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NESTLING DEVELOPMENT OF JACKDAWS *CORVUS MONEDULA* IN AGRICULTURAL LANDSCAPE

ABSTRACT

A Jackdaw colony of over 200 nests, built in cavities of old willow trees along 3 km of a small road running through meadows next to the river Narew in an agricultural landscape (15 km southwest of Białystok, NE Poland), was studied to determine nest locations and construction, onset of egg laying, incubation period, egg parameters, clutch size and hatching success, nestling growth and mortality, breeding success as well as predation. The onset of laying and clutch size were correlated with ambient temperature and precipitation ($p < 0.001$). Hatching success was also determined by these environmental factors as well as by the degree of predation ($p < 0.001$). There was a statistically significant correlation between clutch size and hatching success ($p < 0.001$) as well as fledging success ($p < 0.001$). Nestlings hatching first or second grew faster, reached a higher body weight, and had a lower mortality rate than those hatching last or second to last. There was also a statistically significant correlation between nestling survival and clutch size as well as ambient temperature ($p < 0.001$ each). Nestling mortality caused by predators, i. e. mainly by martens *Martes foina* and domestic cats *Felis domestica*, was high in periods of intensive burning of the meadows surrounding the Jackdaw colony. However, mortality rate of the youngest nestlings was almost 100% lower in periods of high predation compared to times of low predatory activity. Several groups of insects constituted a high amount of nestling food, e. g. 60% of all *Orthoptera* occurring in the meadows next to the breeding colony. In that area the total dry body mass of phytophagous invertebrates amounted to 1.4-2.0 g per m², of which 0.3 g were fed to the nestlings. The percentage of zoophagous invertebrates delivered to the offspring was high with about 30-35%. From an economical point of view, Jackdaws during the breeding season are advantageous in an agricultural landscape because they reduce pest insects significantly while consuming only an insignificant amount of all seeds applied.

Key words: Jackdaw, *Corvus monedula*, breeding ecology, hatching success, breeding success, nestling mortality, predation

INTRODUCTION

Corvids clutch size is determined by environmental factors (Haartman 1967). Several studies revealed that a great majority of young birds reach independence late, hatch from a rather big egg and depend on the parents as nestlings (Ricklefs 1968, 1969, 1973, Blem 1975, O'Connor 1978a, b, Dunn 1980). It has even been demonstrated that variation in first clutches and in brood size is genetically determined by 40% (Van Noordwijk et al. 1981a, b, c) and variation in egg size can be as high a 60-80% (Ojanen et al. 1979, Van Noordwijk et al. 1980). In the higher latitudes breeding starts later and nestling development is shorter. However, in regions far north many species which reproduce late in the course of the year start breeding at a lower temperature and phenologically earlier, which is an advantageous adaptation (Haartman 1963, Danilov 1967, Hussell 1972, Slagsvold 1975a, b, Vogel 1990, Kamiński 1991, Strebel 1991). Of course the limiting factor for an early onset of breeding is a sufficient food supply for females to produce eggs (Perrins 1970, Schmidt 1988). Supplementary food significantly increased fledging success in less than half of experimental studies in Jackdaw colonies. The key to this problem is probably the species' breeding strategy; supplementary food significantly increased fledging success in species exhibiting brood-reduction strategies but not in species which directly adjusted their clutch size (Soler & Soler 1996). Jacobs et al. (2013) reported that food caching is a paramount model for studying relations between cognition, brain organisation and ecology in crows and Jackdaws. In contrast, behaviour towards inedible objects is poorly examined and understood.

Migration and wintering of Jackdaws have already been investigated (Grodziński 1971) but data on the reproductive ecology of populations nesting in naturally flooded meadows and farmland are still missing. As far as other corvid species are concerned, the spatial structure and the mechanisms of self-regulation of Rook *Corvus frugilegus* populations (Józefik 1976) as well as changes in distribution and abundance of the Common Raven *Corvus corax* in Central Europe have been studied (Dobrowolski et al. 1962). On the other hand, Verhulst and Salomons (2004) stated that social dominance is intuitively assumed to be associated with higher fitness, because social dominance implies better access to resources. Jolles et al. (2013) analyzed heterogeneous structure in mixed-species corvid flocks in flight. Schwab et al. (2008) suggested that affiliated social relations may facilitate information transfer between Jackdaw individuals. de Kort et al. (2006) explored the extent and pattern of food sharing in a group of juvenile Jackdaws.

The aim of the present study was to determine important ecological parameters of the breeding ecology of Jackdaws nesting in natural tree cavities and to investigate the dependence of these parameters on environmental factors.

STUDY AREA AND METHODS

From 1981 to 1994, a population of Jackdaws nesting in naturally flooded meadows and farmland near the river Narew, about 15 km southwest of the city of Białystok (north-eastern Poland), was studied. 200 nests were investigated, all of which were located in natural cavities of old willow trees, mainly Sallow willow *Salix caprea*, along an agricultural road crossing flooded meadows of the river Narew.

A total of 490 nests were checked daily, and the date of the first egg laid, time until clutches were complete, period of incubation, size and weight of eggs, hatching success, mortality of nestlings and breeding success were determined. The following parameters were estimated: hatching success (percentage of eggs that hatched per nest for each clutch size separately), breeding success (percentage of hatched nestlings that fledged per nest for each clutch size separately), and nestling mortality (percentage of hatched nestlings that died at successive days of life). In addition, the location of the nest site was recorded and observations on nest building were made. Eggs were weighted with a spring scale (Pesola Co. Ltd.) to the nearest 0.1 g and measured with a cruising rod. Eggs for the biochemical analysis were dried at 65°C for 48 h and grinded in an electrical mill. Water content was determined from the egg weight before and after drying. Protein content was determined with the Kjeldahl method and fat content with the gravimetric method (A sample of about 1 g was extracted with a mixture of chloroform and methanol (2:1) at 60°C and then with a cold mixture of chloroform and ether (1:1). After evaporation at 50°C and extrusion of air, the samples were dried to dry weight. The resulting mass difference equals the extracted amount of fat.). The energy value was determined with a KL-5 closed calorimetric system after Berthelot.

RESULTS

Nest site and construction

In the study area, Jackdaws bred colonially and located their nests in natural, decayed cavities of Willow trees, growing along an agricultural road for about 3 km. Most often nest were built in a height of 3-7 m and only rarely as low as 1-1.5 m or above 15 m. Cavity depth and entrance width varied, but nests were mainly built in cavities 60-80 cm deep and 30-40 cm wide. However, some nests were found in very short (depth 2-5 cm and entrance width 15-20 cm) as well as in very deep (more than 3 m) and varying holes, with several crooked passages within the tree, a couple of entrances and entrance diameters of 8-50 cm were recorded. Nests were mainly constructed of thin (0.5 cm) twigs and were bolstered with hair of various types, e.g. from horses, and scraps of paper. Nest in short cavities contained a lot of nesting material, which was almost missing in deep cavities where egg and young simply lay on decaying wood.

Egg laying and incubation

The beginning of egg-laying differed between years, with a maximum range of 21 days. The earliest date recorded was April 8 (1984), the latest April 28 (1986). Most often clutches were initiated around mid-April. The start of egg-laying was determined by a mean daily ambient temperature of about 10⁰ C as well as by air humidity and precipitation (Tab. I, Figs. 1-3). Clutch size varied between 2 and 6 eggs which were laid at an interval of 1-2 and rarely 3-5 days. Mean clutch size was 4.9 ± 0.3 eggs. The entire period of egg-laying lasted 6-15 days, on average 8.6 days. Females started incubating when the first egg was laid. The incubation period lasted 17-20 days, on average 18.3 days. A second clutch were observed only twice (initiated on June 2 and 4, respectively, in 1981), a few days after the young of the first brood had fledged. Both clutches were abandoned after two weeks of incubation.

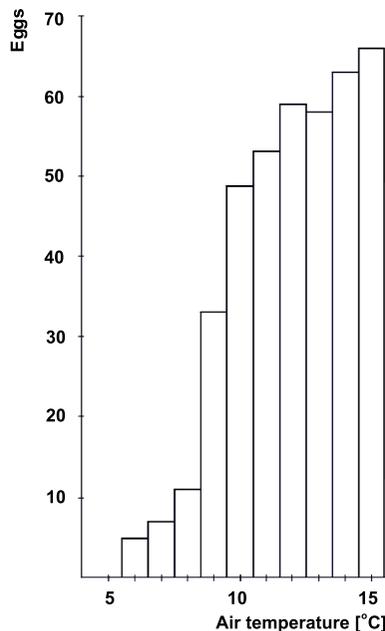


Fig. 1. Cumulative number of eggs laid between 12 and 21 April 1981 in relation to mean daily air temperature

Mean egg size was 35.2×24.9 mm, with the length ranging from 31.3 to 40.8 mm and the width from 22.8 to 26.5 mm. Average egg weight was 11.3 (9.6-12.9) g. Measurements were made on 465 eggs. The chemical analysis of 10 eggs revealed water as the main component (86.9% of the fresh weight), as well as protein ($6.1 \pm 1.07\%$), fat ($4.3 \pm 0.88\%$), ash ($2.4 \pm 0.57\%$), and undetermined compounds ($0.4 \pm 0.12\%$), mainly

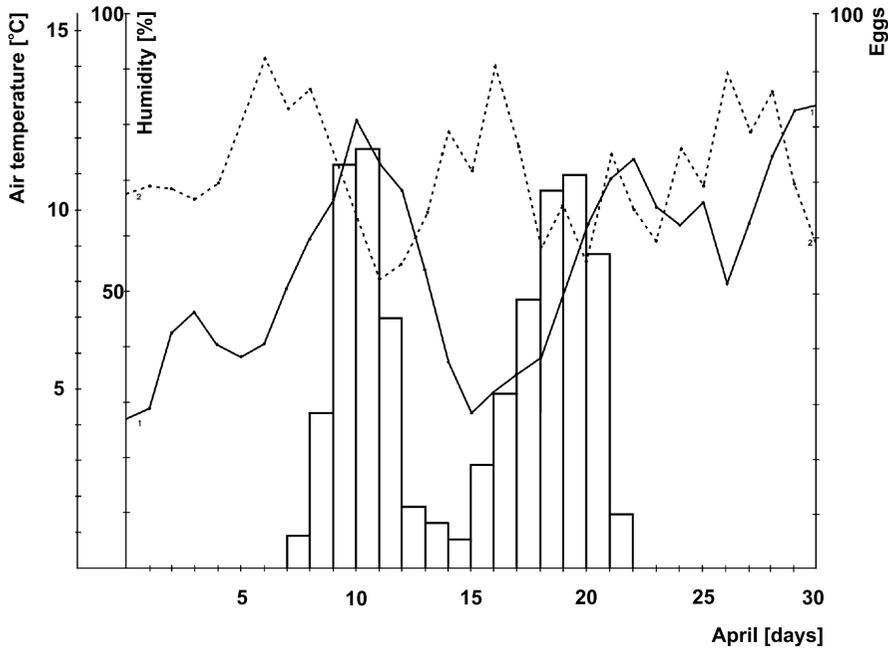


Fig. 2. Course of egg laying and mean daily air temperature (1 = solid line) and humidity (2 = broken line) in April 1984

carbohydrates. The energetic value of the dry egg mass was $28.5 \pm 0.93 \text{ KJ x g}^{-1}$, of the biomass $3.7 \pm 0.76 \text{ KJ x g}^{-1}$, and of the dry mass without ash $33.8 \pm 1.14 \text{ KJ x g}^{-1}$.

Table 1. Correlation between clutch size and ambient temperature as well as air humidity during different periods of egg laying.

Period	Ambient temperature			Air humidity		
	Correlation	Coeff. r	P value	Correlation	Coeff. r	P value
08.-11.04.84	$y = 22.6 x - 200.0$	0.934	< 0.001	$y = -2.3 x + 201.9$	-0.957	< 0.001
11.-15.04.84	$y = 9.1 x - 44.7$	0.881	< 0.001	$y = -2.4 x + 185.3$	-0.868	< 0.001
15.-21.04.84	$y = 8.2 x - 14.3$	0.802	< 0.001	$y = -1.3 x + 137.9$	-0.635	< 0.001
10.-17.04.82	$y = 15.0 x - 14.4$	0.944	< 0.001	$y = -2.0 x + 180.9$	-0.668	< 0.001
17.-23.04.82	$y = 7.3 x + 37.4$	0.502	< 0.001	$y = -1.2 x + 145.5$	-0.258	< 0.05

Hatching success

The most important factors which determined hatching success were weather conditions and density of predators. The results clearly revealed an influence of the change in ambient temperature and amount of precipitation (Tab. 1). In most nests, a sudden decrease in temperature down to a few degrees above 0°C , in combination with intensive precipitation in the form of hail, sleet or snow, caused a decline of up to 40%

in the number of eggs from which young birds hatched. The same effect occurred during heavy rains in May 1982, even at an air temperature of 10°C, when several clutches were submerged. The percentage of successfully hatched eggs was high (mean $82.3 \pm 3.69\%$) between periods of heavy rainfall and considerable decrease in air temperature (Fig. 3).

Table 2. Correlation between the number of hatchlings and ambient temperature as well as air humidity during different periods of hatching.

Period	Ambient temperature			Air humidity		
	Correlation	Coeff. r	P value	Correlation	Coeff. r	P value
28.04.-06.05.82	$y = 4.5x + 17.9$	0.836	0.001	$y = -1.9x + 181.7$	-0.822	< 0.001
06.-13.05.82	$y = 4.8x + 4.7$	0.653	0.001	$y = -1.0x + 144.2$	-0.704	< 0.001
13.-18.05.82	$y = 5.8x - 3.1$	0.828	0.001	$y = -2.3x + 220.7$	-0.644	< 0.001

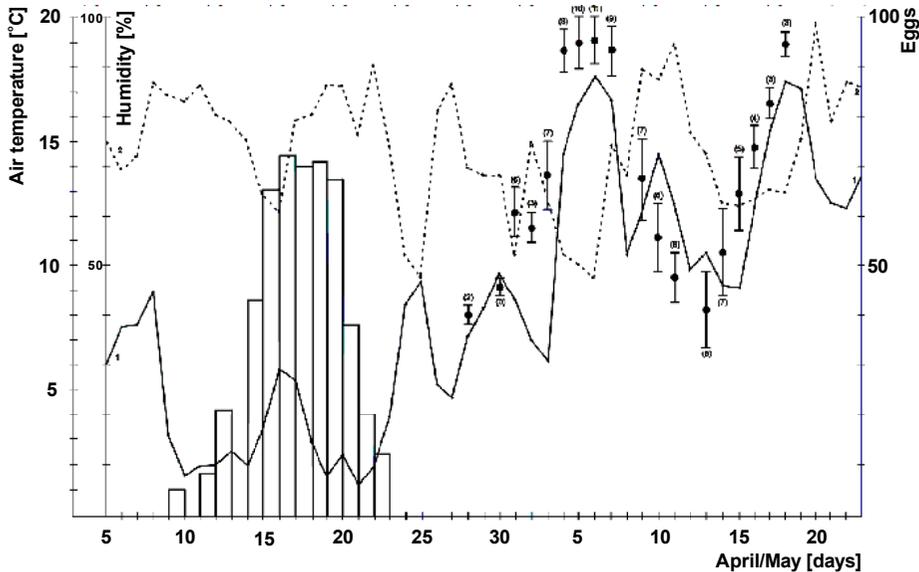


Fig. 3. Course of egg laying (columns), mean (+ SD) number of hatchlings (% of eggs laid), ambient temperature (1 = solid line), and air humidity (2 = broken line) during the breeding season 1982. The number of clutches from which the last nestling hatched that day is given in brackets

The number of successfully incubated eggs depended on the clutch size ($p < 0.001$). Hatching success was 100% in clutches with 2 or 3 eggs. Clutches with 4 eggs sometimes resulted in only 3 nestlings (hatching success $87.8 \pm 5.3\%$), and in clutches of 5 or 6 eggs sometimes only 1 or 2 young birds hatched (hatching success $71.9 \pm 6.3\%$ and $57.6 \pm 3.2\%$, respectively) (Fig. 4).

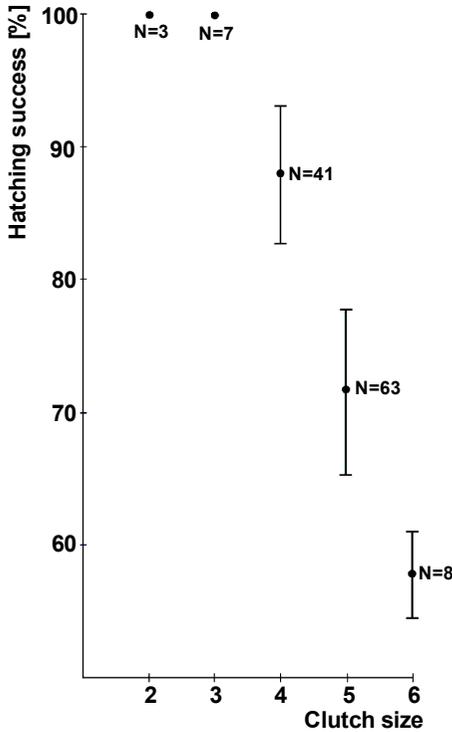


Fig. 4. Hatching success (mean % (+ SD) of eggs hatching) for clutches of different size during the breeding season 1981. Numbers next to the mean indicate the number of clutches investigated

Nestling mortality

33.4% of a total of 202 young birds from 42 nests died during the nestling period (Fig. 5). The most important factors influencing nestling mortality were ambient temperature, precipitation and clutch size. A sudden decrease in temperature (below 10°C) together with rainfall was the main reason for a higher mortality (29.2%), especially in nestlings 1 to 2 days of age (Fig. 5). During the breeding season 1982 the mortality of 1 day old nestlings was 75.4%, corresponding to a total of 23% of all hatched young. The respective value for nestlings 2 days of age was substantially lower with 13.1%, accounting for a little more than 5% of all hatchlings (Fig. 6).

Juvenile mortality was positively correlated with clutch size. Some clutches with 2 or 3 eggs resulted in a 100% survival rate of the later nestlings. From clutches with 4 eggs sometimes one of the nestlings died (nestling survival rate $92.3 \pm 4.5\%$), while from clutches of 5 eggs mostly one and sometimes two nestlings did not survive (rate $78.6 \pm 5.3\%$). Clutches with 6 eggs always resulted in one to two or more dead nestlings (rate $65.7 \pm 2.5\%$).

Mortality differed between young birds which had hatched first or second and those hatched last or second to last. Nestlings from the latter group were smaller, weaker

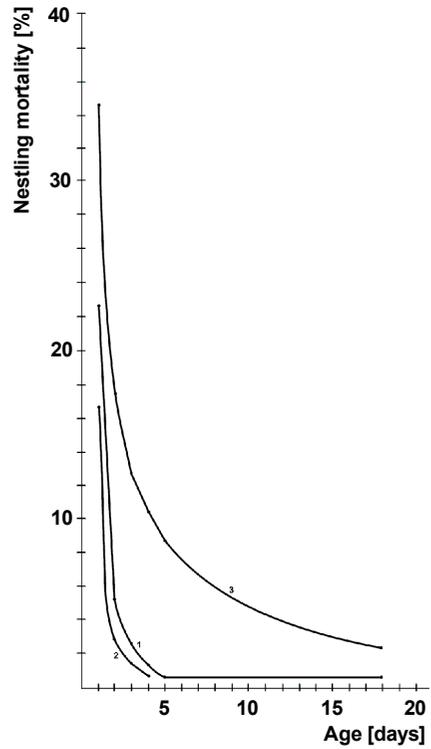


Fig. 5. Age-dependent nestling mortality (number of dead nestlings as % of all nestlings) during the breeding season 1982. 1 – all nestlings, 2 – nestlings which hatched first or second, 3 – nestlings which hatched last or second to last

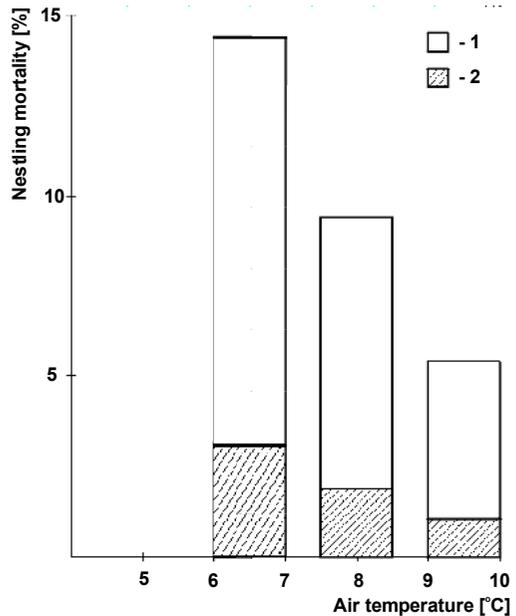


Fig. 6. Mortality of nestlings 1 or 2 days of age (number of dead nestlings as % of all nestlings) and ambient temperature in the breeding season 1981 (1 = 1 day old and 2 = 2 days old)

and had a lower body weight (fig. 8). The mortality rate in 1-day old nestlings which had hatched last or second last was 34.3%, while the corresponding value in nestling hatching first was only 16.8%. Most critical for young Jackdaws were the first 5-days, during which period 98% of all nestlings died (Fig. 5).

Relative nestling survival was highest in smaller broods, i. e. in those from clutches with 2-4 eggs. In broods consisting from 2 and 3 eggs always 2 and 3 young survived until fledging, respectively. Broods from 4 eggs resulted in a mean of 3.7 ± 0.3 surviving nestlings (survival rate $92.3 \pm 4.5\%$), while the corresponding values for broods from 5 and 6 eggs were 3.9 ± 0.5 and 3.9 ± 0.6 nestlings, respectively (survival rate $78.6 \pm 5.3\%$ and $65.7 \pm 2.5\%$) (Fig. 7).

During the breeding season 1986 a clear influence of natural predators, especially stone marten *Martes foinea* and domestic cat *Felis domestica*, was evident. The Jackdaw colony was heavily frequented by these species, caused by an intensive burning of the surrounding meadows (which had not been burned in the previous breeding seasons). 21 out of 38 nest studied in 1986 were preyed upon by martens and cats, which killed 31.6% of all nestlings (Fig. 9). At the same time a lower mortality (17.3%) of nestlings up to 5 days of age was found, in comparison of 32.7% in breeding seasons without the influence of martens and cats (Figs. 5, 9).

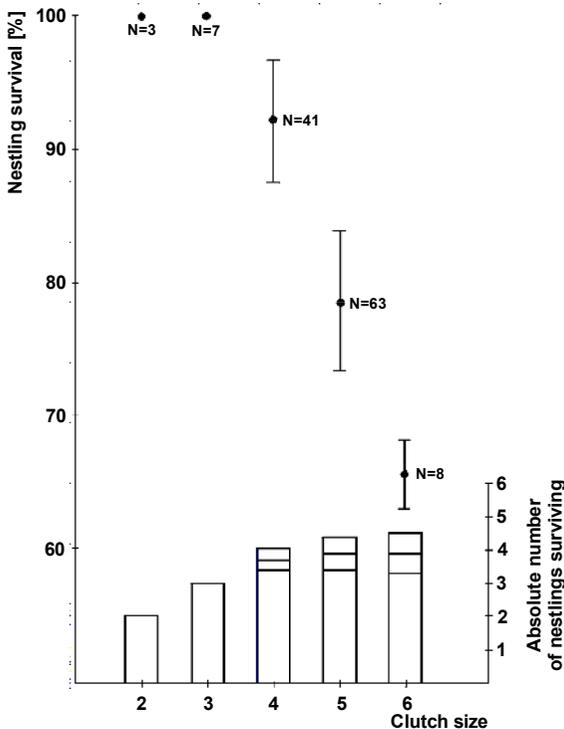


Fig. 7. Relative (mean % (+ SD) of all nestlings) as well as absolute nestling survival rates and clutch size in the breeding season 1981. Numbers next to the mean are the number of broods examined

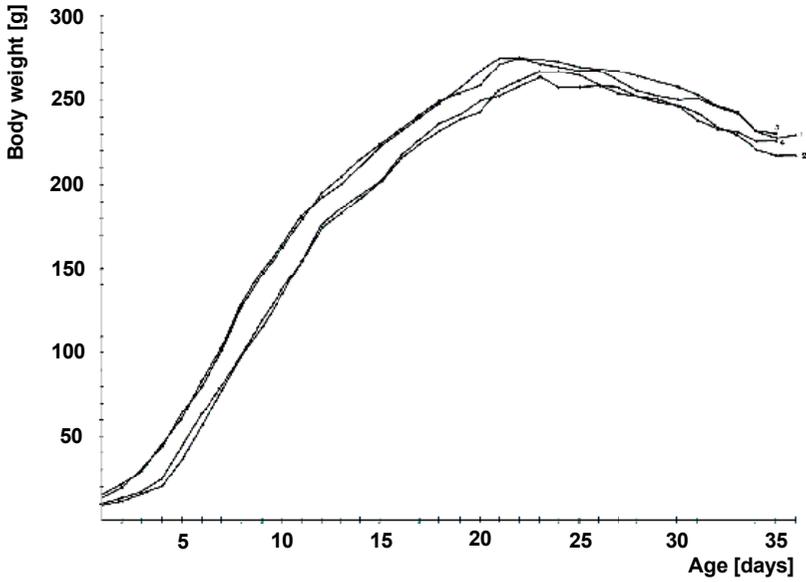


Fig. 8. Growth of nestlings hatching first or second in a clutch (curves 1 and 3; $K_G = 0.280$ and 0.286) and last or second to last (curves 2 and 4; $K_G = 0.243$ and 0.233)

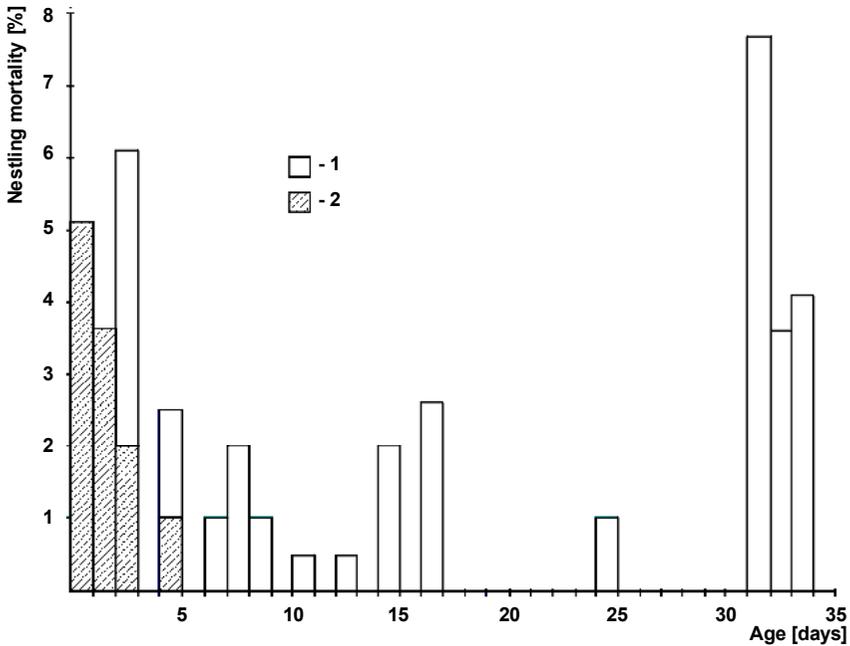


Fig. 9. Age-dependent nestling mortality (number of dead nestlings as % of all nestlings) during the breeding season 1986. 1 – predation, 2 – unknown cause

DISCUSSION

The results of the present study on the reproductive ecology of the Jackdaw (nest construction, egg laying, incubation, hatching success, mortality) are in line with the findings of other authors (Emmet 1933, Kalitsch 1934, Schindler 1949, Riggerbach 1951, 1970, 1979, Zimmermann 1951a, b, Lockie 1955, Eigelis 1958, Folk 1967, 1968, Röell 1978, Hund & Prinzinger 1981, Soler & Soler 1987, Dwenger 1989, Kamiński 1991, Strebel 1991), although none of these investigated Jackdaws breeding in tree cavities. Studied were single nests as well as entire Jackdaw colonies in urban parks.

Our study (this paper) revealed a correlation between the date of egg laying and clutch size as well as weather, i. e. ambient temperature and humidity (Figs. 1-3), which has been observed in investigations on other hole-breeding passerines. Järvinen (1983, 1984) mentions that weather can modify the different stages of the reproductive cycle by (1) influence on the number of pairs which start breeding, (2) determination of timing of egg laying and duration of breeding season, (3) decline in survival of adult birds, (4) reduction in brood size, (5) abandoning clutches or nestlings, (6) increase in incubation time which causes a lower chance of successful hatching and a stronger influence of predators, and (7) nestling growth (a lower growth rate decreases survival probability). Similar conclusions have been made by Järvinen & Lindén (1980) and Järvinen & Väisänen (1983, 1984). The latter authors conclude that females are heavier and initiate clutches, with larger and more eggs, earlier under favourable weather conditions, i. e. in an early and warm spring. This results in a high hatching success and a considerably lower juvenile mortality. A similar influence has been demonstrated for abundant food resources (Järvinen 1983, 1984, Kamiński 1991).

The beginning of nest building and egg-laying in Jackdaws (as well as in other species of the family *Corvidae*) does not only depend on weather conditions but also on food availability. Lockie (1955), for example, showed a dependence of early breeding in rooks *Corvus frugilegus* on the availability of *Lumbricidae* and larvae of *Lepidoptera*, which constitute the main nestling food, in the vicinity. Such a correlation is also evident in other insectivorous birds, e.g. Pinon jay *Gymnorhinus cyanocephalus* (Balda & Bateman 1973), Starling *Sturnus vulgaris* (Dunnet 1955), Blackbird *Turdus merula* (Graczyk 1961), Tits *Paridae* (Mertens 1977a, b), Warblers *Sylviidae* (Stewart et al. 1978, Tiainen 1983), Flycatchers *Muscicapidae* and Finches *Fringillidae* (Perrins 1970, Järvinen & Lindén 1980, Järvinen 1984). In insectivorous birds the breeding success also depends on the type of nesting tree and height of nest site. The Pinon jay, for example, prefers to nest on trees of 6 m height, where nests can absorb radiation of sun and are not exposed to strong winds, and on their southern side where most sunshine is available (Balda & Bateman 1973). Similar preferences were found for the House wren *Troglodytes aedon* (Kendeigh 1963) and for warblers of the family *Sylviidae* (Mac Arthur 1958). In the Cactus wren *Campylorhynchus brunneicapillus* the nest entrance is exposed to cooling winds during the hot period of the breeding cycle, resulting in a higher

number of fledglings (Austin 1974). Such correlations could not be observed in the Jackdaw population investigated in the present study. Other factors which can influence time of nest building, egg laying and breeding success in corvids and other species are the distance of nests from the colony periphery (Balda & Bateman 1973), colony size and density (Lack 1958, Havlin & Folk 1961, Horn 1970, Ralph & Pearson 1871), and rank order of individuals within a colony (Orians 1961, Balda & Bateman 1971). Jackdaws preferred safe cavities with small minimum nest-entrance dimensions and avoided those with a high risk of nest predation (Soler & Soler 1996).

The chemical composition and energy value of the investigated Jackdaw eggs were similar to those reported for other corvid species (Carey et al. 1980).

An influence of the location of nests within the colony on the timing of nest building and egg-laying as well as on hatching success could not be determined. However, the study revealed that hatching success depends on clutch size (Fig. 4). A similar correlation has been described for Jackdaws and Rooks by Lockie (1955) and Owen (1959) and for European starlings by Lack (1948), Royall (1966), Westerterp et al. (1982) and Kamiński (1991). Clutch size depends on the date of the first egg laid and declines during the breeding season by about 0.08 eggs per day (Järvinen & Lindén 1980). Moreover, Verhulst and Salomons (2004) stated that social dominance is intuitively assumed to be associated with higher fitness, because social dominance implies better access to resources. They found that, in a colony of Jackdaws, the dominant males consistently produced fewer fledglings, which had lower chances of survival to 1 year of age. Laying date and clutch size were independent of dominance, but females that mated with dominant males were in poorer condition and laid smaller eggs. Parental survival was independent of social dominance, and the frequency of extra-pair fertilizations in Jackdaws is negligible. Dominance was a stable trait of individuals, and not a state that all individuals attained. In this colony, dominant Jackdaws had lower fitness. It can be hypothesized that the high density of Jackdaw colony resulted in high testosterone titres, which suppressed paternal care of mate and offspring to the extent that it outweighed the benefits of higher resource access Verhulst and Salomons (2004).

A high mortality of nestlings, especially during the first days of life (Fig. 5), as well as a correlation between nestling mortality and clutch size (Fig. 7) has also been found in young Jackdaws ($\pm 30\%$) and Rooks ($\pm 35\%$) studied by Lockie (1955). An increase in nestling mortality resulting from an increase in clutch size has been determined for Rooks by Van Koersveld (1958), Owen (1959) and Shurakov et al. (1973), and for Starlings by Lack (1948), Dunnet (1955), Hudec & Folk (1961) and Royall (1966). A high juvenile mortality during the first days of life was found for the European robin *Erithacus rubecula* by Lack & Silva (1949). However, Tiainen (1983) determined a higher nestling mortality at days 1-7 than at other developmental stages in the Willow warbler *Phylloscopus trochilus*. During the entire period of nestling development the mortality of the Jackdaw nestlings investigated in the present study (33.4%) was lower than for the above mentioned Willow warbler in the study of Tiainen

(1983). Mackowicz et al. (1970) described that most nestlings of Tree sparrows *Passer montanus* and House sparrows *Passer domesticus* died during the first 5 days, although in these species some perish between days 6 and 10 (Pinowski & Wieloch 1972).

Important factors influencing juvenile mortality are ambient temperature and precipitation, affecting especially the youngest nestlings of a brood (Fig. 6). Similar effects have been determined for other insectivorous bird species (Lack & Silva 1949, Dunnet 1955, Balda & Bateman 1973, Stewart et al. 1978, Järvinen 1983, 1984).

The present study revealed a clear influence of martens and cats on nestling survival (Fig. 9), especially in times when the adjacent meadows had been burned intensively (e.g. during the breeding season 1986). The results of many studies point to a considerable lower survival rate of nestlings of other species caused by predators, mainly Least weasel *Mustella nivalis*, and *Cyanocitta sp.*, but also Squirrel *Sciurus vulgaris*, birds of prey such as Sparrowhawk *Accipiter nisus*, and Raven *Corvus corax* (Lack & Silva 1949, Dunnet 1955, Royall 1966, Balda & Bateman 1973, Stewart et al. 1978, Tiainen 1983).

Ricklefs (1982), Kamiński (1991), and Strebel (1991) found a correlation between the developmental speed (efficiency) and its consequences and the number of siblings: Nestlings of smaller broods grow at a slower rate than those of larger broods, and their development is less differentiated. Järvinen (1983) reports that clutches with 5 eggs usually result in fewer nestlings, compared with clutches of more eggs. Such an effect could not be determined for the investigated Jackdaw nestlings, in which larger broods showed a higher degree of differentiation and a slower development of the nestlings which hatched late, resulting in a higher mortality (Fig. 5, 8). The differences in body weight of nestlings hatching first or second and those hatching last or second to last which was noted in this study (Fig. 8) have also been found for Rooks (Lockie 1955, Shurakov et al. 1973) and Starlings (Hudec & Folk 1961).

Soler and Soler (1996) who studied Jackdaw colonies found that in Jackdaw experimental (fed) colonies, there was a tendency to use all cavities, which resulted in an increased breeding density. No nests were preyed upon by Ravens *Corvus corax* in the experimental colonies because supplemental food favoured group defense by increasing colony size and by increasing the time the Jackdaws spent in the colony. Additional food advanced laying date, increased clutch size independently of laying date and increased fledging success. Supplementary food significantly increased fledging success in less than half of experimental studies. The key to this problem is probably the species' breeding strategy; supplementary food significantly increased fledging success in brood-reduction strategist species but not in species which directly adjusted their clutch size (Soler & Soler 1996). On the other hand, Jolles et al. (2013) analyzed heterogeneous structure in mixed-species corvid flocks in flight. They found that flocks of corvids in flight represent a striking example of collective behaviour. Models of self-organization suggest that repeated interactions among individuals following

simple rules can generate the complex patterns and coordinated movements exhibited by flocks. However, such models often assume that individuals are identical and interchangeable, and fail to account for individual differences and social relationships among group members. These authors show that heterogeneity resulting from species differences and social structure can affect flock spatial dynamics. Using high-resolution photographs of mixed flocks of Jackdaws and rooks, they show that birds preferentially associated with conspecifics and that, like high-ranking members of single-species groups, the larger and more socially dominant rooks positioned themselves near the leading edge of flocks. Neighbouring birds showed closer directional alignment if they were of the same species, and neighbouring Jackdaws in particular flew very close to one another. Moreover, birds of both species often flew especially close to a single same-species neighbour, probably reflecting the monogamous pair bonds that characterize these corvid social systems. Jolles et al. (2013) demonstrated that the characteristics of individuals and their social systems are likely to result in preferential associations that critically influence flock structure.

Additionally, Schwab et al. (2008) suggested that affiliated social relations may facilitate information transfer between individuals. They tested this rarely examined hypothesis with juvenile and adult Jackdaws in three stimulus enhancement tasks, both in a non-food context and in a food context. They show that siblings and pair partners maintain stronger bonded social relations than do non-siblings and non-pair partners. They tested individuals in sibling and non-sibling dyads and, later in ontogeny, in pair and non-pair dyads. Jackdaws either did not learn from any other con-specific, or they learned from non-affiliated individuals (non-siblings, non-pair partners). This may be related to two main characteristics of Jackdaws' affiliated relationships. First, affiliates share food at a high rate and may rely on their knowledgeable partners to secure food rather than learning from them. Second, affiliates spend most time in close spatial proximity to each other which increases the probability that they simultaneously experience occurrences in their environment. Hence, spatially more distant individuals, which are more likely to be non-affiliated, face different foraging situations and may therefore provide more relevant information which may lead to selective social learning (Schwab et al. 2008).

Summarizing, the following conclusions can be drawn from the results of the present study: (1) weather conditions, i. e. mainly ambient temperature and precipitation, determine the beginning of egg laying, the number of eggs, hatching success, and nestling mortality, especially of the youngest siblings; (2) clutch size determines hatching success and nestling survival (larger clutches result in a relatively lower number of nestlings and in a higher nestling mortality); (3) larger clutches, i. e. those with 5-6 eggs, have a negative influence on nestling development, they result in a larger differentiation and correspond to a slower development and higher mortality of nestlings which hatch late; (4) predators can have a strong influence on reproductive success. However,

mortality of the youngest nestlings was lower in seasons when predators were abundant in comparison to years without predatory influence, obviously caused by an effective nest defense by the adult birds.

The role of Jackdaws in an agricultural landscape

The Jackdaws and Magpies showed a strong preference for agricultural land and they mainly preyed upon dummy nests in agricultural land (Andren 1992). During the breeding season of Jackdaws studied in this paper, i. e. between the beginning of April and June, phytophagous insects dominate in fields and meadows and make up 60-80% of the respective entomofauna (Andrzejewska 1979a, b). The most numerous taxa were *Lepidoptera* (larvae), *Coleoptera* (larvae; mainly *Curculionidae*, *Scarabaeidae*, and *Elateridae*), *Diptera* (larvae), *Orthoptera*, *Homoptera*, and *Heteroptera* (Andrzejewska 1979a, b). Representatives of these orders constitute the main part of Jackdaw food (Kamiński 1985). The mean dry weight of all phytophagous invertebrates inhabiting meadows at that time is 1.4-2.0 g per m² (Andrzejewska 1979a, b), of which about 0.3 g are feed to Jackdaw nestlings by the adult birds. Especially *Orthoptera* are preyed upon by Jackdaws, although they are not among the dominant taxa of phytophagous species. Of the 0.015 g dry mass per m² (Andrzejewska 1979a, b) on the meadows bordering the investigated Jackdaw colony, the birds take about 60%, i. e. about 0.01 g. This rather high proportion is probably due to the conspicuousness of *Orthoptera*, especially of the genus *Tettigonia* and *Gryllus*.

Of the dominant phytophagous insects (larvae of *Lepidoptera*, *Coleoptera*, and *Diptera*) which occur on the meadows in a total dry body mass of 0.1 g (*Diptera*) to 1.4 g per m² (*Lepidoptera*) (Andrzejewska 1979a, b), Jackdaws take about 10% (larvae of *Lepidoptera*) to 20% (larvae of *Diptera*). Also remarkable is the amount of consumed *Homoptera*, which is about 15% of the approximately 0.02 g dry body mass per m² (Andrzejewska 1979a, b).

The proportion of zoophagous invertebrates consumed by young Jackdaws is higher, although they are less abundant on the meadows. Of the approximately 0.4 g dry body mass per m² of mainly *Hymenoptera*, *Odonata*, *Chilopoda*, *Opiliones*, *Diptera* (*Tabanidae*, *Syrphidae*), *Coleoptera* (*Carabidae*, *Cantharidae*, *Staphylinidae*), and *Aranea*, which occur on the meadows during the breeding season (Brey Meyer 1971, Kajak et al. 1971), Jackdaws consume an average of 30-35%. The highest amount is taken from *Coleoptera* and *Diptera* (23-25% = 0.08-0.10 g dry body mass per m²) and *Hymenoptera* (about 17% = 0.04 g dry body mass per m²). Of all *Aranea* Jackdaws consume about 3% (0.001 g dry body mass per m²), of *Chilopoda* about 9% (0.001 g dry body mass per m²), and of *Lumbricidae* (Nowak 1971) approximately 4% (0.008 g dry body mass per m²).

Some other authors studied eco-determinations in foraging ecology and behaviour of Jackdaws. de Kort et al. (2006) explored the extent and pattern of food sharing in

a group of juvenile Jackdaws. The birds shared food with a number of individuals, regardless of sex and kinship. The frequency of food sharing and the number of recipients per donor decreased over time. Active food sharing, where the initiative for the transfer lies with the donor, appeared to be much more common in Jackdaws than in any primate species studied so far. In addition, Jackdaws shared more of a preferred food than of a less preferred food. Three functional explanations for food sharing between peers were tested: reciprocity, harassment avoidance and food sharing as a signal of social status de Kort et al. (2006). Moreover, Jacobs et al. (2013) reported that food caching is a paramount model for studying relations between cognition, brain organisation and ecology in crows and Jackdaws. In contrast, behaviour towards inedible objects is poorly examined and understood. The captive adult birds were presented with an identical set of novel objects adjacent to food. All three species cached objects, which show the behaviour not to be restricted to juveniles, food catchers, tool-users or individuals deprived of cacheable food. The pattern of object interaction and caching did not mirror the incidence of food caching: the intensely food caching ravens indeed showed highest object caching incidence, but the rarely food caching Jackdaws cached objects to similar extent as the moderate food caching crows. Ravens and Jackdaws preferred spherical objects, but crows preferred stick-like objects (similar to tools). The observed object caching might have been expressions of exploration or play, and deserves being studied in its own right because of its potential significance for tool-related behaviour and learning, rather than as an over-spill from food-caching research (Jacobs et al. 2013).

It also should be emphasized that amongst population trends of Jay *Garrulus glandarius*, Magpie *Pica pica*, Jackdaw *Corvus monedula* and Carrion Crow *Corvus corone*, the population growth has been highest in the Magpie and Carrion Crow, although both these have shown a reduction in the rate of growth. The densities of these corvids increased on farmland, whereas only Magpie and Carrion Crow increased in woodland. Population trends were associated with farmland type in all the corvids; the strongest increases were on mixed and grazing farms and the smallest on arable farms (there were strong regional differences in trends within woodland and farmland); Gregory & Marchant (1996).

The results of this paper indicate that during the breeding season Jackdaws are able to reduce the number of insects in areas adjacent to the breeding colony, because insects not only constitute the main nestling food but also comprise 30-40% of what adult birds consume. In total, the Jackdaws of the studied breeding colony provided their nestlings with more than 1.5 tons of insects from a foraging area of about 0.5 km².

During the nestling phase the young Jackdaws also consumed crop seeds, amounting to about 400 kg for the entire breeding colony. At the beginning of this period the adult birds mainly collected seeds from 0.2 km² adjacent fields (a total of 50 kg, which is less than 20% of all seeds applied). After nestlings were 16 days old, however, adults

foraged for seeds mainly on the surrounding farms and provisioned their offspring with about 350 kg.

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