

## Effects of experimental food provisioning on reproduction in the Jackdaw *Corvus monedula*, a semi-colonial species

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Two Jackdaw *Corvus monedula* colonies were given supplementary food before and during breeding in 1983. Breeding density and cavity use were compared with those of the same colonies in previous years, when no food was provided. Predation rate and reproductive parameters were compared with those in the same colonies in previous years and with those of two control colonies, without experimental food. Jackdaws preferred safe cavities with small minimum nest-entrance dimensions and avoided those with a high risk of nest predation. In experimental (fed) colonies, however, 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 defence 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 all experimental studies on birds. We suggest that the key to this problem is the species' breeding strategy, and we show that supplementary food significantly increased fledging success in brood-reduction strategist species but not in species which directly adjusted their clutch size.

Food is the most important proximate factor influencing reproduction in birds (Lack 1947, 1954). This widely accepted hypothesis has received strong support from both observational (e.g. Sealy 1980, Catterall *et al.* 1982, Strehl and White 1986, Blancher & Robertson 1987, Hamer *et al.* 1993) and experimental studies (e.g. Yom-Tov 1974, Högstedt 1981, Ewald & Rohwer 1982, Hochachka & Boag 1987, Arcese & Smith 1988, Simons & Martin 1990, Nilsson 1991, Richner 1992, Nilsson & Svensson 1993). Experimentally increased food availability has, in some species, produced changes in laying date, clutch size, egg mass, hatching success, number of fledglings, fledgling mass and survival/and the incidence of second broods (reviewed in Hochachka & Boag 1987, Martin 1987, Arcese & Smith 1988, Boutin 1990).

Artificial food provisioning has been shown to increase the breeding density in some open-nesting birds (Davies & Lundberg 1985, Knight 1988), although there are exceptions (Yom-Tov 1974, Högstedt 1981, Dhindsa & Boag 1990). The effect of extra food is particularly clear in hole-nesting passerines (Krebs 1971, Jansson *et al.* 1981, Källander 1981, Enoksson & Nilsson 1983). However, these studies provided no information on the quantity and characteristics of available natural holes (or the experiments carried out using nestboxes).

The effect of supplementary food on nest predation rates has been analysed in only a few studies. Arcese and Smith (1988) found that nest predation did not differ significantly

between food-supplemented and control nests in an island population of Song Sparrows *Melospiza melodia*, whereas a significant effect was documented in Carrion Crows *Corvus corone* (Yom-Tov 1974). However, as far as we know, nobody has tested the possible effects of extra food on predation rates in passerines where group nest defence is employed.

The Jackdaw *Corvus monedula* is a monogamous and semi-colonial corvid that usually nests in cavities in buildings, trees or cliffs (Soler & Soler 1987). In our study area, Jackdaws nest in cliffs. There, a high percentage of Jackdaw nests (23.7%,  $n = 194$ ) failed due to predation, with Ravens *Corvus corax* responsible for 61% of these losses (Soler 1989). Previously, we pointed out that the risk of nest predation depended mainly on the minimum nest-entrance dimension (Soler & Soler 1993). Furthermore, we pointed out that sites where breeding was successful in one year were frequently used in the following year, while nests whose contents were preyed upon were less frequently reused (Soler & Soler 1993).

In this paper we first compare nest cavity occupation by Jackdaws in the two experimental colonies from 1980 to 1982 (nonexperimental years) with that in 1983, when supplemental food was provided. Second, we present data on predation rate in relation to minimum nest-entrance dimension in the same two colonies during 1980-1983. We then compare predation rates in the two experimental colonies with that in two control colonies (during 1983), as well as with that in the experimental colonies during 1980-

1982, when the Jackdaws were not experimentally fed. Third, we test the following predictions: if food limits reproduction, then we should expect that pairs given supplementary food would (1) lay earlier, (2) lay larger clutches, (3) lay larger eggs, (4) feed the young for a shorter nestling period, (5) hatch a larger proportion of their eggs and (6) fledge a larger proportion of laid or hatched eggs than control pairs and pairs in experimental colonies during years prior to the experiment.

## METHODS

### Study area and colonies

This study was conducted in the Hoya de Guadix, southern Spain (37°18'N, 3°11'W), a cereal-producing plain 900–1100 m a.s.l. This area is sparsely vegetated and is dominated by agricultural crops. There are numerous gullies and clay cliffs with many crevices and holes used by nesting Jackdaws. For this reason, the structure of Jackdaw colonies is always linear; the nests occupy existing natural holes on both sides of the bank. As they depend on the existence of cliffs with cavities, nests are not uniformly distributed. Therefore, several nests are sometimes close together while elsewhere the nests can be several hundred metres apart (Soler 1990).

Isolated nests and areas of the gullies with only a few holes were not considered in this study. Two colonies were provided with supplementary food (experimental colonies) and two others were used as controls. The distance between the experimental colonies (A and B) was 800 m, the distance between the two control colonies was 400 m and the minimum distance between control and experimental colonies was 1500 m. As a second control, we used data from nests in the experimental colonies in the nonexperimental years, 1980–1982. This type of control is of value because adult pairs often establish themselves in the same hole in successive years (Soler 1988a). Thus, this second control allowed values for reproductive parameters when extra food was supplied to be compared with values for the same pairs when no experimental food was provided.

### General methods

Between 1979 and 1983, 228 Jackdaw nests were studied in the Hoya de Guadix. Each nest was visited every 2–4 days until the end of the nestling period. Egg length and breadth were measured to the nearest 0.1 mm with callipers. The young were ringed with standard numbered Spanish metal rings when 9–11 days old.

Because only the minimum nest-entrance dimension significantly affected the probability of nest predation (Soler & Soler 1993), it was the only dimension considered in this study.

The laying date was defined as the day when the first egg was laid, assuming that one egg was laid daily. Clutch size was defined as the number of eggs in the nest remaining

constant through two consecutive visits. Egg volume was estimated using Coulson's (1963) formula,  $V = (\pi \times K \times A^2 \times L)/6$ , where  $A$  is breadth and  $L$  is length (in mm).  $K$  is a constant derived from a sample of eggs whose volume is known (0.00096 for the Jackdaw; Soler 1988a). Egg size was defined as the mean volume of all eggs laid in each nest. The nestling period was defined as the mean of the number of days that the chicks in a brood spent in the nest from hatching to fledging. Only nests where the fledging period was determined with a maximum error of 1 day were considered.

Sometimes nests were in cavities too deep for us to gain access to the clutch or brood. In these cases, we considered breeding to have been successful if adults were carrying food to the nests at the end of the nestling period. For this reason, sample sizes for predation rates are larger than those for reproductive parameters.

Supplementary food significantly affected the predation rate and also clutch size (see below). To study the effect of extra food on reproductive success without the influence of these factors, we analysed reproductive success excluding nests that were preyed upon and calculated reproductive success as a percentage. We defined hatching success as the mean percentage of eggs laid that hatched, fledging success as the mean percentage of hatchlings that fledged and breeding success as the mean percentage of eggs that produced fledglings. Values given are means  $\pm$  s.d.

### Experimental procedure

Two Jackdaw colonies were supplied with extra food of hen's eggs and bread in 1983, while two other colonies were used as controls (see above). Twice a week, from 16 February (9–10 weeks before the beginning of egg laying) until the beginning of July (the end of the nestling period), we placed four hen's eggs per pair of Jackdaw in each experimental colony and approximately 7 kg of bread in colony A and 4 kg in colony B. The Jackdaws usually consumed the eggs in about 2 days, whereas new bread was always supplied before the old bread had all been consumed. Thus, bread was continuously available.

We know that nests in a colony are not independent in a statistical sense. However, considering that all colonies were included within the home ranges of a similar number of Ravens, nests were considered to be independent estimates of predation risk.

## RESULTS

### Food use

Direct observations showed that Jackdaws were largely responsible for the disappearance of the supplementary food. Colony A was easily observed from a road, and we frequently saw one or more Jackdaws eating bread. Twice we observed a group of Jackdaws chasing a Carrion Crow from the feeding site. When we put out the extra food, Jackdaws

**Table 1.** Available cavities and percentage used by Jackdaws during 1980, 1981 and 1982 for birds receiving no supplementary food and during 1983 when supplementary food was provided

Colony	Total available cavities	Number and percentage of cavities used							
		1980		1981		1982		1983	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
A	16	9	56	10	63	9	56	14	88
B	6	3	50	4	67	2	33	6	100

often stayed near by and began to eat the eggs as soon as we left. The birds used the extra food mainly for themselves, but we also observed males offering bread to incubating females, and both males and females fed their young with bread (mainly during the last week of the nestling period). Jackdaws that received supplementary food also fed on natural food throughout the breeding season.

### Breeding density

Breeding density depended on the existence of appropriate cavities in the cliffs. There were 16 available cavities in colony A. Between 56% and 63% of these were used in the years preceding the experiment. When supplementary food was provided, 88% of the cavities were occupied (Table 1). Although this increase in occupation suggests an increase in breeding density in this colony, it was not statistically significant (Fisher's exact test,  $P = 0.06$  between 1983 and 1980 and 1982 and  $P = 0.11$  between 1983 and 1981). There were six available cavities in colony B. During the years prior to the experiment, a maximum of four (1981) of these cavities were used; in 1983, however, when food was provided, all six were used (Table 1). Differences between 1983 and the previous years were significant only in 1982 (Fisher's exact test,  $P = 0.03$ ) but not in 1980 and 1981 (Fisher's exact test).

The number of Jackdaws staying in the experimental colonies while we checked the nests was higher in the year when extra food was supplied than during the previous

years. The difference was significant in both colonies (colony A:  $6.2 \pm 1.83$  [ $n = 16$ ] Jackdaws in 1983 v  $3.3 \pm 1.49$  [ $n = 45$ ] during 1980–1982,  $z = -4.38$ ,  $P < 0.001$ ; colony B:  $2.6 \pm 1.39$  [ $n = 13$ ] Jackdaws in 1983 v  $1.1 \pm 0.72$  [ $n = 36$ ] in 1980–1982,  $z = -3.36$ ,  $P < 0.001$ ).

### Cavity use, cavity dimensions and nest predation

The predation rate on Jackdaws nests was affected mainly by the minimum nest-entrance dimension (see above). Nests with a small minimum nest-entrance dimension had lower predation rates (almost 0) than nests with a large minimum nest-entrance dimension (100%) (Soler & Soler 1993). Thus, nest predation is probably a strong selective factor in the evolution of nest-site selection and, as reflected in Table 2, we might expect Jackdaws to prefer safe cavities and to avoid those with a large minimum nest-entrance dimension. Cavities frequently occupied (used in 2 or 3 years) had a significantly smaller mean minimum nest-entrance dimension than those not used or used only rarely (one or zero years) (Mann-Whitney  $U$ -test,  $z = -3.12$ ,  $P < 0.002$  and  $z = -1.96$ ,  $P < 0.05$  for colonies A and B, respectively; Table 2). The latter also had a significantly higher predation rate than the former (Fisher's exact test,  $P < 0.002$  and  $P < 0.03$ , respectively, for colonies A and B; Table 2).

None of the nests in colonies provided with supplementary food was preyed upon by Ravens, which preyed upon 22% of the control nests (Table 3). This difference was sta-

**Table 2.** Minimum nest-entrance dimension (mean  $\pm$  s.d.) and nest predation<sup>a</sup> rate in frequently or rarely occupied cavities (2 or 3 and 1 or 0 years, respectively) used by Jackdaws in both experimental colonies during the years prior to the experiment

	Colony A		Colony B	
	Cavities used in 2 or 3 years	Cavities used in 1 or 0 years	Cavities used in 2 or 3 years	Cavities used in 1 or 0 years
Minimum nest-entrance dimension (number of cavities)	13.8 $\pm$ 2.6 cm (11)	31.8 $\pm$ 9.0 cm (5)	16.7 $\pm$ 7.1 cm (3)	35.7 $\pm$ 14.6 cm (3)
Predation rate (number of nests)	0% (21)	50% (4)	25% (8)	100% (4)

<sup>a</sup> Only nests preyed upon by Ravens were considered (the other main predator is humans).

**Table 3.** Minimum nest-entrance dimension (mean  $\pm$  s.d.) and nest predation rate in experimental and control Jackdaw colonies in 1983 when food was experimentally provided

	Control nests			Experimental nests	
	Preyed upon <sup>a</sup>	Successful	Total	Total <sup>b</sup>	
Minimum nest-entrance dimension (number of cavities)	29.7 $\pm$ 8.4 cm (6)	13.0 $\pm$ 3.8 cm (21)	16.7 $\pm$ 8.7 cm (27)	19.4 $\pm$ 10.0 cm (20)	
Predation rate (number of nests)	100% (6)	0% (21)	22% (27)	0% (20)	

<sup>a</sup> Only nests preyed upon by the Raven have been considered.

<sup>b</sup> No nest was preyed upon in experimental colonies.

tistically significant (Fisher's exact test,  $P < 0.05$ ). Minimum nest-entrance dimension was significantly smaller in control nests that were not preyed upon than in control nests that were preyed upon (Mann-Whitney  $U$ -test,  $z = -3.65$ ,  $P < 0.001$ ; Table 3). Cavities occupied in the two experimentally fed colonies were similar in size to those of the control colonies (Mann-Whitney  $U$ -test,  $U = 215.5$ , n.s.; Table 3). However, the predation rate was significantly lower in experimental colonies than in the controls (Fisher's exact test,  $P < 0.05$ ; Table 3). Thus, we may conclude that supplementary food increased the number of breeding pairs and probably facilitated active nest defence, thereby preventing nest predation by the Raven.

### Reproductive parameters

The mean date of laying was significantly earlier (by 1.8 days,  $P < 0.05$ ) in experimental nests than in control ones (Table 4).

Clutch size was larger in colonies with supplementary food than in either controls or the same colonies in the preceding years (Table 4). There was a significant negative correlation between laying date and clutch size in control

nests ( $r_s = -0.57$ ,  $P < 0.01$ ,  $n = 18$ ) but not in experimental nests ( $r_s = -0.21$ , n.s.,  $n = 13$ ). Did supplementary feeding affect clutch size independently of the laying date? To answer this question, we analysed the data by pairing data according to the laying date, i.e. clutch size of control and experimental nests where the first eggs were laid on the same day. We found that fed pairs laid significantly larger clutches than unfed pairs independently of laying date (Wilcoxon matched-pairs test,  $z = 2.02$ ,  $P < 0.05$ ).

Egg size and nestling period were not significantly influenced by supplementary feeding. We found no difference in the mean egg size or mean nestling period between experimental and control nests (Table 4).

Two of the indices of reproductive success (fledging and breeding success) differed significantly in the two experimental colonies between the year with supplementary food and the three preceding years (Table 5). Hatching success was not affected by supplementary food; its value was identical in experimental and control nests (Table 5). However, fledging and breeding success were significantly higher in colonies with supplementary food than in either controls or the same colonies in the preceding years (Table 5).

Nestling losses occurred in all broods, in both control and

**Table 4.** Breeding parameters of Jackdaws in experimental and control nests

	Experimental nests 1980–1982 (unfed)				Experimental nests 1983 (fed)				Control nests 1983 (unfed)		
	<i>n</i>	Mean	s.d.	Prob- ability level <sup>a</sup> ( <i>P</i> )	<i>n</i>	Mean	s.d.	Prob- ability level <sup>b</sup> ( <i>P</i> )	<i>n</i>	Mean	s.d.
Laying date <sup>c</sup>	8	27.0	2.33	n.s.	13	25.1	3.33	<0.05	18	26.9	3.41
Clutch size	9	5.4	0.56	<0.01	13	6.0	0.58	<0.05	18	5.4	0.62
Egg size (cm <sup>3</sup> )	9	10.4	0.48	n.s.	10	10.3	0.69	n.s.	16	10.1	0.53
Nestling period (days)	7	31.5	1.20	n.s.	7	33.2	1.22	n.s.	11	32.6	2.19

<sup>a</sup> Statistical test used was Wilcoxon matched-pairs test. Comparison between experimentally fed nests in 1983 and the same nests (unfed) during 1980–1982.

<sup>b</sup> Statistical test used was the Mann-Whitney  $U$ -test. Comparison between experimentally fed nests and control nests in 1983 (unfed nests).

<sup>c</sup> Laying date: 1 = 1 April.

**Table 5.** Reproductive success of Jackdaws in experimental and control nests

	Experimental nests 1980–1982 (unfed)				Experimental nests 1983 (fed)				Control nests 1983 (unfed)		
	<i>n</i>	mean	s.d.	Prob-ability level <sup>a</sup> ( <i>P</i> )	<i>n</i>	mean	s.d.	Prob-ability level <sup>b</sup> ( <i>P</i> )	<i>n</i>	mean	s.d.
Hatching success (%)	8	69.2	29.8	n.s.	13	85.6	28.0	n.s.	18	83.3	31.8
Fledging success (%)	8	30.0	11.2	<0.05	12	57.2	10.5	<0.001	16	35.6	20.6
Breeding success (%)	9	20.1	13.7	<0.02	13	48.2	15.7	<0.01	18	29.4	20.8

<sup>a</sup> Statistical test used was Wilcoxon matched-pairs test. Comparison between experimentally fed nests in 1983 and the same nests (unfed) during 1980–1983.

<sup>b</sup> Statistical test used was the Mann-Whitney *U*-test. Comparison between experimentally fed nests and controls (unfed) nests in 1983.

experimental nests. However, when we consider the actual numbers of nestlings involved, 30 starved to death in the 12 food-supplemented nests (mean =  $2.5 \pm 1.00$  s.d. nestlings per nest,  $n = 12$ ) compared with 41 nestlings in the 12 control nests (mean =  $3.4 \pm 0.79$ ,  $n = 12$ ), a significant difference (Mann-Whitney *U*-test,  $z = -2.08$ ,  $P < 0.05$ ).

## DISCUSSION

### Breeding density and nest predation

Availability of nest sites often limits numbers of cavity-nesting birds (Dhondt & Eyckerman 1980, van Balen *et al.* 1982, Cody 1985), and intraspecific competition for nest sites may be strong in hole-nesting birds (Haartmann 1957). Cavities vary in quality, and availability of high-quality (safe) cavities may be especially limited by competition for such sites (Nilsson 1984). In our study area, intraspecific competition among Jackdaws for safe sites occurred, since cavities that had not been preyed upon frequently were used the following year, while cavities that had been preyed upon were reused less frequently (Soler & Soler 1993). Also, cavities with a small minimum nest-entrance dimension were occupied more frequently (and with a higher breeding success) than those with a large minimum nest-entrance dimension (Table 2).

Our results demonstrated that when food was abundant near the colony, Jackdaws tended to occupy all cavities, yet Raven nest predation was completely avoided (Table 3). Experimental and observational studies have shown that aggressive birds are sometimes able to deter predators and thereby increase nesting success (Göransson *et al.* 1975, Blancher & Robertson 1982, Knight & Temple 1986, Weatherhead 1990). This is the case in colonially breeding birds using group defence (Wiklund & Andersson 1980, Wiklund 1982, Götmark & Andersson 1984, Robinson 1985). With respect to Jackdaws, Johnsson (1994) found that as the colony size increased, the nest predation rate significantly decreased. This effect was explained by the de-

fending Jackdaws benefiting from group defence against predators.

In our study area, Jackdaws were able to avoid nest predation in nests which were easily accessible to Ravens because the increase in breeding density favoured group defence, which can effectively deter nest predators (see references above), and because food in the proximity of the nests allowed breeding Jackdaws to spend more time close to and defending their nests.

### Reproductive parameters

Almost all supplementary feeding experiments have resulted in advancement of laying (for reviews see Martin 1987, Arcese & Smith 1988, Boutin 1990). In our study, Jackdaw pairs given additional food laid on average 1.8 days earlier than controls (Table 4). However, when provided with extra food, passerines do not increase their clutch size or do so only slightly. Of 14 food supplementation studies, only five reported increases in clutch size (Arcese & Smith 1988). In the present study and other studies on nonpasserines (Arcese & Smith 1988, Nilsson 1991), a significant effect of supplementary food on clutch size was found. Why then do different species (studies) show different responses to food supplementation with respect to clutch size? Three explanations have been offered: (1) the quality of the food supply used is not always the same in all the experiments, and this may be of critical importance (Ewald & Rohwer 1982); (2) the relationship between food availability and clutch size may be nonlinear, such that clutch sizes are strongly depressed only at very high population densities (Arcese & Smith 1988) and (3) clutch size is not constrained at laying but is adjusted to the future requirements of dependent young (Nilsson & Svensson 1993).

The nestling period was not significantly influenced by supplementary feeding (Table 4). Contrary to our expectations (see prediction 4) the fledging periods were not significantly different and actually tended to be shorter in control than in experimental nests. This was because pairs given

extra food reared more young than control pairs, and larger broods in the Jackdaw have markedly longer fledging periods than smaller ones (Soler 1988b).

The normally unused holes, which are of sub-standard quality because of their generally larger nest openings that are more likely to allow entry by predators, are usually used by young individuals which lay significantly later and smaller clutches (Soler, 1984, PhD thesis, University of Granada). Birds responsible for the increase in breeding density in the experimental colonies in the food supplementation year are likely young individuals. Hence, the advancement of breeding, larger clutch size and higher breeding success found in the experimentally fed colonies are even more striking.

The effect of supplementary food on fledgling production remains unclear. According to Arcese and Smith (1988:table 6), fledging success increased as a consequence of food provisioning in only 4 of 11 studies. We suggest that the key to this problem is the breeding strategy of the species. Lack's hypothesis (1947) is that clutch size is adapted to the maximum number of young that the parents can feed adequately. When the food supply is predictable, birds can directly adjust their clutch size. But if food supply at the time of hatching is highly variable or unpredictable, then the birds cannot predict at laying the amount of food available for their young. In the latter case, birds tend to lay more eggs, and later, during the nestling period, the number of young becomes adjusted to the food supply (the brood reduction strategy; Lack 1947). We predict that supplementary food should increase fledgling success in brood-reduction species but not in species which directly adjust clutch size. If all the hatched young usually fledge in fed and unfed pairs, the number of fledglings would depend on the effect of the extra food on clutch size. This hypothesis is clearly supported by analysing the results in previous studies. According to Arcese and Smith (1988), experimentally supplemented food significantly increased fledging success in the Carrion Crow, Magpie *Pica pica* (two studies) and Song Sparrow but showed no effect in the Crested Tit *Parus cristatus*, Willow Tit *Parus montanus* and Dunnock *Prunella modularis*. As predicted, in the Carrion Crow and Magpie, as in corvids in general, eggs hatch asynchronously (Lack 1968), and the Song Sparrow is also a brood-reduction strategist (Arcese & Smith [1988] found that brood reduction was nearly twice as common in unfed nests). On the other hand, eggs hatch synchronously in the family Paridae (with the exception of second broods of the Great Tit *Parus major*; Lack 1968) and in the Dunnock (N.B. Davies, pers. comm.). Finally, the experimental study on the Song Sparrow where fledging success was not affected by supplementary food (Smith *et al.* 1980) was performed in winter, and food provided outside the breeding season cannot affect fledging success. Thus, we can conclude that supplementary food significantly increases fledgling success in brood-reduction strategist species but not in species which directly adjust their clutch size to food supply while feeding young.

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## REFERENCES

- Arcese, P. & Smith, J.N. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *J. Anim. Ecol.* 57: 119–136.
- Blancher, P.J. & Robertson R.J. 1982. Kingbird aggression: Does it deter predation?. *Anim. Behav.* 30: 929–930.
- Blancher, P.J. & Robertson, R.J. 1987. Effect of food supply on the breeding biology of Western Kingbirds. *Ecology* 68: 723–732.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Can. J. Zool.* 68: 203–220.
- Catterall, C.P., Wyatt, W.S. & Henderson, L.J. 1982. Food resources, territory density and reproductive success of an island Silvereye population *Zosterops lateralis*. *Ibis* 124: 405–421.
- Cody, M.L. 1985. An introduction to habitat selection in birds. In Cody, M.L. (ed.) *Habitat Selection in Birds*: 3–56. Orlando, Fla.: Academic Press.
- Coulson, J.C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating the age and composition of populations. *Proc. Zool. Soc. Lond.* 140: 211–227.
- Davies, N.B. & Lundberg, A. 1985. The influence of food on the time budgets and timing of breeding of the Dunnock (*Prunella modularis*). *Ibis* 127: 100–110.
- Dhindsa, M.S. & Boag, D.A. 1990. The effect of food supplementation on the reproductive success of Black-billed Magpies *Pica pica*. *Ibis* 132: 595–602.
- Dhondt, A.A. & Eyckerman, R. 1980. Competition between the Great and the Blue Tit outside the breeding season in field experiments. *Ecology* 61: 1291–1298.
- Enoksson, B. & Nilsson, S.G. 1983. Territory size and population density in relation to food supply in the Nuthatch *Sitta europaea* (Aves). *J. Anim. Ecol.* 52: 927–935.
- Ewald, P.W. & Rohwer, S. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in Red-winged Blackbirds *Agelaius phoeniceus*. *J. Anim. Ecol.* 51: 429–450.
- Göransson, G., Karlsson, J., Nilsson, S.G. & Ulfstrand, S. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: An experimental study. *Oikos* 26: 117–120.
- Götmark, F. & Andersson, M. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). *Anim. Behav.* 32: 485–492.
- Haartmann, L. von 1957. Adaptation in hole-nesting birds. *Evolution* 11: 339–347.
- Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P. & Burns, M.D. 1993. The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. *Ibis* 135: 255–263.
- Hochachka, W.M. & Boag, D.A. 1987. Food shortage for breeding Black-billed Magpies (*Pica pica*): An experiment using supplemental food. *Can. J. Zool.* 65: 1270–1274.
- Högstedt, G. 1981. Effect of additional food on reproductive success in the Magpie (*Pica pica*). *J. Anim. Ecol.* 50: 219–229.
- Jansson, C., Ekman, J. & Brömssen, A. von. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* 37: 313–322.
- Johnsson, K. 1994. Colonial breeding and nest predation in the

- Jackdaw *Corvus monedula* using old Black Woodpecker *Dryocopus martius* holes. *Ibis* 136: 313-317.
- Källander, H. 1981. The effects of provision of food in winter on a population of the Great Tit *Parus major* and the Blue Tit *P. caeruleus*. *Ornis Scand.* 12: 244-248.
- Knight, R.L. 1988. Effects of supplemental food on the breeding biology of the Black-billed Magpie. *Condor* 90: 956-958.
- Knight, R.L. & Temple, S.A. 1986. Nest defense in the American Goldfinch. *Anim. Behav.* 34: 887-897.
- Krebs, J.R. 1971. Territory and breeding densities in the Great Tit. *Ecology* 52: 2-22.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89: 302-352.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Martin, T.E. 1987. Food as a limit on breeding birds: A life-history perspective. *Ann. Rev. Ecol. Syst.* 18: 453-487.
- Nilsson, J.-A. 1991. Clutch size determination in the Marsh Tit *Parus palustris*. *Ecology* 72: 1757-1762.
- Nilsson, J.-A. & Svensson, E. 1993. Energy constraints and ultimate decisions during egg-laying in the Blue Tit. *Ecology* 74: 244-251.
- Nilsson, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scand.* 15: 167-175.
- Richner, H. 1992. The effect of extra food on fitness in breeding Carrion Crows. *Ecology* 73: 330-335.
- Robinson, S.K. 1985. Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *Auk* 102: 506-519.
- Sealy, S.C. 1980. Reproductive responses of Northern Orioles to changing food supply. *Can. J. Zool.* 58: 221-227.
- Simons, L.S. & Martin, T.E. 1990. Food limitation of avian reproduction: An experiment with the Cactus Wren. *Ecology* 71: 869-876.
- Smith, J.N.M., Montgomerie, R.D., Taitt, M.J. & Yom-Tov, Y. 1980. A winter feeding experiment on an island Song Sparrow population. *Oecologia* 47: 164-170.
- Soler, M. 1988a. Egg size variation in Jackdaw *Corvus monedula* in Granada, Spain. *Bird Study* 35: 69-76.
- Soler, M. 1988b. Nestling period variation in Jackdaw *Corvus monedula* in relation to brood size. *Bird Study* 36: 73-76.
- Soler, M. 1989. Fracaso reproductor en Grajilla (*Corvus monedula*): Pérdidas de huevos y mortalidad de pollos. *Ardeola* 36: 3-24.
- Soler, M. 1990. Breeding success and productivity in the Jackdaw (*Corvus monedula* L.) in Granada (Spain). In Pinowski, J. & Summers-Smith, J.D. (eds) *Granivorous Birds in the Agricultural Landscape*: 253-261. Warszawa: Intecol.
- Soler, M. & Soler, J.J. 1987. Selección del lugar de nidificación en Grajilla (*Corvus monedula*). *Alytes* 5: 87-98.
- Soler, M. & Soler, J.J. 1993. Does the risk of nest predation affect clutch size in the Jackdaw *Corvus monedula*? *Bird Study* 40: 232-235.
- Strehl, C.E. & White, J. 1986. Effects of superabundant food on breeding success and behaviour of the Red-winged Blackbird. *Oecologia* 70: 178-186.
- van Balen, J.H., Booy, C.J.H., van Franeker, J.A. & Odieck, E.R. 1982. Studies on hole-nesting birds in natural sites. 1. Availability and occupation of natural nest-sites. *Ardea* 70: 1-124.
- Weatherhead, P.J. 1990. Nest defense as shareable paternal care in Red-winged Blackbirds. *Anim. Behav.* 39: 1173-1178.
- Wiklund, C.G. 1982. Fieldfare (*Turdus pilaris*) breeding success in relation to colony size, nest position and association with Merlins (*Falco columbarius*). *Behav. Ecol. Sociobiol.* 11: 165-172.
- Wiklund, C.G. & Andersson, M. 1980. Nest predation selects for colonial breeding among Fieldfares *Turdus pilaris*. *Ibis* 122: 363-366.
- Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the Crow (*Corvus corone*). *J. Anim. Ecol.* 43: 479-498.

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