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Does the risk of nest predation affect clutch size in the Jackdaw *Corvus monedula*?

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The nest predation hypothesis predicts that clutch size should be inversely related to the risk of nest predation. In this paper we analyse data on nest predation, clutch size and fledgling production in 128 Jackdaw nests in order to test if clutches are larger in the safer sites. The predation rate was positively correlated with the minimum nest-entrance dimensions (predation is greater in nests with large entrances). Clutch size was not related to the risk of nest predation, and our data do not therefore support the nest predation hypothesis.

Nest predation may have had a strong selective influence on the life history of hole-nesting birds[1] and on nestling growth patterns.[2] Several hypotheses have been proposed for the observed variation in the clutch size of birds.[3–5] One, the nest predation hypothesis, states that the risk of nest predation negatively affects the clutch size.[5–7] The risk of predation is directly related to clutch size, because the time needed for feeding during the pre-laying, egg-laying, incubation, and nestling period is dependent upon the number of eggs that the nest contains. In addition, the frequency of feeding visits is a function of the number of nestlings. For this reason it has been suggested that when nest predation rates are high, a reduction in clutch size should be adaptative.

The importance of predation in clutch size evolution is controversial. Some authors contend that predation has a negligible effect,[3,9] whereas others suggest that it might influence clutch size only under certain circumstances.[5,8,10]

In this paper we analyse data on nest predation, clutch size and fledgling production in the Jackdaw *Corvus monedula* in order to test whether clutches are larger in safer sites (those with smaller nest-entrances) as predicted by the nest predation hypothesis.

STUDY AREA, MATERIALS AND METHODS

Between 1979 and 1983 a total of 228 Jackdaw nests were studied in the Hoya de Guadix (37°10′ N, 3°11′ W), southern Spain, a cereal-producing plain at 900–1100 m asl. In this area there are numerous gullies and clay cliffs with many crevices and holes used by Jackdaws for nesting. In the analyses presented here we have used only those nests for which all data (nest-dimensions, clutch size and fledgling production) were known (n= 128). Climbing equipment was used to gain access to nests. Each nest was visited every two to four days until the end of the nestling period.

Four nest-cavity dimensions were measured: the width and height of the nest entrance (the smaller of the two was taken as the minimum nest entrance), the depth of the cavity and the height above the ground. All were measured to the nearest cm except height above the ground, which was measured to the nearest metre.

Clutch size was measured at the end of laying. Only one nest suffered partial predation during the incubation stage and none during the nestling stage.[11] For this reason the sample size in the clutch-size analysis (n= 127) differs slightly from that in other analyses (n= 128). Fledgling production was considered to be the number of chicks in the nest at day 30 of the nestling period or later, and the predation rate of the proportion of clutches or broods that suffered total losses.

There were no significant differences between years in either clutch size (ANOVA, $F_{4,122}$ = 1.473, P= 0.21) or nest-cavity dimensions (MANOVA, Wilks' lambda= 0.82, df= 20, 295; P = 0.24), and we have therefore analysed data from all years combined.

Logistic regression was used to study the relationship between nest predation (dependent variable) and nest-cavity dimensions (independent variables). Initially, a logistic model was fitted to the pooled data which considered the effects of all five nest variables using the maximum-likelihood method of Cox.[12] The deviance (2*log-likelihood) associated with this model was also calculated. The effects of omitting each of the nest variables in turn was then examined by fitting the model with that variable excluded. The significance of the effect of each variable was assessed by considering the difference in deviance between models including and excluding the variable being tested as a chi-squared statistic with one degree of freedom. The final model was considered to have been identified when omission of any of the remaining variables would have caused a significant (P < 0.05) increase in the deviance. To test for the significance of clutch size on nest predation, we included clutch size as an additional independent variable and computed the difference in the deviance for models with and without clutch size.

The relationships between clutch size, fledgling production and nest-cavity dimensions were analysed using the Spearman Rank correlation coefficient.[13] The correlation analyses were carried out using each individual nest as an independent observation.

RESULTS

A high percentage of Jackdaw nests (23.7%, n= 194) were completely predated, mainly by the Common Raven *Corvus corax*.[11]

The relationships between cavity dimensions and nest predation, clutch size and fledgling production are presented in Fig. 1. These plots suggest that predation rate is affected mainly by nest-entrance dimensions, but the logistic regression analysis indicated that only the minimum nest-entrance significantly affected the probability of predation (Table 1). A logistic regression model incorporating only the effect of minimum nest-entrance dimension on nest predation described the data just as well as a model incorporating all five nest dimension variables (difference in deviance between these two models = 6.39, P = 0.17). Therefore, the risk of nest predation depends mainly on the minimum nest-entrance dimension. Nests with small minimum nest-entrance dimensions experience lower predation rates than nests with large minimum nest-entrance dimensions (Fig. 1c).

Clutch size was not related to the risk of nest predation, since there was no significant difference between the deviances of the logistic model incorporating only the effect of minimum nest-entrance (deviance= 130.79, number of parameters= 2) and a model also including clutch size (deviance = 128.03, number of parameters= 3; P = 0.140).

There was some evidence that fledgling production was greater in nests with a relatively small entrance. The correlations between fledgling production and nest-entrance width, nest-entrance height and minimum nest-entrance dimension were all significant (r_s= −0.39, P < 0.0001, n= 128; r_s = −0.31, P < 0.0005 n= 128; r_s= −0.36, P < 0.0001, n = 128; respectively). Fledgling production was not correlated with cavity depth (r_s= −0.001, P = 0.99, n = 128). A nest with a shallow cavity cannot be predated if it has a narrow entrance.

A curious result was obtained during analysis of fledgling production with respect to the height above the ground. Contrary to expectation, fledgling production was significantly higher in lower holes (r_s = −0.282, P < 0.002, n = 128, Fig. 1e). The likely explanation for this is that in the Guadix area the Green Woodpecker *Picus viridis* frequently excavates its nest in clay cliffs between 2 m and 5m above the ground.[14] These holes have a narrow entrance and are preferred by Jackdaws because they are safe from predation.[14]

DISCUSSION

According to the nest predation hypothesis average clutch size should be smaller at nest-sites with a greater risk of nest predation.[5,15] In this study there was no evidence for such an

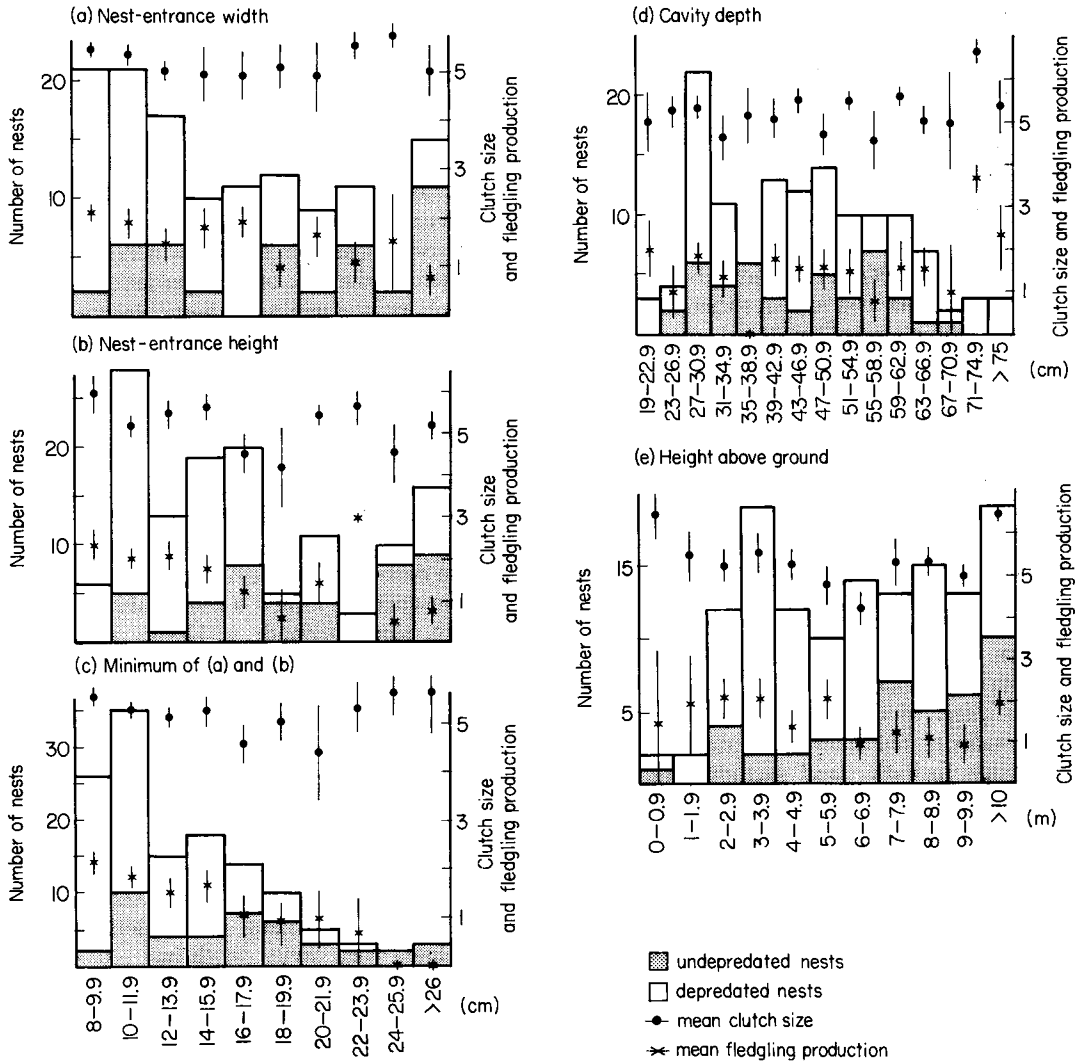

Figure 1. Relationship between nest cavity dimensions and nest predation, mean clutch size and mean fledgling production. Only nests where all variables are known have been considered. Vertical bars represent standard errors. Nest-dimensions have been categorized into these number of classes to enable a depredation rate to be calculated.

effect on the Jackdaw. There was evidence that the nest-entrance dimensions affect the risk of nest predation, but not clutch size. Nest predation is a major cause of nest failure and is a major factor in reducing the number of fledged young.[16–19] Thus, nest predation should be a strong selective factor in the evolution of nest-site selection and nesting habits in birds. This idea is supported by the observation that in hole-nesting birds the minimum nest-entrance widths are correlated with the size of the species[19] and, in this study, by the correlation between predation rate and the minimum nest-entrance dimension.

Intraspecific competition for nest-sites may be strong in hole-nesting birds[20] and may limit the availability of suitable nesting places.[21,22] In our study area, intraspecific competition for nest-sites can be expected given that the unpredated safe cavities were very frequently used in the following year (mean = 69.4%, se = 3.8%; n = 4 years) while the cavities that were predated were less frequently reused (mean = 30.7%; se = 2.8%; n = 4 years).

Table 1. Maximum likelihood estimates of the slope parameters (S) of logistic models considering the effects of 5 Jackdaw nest-cavity dimension variables on nest predation rates. Differences between deviances (D) for models with and without the variable to be tested are also presented

	All nest variables in the model				*Final model*	
Variable	*S*	P	D	P	*Slope*	P
Nest-entrance width	0.041	0.256	2.04	0.153	—	—
Nest-entrance height	0.003	0.858	0.45	0.833	—	—
Minimum nest-entrance dimension	0.196	0.007	11.24	0.001	0.223	0.0002
Cavity depth	−0.032	0.162	3.14	0.076	—	—
Height above the ground	0.082	0.333	1.36	0.244	—	—

In general, the breeding success of hole-nesting birds is higher than that of open-nesting species.[16,23] Considering that a safe cavity (with a narrow entrance and/or a very deep hole) cannot be predated and given the strong competition for nest-sites, we suggest that in the case of the Jackdaw, and perhaps in other hole nesters, the risk of nest predation affects nest-site selection but not clutch size.

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