LATITUDINAL TRENDS IN CLUTCH SIZE IN SINGLE BROODED HOLE NESTING BIRD SPECIES: A NEW HYPOTHESIS

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ABSTRACT In the Jackdaw *Corvus monedula* clutch size decreases significantly with increasing latitude. Our data provide an exception to the commonly accepted observation that avian clutch size tends to increase with latitude. We suggest that (1) the advantages of small clutches are not important in the Jackdaw, since larger clutches are the most productive ones, and (2) an opposite latitudinal trend between clutch size and egg size suggests a trade-off between laying few large eggs or many small eggs. We hypothesize that in the Jackdaw, and in general, in other single brooded hole nesters, large clutches are advantageous. and clutch size decreases with latitude because it is limited by proximate constraints put on the females of producing large eggs given that in the north large eggs provide a selective advantage.

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INTRODUCTION

Many studies have analysed the factors affecting clutch size. Many of them give special attention to patterns of geographic variation (Von Haartmann 1967, Owen 1977, Ricklefs 1980, Järvinen & Väisänen 1983, Møller 1984, Isenmann 1987), but other factors also have been studied (Perrins 1970, Loman 1977, Finney & Cooke 1978, Ojanen *et al.* 1978, Orell & Ojanen 1983, Järvinen 1986, 1989). Now, clutch size is considered in a life history context, with the perspective of a trade-off between current investment and future prospects, and with a focus on individual differences in quality (Pettifor *et al.* 1988, Slagsvold & Lifjeld 1988, 1990).

The increase of clutch size with increasing latitude is one of the most striking and best documented variations in clutch size both between and within species (Perrins & Birkhead 1983), having been found in many studies (Lack 1947, 1948, Ashmole 1961, 1963, Cody 1966, Royama 1969, Slagsvold 1975, Ojanen *et al.* 1978, Owen 1977). However, exceptions are not rare (Ojanen *et al.* 1978, Orell & Ojanen 1983, Isenmann 1987, Järvinen 1989). This trend of latitudinal increase towards the north has been the subject of three major hypotheses in nidicolous birds:

(1) The longer spring day in the north permits the parents to collect more food for their young (Lack 1947, 1966). This hypothesis has been extended and modified in some cases (Royama 1969, Owen 1977).

(2) The resource abundance during the breeding season relative to the breeding population density is greater in the north, allowing the production of more eggs and thus more offspring (Ashmole 1963, Ricklefs 1980, Hussell 1985).

(3) The risk of nest predation negatively affects the clutch size (Skutch 1949, Cody 1966, Slagsvold 1982). This hypothesis suggests a reason for the latitudinal decrease in clutch size, because nest predation risks decrease at high compared with low latitudes (Ricklefs 1969).

In this paper, we present data which contradict the general pattern that clutch size increases with latitude, discuss the influence of this pattern on the hypothesis concerning the evolution of clutch size, and propose a new hypothesis to explain the "reversed" latitudinal trend in clutch size for the Jackdaw and other hole nesting birds which only lay one clutch per season. We suggest that in single brooded hole nesting bird species, large clutches are advantageous and decrease with latitude as a consequence of the trade-off between clutch size and eggs size.

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MATERIAL AND METHODS

Between 1979 and 1983 a total of 228 Jackdaw nests were studied in the Hoya de Guadix (Granada, Southern Spain), an area described in earlier papers (Soler *et al.* 1982, Soler 1989a). The nests were visited every two or four days until the end of the nestling period. Eggs were marked with a number, according to the order of laying, if this was known. More information about the methods and colonies is given in previous papers (Soler 1988, Soler 1989b, Soler & Soler 1991). Egg volume of Jackdaw eggs was estimated using Coulson's (1963) formula, $V = \pi \cdot K \cdot A^2 \cdot L/6$, where A is breadth, L is length and K is a constant derived from a sample of eggs whose volume is known. We considered the K value obtained previously for the Jackdaw in our study area (Soler 1988) valid for all Jackdaw populations whose eggs breadth and length are cited in the literature. The statistical analyses used were standard ones (Sokal & Rohlf 1979).

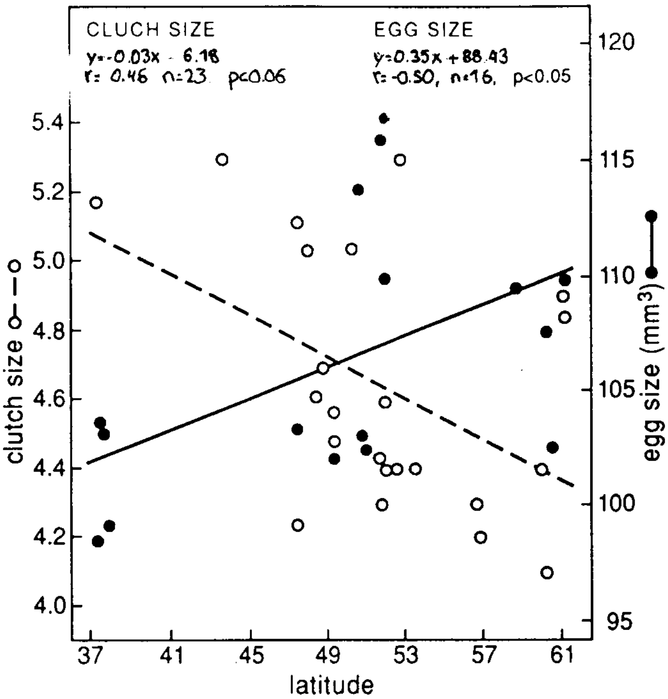

Fig. 1. Relationship between clutch size, egg size and latitude in the Jackdaw. More detailed information and sources in Soler & Soler (1991).

RESULTS

Lack (1947) assumed that there was no increase in Jackdaw clutch size with increasing latitude. However, analyzing data on Jackdaw clutch size from this and other published studies (see table 2 in Soler & Soler 1991) there is a negative and significant correlation between latitude and clutch size (Fig. 1). This represents the first case in which a statistically significant negative correlation has been found between increasing clutch size and latitude.

In our study area Jackdaw eggs are shorter than elsewhere (Soler 1988). Analyzing data in the literature (Schönwetter 1967, Makatsch 1976, Dwenger 1989, Hucke 1990, and references in Soler 1988 (table 9)) and three unpublished data (Central Spain: 32.07 mm x 24.73 mm, n = 8, eggs from Museo de Ciencias Naturales de Madrid; Mures: 33.91 mm x 24.52 mm, n = 31, own data; Hueneja: 32.24 mm x 24.59 mm, n = 18, own data) there is a positive significant correlation between egg size (volume) and latitude ($r = 0.50, p < 0.05, n = 16$) which is stronger between the egg length and latitude ($r = 0.67, p < 0.005, n = 16$). Egg size reported by Antikainen (1978) in a northern population in SW Finland was abnormally small. Without these data, the correlations between egg size and latitude are clearer ($r = 0.60, p < 0.02, n = 15$ and $r = 0.73$, $p = 0.002$, $n = 15$ respectively for egg volume and egg length).

These inverse trends of clutch size and egg size with latitude may be interpreted as a latitudinal pattern because in our study area there is no correlation between clutch size and egg size ($r = 0.08, p > 0.4$, $n = 126$, using clutch means for egg dimensions).

DISCUSSION

Not all bird species show increasing clutch size with increasing latitude. Slagsvold (1982) found that the mean clutch size for 83% of the open-nesting species were higher in Finland than in Switzerland, while only 58% of hole and semi-hole nesters laid larger clutches in Finland. Järvinen (1986), comparing the clutch size of 15 species in NW Lapland with other northern areas in Fennoscandia, found that in only one case the northern population did have larger clutches. In eight cases, clutch size was equal and in six cases smaller than in the southern populations. However, Järvinen (1986) supposed that these results were the consequence of harsh conditions in his study area. Although the latitudinal increase in clutch size is not a general phenomenon, the Jackdaw is the only altricial species in which the opposite tendency is known to be statistically significant.

Within a species large eggs confer important benefits because of the positive relationship between egg size and growth rate and survival of hatchlings, respectively (Schifferli 1973, O'Connor 1979). Small clutches also have many advantages (see review in Slagsvold 1982). The most important can be summarized as follows: (1) The risk of predation will be reduced, because (a) less time needs to be spent feeding during the pre-laying, egg-laying and incubation stages; (b) the nestling period may be shortened; and (c) the adults need to make fewer feeding visits to the nest. (2) The young will be reared more quickly and each fledgling will be heavier. (3) The energy reserves available for producing second broods will be increased and such repeated nesting will take place more quickly. (4) The chances of survival of the adults to the next year will also be enhanced.

If laying large eggs and reducing the clutch size is advantageous, why do Spanish Jackdaws show the opposite tendencies? If we analyze the above mentioned advantages of small clutches for the Jackdaw, the first advantage related to nest predation does not seem to affect clutch size since in the Jackdaw, the risk of nest predation influences nest site selection, but does not affect clutch size because a cavity with a narrow entrance cannot be predated regardless of clutch size (Soler & Soler, submitted). On the other hand, a long nestling period accompanied by a slow growth rate may permit the raising of a greater number of young, given that those young individually need less food per unit time (Ricklefs 1968). Birds, which nest in relatively secure places such as holes, can adopt this strategy for feeding the brood (Lack 1968). The first and the second advantages arguably are not important for birds nesting in secure holes. The third advantage would be relevant in birds which rear two broods, but Jackdaws only lay one clutch; even replacement clutches are very rare (Soler & Soler 1991). With respect to the fourth advantage, certainly, an individual may increase its lifetime reproductive success by reducing clutch size, or more specifically by reducing current reproductive effort (Williams 1966, Charnov & Krebs 1974). We suggest that the chances of adult survival to the next season is larger in species with only one clutch per year than in those with two, even though the latter may lay smaller clutches. As a matter of fact, corvids lay only one clutch and are one of the bird families with a long life expectancy (Perrins 1987).

To lay only one clutch has another advantage. This allows more flexibility and reduces the time pressure of having to lay two clutches, enabling the birds to take advantage of the optimal food availability period. In the Guadix area, Jackdaws lay later than in most other places ($\bar{x}$ = 28.1 April, Soler & Soler 1987). This delay is advantageous because then the last week of the nestling period coincides with the timing of barley germination. This food is the most important component in the diet of adults (Soler *et al.* 1990), allowing them to give more of the insects they capture to the nestlings. Furthermore, in the last days of the nestling period, they use to feed offspring with germinating barley grain (M. Soler own obs.).

Are there any advantages in laying a larger number of eggs? Lack (1947, 1954, 1968) hypothesized that clutch size in nidicolous birds is determined by the maximum number of young that the parents are able to feed, and that, as a result of natural selection, the most common clutch size is the most productive. He suggested that females which laid more eggs than usual could be less successful because the nestlings might be undernourished. However, many studies have failed to support this assumption. Frequently, the most productive clutch size has been found to be larger than the observed mean clutch size (Perrins & Moss 1974, Crossner 1977, Loman 1977, Murphy 1978, De Steven 1980, Nur 1984). This is also the case in our Jackdaw population; clutches of six and seven eggs ($\bar{x}$ = 1.84 ±

1.35, $n = 64$) are more productive than smaller ones ($\bar{x} = 1.18 \pm 1.23$, $n = 74$; $t = 2.87$, $p < 0.003$). Larger clutches have a very important advantage if they produce more offspring.

Clutch size and egg size represent an energy investment by the female. Thus, the opposite latitudinal trend between clutch size and egg size in the Jackdaw may suggest a trade-off between laying a few large or more small eggs. This idea may be supported by the fact that clutch size is determinate (Soler & Soler 1991), and that extra food leads to an increase in clutch size as compared to natural conditions (Soler & Soler in prep.).

Larger eggs offer important advantages (for references, see below). Järvinen & Väisänen (1983), studying egg size in the Pied Flycatcher *Ficedula hypoleuca*, suggested that selection pressures for larger eggs are stronger in the north because losses due to hatching failure are more common in the far north than in the south, and small eggs tend to hatch poorly in the north. Furthermore, large eggs have more reserves (Nisbet 1978, Ankney 1980) which are mainly important during the first days of life (Wiley 1950). Small nestlings are more easily affected by adverse environmental conditions, which in northern latitudes are more common (Järvinen 1986).

We can therefore conclude that:

(1) The advantages of small clutches are not important in the Jackdaw because (a) the risk of the nest predation influences nest site selection, but does not affect clutch size; (b) birds nesting in relatively secure places can adopt the strategy of increasing the nestling period and decreasing the growth rate which permits the raising of a larger number of young. (c) The Jackdaw only lays one clutch per season, replacement clutches being very rare. This may increase the chances of adult survival until the next season and permits rearing of offspring during the optimal food availability period.

(2) Larger clutches have the very important advantage of producing a larger number of offspring. Selection should, therefore, favour a large clutch size in the Jackdaw.

On the other hand, we must consider:

(1) In hole and semi hole nesters, the latitudinal trend is less clear than in open nesters. (2) Selection pressures for large egg size are stronger in the north. (3) The opposite latitudinal trend found between clutch size and egg size may mean a trade-off between laying few large or many small eggs.

Therefore we suggest that in the Jackdaw clutch size tends to be large, but in the north where large eggs may be selectively advantageous as a consequence of the trade-off between eggs size and clutch size, clutch size is smaller. As latitude decreases selection pressures for large eggs decreases and clutch size increases.

This may be the way Jackdaws, and other species, which breed in holes and do not lay second nor replacement clutches, may optimize clutch size. This hypothesis may be tested by analyzing data for species having the same characteristics and having a wide latitudinal distribution range such as the Chough *Pyrrhocorax pyrrhocorax*, the Swift *Apus apus* and the Little Owl *Athene noctua*.

In the Chough, according to Bullock *et al.* (1983), the most frequent clutch size is five eggs. The mean clutch size recorded in Guadix ($\bar{x} = 4.15$, $SE = 0.66$; Soler *et al.* 1983) is larger than that reported by Bullock *et al.* (1983) for the British Isles ($\bar{x} = 3.88 \pm 0.99$, $n = 236$), but the difference is not significant ($t = 1.19$, $p > 0.1$). There exists very little data with respect to Chough egg size. In our area the mean egg size is 40.0 mm x 27.1 mm (SE = 1.82 and 5.06, respectively, $n = 31$; Soler *et al.* (1983)). These dimensions are smaller than those measured in other areas (40.37 mm x 27.50 mm, Guichard 1962; 40.6 mm x 28.7 mm, Harrison 1983) and narrower than those cited by Witherby *et al.* (1938; 39.4 mm x 27.9 mm). We cannot compare means because standard deviations are not available in the literature.

Analyzing the data for the Little Owl cited in Glutz & Bauer (1980) and Cramp (1985), a significant negative correlation have been found between clutch size and latitude (Fig. 2). With respect to egg size, data available (Rey 1905, Niethammer 1938, Schönwetter 1967, Verheyen 1967, Makatsch 1976, Glutz & Bauer 1980, Cramp 1985) show a significant positive correlation with latitude (Fig. 2) as our hypothesis predicted.

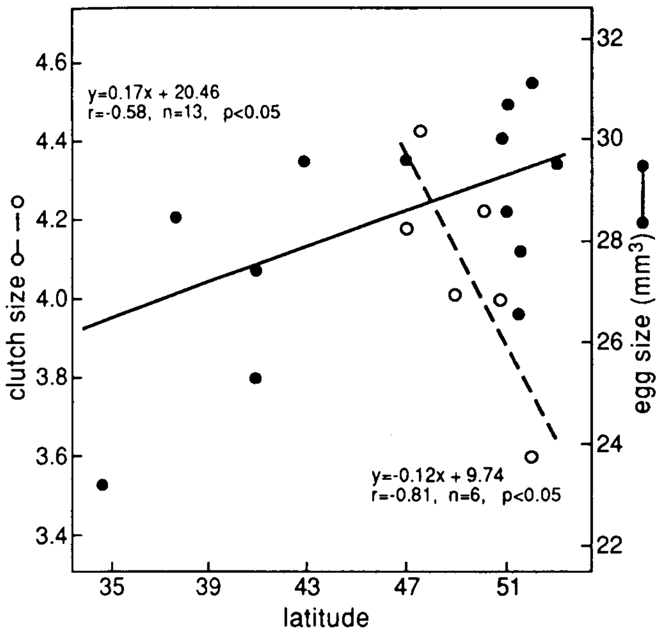

Fig. 2. Relationship between clutch size, egg size and latitude in the Little Owl.

Data provided by Glutz & Bauer (1980) and Cramp (1985) on clutch size of the Swift are also negatively correlated with the latitude (r = -0.65, p < 0.06, n = 9). However, egg size (Rey 1905, Niethammer 1938, Verheyen 1967, Makatsch 1976, Glutz & Bauer 1980, Cramp 1985) does not show any relationship with latitude (r = -0.07, p > 0.8, n = 10), but this may be because seven data points have a very similar latitude (51°- 53°) and present great variation.

These results, in these species support the aforementioned hypothesis. Besides, the swift and the little owl are also species with a high adult survival rate (Saether 1989).

Other single brooded open-nesting corvids may show the same latitudinal trend in clutch size as the Jackdaw. However we have analyzed data on clutch size of the Magpie *Pica pica* (Holyoak 1967, Love & Summers 1973, Högstedt 1980, Baeyens 1981, Tatner 1982, Balança 1984, Arias-de-Reyna *et al.* 1984, Eden 1985, Husby ... Crow *Corvus corone* (Wittenberg 1966, Holyoak 1967, Yom-Tov 1974, Picozzi 1975, Loman 1977) and the correlation between clutch size and latitude in both species is positive (r = 0.33, p > 0.3, n = 9 and r = 0.18, p > 0.7, n = 5, respectively).

Thus, other species laying only one clutch and having a high adult survival rate do not follow the same latitudinal trend as the Jackdaw. Therefore, the most important characteristic of species showing a decrease of the clutch size with latitude is being a hole-nester.

We can conclude that in Jackdaws, and in single brooded hole nesters in general, large clutches are advantageous and decrease with latitude as a consequence of the trade-off between clutch size and egg size given that in the north large eggs have a selective advantage. This strategy is advantageous because the most productive clutch is laid each year and reproductive success may increase throughout life. Hole nesters laying only one clutch do not support the nest predation hypothesis which only applies to open nesters and hole nesters laying two or more clutches.

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SAMENVATTING

Bij de Kauw blijkt de gemiddelde legselgrootte (statistisch significant) af te nemen van zuid naar noord (Fig. 1). Dat is nogal uitzonderlijk onder nestblijvers. Daarbij is in het algemeen juist sprake van een (al door Lack in