

Seasonal variation of clutch size in the European blackbird *Turdus merula*: a new ultimate explanation

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Summary

1. Seasonal patterns of clutch size, partial hatching, fledging and breeding losses were analysed in an urban blackbird population in Budapest during four successive breeding seasons from 1986 to 1989.

2. Average clutch size was maximal mid-season, but timing of the clutch size peak varied from year to year according to the beginning of the breeding season.

3. Contrary to expectation, partial losses both in egg and nestling stages were greatest mid-season, and seasonal patterns of successes corresponded well with the pattern of precipitation preceding egg laying. The amount of rainfall proved to be a good indicator of earthworm abundance, the main food of urban blackbirds.

4. Seasonal patterns of hatching success proved to be quite different between four- and five-egg clutches, while fledging success did not differ significantly. The pattern of breeding success of females laying five eggs followed precipitation closer and earlier, while females laying only four eggs lost eggs or nestlings only when the amount of precipitation fell below a threshold level. Productivity of clutch size four reached that of clutch size five at the beginning and at the end of the season but not in the middle.

5. Our results suggest a new ultimate explanation for the seasonal clutch size maximum in this species. Although the key factor seems to be changes in food supply during egg formation, it affects clutch size indirectly by changing the trade-off between fertility and hatching success throughout the season.

Key-words: egg hatchability, food supply, trade-off.

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Introduction

Two main types of seasonal variation in clutch size occur among temperate-zone passerines (Klomp 1970). Single-brooded species usually show a seasonal decline (Kluijver 1951; von Haartmann 1967; Murphy 1986; Stutchbury & Robertson 1988; Igniatuk & Clark 1991), while multiple-brooded species, like the European blackbird *Turdus merula* L., lay their largest clutches in the middle of the breeding season (Snow 1955, 1958; Seel 1968; Dixon 1978; Murphy 1978; Davies & Lundberg 1985; Kuitunen 1987).

The first group of explanations for the decreasing seasonal pattern hypothesizes ultimate mechanisms, i.e. that there is a trade-off between clutch size and some other fitness component. For example, clutch size and fledging success may be traded-off (Lack 1947), and the declining food supply for the nestlings during the season leads to the adaptive response of

decreasing clutch size by the end of the breeding season (Perrins 1970). Another mechanism hypothesizes that the parental cost of reproduction (Williams 1966), i.e. the slope of the trade-off between clutch size and parental survival, increases by the end of the breeding season because parents have to prepare for moult and/or migration (Hussel 1972). Reduction of parental survival can be avoided by reduced reproductive effort, consequently parents should reduce either their clutch size and/or parental care by the end of the season.

From these ultimate hypotheses only the former could be applied to species with a seasonal clutch size maximum (Snow 1955, 1969; Seel 1968; Kuitunen 1987). Besides seasonal variation of food supply, these authors also considered the possible role of seasonal variation of day length, i.e. time available for foraging.

Proximate mechanisms suppose that clutch size is determined directly by the laying ability of females

(von Haartmann 1971). In some species where repeat or second clutches are frequent, body reserves of females may be decreased by the first breeding attempt, such that they can only lay smaller clutches in a second attempt (Pinkowski 1977). According to another explanation, individual differences exist among females (age or territory) and those in better condition both lay earlier and larger clutches, resulting in a negative correlation between laying date and clutch size (Askenmo 1982; Daan *et al.* 1988).

These proximate hypotheses do not explain an early seasonal increase in clutch size. On the other hand, Murphy (1978), finding 'no concordance between seasonal changes in clutch size and in fledging success' in house sparrows *Passer domesticus* L., supposed that the seasonal variation of clutch size was determined directly by changes in food supply during the egg formation period.

In this paper we analyse seasonal patterns of partial hatching, fledging and breeding losses, and their connection with changes in precipitation, a good indicator of food supply in urban blackbirds. Our results show the existence of a trade-off between clutch size and hatching success. Changes in food supply during the egg formation period appear to change the slope of this trade-off during the season, so that clutches with five eggs are no more productive than clutches with four eggs at the beginning and at the end of the breeding season.

Materials and methods

STUDY AREA, DATA COLLECTION

Our data were collected in a 13-ha urban park (Vérmézö) in the centre of Budapest, Hungary, during four breeding seasons from 1986 to 1989. The park consists of pathways and lawn areas of different sizes with a great variety of evergreen and broad-leaved bushes and trees. About 70–80 pairs of blackbirds breed in the area each year. They lay two or three clutches during a season, resulting in about 150–200 nests each year.

The area was searched for new nests once a week from the beginning of March until the end of June. Each accessible nest was visited at least once a week, so hatching, fledging and breeding success could be determined accurately. If laying date of the first egg was unknown, it could be calculated from the date of hatching, assuming that eggs were laid daily and that the duration of the incubation period was about 12 days.

In 1986 the seasonal dynamics of earthworm abundance was studied. Five 0.25-m² quadrats were sampled with the extraction method (Evans & Guild 1948) on five occasions from the end of April until mid-July. Earthworms were counted and total dry weight (mg) was estimated from measurements of length (mm) on the basis of a linear relationship (dry weight = 1.2 × length).

Precipitation data were obtained from the Budapest Weather Station of the Hungarian Meteorological Service, located about 1 km from our study area.

DATA ANALYSES

To analyse the seasonal patterns of clutch size and other breeding parameters, data were arranged in overlapping time-intervals on the basis of laying date (Vanicsek & Ludvig 1992). Different interval-lengths from 5 to 30 days were tried; results obtained by using 15-day overlapping intervals are presented in this paper. The starting point of the first interval was determined so that the first interval contained at least one datum, then each interval began a day later. Consequently, in the case of 15-day intervals, each pair of neighbouring intervals overlapped by 14 days, and each fifteenth interval did not overlap with each other.

During the 4 years, 365 nests were considered complete, as females had begun to incubate them. Data from these nests were used only in the calculation of average clutch size throughout the seasons, while in the analyses of seasonal patterns of partial losses only data from nests which fledged at least one offspring were included. Hatching, fledging and breeding success were calculated for individual clutches [number of successful eggs (nestlings) per number of all eggs (nestlings)], then averaged for the 15-day overlapping intervals. Because the number of successful nests was quite low in each year (25, 47, 42 and 51 in 1986, 1987, 1988 and 1989, respectively), but the seasonal patterns of their hatching, fledging and breeding success tended to be similar in each year, data for the 4 years were combined.

Concordance between the seasonal patterns of successes and precipitation was calculated by using a modified cross-correlation analysis. The 15-day averages of successes and precipitation were correlated with various time lags. For example, time lag 10 meant that precipitation data were taken from intervals preceding those of successes by 10 days, e.g. precipitation average of interval 1 (1–15 March) was paired with success averages of interval 11 (11–25 March), precipitation average of interval 2 (2–16 March) with success averages of interval 12 (12–26 March), etc. The best time lag was considered to be when the correlation coefficients were maximal. The best results were obtained when the first 15 intervals and intervals containing less than 10 data points were excluded from the analysis. Thus correlations were calculated in the case of all clutches only for intervals 16–90, in the case of clutch size four only for intervals 16–81, and in case of clutch size five only for intervals 22–74.

As our time series consisted of non-independent elements, the significance of correlations between two series of averages from overlapping intervals could not be taken from standard statistical tables. Consequently, we calculated our own critical values of correlation coefficients at a 0.05 level of significance.

Daily precipitation data—combined for the 4 years according to timing of breeding—were randomized 10 000 times, then the 15-day overlapping averages were calculated and finally correlated with the 15-day averages of hatching, fledging and breeding successes. Thus in each case 10 000 correlation coefficients were obtained, from which the highest 500th one gave the critical value at $P = 0.05$.

On the basis of the seasonal patterns of breeding success in four- and five-egg clutches, the breeding season was divided into three parts. Part 1 contained clutches laid between days 1 and 30, part 2 between days 31 and 70 and part 3 after day 71. Day 1 meant 13 March in 1986 and 1987, 9 March in 1988 and 1 March in 1989. Hatching, fledging, breeding success and the number of fledglings per clutch were compared using the Mann-Whitney U -test between the two clutch types in the three parts of the season. Hierarchical log-linear models were used to analyse the effect of season on the interaction between clutch size and hatching and breeding successes.

Results

TIMING OF BREEDING AND CLUTCH SIZE

The number of complete nests arranged in 15-day overlapping intervals showed two peaks each year (Fig. 1 crosses). The slopes of the first peaks seemed to be similar in all years, but the intercepts of the slopes were different. Considering the intercept of

slopes as the start of breeding, the breeding season began 12 days later in 1986 (Fig. 1a) and 1987 (Fig. 1b) and 8 days later in 1988 (Fig. 1c), than in 1989 (Fig. 1d).

The 15-day running averages of clutch size showed a symmetrical curve, with maximum values in the middle of the season each year (Fig. 1 triangles). The increase in the average clutch size in the second part of the season was due to the increase in the proportion of five-egg clutches, reaching 50% at this period. The proportion of four-egg clutches decreased by this time, while the proportion of clutches with three eggs did not change significantly and remained under 25% throughout the season. The position of maximum clutch size averages seemed to shift according to the timing of breeding in each year. In 1986 and 1987 maximal values were obtained in intervals around 61, in 1988 the maximal averages could be found in intervals 43–71 (mean 57), and in 1989 two smaller peaks formed the middle maximum, one around interval 44 and the other around interval 58 (mean 51).

HATCHING, FLEDGING AND BREEDING SUCCESSES

Contrary to the predictions of the Lack hypothesis, both average hatching and fledging successes, and consequently breeding successes, also had minimum values mid-season (Fig. 2a, b, c), at the same intervals where clutch size had its maximal averages. These seasonal patterns of partial losses seemed to be attri-

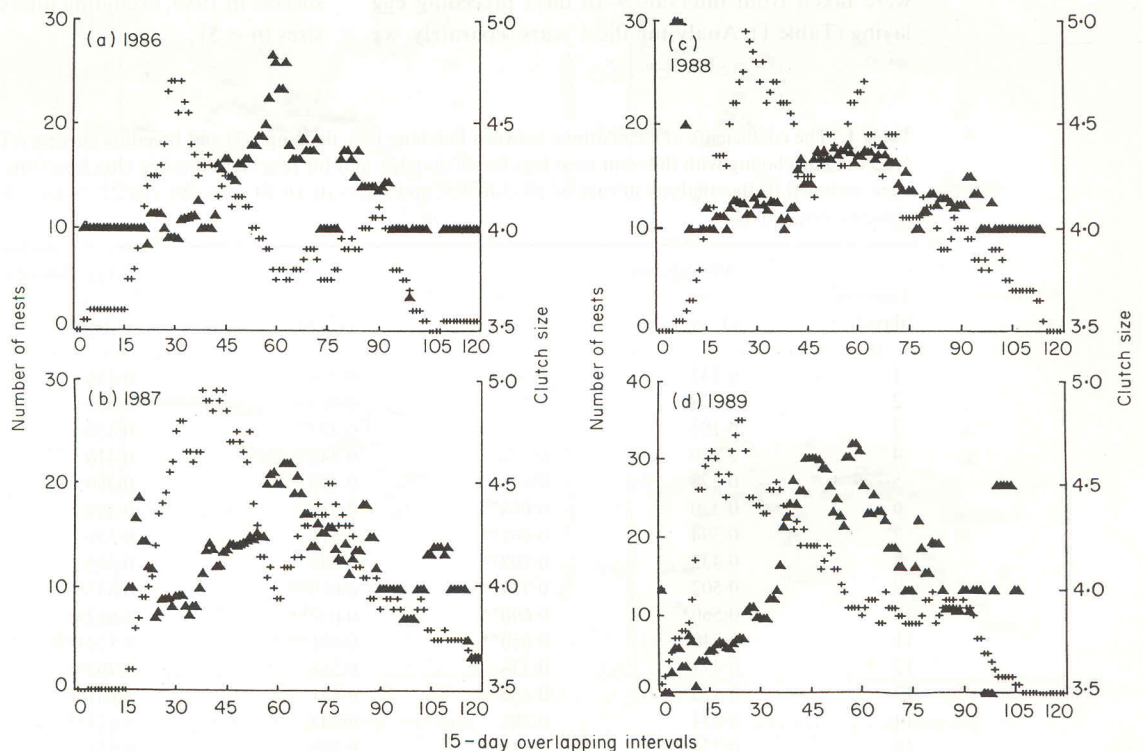


Fig. 1. The number of complete nests (crosses) and the averages of clutch size (triangles) in 15-day overlapping intervals in (a) 1986, (b) 1987, (c) 1988 and (d) 1989. First interval began on 1 March in each year.

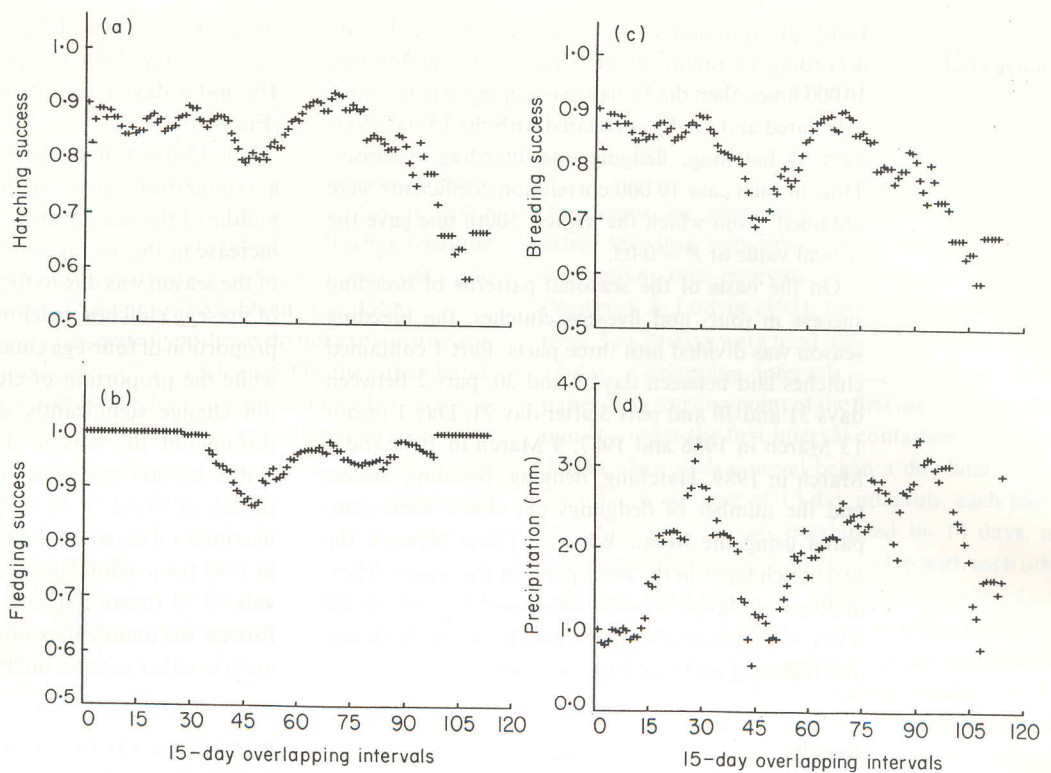


Fig. 2. The averages of (a) hatching, (b) fledging, (c) breeding success and (d) daily precipitation in 15-day overlapping intervals. Data from the 4 years are combined. The first interval began on 13 March in 1986 and 1987, on 9 March in 1988 and on 1 March in 1989 for successes, and 10 days earlier for precipitation in each year.

buted to seasonal changes of precipitation preceding egg laying (Fig. 2d). Correlating the 15-day averages of successes with the averages of precipitation, the best results were obtained when averages of precipitation were taken from intervals 9–10 days preceding egg laying (Table 1). Analysing the 4 years separately, we

also found significant correlations between precipitation and all three successes in 1987 and 1988, between precipitation and hatching and breeding successes in 1986, and between precipitation and fledging success in 1989, excluding intervals with small sample sizes ($n < 5$).

Table 1. The coefficients of correlations between hatching (s1), fledging (s2) and breeding success (s12) and precipitation (pr) preceding egg laying with different time lags for all clutches and for four- and five-egg clutches. Only intervals 16–90 ($n > 10$) were included in the analysis in case of all clutches, and intervals 16–81 ($n > 10$) and 22–74 ($n > 10$) for four- and five-egg clutches, respectively

Time lag (days)	All clutches			4-egg clutches	5-egg clutches
	s1-pr	s2-pr	s12-pr	s12-pr	s12-pr
1	0.133	0.360	0.274	0.256	0.323
2	0.158	0.423	0.319	0.301	0.404
3	0.183	0.494	0.373	0.354	0.467
4	0.230	0.574	0.444	0.410	0.555
5	0.278	0.616	0.495	0.466	0.576
6	0.320	0.664**	0.554	0.508	0.605**
7	0.394	0.691**	0.571	0.549	0.664**
8	0.432	0.708**	0.588	0.595	0.631**
9	0.502	0.714**	0.619**	0.635**	0.606**
10	0.560*	0.690**	0.637**	0.682**	0.591**
11	0.540	0.650**	0.601**	0.724***	0.518
12	0.499	0.578	0.538	0.705**	0.451
13	0.425	0.486	0.451	0.681**	0.350
14	0.334	0.388	0.343	0.623**	0.228
15	0.274	0.285	0.245	0.558	0.114

* $P < 0.06$; ** $P < 0.05$; *** $P < 0.01$.

Precipitation is a good indicator of earthworm abundance, as we found a significant correlation ($r = 0.968$, $n = 5$, $P < 0.05$) between the amounts of earthworms extracted and the 5-day averages of precipitation preceding sampling in 1986. In another study (Török & Ludvig 1988) a positive correlation ($r = 0.710$, $n = 10$, $P < 0.02$) was found between the amount of rainfall and the proportion of earthworms in the nestlings' diet, which reached 80% in the rainy periods, indicating that earthworms are important food for urban blackbirds.

PARTIAL LOSSES IN CLUTCHES WITH FOUR AND FIVE EGGS

In the following, the seasonal patterns of partial losses in four- and five-egg clutches were analysed separately so as to reveal whether they responded to food shortage differently or not. In the case of hatching success (Fig. 3a), clutches with five eggs had much lower success in the first and third part of the breeding season than clutches containing only four eggs (Table 2). On the other hand, the seasonal patterns of fledging success were similar in the two clutch size types (Fig. 3b), both having minimum values in the second part of the season (Table 2). Patterns of breeding success (Fig. 3c) and cross-correlation analyses (Table 1) suggest that the breeding success of clutch size five

responded to the pattern of precipitation earlier than that of clutch size four. Moreover, the breeding success of females laying four eggs seemed to be reduced significantly only in cases where precipitation, and consequently earthworm abundance, decreased under a threshold level, which appeared to be about 2 mm precipitation per day. Although the amount of rainfall was under this threshold at the beginning of the season, melting snow could contribute to the moisture of soil at this period, and consequently earthworm abundance might not have decreased under the threshold level causing partial losses in clutches with four eggs. On the other hand, partial losses in clutches with five eggs occurred throughout the season but were least when egg laying was preceded by rainfalls. Moreover, losses occurred almost exclusively in the egg stage at the beginning and at the end of the season, while females lost eggs as well as nestlings in the middle of the breeding season.

Different patterns of breeding success in four- and five-egg clutches meant clutches with four eggs fledged about as many offspring as clutches with five eggs in the first and third parts of the breeding season. On the other hand, as the breeding success of both clutch size types was reduced mid-season, clutches with five eggs were more productive during this period (Fig. 3c, d and Table 2).

These results suggest that the trade-off between clutch size and hatching success, and consequently

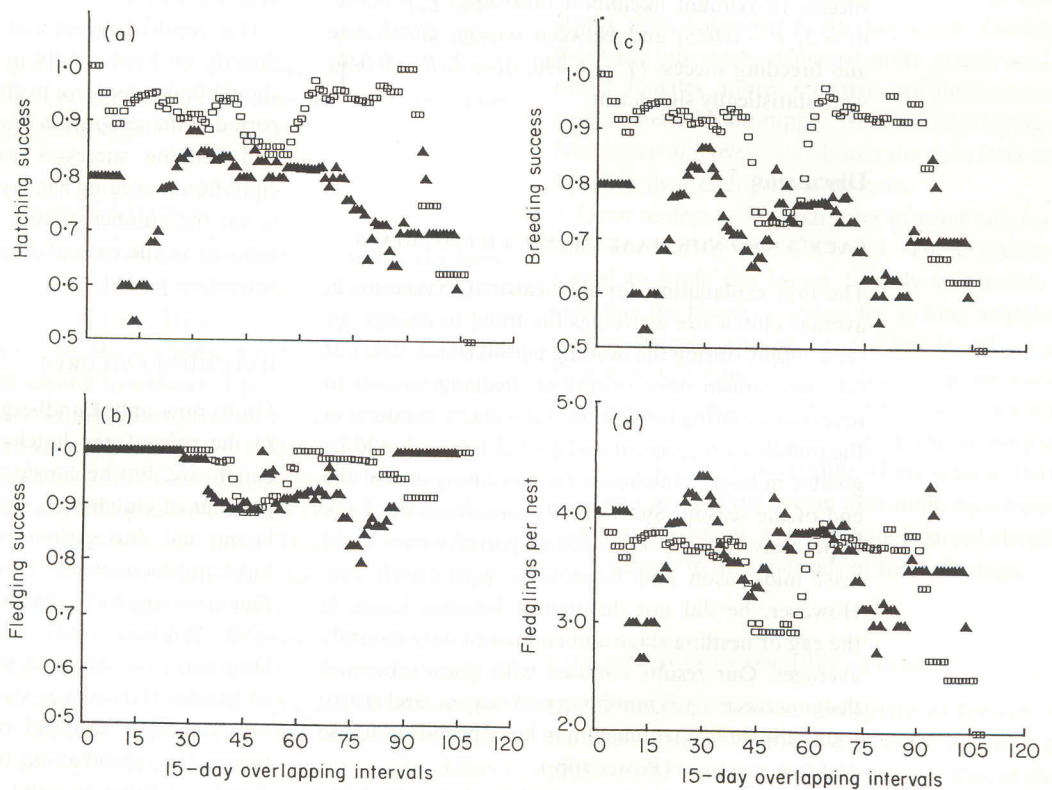


Fig. 3. The averages of (a) hatching, (b) fledging, (c) breeding success and (d) number of fledglings per nest in 15-day overlapping intervals in clutch size four (rectangles) and clutch size five (triangles). Data from the 4 years are combined. First interval began on 13 March in 1986 and 1987, on 9 March in 1988 and on 1 March in 1989.

Table 2. Comparison of hatching (s1), fledging (s2), breeding (s12) success and the number of fledglings per clutch (fl) in clutch sizes four and five with the Mann-Whitney *U*-test in the three parts of the breeding season

Clutch size		Part 1 (days 1-30)			Part 2 (days 31-70)			Part 3 (days 71-130)		
		Mean	<i>U</i>	<i>P</i>	Mean	<i>U</i>	<i>P</i>	Mean	<i>U</i>	<i>P</i>
T s1	4	0.950	-2.820	0.005	0.891	-0.465	NS	0.933	-3.104	0.002
	5	0.640			0.834			0.737		
T s2	4	1.000	0.000	NS	0.961	-0.433	NS	0.981	-1.534	NS
	5	0.640			0.834			0.737		
T s1	4	0.950	-2.820	0.005	0.841	-0.865	NS	0.913	-3.117	0.002
	5	0.640			0.733			0.688		
T fl	4	3.800	-1.209	NS	3.364	-2.524	0.012	3.654	-0.429	NS
	5	3.200			3.867			3.436		

Data from the 4 years are combined. Number of clutches are 15 and 5, 33 and 30, and 26 and 16 for clutch types four and five in the three parts of the season, respectively.

between clutch size and breeding success, changes seasonally. The effect of season on these trade-offs was tested by using hierarchical log-linear models with three factors (season, clutch size and success). Season was divided into three parts, as in Table 2. Two success categories were set up on the basis of whether clutches were totally successful or had partial losses. According to the hierarchical log-linear analyses, both three-way interactions between season, clutch size and hatching success (maximum likelihood ratio test, $\chi^2 = 7.391$, $df = 2$, $P = 0.025$) and between season, clutch size and breeding success ($\chi^2 = 6.446$, $df = 2$, $P = 0.040$) were statistically significant.

Discussion

LACK'S AND VON HAARTMANN'S HYPOTHESES

The first explanation for the seasonal maximum in average clutch size attributes the trend to changes of food supply during the nestling period (Lack 1947). If this mechanism were operating, fledging success in nests not suffering total failures should be maximal in the middle of the season and partial losses should be greater in larger clutches at the beginning and at the end of the season. Snow (1969) considered the Lack hypothesis verified, as he found partial losses to be least mid-season and to increase with clutch size. However, he did not distinguish between losses in the egg or nestling stage and compared only monthly averages. Our results contrast with Snow's because fledging success was minimum mid-season. Seel (1970) found the same phenomenon in large broods of house and tree sparrows (*Passer* spp.).

The other explanation is that food supply determines clutch size directly by constraining the laying ability of females (von Haartmann 1971; Murphy

1978). There are many examples where females lay larger clutches in more favourable food years or with better territories (reviewed in Martin 1987; Arcese & Smith 1988; Nillson 1991). Artificial increase of food supply, however, resulted in increased reproductive success rather than clutch size (reviewed in Martin 1987 and Boutin 1990). Other studies have documented that females in better condition also lay larger clutches (Jones & Ward 1976; Askenmo 1982; Wiklund 1985).

Our results suggest that clutch size is not limited directly by food supply in blackbirds, otherwise we should find a decrease in clutch size in the middle dry period of the season. On the other hand, both hatching and fledging successes were correlated with precipitation preceding egg laying, which suggests that it is not the number of eggs but their quality which is reduced in the case of food shortage during the egg formation period.

HATCHING FAILURES

Up to now only Lundberg (1985) has paid attention to the role of egg hatchability in the evolution of clutch size, but he considered hatching failures independent of clutch size, leading to compensatory egg laying and thus greater modal clutch size than the most productive one. However, there are examples that more eggs fail to hatch in larger clutches (Murphy 1978; Wiklund 1985). Food supply (Bryant 1973; Högstedt 1981; Arcese & Smith 1988) or the condition of females (Jarvinen & Vaisanen 1983; Roskaft 1985) also can have an effect on hatching success. Comparing the reproduction of pied flycatchers *Ficedula hypoleuca* Pallas in good and bad breeding seasons, Jarvinen & Vaisanen (1984) found that it was mainly the hatching success which differed, although they

could not separate the effects of bad weather and larger clutch size as both occurred at the beginning of the season.

Egg size has proved to be a good indicator of egg quality, as in some species (Laridae, Corvidae, *Apus apus* L., *Sturnus vulgaris* L.) smaller eggs fail to hatch more often (Högstedt 1981; O'Connor 1979; Slagsvold *et al.* 1984). There are several studies in which ambient temperature (Howe 1978; Ojanen, Orell & Vaisanen 1981), food supply (March & Biely 1963; Nisbet 1973; Otto 1979) or the condition of females (Pikula 1976; Murphy 1978; Jarvinen & Vaisanen 1983; Murphy 1986) affected egg size. In a similar long-term study of the blackbird in Cambridge, UK, Magrath (1992b) found that egg size was related to the daily minimum temperatures during rapid yolk synthesis. However, he failed to find an effect of rainfall and supplemental feeding on egg size. Moreover, he found that hatching success did not depend on clutch size and egg size excluding very small eggs (Magrath 1992c). His results suggest that either egg size is not a good measure of egg quality, or food supply during the egg formation period has no significant effect on egg quality via egg size in Cambridge blackbirds.

It is possible that the laying sequence can also influence hatching success, as later eggs might be of inferior quality because of depletion of reserves of females. In the above-mentioned species, where unhatched eggs proved to be smaller, egg size usually decreased with laying sequence (Slagsvold *et al.* 1984). On the other hand, in blackbirds the last or penultimate eggs are the largest (Ryden 1978; Magrath 1992a), and as the size of the last egg is similar to the mean of the others (Magrath 1992a) it may explain why the size distribution of unhatched eggs does not differ from that of successful eggs.

BROOD REDUCTION

Nestling losses are usually attributed to the size hierarchy among siblings caused by asynchronous hatching (Ricklefs 1965; Howe 1976, 1978). However, not only the incubation pattern can cause weight differences among hatchlings. Egg size influences the size and sometimes subsequent survival of nestlings in several passerine (Schifferli 1973; Murphy 1978; Rofstad & Sandvick 1987; Grieg-Smith *et al.* 1988; Magrath 1992c) and non-passerine species (Parsons 1970; Nisbet 1973; Ricklefs *et al.* 1978; O'Connor 1979; Grant 1991). In the house martin *Delichon urbica* L., Bryant (1978) found that relative weight differences between nestlings were primarily due to food shortage during the egg-formation period. Besides the possible adaptive value of brood reduction in the case of food shortage (Lack 1954; Ricklefs 1965; Wiklund 1985; Lessels & Avery 1989; Magrath 1989), great weight differences may lead to elimination of the smallest sibling even if food supply is adequate at the time of the nestling period (Bryant 1978; Skagen 1988; Stouffer

& Power 1990). In our study, broods losing one or two nestlings were quite rare (17% of broods fledging at least one nestling), and brood reduction occurred in both synchronous and asynchronous broods laid mid-season. They lost one or two nestlings at an early age and at the time when food was already not limiting. However, when food shortage occurred at the time of the nestling care, only eight broods (5% of all broods not suffering total failures because of other causes) succumbed because of starvation during the 4 years. Snow (1958) also reported total failures because of starvation in blackbird clutches at times of droughts at Oxford, UK.

EGG QUALITY AND FEMALE CONDITION

The highest correlation was found between the pattern of breeding success and the pattern of precipitation preceding egg laying, suggesting that partial breeding losses either in egg or nestling stages were due to egg quality determined by the condition of females during the period of egg formation. The difference between the seasonal patterns of breeding success of females with four and five eggs can be explained by the fact that egg formation is a process of great energy demand. The maximum daily energy requirements of egg production can reach 50% of a female's standard metabolic rate in passerines (King 1973; Kremetz & Ankney 1986), which can be covered by the female's endogenous reserves (Jones & Ward 1976) and/or exogenous nutrients (Kendeigh, Kramer & Hamerstrom 1956; Kremetz & Ankney 1986). Laying one more egg obviously demands more energy and can make females more sensitive to fluctuations of environmental food supply, while females laying only four eggs could overcome shorter drops in food supply by using their endogenous reserves.

Open nesters suffer high rates of total failures and thus are usually multi-brooded. These species are forced to begin egg laying as early as possible and continue the breeding season for as long as possible, so that one pair can rear at least one brood per year. Consequently, conditions for egg laying are worse at the beginning and at the end of the season. Our results also suggest that although losses in the nestling stage occurred mainly in the middle of the season, the first and third parts of the season were more disastrous for clutches of five eggs, as losses had occurred already at the egg stage in these periods of food shortage.

EVOLUTIONARY CONSIDERATIONS

In our case the different sensitivity of females with the two clutch types to food shortage was such that productivity of clutch size four reached that of clutch size five at the beginning and at the end of the season. On the other hand, clutches with five eggs initiated mid-season produced more fledglings in spite of the

bad conditions for egg-laying, as the breeding success of clutches with four eggs also decreased at this period.

Although woodland blackbirds might be not so dependent on earthworm abundance (and consequently on precipitation), mainly in the latter part of the breeding season when they feed on caterpillars (Koródi-Gál 1967; Dyrz 1969; Török 1981), it is probable that their food supply is also limited at the beginning and at the end of the season. Consequently, it is likely that the same mechanism determines a similar seasonal pattern of clutch size in woods (Snow 1955; Havlin 1963; Ribaut 1964; Perez, Fournet & Bertran 1979).

Our results, that the clutch size maximum varied between years according to the starting of breeding and the fact that in northern populations maximal clutch size averages occur later in the season (Venables & Venables 1952; Snow 1955), suggest that the timing of laying large clutches is linked with the progress of the breeding season and not calendar time. In some passerines, which usually lay only one clutch per season, the heritability of clutch size was estimated to be about 30–40% (Boag & van Noordwijk 1987). In the blackbird, often laying three clutches during a season, it is possible that the size of the three subsequent clutches is heritable, so that clutch size five is selected against for the first and third breeding attempt. Unfortunately, there are few data on clutch size series of individually marked blackbirds from consecutive years (Snow 1958; Ribaut 1964), but they show some sign of repeatability. In a similar multiple-brooded passerine, the song sparrow *Melospiza melodia* Wilson, Hochachka (1990) found that although the average clutch size of the population declined through the season, the clutch size of individuals was largest for the second breeding attempt.

Summing up our results suggests that the seasonal pattern of clutch size in the blackbird is determined by seasonal changes of food supply during the time of egg formation. However, low food supply does not limit clutch size directly, but reduces egg quality selectively in different-sized clutches. Changes in the food supply during the season alter the trade-off function between clutch size and hatching, and consequently breeding success so that clutches of five eggs are no more productive than clutches of four eggs at the beginning and at the end of the season.

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