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Costs and benefits of surplus offspring in the lesser kestrel (*Falco naumanni*)

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Abstract Lesser kestrels (*Falco naumanni*) lay clutches which appear excessive as only 3% of them yield as many young as eggs laid. Four hypotheses may explain the adaptive value of producing surplus eggs: (1) the bet-hedging hypothesis assumes that the environment varies unpredictably and surplus eggs serve to track uncertain resources; (2) the ice-box hypothesis suggests that surplus offspring serve as a reserve food during a period of shortage; (3) the progeny choice hypothesis says that parents produce surplus offspring in order to choose these with higher fitness; and (4) the insurance-egg hypothesis proposes that extra eggs are an insurance against the failure of any egg. To test the significance of this strategy in the lesser kestrel, an experiment manipulating brood size at hatching was carried out over 2 years, with good and bad feeding conditions. The experiment consisted of adding a chick to experimental broods where one egg failed to hatch or removing a randomly selected chick from experimental broods where all eggs had hatched. Independently of annual food availability, pairs with brood sizes reduced by one chick fledged more nestlings than pairs with brood size equalling their clutch sizes. Body condition of young was also better in the former group, but only in 1993 (a high-food year). Independently of year, mean local survival of parents with complete broods at hatching was lower than for parents raising reduced broods. These results supported only the insurance-egg hypothesis which says that surplus eggs may be an insurance against the failure of any egg, but parents may suffer reproductive costs when all eggs hatch.

Key words Brood reduction · Clutch size · *Falco naumanni* · Insurance-egg · Surplus offspring

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Introduction

Nidicolous birds seem to adjust their clutch sizes individually to the maximum number of young which the parents can feed adequately without risking their own survival (e.g., Högstedt 1980; Gustafsson and Sutherland 1988; Pettifor et al. 1988; Dijkstra et al. 1990; Lindén 1990; Pettifor 1993). However, in some bird species, parents are rarely capable of rearing all chicks produced, some of which must be actively or passively eliminated (e.g., Nelson 1978; Stinson 1979; Edwards and Collopy 1983; Anderson 1990). Nevertheless, the production of surplus offspring may be an adaptive strategy for four reasons:

1. Bet-hedging hypothesis. Parents living in an unpredictable environment lay optimistically large clutches in order to maximize reproductive success in high-food years, but they would have redundant nestlings in poor-food years (Lack 1947, 1954; Temme and Charnov 1987; Kozlowski and Stearns 1989).
2. Ice-box hypothesis. Younger surplus offspring serve as a food supply for older siblings during a period of shortage (Alexander 1974). Although the food value is small, the surplus offspring may be important if they provide a critical meal (Bortolotti et al. 1991).
3. Progeny-choice hypothesis. Parents produce surplus offspring and kill or abandon those with lowest fitness (Kozlowski and Stearns 1989).
4. Insurance-egg hypothesis. Parents may be able to predict future feeding conditions for rearing offspring, but their clutches are larger than optimal brood sizes because surplus eggs are an insurance against the failure of any egg. Parents would have redundant nestlings if the whole clutch hatches (Dorward 1962; Stinson 1979; Lundberg 1985; Forbes 1990, 1991).

These four hypotheses are not mutually exclusive and they could operate in any combination. However, their predictions differ when a nestling selected at random is experimentally eliminated (Table 1). Experimental brood reduction may be beneficial for parents using a

Table 1 Mean reproductive success predicted from the hypotheses which explain the significance of surplus offspring. B0 are broods with redundant chicks and B− are broods with random elimination of redundant chicks

Hypotheses	Reproductive success according to annual food abundance:	
	Good years	Bad years
Bet-hedging	B0 > B−	B0 < B−[a]
Ice-box	B0 = B−[b]	B0 > B−
Progeny-choice	B0 > B−	B0 > B−
Insurance-egg	B0 < B−[a]	B0 < B−[a]

[a] B0 = B− if brood reduction is not costly

[b] B0 > B− if ice-box strategy is combined with bet-hedging

bet-hedging strategy in years with bad feeding conditions, but not in good years. In contrast, if the surplus young serves as food supply during a period of shortage, the experimental brood reduction would be detrimental for parental reproductive success in poor years. If the progeny-choice hypothesis is operating any random elimination would reduce the possibilities to choose between offspring and thus the benefits of this strategy. Under the insurance hypothesis, females always lay clutches larger than their particular optimal brood size. When extra eggs are an insurance against the failure of eggs rather than failure of chicks, experimental brood reduction at hatching may be advantageous whenever all eggs hatch successfully, even in "good years".

The lesser kestrel (*Falco naumanni*) is a small raptor that breeds colonially in old buildings. It lays between two and six eggs, but most frequently four or five. Its clutch size is therefore similar to those of the American (*F. sparverius*) and European kestrels (*F. tinnunculus*) living at similar latitudes (Balgooyen 1976; Aparicio 1994). Considering only partial failures, its eggs fail to hatch with a frequency of *c*. 17% which is higher than in other kestrels (10% for the American kestrel: Balgooyen 1976; and 6–8% for the European kestrel: Cavé 1968; Aparicio 1993). Moreover, lesser kestrels usually produce *c*. 2 fledglings per brood, i.e., about one fewer than their congeners (Balgooyen 1976; Aparicio 1993). In the lesser kestrel, both parents share incubation and chick-rearing. Nestlings hatch asynchronously at intervals of up to 5 days. Nestlings are normally fed with arthropods, which are delivered in single prey loads. Clutches appear excessive as only 3% of clutches yield as many young as eggs laid.

In this study I attempted to answer two questions: whether the production of extra eggs is an adaptive strategy in the lesser kestrel and, if so, why. If surplus eggs are an adaptive strategy, kestrels would obtain a net benefit from laying clutches as large as they do. Hence, their reproductive success would be lower on average when their clutches are experimentally reduced by one egg, independently of the viability of another. An experimental test of this question is, therefore, easy to perform, by removing an egg from some nests after clutch completion, but this experiment may be very harmful for kestrel populations, because reproductive success of experimental pairs with reduced clutches could be reduced and the egg removed could not be added to other clutches without decreasing their reproductive output. Thus, I preferred to use observational data to analyze benefits of surplus eggs. To test which of the four adaptive hypotheses explains surplus offspring in the lesser kestrel, I manipulated broods by adding one chick when an egg failed to hatch or eliminating one when the whole clutch had hatched, in a group of randomly selected pairs. This experiment was not harmful for the population (see below), because mean brood size and its variance did not changed within populations. I only changed which individuals had a reduced brood size at hatching. The experiment was carried out over 2 years with good and bad feeding conditions for rearing nestlings. Broods were manipulated immediately after hatching when energy demand by nestlings is low and there is no reason for food shortage. As was shown above, predictions from the experiment differ depending on annual feeding conditions and the significance of the surplus egg strategy (Table 1).

Materials and methods

Study area

This study was conducted between 1991 and 1993 on eight lesser kestrel colonies in an area of 100 km^2 in La Mancha, Central Spain (39°20′N, 3°15′W). The study area is an agricultural plain cultivated mainly with barley, wheat and vineyards. Lesser kestrels breed colonially in farmhouses, usually under tiled roofs or inside holes in walls. The colony sizes varied from 3 to 60 pairs.

Egg-laying occurs at the end of April and beginning of May. In this period, maximum temperatures average 20 °C. When the earliest chicks hatch, maximum temperatures are normally over 25 °C, and usually reach 30 °C in the middle of June, when most kestrel parents are rearing nestlings 7–15 days old. In 1992, there was an unusually long period of rain during June, and maximum temperatures were low (20–21 °C) until the 3rd week of June. After that, temperature increased, but did not reach 30 °C until 2 weeks later. That period of bad weather caused a high mortality among nestlings.

General methods

Nest-sites were located before the onset of laying by watching mated pairs. Each potential nest was monitored every 6 days from the middle of April to find the first eggs, and then every 2 days until the clutch was finished. Thus, since females usually lay four or five eggs with mean intervals of 2 days, I was able to find the maximum number of unfinished clutches with minimum disturbance of the colonies. Eggs were labelled with a water proof felt-tip pen to identify the last egg.

Incubation of the last egg usually lasts 26–27 days. Nests were checked 20 days after clutch completion to determine possible egg-failures during incubation, and then a week later to record hatching success. Chicks were weighed at hatching with a 100-g spring balance and their tarsus and wing lengths were measured. I was unable to record hatching date of all chicks because time of incubation is quite variable. When necessary, I estimated hatching date by using a model of growth of wing length of nestlings of known age. I measured hatching asynchrony as the difference in age between the oldest and the youngest chicks.

Each chick was marked at hatching with a felt-tip pen or with nail varnish. They were banded with coloured plastic rings when they were 5–7 days old, and later with numbered metallic rings at 20–21 days. Nestlings were measured again and sexed at 20 and 30 days. Male and female young were distinguished by the colour of their upper tail coverts (Negro and Hiraldo 1992). Body condition of nestlings and adults was assessed using the thickness of the pectoral muscle. This variable is positively correlated with the probability of recruitment of young (logistic regression: *Wald* = 4.86, $P = 0.027$) and, therefore, it may be a realistic measure of body condition. Pectoral thickness can be accurately measured on live birds using ultrasound. This technique has been described in detail and tested on mute swans (*Cygnus olor*) by Sears (1988). To measure the pectoral muscle, I used a portable ultrasonic meter, model Krautkrämer Branson USK 7B. Breast feathers were soaked with alcohol and then carefully parted. The probe was placed on the skin surface, at 7 mm from the sternum. Pectoral thickness was measured in arbitrary units. These units accurately measure individual variation in pectoral thickness. I measured the pectoral of 75 kestrels twice and measurements were highly repeatable ($r = 0.98$, $F = 120$, $df = 73, 74$, $P < 0.00001$). I pooled male and female young to analyze pectoral thickness because it does not differ with respect to sex ($F = 0.8$, $df = 1{,}160$, $P = 0.37$) when year and hatching order are statistically controlled.

Adults were trapped with a noose carpet or during incubation, measured, and individually marked with metallic and coloured plastic rings. Parental survival was assessed from local recoveries in subsequent breeding seasons. Kestrels usually nested in the same colony in different years; however some individuals moved to another colony. Using stepwise logistic regression, I found that unsuccessful breeding had a significant effect on probability of changing colony in the following year (*Wald* = 4.2, $P = 0.04$), but neither year, nor sex, nor number of young fledged, nor laying date (all Ps > 0.3) appeared to be related to parental dispersal. Thus, I excluded unsuccessful parents from survival analyses. In 1994 and 1995 adults were also trapped to determine their survival, but only in two colonies. Pairs which were breeding in other colonies during 1993 were excluded from survival analyses.

Experimental procedure

Brood size was manipulated at hatching in 1992 and 1993. I randomly selected experimental and control nests before hatching. Then, a chick selected at random was removed from experimental nests where all eggs hatched (treatment E−). In control nests all eggs hatched, but no chick was removed (treatment C0). On the other hand, a chick of appropriate age was introduced into experimental nests where one egg failed to hatch (treatment E0). Their controls (treatment C−) also contained a failed egg, and a chick was exchanged for another of similar age and physical condition.

Chicks were transported inside cloth bags. Manipulations took less than 15 min. No adopted chicks were abandoned by their foster parents. There was no initial difference among treatments in clutch size, laying date, hatching asynchrony or parental condition.

Results

Reproduction in natural conditions

The most frequent clutch sizes were four (54%) and five (33%) in the three years of study. Mean clutch size did not vary significantly between years ($F = 0.6$, $df = 2, 207$, $P > 0.5$), perhaps because pre-laying weather conditions were similar in each year. Hatching success was 83% in 178 clutches that produced at least one chick. In those clutches, 26% of 130 failed eggs disappeared or were damaged during incubation, 35% suffered embryo mortality and 39% did not contain a visible embryo. Mean hatching success was similar among years ($F = 0.8$, $df = 2, 175$, $P > 0.4$), among clutch sizes ($F = 1.35$, $df = 3, 174$, $P > 0.25$), among individuals (females: $F = 1.3$, $df = 17, 20$, males: $F = 0.9$, $df = 12, 16$; in both cases $P > 0.25$), among nest sites ($F = 1.1$, $df = 41, 94$, $P = 0.35$) and was independent of laying date ($r_s = -009$, $n = 173$, $P = 0.23$). Hatching success was also independent of laying order (first egg: 77.9%, $n = 68$; middle eggs: 84.7%, $n = 164$; last egg: 83.3% $n = 68$; $\chi^2_2 = 1.56$, $P = 0.46$). The number of unhatched eggs within clutches was not different from that expected from a binomial distribution ($\chi^2_1 = 0.1$, NS, $\chi^2_2 = 2.7$, NS, $\chi^2_2 = 2.2$, NS; for clutches of 3, 4 and 5 eggs respectively).

Incubation started before clutch completion and eggs hatched asynchronously with differences of up to 5 days. The degree of hatching asynchrony did not differ among years ($F = 0.7$, $df = 2, 78$, $P = 0.5$), but was significantly positively correlated with clutch size ($r = 0.42$, $n = 151$, $P < 0.00001$).

In this population, the number of fledglings per breeding attempt was lower in 1992 than in 1991 and 1993 ($F = 19.8$, $df = 2{,}119$, $P < 0.0001$). Compared to fledging success in other parts of Spain, in different years, 1992 was a bad year with the lowest number of fledglings per breeding attempt of those records. Fledging success in 1991 and 1993, however, was among the highest recorded (Table 2). Continuous rain and low temperatures characterized the nestling period in 1992, whereas this period was warm in both 1991 and 1993.

During the study only 3 of 110 pairs (< 3%) reared as many young as eggs laid. This suggests that clutch sizes were not adjusted to the number of nestlings that parents are normally able to rear. On the other hand, large clutches yielded more young per nest than smaller

Table 2 Clutch size and number of fledglings [mean ± SD (n)] produced by lesser kestrels in several Spanish regions and years. Means were compared using the Tukey-Kramer method for multiple comparisons. Values followed by the same letter are not significantly different

Area	Year	Clutch size	No fledglings	Source
Extremadura	1987	$4.1 \pm 0.8\ (71)^{A}$	$2.1 \pm 1.6\ (61)^{B}$	Bijlsma et al. 1988
Andalucía	1988	$3.9 \pm 0.6\ (19)^{A}$	$2.2 \pm 1.4\ (112)^{B}$	Negro 1991
Andalucía	1989	$4.1 \pm 0.9\ (87)^{A}$	$1.5 \pm 1.2\ (126)^{CD}$	"
Andalucía	1990	$4.1 \pm 0.8\ (26)^{A}$	$1.8 \pm 1.2\ (125)^{BC}$	"
La Mancha	1991	$4.2 \pm 0.7\ (55)^{A}$	$2.2 \pm 1.1\ (43)^{B}$	This study
La Mancha	1992	$4.3 \pm 0.6\ (64)^{A}$	$1.0 \pm 0.9\ (34)^{D}$	"
La Mancha	1993	$4.2 \pm 0.7\ (96)^{A}$	$2.0 \pm 1.3\ (33)^{BC}$	"

clutches (Fig. 1) and there were no significant differences in fledgling pectoral thickness among clutch sizes ($F = 1.0$, $df = 3{,}45$, $P = 0.4$). The father's wing-length, which could be a measurement of flying capacity (Masman and Klaassen 1986), was positively correlated with clutch size ($r = 0.32$, $n = 109$, $P < 0.001$), male's provisioning rate ($r = 0.49$, $n = 17$, $P < 0.05$), and number of fledglings ($r = 0.35$, $n = 54$, $P = 0.01$). Thus, these results seem to indicate that, although there may be an individual optimization of clutch size, all individuals lay optimistically large clutches.

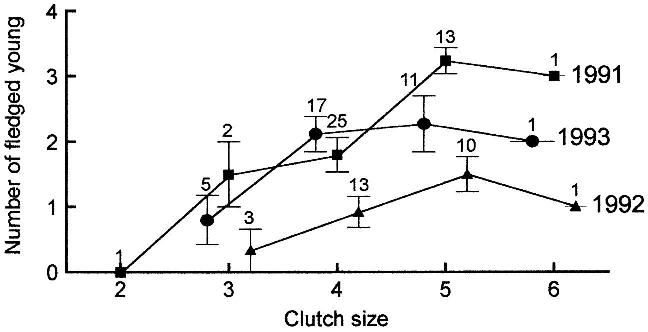

Fig. 1 Number of fledged young in relation to clutch size for different years (mean ± SE)

Benefits from the last egg

Observational data were used to analyze benefits of surplus eggs. I assume that if there is a surplus egg, this is the last egg. An alternative strategy to producing a surplus egg should be to produce a smaller clutch size; thus the "last" egg is not laid. If the production of a surplus egg is an adaptive strategy, parents would obtain no benefit when the last fails. By contrast, if this egg hatches, parents could suffer reproductive costs when all eggs hatch, but on average its contribution would be positive. Thus, parents whose last egg hatches (called LE+) are representing a surplus egg strategy in this analysis, whereas parents whose last egg failed (called LE−) are equivalent to experimental individuals whose clutches are reduced by one egg, and they represent an alternative to the surplus egg strategy. This equivalence is possible because hatching success was independent of year, laying date, parents, nests, and laying order, and the number of unhatched eggs within clutches was not different from a binomial distribution (see above). Thus egg hatching is apparently a random event. If surplus eggs are adaptive for kestrels then reproductive success will be better for LE+ pairs than for LE− pairs.

The last egg in the laying sequence was identified in 89 non-manipulated clutches where at least one egg hatched. The last egg failed in 16 clutches (LE−) and hatched in 73 which were called (LE+). Both groups did not differ in mean clutch size, and mean hatching rate of non-last eggs. As expected, brood sizes at hatching, and hatching asynchrony, were greater in LE+ broods than in LE− broods (Table 3). Given that hatching asynchrony was closely dependent on clutch size (see above), I performed an ANCOVA including clutch size as covariate. In this analysis, LE− clutch size were included with one egg minus, because a non-surplus egg strategy (as LE− broods represent) would imply a smaller original clutch size. Controlling clutch size, hatching success of the last egg had no effect on asynchrony ($F_{1,76} = 0.55$; $P > 0.4$). Hence, there are no basic differences between both groups, LE− and LE+, except in brood size at hatching, which is a distinguishing feature of these two hypothetical strategies.

The number of fledglings per attempt and body condition of young was standardized with respect to annual means to compare fledging success between LE+ and LE− using the Mann-Whitney *U*-test. Broods where the last egg hatched (LE+) yielded more young at fledging than LE− ($Z = 2.17$, $P = 0.03$), but there were no significant differences in body condition ($Z = 0.4$, $P = 0.7$; Fig. 2). When all eggs hatched, the youngest chick survived until fledging only in 7% of 44 cases, but its survival rate increased to 48% ($n = 29$) if any other egg failed to hatch.

A logistic regression showed that parental survival was not affected by hatching success of the last egg (mean survival for LE+ 0.36, $n = 64$; for LE− 0.35, $n = 15$; $Wald = 0.04$; $P = 0.8$), year ($Wald = 0.3$, $P = 0.8$), sex ($Wald = 0.005$, $P = 0.9$) or interaction between hatching success and year ($Wald = 1.3$, $P = 0.5$) . In short, LE+ parents, which would represent a surplus egg strategy in this analysis, were more successful because they were able to fledge more young without sacrificing body condition of offspring or reducing their own lifespan.

The costs of redundant chicks

The effect of redundant chick manipulation on fledgling production was analyzed using ANOVAs with three

Table 3 ANOVA on clutch size, hatching rate of eggs other than the last one, brood size at hatching and hatching asynchrony in LE+ (clutches whose last egg hatched) and LE− (clutches whose last egg did not hatch). Data are given as mean ± SE (*n*)

	LE+	LE−	*F*-value
Clutch size	4.3 ± 0.1 (73)	4.2 ± 0.2 (16)	0.41NS
Hatching rate (for non-last egg)	0.82 ± 0.04 (73)	0.78 ± 0.09 (16)	0.29NS
Brood size at hatching	3.8 ± 0.1 (73)	2.5 ± 0.3 (16)	20.5^{*4}
Hatching asynchrony	2.1 ± 0.1 (66)	1.2 ± 0.2 (13)	7.33^{*2}

$^{*2}P \leq 0.01$, $^{*4}P \leq 0.0001$

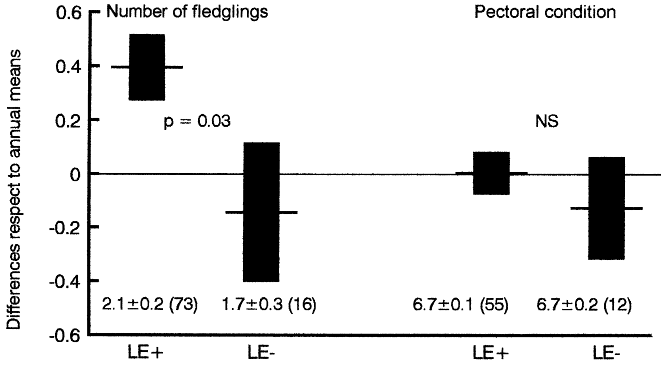

Fig. 2 Number of fledglings and pectoral condition (mean ± SE) in broods where the last egg failed (LE−) or hatched (LE+). Data were corrected with respect to annual means. Absolute values and sample sizes are given below

factors: year, original hatching success, and difference between brood and clutch size after manipulation. By including these last two factors, the effect of a redundant chick is distinguished from parental quality in the event that hatching success and parental quality are correlated.

There was a strong year effect on number of young raised, nestling survival, and pectoral condition of young at fledging ($F = 22$, $df = 1{,}86$; $F = 30$, $df = 1{,}86$; and $F = 39$, $df = 1{,}70$ respectively, in all cases $P < 0.0001$). Pectoral condition was better in 1992 (a poor-food year) than in 1993 (a high-food year).

Original hatching success affected the number and proportion of nestlings surviving ($F = 4$ and $F = 5$, respectively, $df = 1{,}86$, $P_s < 0.05$), but not their pectoral condition ($F = 2$, $df = 1{,}70$, $P > 0.1$). Pairs which did not originally have egg failures (i.e., E− and C0) fledged more young than E0 and C− (Table 4). The three variables were also affected by chick redundancy (number of fledglings: $F = 9$, $df = 1{,}86$, $P < 0.005$; nestling survival: $F = 39$, $df = 1{,}86$, $P < 0.0001$; pectoral condition: $F = 6.3$, $df = 1{,}70$, $P = 0.015$), i.e. pairs with brood sizes as large as clutch sizes after manipulation (E0 and C0) were less successful than reduced broods (C− and E−). These results were independent of year, since no interaction between these two factors were significant for any variable, except for pectoral condition of young ($F = 4.3$, $df = 1{,}70$, $P = 0.04$). This interaction was significant because pectoral condition was better for reduced broods in 1993, but there were no differences between groups in 1992 (Table 4).

Fledging success depended also on which chick was eliminated. Pairs with complete broods had similar fledging success to reduced-brood pairs, whose youngest chick was experimentally removed or whose last egg failed to hatch. However, reduced broods were more successful than complete broods when an older egg or chick failed or was eliminated. Such a difference occurred in the high-food year because survival of the youngest chick was better in reduced broods than in complete broods, whereas in the poor-food years reduced broods were more successful than complete broods because they produced more older chicks. Pectoral condition of young shows a similar tendency. In short, parents were more successful only when a elder chick failed or was removed (Table 5).

A logistic regression model was used to determine which factors affected parental survival. The probability of surviving differed in relation with chick redundancy. Thus, mean local survival of parents with complete broods at hatching was lower than survival of those raising reduced broods (0.26 ± 0.07 SE [38] vs 0.50 ± 0.09 SE [34]). However there was no effect of sex, year, or original hatching success (Table 6). Parents with complete broods tended to raise fewer nestlings than parents with reduced brood in the next season (1.00 ± 0.33 SE [9] vs 1.54 ± 0.31 SE [13]), but this difference was not statistically significant ($Z = 1.14$, $P = 0.25$).

The experiment did not impair mean reproductive success in the population. Experimental and control pairs produced similar numbers of fledglings with equal body condition, and parental survival did not differ between the two groups (Table 7).

Table 4 Fledging success in experimental and control broods. E0 and C0 treatments had brood sizes as large as their original clutch sizes. E− and C− treatments had brood sizes reduced by one chick with respect to their original clutch sizes. Values are given as mean ± SE (*n*)

	Broods originally with one egg failing to hatch		Broods originally with all eggs hatching successfully	
	E0	C−	E−	C0
1992:				
Number of fledglings	0.75 ± 0.31	1.33 ± 0.29	1.89 ± 0.39	0.93 ± 0.25
Nestling survival	0.18 ± 0.08 (8)	0.39 ± 0.08 (9)	0.56 ± 0.12 (9)	0.21 ± 0.05 (14)
Pectoral condition	6.62 ± 0.27 (4)	6.69 ± 0.20 (7)	6.71 ± 0.42 (7)	6.89 ± 0.28 (8)
1993:				
Number of fledglings	1.45 ± 0.25	2.40 ± 0.27	2.47 ± 0.22	2.29 ± 0.29
Nestling survival	0.33 ± 0.05 (11)	0.79 ± 0.05 (10)	0.76 ± 0.07 (15)	0.54 ± 0.07 (17)
Pectoral condition	5.00 ± 0.32 (10)	6.02 ± 0.11 (10)	5.98 ± 0.16 (15)	5.58 ± 0.15 (16)

Table 5 Comparisons of fledging success (mean ± SE) of reduced broods with and without the last chick against complete broods. Mann-Whitney *U*-test, two tailed

	Number of fledged young per nest				Pectoral condition
	n	Youngest chick	Elder chicks	Total	
1992					
Complete broods (*C0 and E0*)	22	0.00 ± 0.00	0.86 ± 0.19	0.86 ± 0.19	6.8 ± 0.2 (12)
Reduced broods (*C*− and E−):					
The youngest chick fails to hatch or is removed	5	0 NS	1.20 ± 0.49 NS	1.20 ± 0.49 NS	6.4 ± 0.5 (3) NS
An elder chick fails to hatch or is removed	13	0.08 ± 0.08 NS	1.69 ± 0.29*	1.77 ± 0.28*	6.8 ± 0.3 (11) NS
1993					
Complete broods (*C0 and E0*)	28	0.04 ± 0.04	1.93 ± 0.21	1.96 ± 0.22	5.4 ± 0.2 (26)
Reduced broods (*C*− and E−):					
The youngest chick fails to hatch or is removed	6	0 NS	1.83 ± 0.31 NS	1.83 ± 0.31 NS	6.0 ± 0.2 (6) NS
An elder chick fails to hatch or is removed	19	0.53 ± 0.12***	2.11 ± 0.15 NS	2.63 ± 0.17*	6.0 ± 0.1 (19)**

NS $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

The role of asynchronous hatching on reproductive costs

In relation to hatching order, asynchrony had a negative effect on survival of the last chick ($r = -0.25$, $n = 87$, $P = 0.017$) but had a positive effect on the number of non-last chicks surviving until fledging ($r = 0.27$, $n = 87$, $P = 0.012$). In total, pairs whose brood sizes after manipulation were as large as their clutch sizes (C0 and E0) produced more fledglings with greater asynchrony in both 1992 and 1993 (Fig. 3A). However, in reduced broods, fledging success decreased in 1992 when hatching asynchrony was more than 2 days, but there was no tendency in 1993 (Fig. 3B).

Discussion

Surplus eggs could serve four adaptive functions: progeny choice, ice-box, bet hedging, or insurance. The experimental manipulation of a redundant chick in a lesser kestrel population showed that, independently of annual feeding conditions, pairs attempting to rear as many chicks as eggs laid were less successful than parents with brood sizes reduced at hatching by one egg, because they raised fewer young, of lower body condition (only in 1993), and their own chance of survival was lower. If progeny-choice operates, the opposite result would be expected, at least for experimental reduced broods (E−). Since the chicks removed were randomly selected, parental choice was reduced and therefore, any advantage from a progeny-choice strategy was eliminated in treatments E−.

The results do not support the ice-box hypothesis because parents with redundant chicks did not get any benefit from these when feeding conditions were bad as in 1992. Moreover, I did not find any evidence for

Table 6 Effect of year, sex, original hatching success and chick redundancy on parental survival analyzed using logistic regression ($n = 72$)

Factor	Wald	*df*	*P*
A Chick redundancy	4.1	1	0.04
B Original hatching success	3.1	1	0.08
C Year	1.1	1	0.30
D Sex	0.7	1	0.39
Interactions:			
A × B	2.0	1	0.16
A × C	2.6	1	0.10
A × B × C	2.4	1	0.12

Table 7 Effects of the experiment on reproductive success [Mean ± SE (*n*)]. Effects on number of fledglings and pectoral condition were analyzed using ANOVA and including year as a factor. Effects on parental survival were analyzed using logistic regression and including year and sex as factors

	Number of fledglings	Pectoral condition	Parental survival
Experimentals (E− and E0)	1.77 ± 0.17 (43)	5.9 ± 0.2 (36)	0.32 ± 0.08 (37)
Controls (C− and C0)	1.76 ± 0.17 (50)	6.1 ± 0.1 (41)	0.42 ± 0.08 (35)
Effects:			
Manipulation	$F_{1,89} = 0.07$ NS	$F_{1,73} = 0.7$ NS	Wald = 0.9 NS
Year	$F_{1,89} = 21^{*4}$	$F_{1,73} = 34^{*4}$	Wald = 0.7 NS
Sex	–	–	Wald = 0.5 NS

$^{*4}P \leq 0.0001$

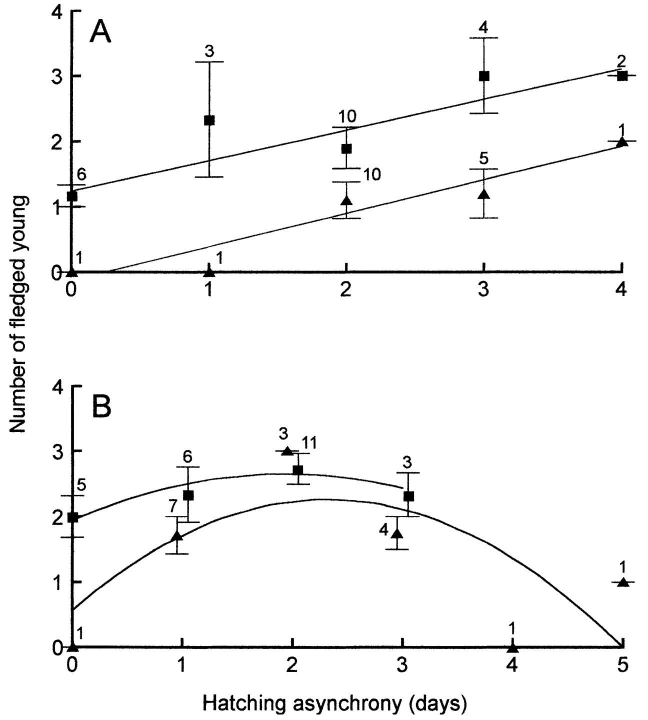

Fig. 3A,B Number of fledged young in relation to hatching asynchrony. **A** For broods with redundant chicks (E0 and C0) in 1992 (*triangles*) and 1993 (*squares*). **B** For reduced broods at hatching (E– and C–) in 1992 (*triangles*) and 1993 (*squares*). Regression lines are: **A** 1992: $y = -0.13 + 0.51x$, $r = 0.52$, $P < 0.02$; 1993: $y = 1.24 + 0.471x$, $r = 0.53$, $P < 0.01$; **B** 1992: $y = 0.57 + 1.45x - 0.31x^2$, $r = 0.61$, $P < 0.04$; 1993: $r = 0.33$, NS

cannibalism as was found by Bortolotti et al. (1991) in the American kestrel. Despite the presence of dead chicks in the nest, none had been partially eaten.

A bet-hedging strategy could evolve when feeding conditions are unpredictable. Kestrel parents were not able to foresee bad weather during the nestling period in 1992. In fact, their clutches were as large as in other years and they suffered, consequently, low reproductive success. Such environmental conditions could be favourable for the evolution of a bet-hedging strategy in this species. However, the bet-hedging hypothesis did not explain the experimental results either, because pairs with all chicks surviving at hatching were less successful, even in a high-food year. By contrast, experimental results agree with the insurance egg hypothesis which proposes that parents lay surplus eggs to compensate for possible egg-failures in both, good and poor-food years. Hence, complete broods should always pay for chick redundancy.

This conclusion in support of the insurance egg hypothesis depends on a correct determination of year quality because the two hypotheses, bet-hedging and insurance-egg, predict different results in good food years but not in poor years (see Table 1). Curiously, pectoral condition was better in 1992 (a poor-food year) than in 1993 (a high-food year). This suggests that year quality was assessed incorrectly. However, this result occurred because surviving nestlings were able to recover from malnourishment when weather and food availability suddenly improved in 1992, and even surpassed their usual condition since most of them had fewer competing siblings. In fact, growth of surviving nestlings was retarded by up to 12 days with respect to normal growth in other years, but they recovered by delaying fledging (J.M. Aparicio, unpublished work). Similar cases of retardation of growth have been found in other species which feed on flying insects whose abundance may decrease unexpectedly with bad weather (Lack and Lack 1950; Bryant 1975; Ricklefs 1976; O'Connor 1977; Emlen et al. 1991).

Perhaps 1993 was not as good as might be expected by parents using a bet-hedging strategy and, therefore, it would be necessary to test this hypothesis in a year with higher food abundance. Obviously, I think that parents should be able to rear complete broods if food availability becomes high enough, but such conditions may be infrequent in real life. In fact, the number of young fledged per breeding attempt in 1993 was not significantly different from the highest record in seven years (Table 2). Therefore, I think the classification of 1993 as a good year may be correct. Although there may be very good years in which surplus eggs could generate extra reproductive success, the most frequent function may be as insurance against the failure of any egg.

The costs of producing surplus eggs are the energy cost for the formation of extra eggs and the reproductive cost when no egg fails to hatch and nestlings must share parental care with a sibling that is going to die. To produce an extra egg does not appear to be too expensive in terms of energy in nidicolous birds (Krementz and Ankney 1986; Murphy 1986; Meijer et al 1989), because the peak of daily energy demand is independent of clutch size (King 1973). However, as was found in this study, redundant chicks are costly in terms of offspring and adult survival. Experimental and control broods whose sizes at hatching were as large as the clutches laid fledged fewer young with reduced body condition at fledging compared to reduced broods. Moreover, parents also paid for chick redundancy with their own survival. Thus, the effects are comparable to those induced by experimental brood enlargement in other altricial birds (review in Dijkstra et al. 1990; Stearns 1992), but note that lesser kestrel brood sizes were never larger than their original clutch sizes. In an experiment with the magpie (*Pica pica*), Husby (1986) also demonstrated costs of redundant chicks when they replaced chicks that died within 7 days after hatching.

Given the costs produced by chick redundancy, there would be a strong selective pressure facilitating the evolution of mechanisms of brood reduction. Species practising an insurance egg strategy could improve parental reproductive success through mechanisms which facilitate early brood reduction such as terminal-egg neglect (Graves et al. 1984). This mechanism allows the elimination of the last egg when hatching is asynchronous by stopping incubation after the first eggs have hatched

(Evans 1990; Evans and Lee 1991). Despite the fact that kestrel chicks hatched asynchronously and that there were opportunities for neglect of terminal eggs, parents appeared to continue incubating the last egg. In fact, hatching success of the last and other eggs were similar. In the lesser kestrel, asynchronous hatching could be sufficient to eliminate the youngest chick when necessary, and without apparent reproductive costs, as happens in some obligate siblicidal species (e.g., Anderson 1989). Older chicks prevent the youngest chick from feeding, and the youngest usually dies within 5 days (J.M. Aparicio, unpublished work). In fact, hatchibility of the last egg does not significantly affect the survival of other chicks. Hence, parents may not be pressed to eliminate the last egg when every egg hatches successfully.

Reproductive costs occurred, however, when all first eggs hatched. In these cases, asynchronous hatching also reduced sibling competition, and parental reproductive success increased with hatching asynchrony, independently of feeding conditions in the year. However, when an egg failed, asynchronous hatching over two days was detrimental to fledging success. Hatching asynchrony had, therefore, different effects, depending on the necessity of brood reduction, as also happens in other species which seem to practice a bet-hedging strategy (Magrath 1989, 1990). Parents usually created brood asynchronous by 2 days, which seems to be a compromise solution for both cases, when one egg fails to hatch or when there are redundant chicks.

As for benefits of the insurance egg strategy, the extra egg may be advantageous when any egg fails to hatch. Thus, as was shown by theoretical studies (Lundberg 1985; Forbes 1990, 1991), the strategy could evolve more easily in species laying large clutch sizes and with low hatching rate. However, the insurance egg hypothesis was originally proposed to explain obligate siblicide in birds which usually lay two eggs (Dorward 1962; Stinson 1979; Cash and Evans 1986; Anderson 1990), and has been rarely invoked for species with larger clutches (but see Graves et al. 1984; Mock and Parker 1986; Tortosa and Redondo 1992). More than half of lesser kestrel pairs (54%) experience a reduced brood size at hatching in this population, with a mean clutch size of 4.2 eggs and a hatching rate of 83%. Hatching success is lower (50–60%) in species which lay two eggs and practise the insurance egg strategy (Anderson 1990), but the probability of least one egg failure is similarly high. Therefore, the last egg frequently has the opportunity to replace an older sibling, and significantly contribute to reproductive output.

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