

CLUTCH ENLARGEMENT IN LESSER GRAY SHRIKES (*LANIUS MINOR*) IN SLOVAKIA WHEN FOOD IS SUPERABUNDANT: A MALADAPTIVE RESPONSE?

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ABSTRACT.—Food abundance influences various aspects of birds' breeding ecology, such as onset of laying, clutch size, and reproductive success. Here, we examine the effects of a natural superabundance of food—cockchafer (*Melolontha melolontha*, Coleoptera)—on nesting success of a monogamous long-distance migrant, the Lesser Gray Shrike (*Lanius minor*). In that species, cockchafers make up 88% of adult and 48% of nestling diet in years with cockchafer outbreaks. We compared timing of egg laying, clutch size, and fledging success in three years and chick development in two years with and without cockchafer outbreaks. In cockchafer years, laying date was advanced by about one day, clutch size increased by about one egg, and heavier chicks were produced. Fledging success, however, did not change (fledgling number in non-cockchafer years: 5.3 ± 0.2 , 5.0 ± 0.2 , and 4.0 ± 0.5 ; in cockchafer years: 4.1 ± 0.7 , 5.4 ± 0.2 , and 4.2 ± 0.5), because more eggs failed to hatch during cockchafer years. Thus, increased clutch size in periods of superabundant food do not always result in increased fledgling production. Limited incubation ability or intrinsic physical egg properties, resulting in inefficient incubation, are the most likely explanations for increased hatching failure in years of food superabundance in our study population of Lesser Gray Shrikes. Received 10 February 2003, accepted 27 January 2004.

RESUMEN.—La abundancia de alimento influye en diversos aspectos de la ecología reproductora de las aves, tales como el comienzo y tamaño de la puesta y el éxito reproductor. En este trabajo examinamos los efectos de una superabundancia natural de alimento (escarabajo sanjuanero, *Melolontha melolontha*, Coleoptera) en el éxito de nidificación de *Lanius minor*, un ave monógama migrante de larga distancia. Los escarabajos sanjuaneros constituyen el 88% de la dieta de los adultos y el 48% de la dieta de los pollos de este ave. En este estudio se compara la fecha de comienzo de puesta, el tamaño de puesta y el éxito de los volantones en tres años con superabundancia de escarabajos y en tres años sin tal superabundancia. También se analizan diferencias en el desarrollo de los pollos en dos años con y sin superabundancia de escarabajos. En años con superabundancia de escarabajos, la fecha de puesta se adelantó aproximadamente un día, el tamaño de puesta aumentó en aproximadamente un huevo y los pollos producidos fueron más pesados. Sin embargo, el éxito de los volantones no varió (número de volantones en años sin superabundancia de escarabajos: 5.3 ± 0.2 , 5.0 ± 0.2 y 4.0 ± 0.5 , en años con superabundancia: 4.1 ± 0.7 , 5.4 ± 0.2 y 4.2 ± 0.5) ya que el fracaso en la eclosión fue mayor en años con superabundancia de alimento. Por tanto, el incremento en el tamaño de puesta durante periodos de superabundancia trófica no siempre resulta en un incremento concomitante en la producción de volantones. Una incubación ineficaz debida a una limitación en la capacidad incubadora y/o propiedades físicas intrínsecas al huevo son las explicaciones más plausibles para el incremento en el fracaso de eclosión en *Lanius minor*.

INCREASED FOOD SUPPLY affects various aspects of breeding ecology in birds, including laying date, clutch size, hatching asynchrony, and hatching success (Lack 1947, 1948; Perrins 1970; Bryant 1973; Emlen and Oring 1977; Martin 1987; Dunn and Hannon 1992; Källander and Karlsson

1993; Nilsson 1993; Hoi et al. 1995; Soler and Soler 1996; Brinkhof 1997). Most of those studies have shown beneficial effects of food abundance on reproduction. The idea that the adaptive benefit of changes in one trait may be limited by constraints imposed by other traits has seldom been considered. For instance, we typically think of increased clutch sizes during periods of food abundance as an adaptive response. However,

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there is evidence that increased clutch size may negatively affect reproductive success (Moreno et al. 1991, Heaney and Monaghan 1995, Monaghan and Nager 1997), imposing a fitness cost on parents. Larger clutches may make greater energetic demands on incubating parents (Biebach 1984, Haftorn and Reinertsen 1985, Moreno et al. 1991), consequently influencing breeding success by affecting the parents and their subsequent brood-rearing abilities (Monaghan and Nager 1997, Reid et al. 2000). In addition, clutch enlargement may directly affect survival or development of embryos; recent studies show that experimental enlargement of clutch size affects intrinsic physical properties of the clutch, resulting in reduced hatching success (Reid et al. 2000, Larsen et al. 2003). However, birds producing naturally larger (as opposed to experimentally manipulated) clutches may be able to reduce incubation costs by adapting physical properties of the eggs to expected clutch size. For instance, females might optimize egg shape, egg size, or shell structure—or allocation of resources to eggs—in relation to expected clutch size (Barta and Szekely 1997, Christians and Williams 2001). We would predict that if females “design” eggs for an expected clutch size, incubation costs might be lower for naturally larger clutches than for experimentally enlarged clutches.

Here, we used insect outbreaks as an extreme case of natural food-variation (Barba et al. 1994, Arlettaz et al. 2001) to examine the “clutch-size versus hatching-failure” trade-off. Specifically, we looked at cockchafer (*Melolontha melolontha*) outbreaks in relation to reproduction of Lesser Gray Shrikes (*Lanius minor*), for which cockchafers make up about 50% to 90% of diet in certain years (Haensel 1964, Kristin and Zilinec 1998). We compared breeding performance between three cockchafer and three non-cockchafer years. Our goals were to (1) understand the role of cockchafers in the diet of Lesser Gray Shrikes; (2) assess the effects of cockchafer outbreaks on various reproductive parameters in the shrikes, including timing of egg laying, clutch size, hatching and fledging success, and chick development; and (3) examine the relationship between clutch size and hatching failure.

MATERIALS AND METHODS

SPECIES

The Lesser Gray Shrike (hereafter “shrike”) is socially monogamous. It reaches the study area in late April or early May. Pairs produce only one brood per

season, but replacement clutches may occur after nest failure. Incubation (starting with the third, fourth, or fifth egg) is mainly by the female, but the young are fed and cared for by both parents (Cramp and Perrins 1993). The shrike is a long-distance migrant, wintering in South Africa (8,000–10,000 km from the study area). Populations are declining in Europe (Kristin 1995), where the species is considered seriously endangered.

The shrike is a foraging specialist that relies mostly on large insects (mean body length 22.1 ± 0.19 mm; Kristin 1995) and quickly adapts its food-exploitation behavior, or impaling, to new prey items (Valera et al. 2001). Specifically, a high abundance of cockchafers significantly influences the composition of its diet and its foraging strategy (Haensel 1964, Kristin and Zilinec 1998). Because cockchafers occur at very high densities, are big and slow-moving (and hence easier to capture than most other shrike prey; see Kristin 1995), and have high energy and protein content (13% fresh and 27.5% dry mass; Kratochvil et al. 1953), they are a very profitable food source for the birds. Cockchafer outbreak years thus provide an opportunity to study the response of breeding birds to a superabundant food supply.

STUDY AREA

The study area, a 20-km² plot in central Slovakia (40°35′–38′N, 19°18′–22′E, 450–850 m above sea level), on the southern slopes of the Polana Mountains Biosphere Reserve, is an extensively managed agricultural landscape characterized by a high diversity of habitats (meadows, fields, bare ground, and orchards with plenty of tall fruit trees; Wirtitsch et al. 2001). Nests were frequently found near farm houses (average = 17.7 m; $n = 298$). The area supports one of the last stable and dense populations of shrikes in central Europe (3.75–4.25 breeding pairs per square kilometer; for details see Kristin 1995, Kristin et al. 2000).

BREEDING BIOLOGY

In six years (1995–1998, 2000, and 2001), we estimated onset of egg laying, clutch size, hatching success, and number of 14-day-old fledglings in first clutches. We recorded chick growth in first broods (May–June) in the first four years. We measured body mass and wing length of nestlings 6–10 days old. To estimate chick condition, we corrected body mass for size (i.e. wing length; correlation between body weight and wing length: $r = 0.85$, $P < 0.001$, $n = 195$ chicks). We did not correct for differences in brood size, because residual body mass per nest was not correlated with brood size ($r = -0.19$, $P > 0.20$, $n = 38$). Body mass data are only available for four years (1995–1998).

From the beginning of May, we checked territories daily and inspected nests every three days to determine breeding parameters. We investigated 23, 73, 65, 70, 37,

and 36 nests during 1995, 1996, 1997, 1998, 2000, and 2001, respectively. The variation in number of nests studied reflects differences in search intensity.

FOOD COMPOSITION

To determine the importance of cockchafers and other food components in the diet of shrikes, prey taken by adults and fed to chicks was studied in all cockchafer and non-cockchafer years (except 1995), using visual observations ($n = 779$; Table 1) taken during 20-min periods before and during egg laying and during chick feeding. Birds were observed through a 40 × 70 telescope or a video camera, mounted 8–10 m from the nest.

FOOD ABUNDANCE

Years 1995, 1998, and 2001 were cockchafer outbreak years in the study area. Onset of outbreaks depends on daily ambient temperatures of $\geq 20^\circ\text{C}$ (Escherich 1923) or mean daily temperature of $\geq 15^\circ\text{C}$ (Decoppet 1920). In central Europe, cockchafer emergence starts in the second half of April or the beginning of May and peaks two weeks after imagoes first appear (Kratochvil et al. 1953, Arlettaz et al. 2001, H. Hoi et al. pers. obs.).

In the study area, cockchafer imagoes (body length 25–31 mm) generally occurred from 10 April through the first days of July. Between 25 April and 20 June in all three cockchafer years, the insects abundantly covered most of the tree and shrub species on which they feed. Peak abundance in those years occurred between 15 and 25 May—coinciding with egg laying and incubation of shrikes—and slowly declined afterwards. At peak abundance, cockchafers reached densities of >50 individuals per meter of twig on some fruit trees (plum, cherry), on oaks (*Quercus* spp.), and on shrubs, such as rose (*Rosa* spp.), frequently causing intense defoliation.

DATA ANALYSES

We used nested ANOVAs with “cockchafer outbreak versus non-outbreak” as the main treatment,

“year” nested within that treatment, and laying date, clutch size, fledgling number, and hatching failure as dependent variables. To express onset of egg laying, days were numbered from 1 April onward.

We tested for differences in number of eggs failing to hatch in outbreak compared with non-outbreak years with a 2×2 chi-square test, rows being “outbreak” and “non-outbreak” years and columns being “0–1 egg failing to hatch” and “ ≥ 2 eggs failing to hatch.” To test for variation in hatching failure with date or clutch size, we used separate logistic-regression analyses for cockchafer and non-cockchafer years; the dependent variable was whether a nest contained at least one unhatched egg or not; the independent variables were laying date and clutch size. To examine chick development, we used residual chick body mass per nest, adjusted for chick age and number of chicks per nest. Range in body mass between chicks in a brood was used to estimate within-brood variation.

Statistical tests were usually parametric. Data were $\log(x + 1)$ transformed when they did not meet assumptions for normality. Hatching failure was arcsin square-root transformed. Means and standard errors (SE) are given throughout.

RESULTS

SEASONAL AND ANNUAL VARIATION IN DIET AND COCKCHAFER AVAILABILITY

Cockchafer availability had a strong effect on composition of shrike diets in all cockchafer years (Table 1). In those years, cockchafers predominated in the diets of male and female shrikes, before and during egg laying (six days prior to egg laying, until the day the penultimate egg was laid). In contrast, no cockchafers were taken by shrikes in non-cockchafer years (Table 1). Adult cockchafers start to swarm in mid-April and survive for only three to four weeks (Kratochvil et al. 1953). They decrease in abundance, therefore, as the shrikes’ breeding

TABLE 1. Mean (\pm SE) percentage of cockchafers in the diet of Lesser Gray Shrikes (male and female adults and 5- to 14-day-old nestlings) in cockchafer and non-cockchafer years (n = number of individuals or nests; FE = number of foraging events).

Year	Males	n	FE	Females	n	FE	Nestlings	n	FE
Cockchafer years									
1995	51.5 \pm 7.6	6	41	53.3 \pm 16	6	27	–	–	–
1998	88.0 \pm 5.2	30	92	80.9 \pm 8.9	14	29	48.4 \pm 9.4	18	32
2001	55.3 \pm 7.6	21	76	48.3 \pm 10.6	15	28	40.8 \pm 11.8	10	33
Non-cockchafer years									
1996	0	29	82	0	29	46	0	29	51
1997	0	18	29	0	18	29	0	18	15
2000	0	23	88	0	17	49	0	13	32

season progresses, but they still make up ~48% of the diet of 5- to 14-day-old young (Table 1). We can thus assume that food abundance during cockchafer years is much higher than in normal years, which suggests a natural experiment to study the effects of surplus food.

EFFECT OF COCKCHAFER AVAILABILITY ON BREEDING PARAMETERS

Laying started earlier and clutch size was larger in cockchafer years; there were no differences between nested years (Fig. 1A,B). The proportion of females producing the maximum number of seven eggs was significantly higher in cockchafer years (22 out of 78; 28.2%) than in non-cockchafer years (9 out of 107; 8.6%; binomial test: $\chi^2 = 12.67$, $P < 0.001$). However, fledging success did not significantly differ between cockchafer and non-cockchafer years (Fig. 1C), probably because hatching failure was ~3× higher in cockchafer years (Fig. 1D). In addition to the consistently higher probability of hatching failure in cockchafer years, there was variation in both number of fledglings produced and hatching failure, even within cockchafer and non-cockchafer years. Residual nestling body mass was significantly higher in cockchafer years; differences were not significant within cockchafer years or within non-cockchafer years (Fig. 2).

Residual intrabrood variation in body mass (controlling for brood size) did not differ between cockchafer and non-cockchafer years (Fig. 3). The lower intrabrood variation (controlling for brood size) in nests with higher average chick body-mass suggests that high nestling growth rates coincided with a more consistent rate of growth among siblings. The relationship between chick body mass and intrabrood variation was significant for cockchafer years (1995: $r_{\text{part}} = -0.41$, $n = 9$; 1998: $r_{\text{part}} = -0.36$, $n = 33$; for both, $P < 0.05$) but not for non-cockchafer years (1996: $r_{\text{part}} = -0.15$, $n = 23$; 1997: $r_{\text{part}} = -0.18$, $n = 36$; for both, $P > 0.4$). Cockchafer food may decrease mass span in chick development within a brood, independently of brood size.

Examining cockchafer years only, a logistic-regression analysis provided a significant model explaining hatching failure (i.e. nests containing at least one unhatched egg vs. nests containing no unhatched eggs; $\chi^2 = 12.1$, $df = 2$, $P = 0.01$). Clutch size (Wald's $\chi^2 = 5.6$, $P = 0.02$), but not start

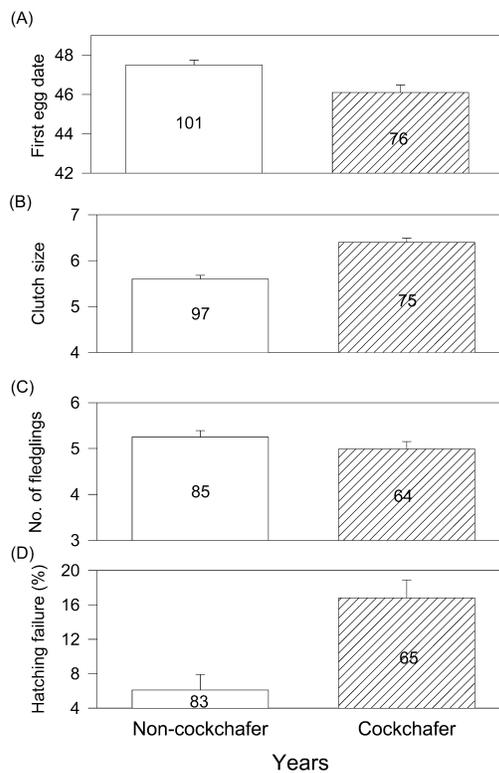


FIG. 1. Comparison of four breeding parameters of the Lesser Gray Shrike for cockchafer years (1995, 1998, 2001; hatched bars) and non-cockchafer years (1996, 1997, 2000; open bars). Shown are (A) day of start of egg laying (numbering days from 1 April), (B) clutch size, (C) number of fledglings, and (D) hatching failure (%). Bars indicate means \pm SE and sample size. See text for sample size for each year. Results of nested ANOVAs with cockchafer years vs. non-cockchafer years as the main treatment and year nested within treatment are highly significant for laying date ($F = 18.3$, $df = 1$ and 176, $P < 0.0001$; nested year effect: $F = 0.03$, $df = 6$, $P > 0.80$) and hatching failure ($F = 19.9$, $df = 1$ and 147, $P < 0.0001$; nested year effect: $F = 2.3$, $df = 6$, $P < 0.007$), significant for clutch size ($F = 4.02$, $df = 1$ and 171, $P = 0.04$; nested year effect: $F = 0.9$, $df = 6$, $P > 0.40$), but not significant for number of fledglings ($F = 0.2$, $df = 1$ and 148, $P > 0.60$; nested year effect: $F = 2.5$, $df = 6$, $P = 0.03$).

of laying, entered the model. Number of eggs failing to hatch increased with clutch size ($r = 0.47$, $P < 0.007$, $n = 64$), but was not related to laying date ($r = 0.04$, $P > 0.50$, $n = 64$). However, the model was not significant when examining non-cockchafer years ($P > 0.30$), and there was no correlation between hatching failure and clutch size ($r = 0.04$, $P > 0.70$, $n = 83$) or laying date ($r =$

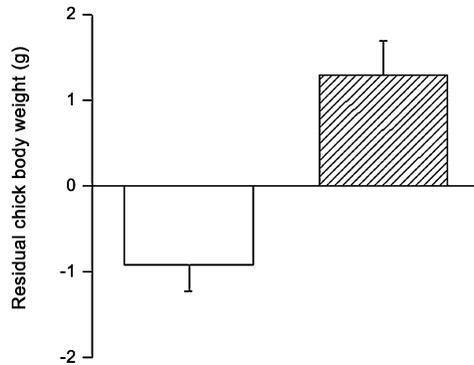


FIG. 2. Differences in nestling body mass between cockchafer (1995, 1998; $n = 40$; hatched bar) and non-cockchafer (1996, 1997; $n = 56$; open bar) years. Bars indicate mean \pm SE residual body mass of Lesser Gray Shrike nestlings (adjusted for brood size and nestling age; see text for details). Results of nested ANOVAs with cockchafer years vs. non-cockchafer years as the main treatment and year nested within treatment are highly significant for nestling body mass ($F = 7.3$, $df = 1$ and 95 , $P < 0.008$; nested year effect: $F = 0.9$, $df = 4$, $P > 0.40$).

0.01, $P > 0.90$, $n = 83$). Furthermore, there was no significant association between cockchafer outbreaks and rate of multiple hatching failure (0 or 1 unhatched egg vs. ≥ 2 unhatched eggs; $\chi^2 = 9.6$, $df = 1$, $P > 0.19$). Those results suggest that increased hatching failure in outbreak years was more likely a result of all nests having a higher probability of containing a single unhatched egg than of a few nests having complete hatching failure (which we did not observe).

DISCUSSION

Our study suggests that cockchafer outbreaks indeed provided a natural food-supplementation experiment, given that our results are in line with most food-supplementation experiments—although the increase in food abundance was more extreme. Superabundant food from cockchafer outbreaks resulted in an earlier laying date and had a positive effect on clutch size and nestling body mass in shrikes (see also Davies and Lundberg 1985, Strehl and White 1986, Hochachka and Boag 1987, Martin 1987, Arcese and Smith 1988, Soler and Soler 1996 for birds; and Arlettaz et al. 2001 for timing of parturition in bats). On one hand, it is not surprising that egg laying starts earlier when there is an abundance of cockchafer available

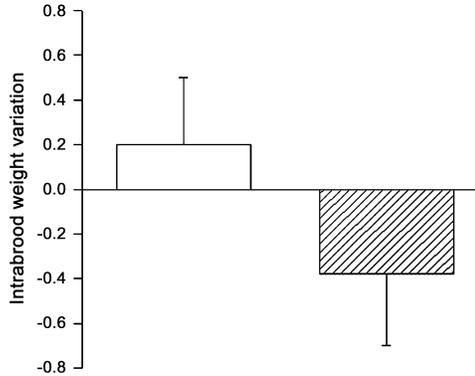


FIG. 3. Differences in intrabrood variation in nestling body mass (range in body mass between the heaviest and the lightest nestling in a nest) between cockchafer (1995, 1998; $n = 42$; hatched bar) and non-cockchafer (1996, 1997; $n = 68$; open bar) years. Bars indicate mean \pm SE residual variation in body mass of Lesser Gray Shrike nestlings (adjusted for brood size and age differences). Results of nested ANOVAs with cockchafer years vs. non-cockchafer years as the main treatment and year nested within treatment are not significant for intrabrood variation in nestling body mass ($F = 0.8$, $df = 1$ and 109 , $P > 0.50$; nested year effect: $F = 0.4$, $df = 4$, $P > 0.50$).

to the shrikes on their arrival from migration. On the other hand, the shrike is a long-distance migrant, and the birds always start breeding as soon as they arrive (see similar results in Martin 1987). The shrikes' arrival dates (28 April to 2 May for the first five breeding pairs) did not differ significantly between years (Kristin et al. 2000, A. Kristin et al. unpubl. data for 1989–2001). However, the great energetic reward of cockchafer (Kratovich et al. 1953) obviously accelerated the start of laying (Fig. 1A).

The significantly larger clutch size in cockchafer years—with almost a third (28%) of the females producing the maximum clutch size of seven eggs (see Cramp and Perrins 1993)—is a crucial prerequisite for examining the possible trade-off between clutch size and hatching failure. Despite higher clutch size in cockchafer years, number of nestlings did not differ between cockchafer and non-cockchafer years. In fact, fewer chicks tended to fledge in cockchafer years. The main reason for the low number of fledglings in cockchafer years was that hatching failure was $\sim 3\times$ higher in those years (Fig. 1D), so that increases in clutch size were offset by reduced hatching success; all eggs examined contained

developed embryos ($n = 28$), which eliminates increased infertility as an alternative cause of higher hatching failure. Clutch size is usually said to be confounded by laying date (Daan et al. 1988), which could also be important in explaining hatching failure, but our analyses revealed no evidence for an effect of laying date on hatching failure in shrikes. There is evidence that experimental enlargement of clutch size affects breeding success (Moreno et al. 1991, Heaney and Monaghan 1995, Monaghan and Nager 1997, Reid et al. 2000) and, more specifically, hatching success (Hills 1983, Delahanty and Oring 1993, Arnold 1999, Reid 2000). However, other studies found no evidence of an effect on hatching success (Sandercock 1997, Wallander and Andersson 2002, Larsen et al. 2003). Reid et al. (2000) pointed out that hatching success is affected by the conditions embryos experience during incubation. Enlargement of clutch size changes the intrinsic physical properties of a clutch, as well as directly changing clutch temperature.

Females laying naturally larger clutches may be able to minimize costs of incubation by adapting their eggs to the expected clutch size. They might adjust, for example, the eggs' shape, size, or shell structure (Barta and Szekely 1997, Reid et al. 2000) or the resource allocation among eggs (Christians and Williams 2001). Thus, the negative effect of larger clutch size on hatching success could result from experimental manipulation of clutch size, where egg "design" has not been properly adjusted. However, our study of a wild bird population does not suggest that eggs are "tailor-made" for larger clutch sizes in years of food superabundance; at least, food supplementation does not seem to have a positive effect on hatching success.

Females incubating larger clutches have a higher daily energy expenditure (Moreno et al. 1991, Monaghan and Nager 1997) and consequently consume more food (Coleman and Whittall 1988) and suffer higher mass losses (Moreno and Carlson 1989). Thus, rather than directly affecting embryos, increased clutch size may affect parents by energetically constraining their incubation abilities or altering their allocation of energy reserves between incubation and later chick-rearing.

Studies of several species have found reduced incubation efficiency in large clutches (e.g. Wood and Bollinger 1997), resulting in a prolonged incubation period, reduced hatching success

(Moreno et al. 1991, Siikamäki 1995, Wallander and Andersson 2002, Larsen et al. 2003), and increased hatching asynchrony (Moreno and Carlson 1989). Monaghan and Nager (1997) reported that the energy requirements of an incubating parent increased with increasing clutch size; hatching failures are likely to occur when the attending adult is unable to maintain an adequate incubation regime, particularly in the later stages of incubation (O'Connor 1984). However, those observations were made in situations where females did not have the benefit of surplus food. When food is superabundant and easily acquired, females should be able to increase their attentiveness during incubation without incurring additional cost. Also, female shrikes are fed by their males during egg laying, incubation, and the early chick-feeding period; they do not need to leave the nest unattended to forage. The assumption that energy resources were not limited is also supported by the finding that chick body condition was better in cockchafer years. Rather than energy constraints on the parents, other factors may more likely influence incubation efficiency in this species. Larger clutches occupy more space, and females probably have difficulty covering all the eggs effectively (Lack 1947, Larsen et al. 2003). Additionally, the nest might be too small to accommodate large clutches, as suggested by our own observations, so that eggs sometimes lie on top of one another.

An alternative explanation for the higher hatching failure is that larger clutches have a longer laying period, which may result in a longer hatching period, which could cause lower hatching success during cockchafer outbreaks (see Moreno and Carlson 1989). If the first-laid eggs begin to hatch days before the last-laid eggs, remaining unhatched eggs will be incubated far less frequently and efficiently, because the female will be off the nest foraging for the already-hatched young. Such a relationship between clutch size and hatching asynchrony, and the consequent effect on hatching success, would be visible in both cockchafer and non-cockchafer years, but we found no relationship between clutch size and hatching success in non-cockchafer years. Thus, inefficient incubation—resulting from limited parental incubation ability or intrinsic physical properties of eggs, or both—is the most likely explanation for increased hatching failure in our study population of shrikes.

Egg production is energetically costly (Monaghan and Nager 1997). In this species, laying of extra eggs is a waste of energy, given that larger clutches did not result in more fledglings—in fact, a tendency toward lower fledgling success was observed. On the other hand, nestlings seemed to be in better condition in cockchafer years; given that good fledgling condition increases survival probability (Ricklefs 1968, Moss and Camin 1970, Magrath 1992), the costs of laying more eggs may thus be outweighed and not necessarily result in fitness costs for the parents.

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LITERATURE CITED

- ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *Journal of Animal Ecology* 57:119–136.
- ARLETTAZ, R., P. CHRISTE, A. LUGON, N. PERRIN, AND P. VOGEL. 2001. Food availability dictates the timing of parturition in insectivorous mouse-eared bats. *Oikos* 95:105–111.
- ARNOLD, T. W. 1999. What limits clutch size in waders? *Journal of Avian Biology* 30:216–220.
- BARBA, E., D. M. GARCIA, J. A. GIL-DELGADO, AND G. M. LOPEZ. 1994. Moth abundance and breeding success in a Great Tit population where moths are the main nestling food. *Ardea* 82:329–334.
- BARTA, Z., AND T. SZEKELY. 1997. The optimal shape of avian eggs. *Functional Ecology* 11:656–662.
- BIEBACH, H. 1984. Effect of clutch size and time of day on the energy-expenditure of incubating starlings (*Sturnus vulgaris*). *Physiological Zoology* 57:26–31.
- BRINKHOF, M. W. G. 1997. Seasonal variation in food supply and breeding success in European Coots *Fulica atra*. *Ardea* 85:51–65.
- BRYANT, D. M. 1973. Breeding biology of House Martin *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117:180–216.
- CHRISTIANS, J. K., AND T. D. WILLIAMS. 2001. Intra-specific variation in reproductive physiology and egg quality in the European Starling *Sturnus vulgaris*. *Journal of Avian Biology* 32:31–37.
- COLEMAN, R. M., AND R. D. WHITTALL. 1988. Clutch size and the cost of incubation in the Bengalese Finch (*Lonchura striata* var. *domestica*). *Behavioral Ecology and Sociobiology* 23:367–372.
- CRAMP, S., AND C. M. PERRINS, Eds. 1993. *The Birds of the Western Palearctic*, vol. 7. Oxford University Press, New York.
- DAAN, S., C. DIJKSTRA, AND T. MEIJER. 1988. Food supply and the annual timing of avian reproduction. Pages 392–407 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). National Museum of Natural Sciences, Ottawa, Ontario.
- DAVIES, N. B., AND A. LUNDBERG. 1985. The influence of food on time budgets and timing of breeding of the Dunnock *Prunella modularis*. *Ibis* 127:100–110.
- DECOPPET, M. 1920. *Le Hanneton*. Payot, Lausanne, France.
- DELAHANTY, D. J., AND L. W. ORING. 1993. Effect of clutch size on incubation persistence in male Wilson's Phalaropes (*Phalaropus tricolor*). *Auk* 110:521–528.
- DUNN, P. O., AND S. J. HANNON. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in Tree Swallows. *Auk* 109:488–499.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection and evolution of mating systems. *Science* 197:215–223.
- ESCHERICH, K. 1923. *Die Forstinsekten Mitteleuropas*. Bd. II. Verlag Paul Parey, Berlin.
- HAENSEL, J. 1964. Zur Ernährungsökologie des Schwarzstirnwürgers nach Gewöllenuntersuchungen im nördlichen Harzvorland. *Beiträge zur Vogelkunde* 10:199–210.
- HAFTORN, S., AND R. E. REINERTSEN. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). *Auk* 102:470–478.
- HEANEY, V., AND P. MONAGHAN. 1995. A within-clutch trade-off between egg production and rearing in birds. *Proceedings of the Royal Society of London, Series B* 261:361–365.
- HILLS, S. 1983. Incubation capacity as a limiting factor of shorebird clutch size. M.S. thesis, University of Washington, Seattle.
- HOCHACHKA, W. M., AND D. A. BOAG. 1987. Food shortage for breeding Black-billed Magpies (*Pica pica*): An experiment using supplemental food. *Canadian Journal of Zoology* 65:1270–1274.
- HOI, H., S. KLEINDORFER, R. ILLE, AND J. DITTAMI. 1995. Prey abundance and male parental behaviour in *Acrocephalus* warblers. *Ibis* 137:490–496.

- KÄLLANDER, H., AND J. KARLSSON. 1993. Supplemental food and laying date in the European Starling. *Condor* 95:1031–1034.
- KRATOCHVIL, J., V. LANDA, K. NOVAK, AND V. SKUHRAVY. 1953. Cockchafers and Their Control. [In Czech.] Czech Science Advanced Views (CSAV), Prague.
- KRISTIN, A. 1995. Why the Lesser Gray Shrike (*Lanius minor*) survives in Slovakia: Food and habitat preferences, breeding biology. *Folia Zoologica* 44:325–334.
- KRISTIN, A., H. HOI, F. VALERA, AND C. HOI. 2000. Breeding biology and breeding success of the Lesser Grey Shrike (*Lanius minor*) in a stable and dense population. *Ibis* 142:305–311.
- KRISTIN, A., AND M. ZILINEC. 1998. Lesser Grey Shrike (*Lanius minor*) diet and foraging strategy during and after cockchafer (*Melolontha melolontha*; Insecta, Coleoptera) swarming. Pages 34–37 in *Shrikes (Laniidae) of the World II: Conservation Implementation* (R. Yosef and F. E. Lohrer, Eds.). International Birdwatching Center, Eilat, Israel.
- LACK, D. 1947. The significance of clutch-size [Parts I and II]. *Ibis* 89:302–352.
- LACK, D. 1948. The significance of clutch-size [Part III]. *Ibis* 90:25–45.
- LARSEN, A., T. LISLEVAND, AND I. BYRKJEDAL. 2003. Is clutch size limited by incubation ability in Northern Lapwings? *Journal of Animal Ecology* 72:784–792.
- MAGRATH, R. D. 1992. The effect of egg mass on the growth and survival of blackbirds—A field experiment. *Journal of Zoology (London)* 227: 639–653.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. *Annual Reviews in Ecology and Systematics* 18: 453–487.
- MONAGHAN, P., AND R. G. NAGER. 1997. Why don't birds lay more eggs? *Trends in Ecology and Evolution* 12:270–274.
- MORENO, J., AND A. CARLSON. 1989. Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica* 20: 123–128.
- MORENO, J., L. GUSTAFSSON, A. CARLSON, AND T. PÄRT. 1991. The costs of incubation in relation to clutch size in the Collared Flycatcher *Ficedula albicollis*. *Ibis* 133:186–193.
- MOSS, W. W., AND J. H. CAMIN. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. *Science* 168:1000–1003.
- NILSSON, J. A. 1993. Energetic constraints on hatching asynchrony. *American Naturalist* 141:158–166.
- O'CONNOR, R. J. 1984. *The Growth and Development of Birds*. John Wiley and Sons, Chichester, New York.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–255.
- REID, J. M., P. MONAGHAN, AND G. D. RUXTON. 2000. The consequences of clutch size for incubation conditions and hatching success in starlings. *Functional Ecology* 14:560–565.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–448.
- SANDERCOCK, B. K. 1997. Incubation capacity and clutch size determination in two calidrine sandpipers: A test of the four-egg threshold. *Oecologia* 110:50–59.
- SIHKAMÄKI, P. 1995. Are larger clutches costly to incubate—The case of Pied Flycatcher. *Journal of Avian Biology* 26:76–80.
- SOLER, M., AND J. J. SOLER. 1996. Effects of experimental food provisioning on reproduction in the Jackdaw *Corvus monedula*, a semi-colonial species. *Ibis* 138:377–388.
- STREHL, C. E., AND J. WHITE. 1986. Effects of superabundant food on breeding success and behaviour of the Red-winged Blackbird. *Oecologia* 70:178–186.
- VALERA, F., A. KRISTIN, AND H. HOI. 2001. Why does the Lesser Grey Shrike (*Lanius minor*) seldom store food? Determinants of impaling in an uncommon storing species. *Behaviour* 138: 1421–1436.
- WALLANDER, J., AND M. ANDERSSON. 2002. Clutch size limitation in waders: Experimental test in Redshank *Tringa totanus*. *Oecologia* 130: 391–395.
- WIRTITSCH, M., H. HOI, F. VALERA, AND A. KRISTIN. 2001. Habitat composition and use in the Lesser Grey Shrike *Lanius minor*. *Folia Zoologica* 50: 137–150.
- WOOD, D. R., AND E. K. BOLLINGER. 1997. Egg removal by Brown-headed Cowbirds: A field test of the host incubation efficiency hypothesis. *Condor* 99:851–857.

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