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Parental body mass changes during the nesting stage in two Lark species in a semi-arid habitat

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Abstract

Parental body mass changes during the nesting period were analysed for Thekla Larks, *Galerida theklae*, and Lesser Short-toed Larks, *Calandrella rufescens*. Body mass of female Thekla Larks declines from the start of incubation until the chicks fledge; laying date, interpreted as the number of renesting attempts, also has a negative effect. Body mass of female Lesser Short-toed Larks was not related to any of these variables, except laying date during the incubation stage. Male Thekla Larks lost body mass during the nestling phase. All female Thekla Larks which were recaptured lost body mass during incubation and female Lesser Short-toed Larks lost body mass during the post-hatching period. Body mass losses throughout the whole nesting period were 14% and 16% for adult female Thekla Larks and Lesser Short-toed Larks, respectively, and 2.5% and 2.6%, respectively, for the males of these two species during the nestling phase. Body mass declines in the two species seem to be related to the number of clutches laid and not to clutch size, but the two show different patterns of body mass variation, which are also different from the only other lark of desert environments in which body mass when nesting has been studied to date.

Keywords: Birds; Larks; Arid habitats; Reproductive costs; *Galerida*; *Calandrella*; Adult body mass; Mediterranean; Breeding; Spain; Incubation; Nestling

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1. Introduction

Body mass variation during the breeding period has been considered as an index of parental reproductive stress by some authors (Hussell, 1972; Ricklefs, 1974, pp. 152–297; Askenmo, 1977; Bryant, 1979; Takagi, 2002), but not by others (Freed, 1981; Moreno, 1989a; Croll et al., 1991; Jones, 1994; Sanz and Moreno, 1995; Cichon, 2001; Kullberg et al., 2002), given that adult birds can decrease their weight in the nestling stage to increase their flying and feeding capacities. However, most of the studies on passerines have been undertaken on cavity-nesting species and in mesic habitats (e.g. Moreno, 1989b), with studies on ground-nesting species of semi-desert or desert environments being very scarce. This is the case in the lark family (*Alaudidae*), where to our knowledge, only one study of this type exists (Williams, 2001). In addition, many larks are multi-brooded species, renesting being a common occurrence after the loss of one or more earlier clutches (i.e. Cramp, 1988; Dean et al., 1992, pp. 13–124).

Two basic models have been established in relation to body mass variation during the nesting phase (Moreno, 1989b). The females of some species, in the so-called Incubatory Mass Loss model, lose body mass during incubation until hatching, then maintain or increase their mass slightly during the post-hatching period. In contrast, other species maintain their body mass during incubation but lose mass during the first part of the post-hatching period, then regaining it at the end of the nestling phase (the Incubatory Mass Constancy model). The majority of female passerines fit the second strategy whereas males show virtually no mass changes during the nesting phase. Nevertheless, this pattern has exceptions and it has been proposed that in environments of poor quality or where prey may be hard to find, as in semi-arid habitats, it would be difficult for females to maintain their incubatory mass (Moreno, 1989b).

We explore and compare the mass changes during the nesting period of two larks of semi-arid habitats, the Thekla Lark *Galerida theklae* and the Lesser Short-toed Lark *Calandrella rufescens*. Our initial hypothesis was that female body mass falls during incubation and in the post-hatching phase, given the low productivity and low food availability of their environment in comparison to more productive mesic habitats.

2. Methods and materials

2.1. Species

Thekla and Lesser Short-toed Larks are medium and small passerines (36 and 19 g, respectively) of semi-arid Mediterranean environments, which also occur in semi-desert habitats in North Africa (Cramp, 1988). Although their ecologies are poorly known, the first appears to be sedentary, forming small family groups in winter that undertake restricted movements, while the second forms wandering groups in the post-breeding and winter periods. In our study area, Thekla Larks start breeding approximately 1 week before Lesser Short-toed Larks and lay larger clutches (3.54 ± 0.72 vs. 3.34 ± 0.60 eggs, $n = 322$ and 238, unpublished data from 5 years). In both species, only the females incubate and they are not fed by the males. The chicks are cared for and fed by both parents, and fledgling care appears to be undertaken by the males while the females lay further clutches. Nest predation rates are very high (between 70% and 95%, Yanes and Suárez, 1996a, 1997) and the number of clutches laid per female is unknown, although Thekla Larks may lay up to three successful clutches. In the study population, it has been estimated that 81% of Thekla Lark females lay within 4 weeks from the date of the earliest clutch found in the population and 82% of Lesser Short-toed Lark females do so within 2 weeks (Yanes and Suárez, 1996b).

2.2. Study area and methods

The study area is in South-eastern Spain (Almería, 36°50′N, 2°25′W; 50 m a.s.l.). It has a semi-arid Mediterranean climate with an annual rainfall of 200 mm. The landscape is flat or gently undulating and the vegetation a shrub-steppe dominated by *Stipa tenacissima*, *Fagonia cretica*, *Thymus* spp., *Crucianella maritima*, etc. A detailed description of the vegetation and bird communities may be found in Yanes and Suárez (1996a) and Tellería et al. (1988).

The study was conducted in 1996 and 1997. Nests were found through systematic searches and observations of adult behaviour during the breeding period (March–June). The birds were caught at the nest during incubation (females) or when feeding chicks (both sexes) using a nest-trap. Traps were only used when females had been incubating for 4 or more days, in order to avoid possible clutch desertions and traps were not left in place for more than 30 min per day. All birds were colour-ringed and some were recaptured. Individuals were weighed on an electronic balance (±0.01 g) and tarsus length was measured with callipers to the nearest 0.01 mm. Sex was established by the presence of an incubation patch in females. A total of 97 Thekla Larks (31 males and 66 females) and 94 Lesser Short-toed Larks (31 males and 63 females) were captured, comprising 94 individuals in 1996 (37 Thekla and 57 Lesser Short-toed Larks) and 97 in 1997 (60 Thekla and 37 Lesser Short-toed Larks). Nest-trapped birds totalled 75 Thekla Larks (26 males and 49 females) and 63 Lesser Short-toed Larks (23 males and 40 females).

Clutch size and first-egg date were recorded for each nest. In nests discovered during the incubation period, clutch size was taken as the maximum number of eggs found in the nest. In nests found during the nestling period, we assumed a clutch size equal to the maximum number of chicks recorded. The date of the first egg laid was estimated assuming a laying rate of one per day (Cramp, 1988). In nests found during the nestling stage, the laying date was estimated allowing for a 13-day incubation period in both species, and using growth curves of chicks constructed for both species, with an estimated error of ±1 day (Shkedy and Safriel, 1992). Given that the difference between first-laying dates in the 2 study years was 10 days in Thekla Lark (26 March in 1996, $n = 37$ nests; 16 March in 1997, $n = 41$ nests), the laying date for each nest was standardized in relation to the earliest laying date for that year for each species by assigning the value 1 to the earliest-clutch date.

2.3. Statistical analysis

Two separate analyses were made for each species, one using data from all the birds captured and the second based only on those birds which were recaptured at least twice. In the first we used General Linear Models (GLM), using body mass as the dependent variable. To avoid pseudoreplication problems resulting from measuring the same individuals on successive days, we used mean weights and mean capture dates, as long as the data related to the same stage of reproduction (incubation or nestling). Same-female recaptures during both incubation and post-hatching phases totalled seven and three for Thekla and Lesser Short-toed Larks, respectively.

Data for females and males were analysed separately. For females, in addition to an analysis covering the whole breeding period, independent analyses were undertaken for the incubation and nestling stages. Male body mass data were only analysed during the nestling phase given that males of neither species incubate. In all models, the year was included as a random factor and clutch size as a fixed, with laying date and nest age as covariates. To eliminate possible effects resulting from differences in the body size of individuals, tarsus length was also included as a covariate (Freckleton, 2002). Two-way interaction terms were tested and removed from the model when insignificant.

The second analysis was based on recaptured individuals, analysing the effects of species, reproductive stage and sex on the daily body mass change between capture dates. Where there were more than two recaptures during one of the periods, the daily body mass change was calculated using the first and last capture dates. Data for females that were captured only once during the incubation period and again during the nestling phase were not included. However, data for birds recaptured during both the incubation and nestling periods were used for both periods. The Sign test was used to test whether the changes were positive or negative and factorial ANOVAS were used to compare rates of daily body mass change between the two species, sexes and periods, controlling for the effect of different body mass of species and sexes by dividing the daily body mass increase by the mean of the two adult weights. The significance level considered was $p = 0.05$. All analyses were undertaken using the SPSS 11.0 (SPSS Inc., 2001) statistical package.

3. Results

Nest age was the only significant variable when considering all the female Thekla Larks captured (Table 1); body mass declined with nest age. In this species, female body mass declined more rapidly during incubation but also continued during the nestling phase (Fig. 1), though no significant differences were found in body mass variation when the incubation and the nestling phases are considered separately (GLM, $p > 0.05$ in all cases). Nest age showed a significant effect on the body mass of male Thekla Larks, as in females, but neither laying date nor clutch size had any significant effect (Table 1).

In Lesser Short-toed Larks, female body mass throughout the breeding period and male body mass during the nestling phase were not related to any of the variables

Table 1
GLM results of the analysis of body mass variation in Thekla Lark males and females in relation to laying date and nest age, clutch size, year and tarsus length throughout the whole reproductive period

Variable	Quadratic mean	d.f.	*F*	*p*
Females				
Laying date	5.052	1	3.459	0.072
Nest age	13.378	1	9.161	0.005
Clutch size	2.343	3	0.441	0.742
Year	0.081	1	0.035	0.881
Tarsus length	3.182	1	2.179	0.149
Males				
Laying date	0.107	1	0.078	0.783
Nest age	7.624	1	5.597	0.032
Clutch size	0.867	3	0.259	0.854
Year	0.130	1	0.026	0.902
Tarsus length	7.327	1	5.379	0.035

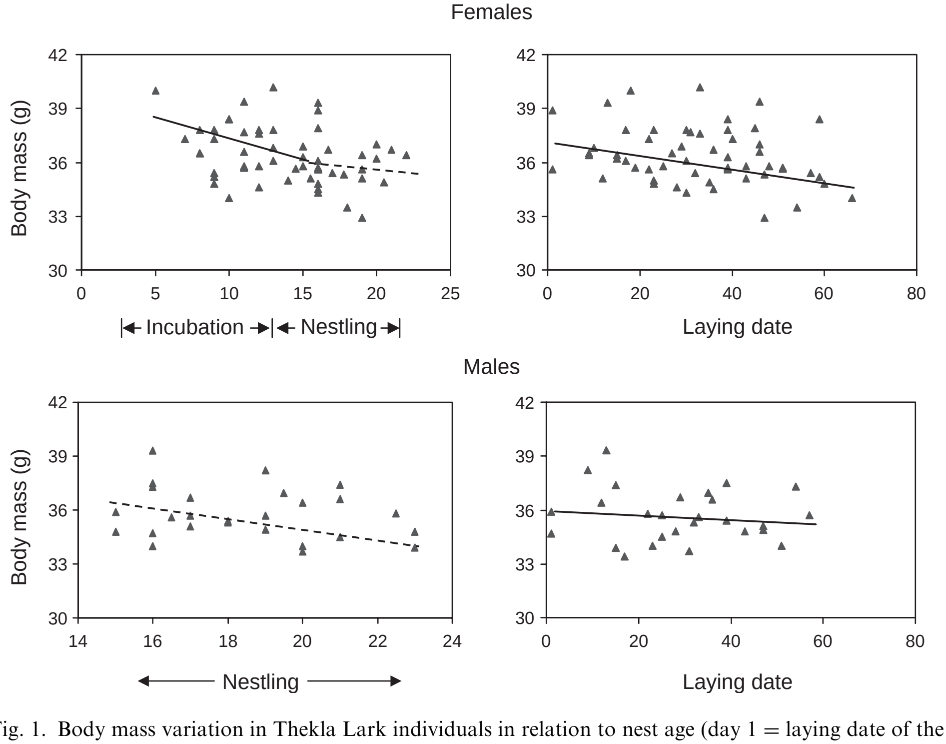

Fig. 1. Body mass variation in Thekla Lark individuals in relation to nest age (day 1 = laying date of the first egg) and the laying date of the first egg (day 1 = 1 March), both relative to the whole population.

($p > 0.1$). Only the clutch size × year interaction was significant in males (Table 2). Female body mass showed a slight increase until hatching, declining thereafter (Fig. 2), while body mass change in the males during the nestling phase was virtually

Table 2
GLM results of the analysis of body mass variation in Lesser Short-toed Lark males and females in relation to laying date and nest age, clutch size, year and tarsus length throughout the whole reproductive period

Variable	Quadratic mean	d.f.	*F*	*p*
Females				
Laying date	0.376	1	0.644	0.429
Nest age	0.075	1	0.129	0.722
Clutch size	3.111	2	195.302	0.922
Year	0.008	1	0.029	0.868
Tarsus length	8.122	1	13.913	0.001
Males				
Laying date	0.872	1	1.684	0.215
Nest age	0.929	1	1.793	0.202
Clutch size	0.036	1	0.010	0.937
Year	0.000	1	0.000	0.993
Tarsus length	0.373	1	0.720	0.410
Clutch size × year	4.091	1	7.898	0.014

absent, as was its variation in relation to laying date (Fig. 2). Considering the incubation and nestling phases in female Lesser Short-toed Larks separately, only laying date showed a significant effect during incubation ($F = 20.718$, 1 d.f., $p = 0.01$).

Most recaptured individuals of both species showed body mass losses during the intervening period (Thekla Lark, 86%, $n = 14$, Lesser Short-toed Lark, 71%, $n = 24$; Sign test, $p = 0.006$ and 0.032, respectively). All the Thekla Lark females lost body mass during incubation (Table 3, Sign test, $p = 0.008$) as did 75.0% of Lesser Short-toed Lark females, although this difference was not significant (Sign test, $p = 0.145$). The females and males of both species appear to lose body mass during the nestling phase (Table 3), although this was only significant in female Lesser Short-toed Larks (Sign test, $p = 0.035$).

Body mass change rates controlled for adult body mass showed no differences between the species, sexes or nesting phases in any of the cases (ANOVA, $p > 0.1$). Considering the rates of change in the two nesting phases (Table 3) and incubation times and the periods during which the chicks remain in the nest (13 and 8 days, respectively, for both species), the mean body mass loss during the nesting period was 5.2 g for Thekla Lark females and 3.1 g for Lesser Short-toed Lark females (14.3% and 15.7%, respectively). In males, during the nestling phase, the mean loss was 0.9 g in Thekla Larks and 0.5 g in Lesser Short-toed Larks (i.e. 2.5% and 2.6%, respectively).

4. Discussion

Laying date appears to be an important variable in relation to the body mass of females in both lark species. Laying date affects negatively the body mass of female

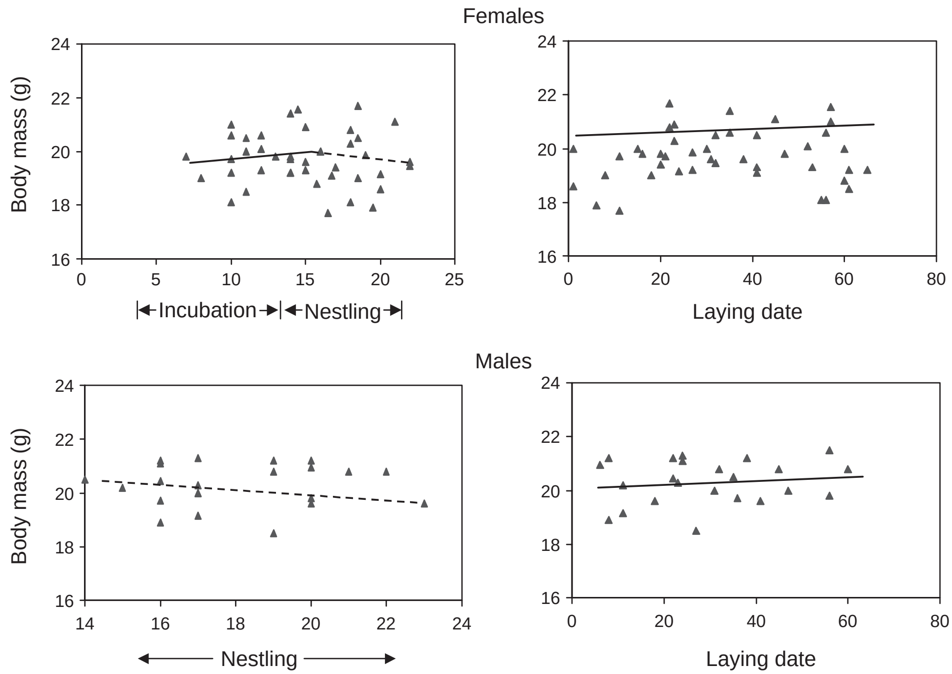

Fig. 2. Body mass variation in Lesser Short-toed Lark individuals in relation to nest age (day 1 = laying date of the first egg) and the laying date of the first egg (day 1 = 1 March), both relative to the whole population.

Table 3
Number of individuals recaptured, percentage which lost weight, mean and standard deviation of the daily mass loss and body mass of adult Thekla and Lesser Short-toed Larks during incubation (females) and the nestling phase (females and males)

	Galerida theklae			*Calandrella rufescens*		
	Females		Males	Females		Males
	Incubation	Nestling	Nestling	Incubation	Nestling	Nestling
Number of measures	7	3	4	8	8	6
% which lost weight	100.0	66.7	75.0	75.0	87.5	66.7
Daily weight loss ($g\,d^{-1}$)	0.323 ± 0.225	0.125 ± 0.193	0.111 ± 0.309	0.158 ± 0.213	0.135 ± 0.093	0.067 ± 0.267
Adult body mass (g)	36.37 ± 1.57 ($N = 49$)		35.69 ± 1.46 ($N = 26$)	19.72 ± 0.96 ($N = 40$)		20.33 ± 0.83 ($N = 23$)

Sample sizes are in parentheses.

Lesser Short-toed Larks during the incubation phase and there is a tendency for body mass to decline throughout the whole nesting period in female Thekla Larks. However, no similar effect on body masses was found in males of either species.

Body mass declines with nest age in both sexes in Thekla Larks. Clutch size has no effect on the female body mass of either species and only influences male Lesser Short-toed Larks in its interaction with year.

The mean laying date in these multi-brooded species is determined by the frequency in the population of second and later replacement clutches, which are practically all those clutches present later than 1 month after the earliest laying date in the population. This is due to the high nest predation rates (75–95%, Yanes and Suárez, 1996a), the fact that the earliest-laying females have already reared their first clutches (Yanes and Suárez, 1996b), and to the very short period before renesting (approximately 4 days in both species, pers. obs.). Therefore, it appears plausible that the effect of laying date on female body mass actually reflects the number of clutches laid. The high predation rates also cause a low number of chicks to rear, explaining the absence of effect of laying date on the body mass of males of either species, whose main energetic expenditure occurs during feeding and rearing of chicks.

The pattern of weight loss observed in Thekla Larks during the nesting stage supports the prediction of the Incubatory Mass Loss hypothesis (Moreno, 1989b). The data from all of the females captured show a loss of body mass throughout the whole nesting period, which is significant in those individuals recaptured during incubation. Although there was a tendency for a decline in body mass for all the individuals captured during the nestling phase (Fig. 1), and most recaptured individuals lost mass (67%), the lack of significance in both cases shows that this is really very slight or non-existent. Male Thekla Larks also lose mass during the nestling phase when all the captures are considered. Therefore, in contrast to the majority of those passerines where the females are not fed on the nest by the males, Thekla Lark females appear to comply with the Incubatory Mass Loss hypothesis, whereas the variation in body mass of the males does not. However, the mass loss of recaptured Lesser Short-toed Lark females occurred during the nestling phase and not during incubation, and body mass of male Lesser Short-toed Larks does not appear to be affected during the nestling phase. The Lesser Short-toed Lark therefore appears to fit the Incubatory Mass Constancy model.

The differences between the two species are difficult to explain and could be due to the fact that Thekla Larks have a longer breeding period and higher body mass. In contrast, the desert-living Dune Lark (*Mirafra erythroclamys*) shows a pattern different from the two species studied here, maintaining its body mass throughout the whole reproductive period (Williams, 2001). This suggests that the lark species of arid and semi-arid environments can show different specific patterns of body mass change during the breeding season and more data are needed to clarify the question.

The proportional body mass loss (approximately 10%; Moreno, 1989b) shown by the females during the nesting period was not very different from other passerines. In both species, there are considerable differences between females and males in body mass losses during the nesting period, which is the norm in other passerines. However, in contrast to other passerine groups, larks normally have a long period of post-fledging care (about 1 month in most of the species; De Juana et al., 2004), largely undertaken by the males. Although in this study males were not weighed after the chicks abandoned the nest, rearing the altricial fledglings implies a cost (e.g. Scott, 1984) that could mirror the larger losses seen in females during the nesting phase itself.

In summary, the body masses of these larks of a semi-arid Mediterranean habitat seem to decline in relation to the number of clutches and not to clutch size. Also, these two species show distinct patterns of variation in body mass, which in turn are different from the only species of desert lark so far studied (Williams, 2001) in this respect.

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