

NEST SIZE AND STRUCTURE VARIATION IN TWO GROUND NESTING PASSERINES, THE SKYLARK *ALAUDA ARVENSIS* AND THE SHORT-TOED LARK *CALANDRELLA BRACHYDACTYLA*

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Herranz J., J. Traba, M.B. Morales & F Suárez 2004. Nest size and structure variation in two ground nesting passerines, the Skylark *Alauda arvensis* and the Short-toed lark *Calandrella brachysactyla*. *Ardea* 92(2): 209-218

We analysed variation in size and weight of 127 Skylark *Alauda arvensis* and 179 Short-toed Lark *Calandrella brachyactyla* nests studied over four years in central Spain. More specifically, we explored three groups of hypotheses: hypotheses based on (1) thermoregulation and past reproductive parental investment, (2) predation, and (3) clutch size. Variables recorded were dry nest weight, inner diameter, outer diameter, nest edge thickness, nest cup depth and percentage of lining layer cover, which were related to laying date, clutch size, geographical orientation, shrub cover, year, and predation rate. Weight and nest edge thickness were negatively correlated with laying date in both species, and with percentage of lining layer cover in the Short-toed Lark. Skylark inner nest diameter varied positively with shrub cover. Three nest measurements varied with year in the Short-toed lark: nest edge thickness, nest cup depth, and inner diameter. In this species, nest cup depth was associated with orientation, while inner diameter varied also with laying date. Neither predation, clutch size nor phenology were correlated with nest size and weight in either species.

Key words: *Alauda arvensis* - *Calandrella brachyactyla* – nest size – nest structure- passerines

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INTRODUCTION

The costs associated with nest building vary considerably among bird species (Collias & Collias 1984; Hansell & Deeming 2002). Such costs are the result of two phenomena. First, the energy investment in additional flights necessary for birds to build the nest. Second, the increase in predation risk both for adults during the time devoted to the gathering of nest material, and for adults and brood due to the greater ease for predators to locate nests (Møller 1990). These costs can

be compensated in altricial birds during incubation through a nest insulation sufficiently effective to create a microclimate that increases the survival probability for eggs and / or nestlings (Ar & Sidis 2002). Consequently, a balance for parents may exist between the costs associated to nest construction (energy invested, predation risk), and the energy saved during incubation (Slagsvold 1989 a), which has been poorly studied so far (Hansell 2000).

Several non-exclusive hypotheses have been proposed to explain variation in nest dimensions

(Palomino *et al.* 1998). These hypotheses can be grouped into three categories depending on the different costs and benefits associated with nest building. (1) Hypotheses based on thermoregulation (Hoi *et al.* 1994) and past reproductive parental investment (e.g., Lens *et al.* 1994). In temperate climates, temperature increases and rainfall and moisture decrease as the season progresses, so that a decrease in nest insulation can be expected. Additionally, in multi-brooded species, the accumulated female costs of producing successive clutches may lead to an expected reduction of the investment in nest construction during the season as a result of a decreasing construction effort in terms of both materials and time, so that birds can optimize the number of clutches laid, thus maximizing their lifetime fitness. In both cases a decrease in nest weight and insulating structure over the season should be found. (2) Predation hypotheses. Predation pressure will favour small nests due to their lower detectability by predators (Slagsvold 1982a). (3) Hypotheses based on sexual display (Moreno *et al.* 1994; Soler *et al.* 1998) and clutch size (Snow 1978; Møller 1982). If investment in nest building is a reliable signal of parental reproductive effort, then nest size might be expected to be correlated with clutch size, to which females would adjust nest volume. Other factors not regarded by these groups of hypotheses, such as female age (Boyer 1988), availability of nest building material (Collias & Collias 1984), or parasite load (Hansell 2000) may also influence nest structure.

Most studies on the variation and determinants of open nest dimensions are based on tree, bush or wall nesting species (e.g. Møller 1982; Slagsvold 1982; Palomino *et al.* 1998) in which the structure constraints of nests are larger due to their need to have a solid, stable base (Collias & Collias 1984). In ground nesting species, however, structure constraints are smaller and nests tend to present wider nest-cups than those of tree nesting birds (Slagsvold 1989), while some ecological constraints such as predation may be stronger. We studied the factors affecting nest weight and size of two ground nesting, multi-brooded lark species with female intermittent incubation, the Skylark *Alda arvensis* and the Short-toed Lark

Calandrella brachydactyla. Specifically, we explored the three categories of hypotheses summarised above using laying date, temperature, predation rates and clutch size as main predictors of nest weight and dimensions in these species.

METHODS

Study area and species

The study area was located in Layna, central Spain (41°05'N, 1°50'W; 1200 m a.s.l.), and characterised by flat short shrub-steppe dominated by *Genista pumila*, *Thymus vulgaris* and *Linum suffruticosum* (Suárez *et al.* 1993). The climate is continental Mediterranean, with an annual rainfall of 500 mm and a yearly average temperature of 10.2 °C. Winters are cold and summers are cool but dry. Rainfall is mainly restricted to autumn and spring. During the nesting season average monthly temperature increases (mean temperatures of May, Jun and Jul, 12.3, 16.2 and 19.5 °C), while monthly rainfall decreases (70, 59 and 27 mm, respectively).

Both study species are sympatric in the study site, sharing the same type of habitat. Skylark females are larger than Short-toed Lark females (mean \pm SD = 33 \pm 2.2 g, n = 15 vs mean \pm SD = 20.9 \pm 1.2 g, n = 24, respectively in the study area, own unpublished data). Skylark and Short-toed Lark nests are built mainly by females, while males contribute only some small sticks placed by females (Cramp 1988). Nests of both species are located on the ground, cup-shaped and lined with grasses. Short-toed larks make more complex nests and usually add a lining layer made of various types of soft material (plume-seeds, wool strings, leaves, and even paper fragments). In some instances, nests of both species have a rim of small sticks at the nest entrance. In the two species, nest building time is always two days, estimated from the moment they finish excavating the nest hole (own unpubl. data). Their respective laying dates in the study site are similar, both starting in the second week of May. Both species suffer high nest predation rates (75 - 80% of nests, Suárez *et al.* 1993).

Data collection

Nests were located by systematic search and observing the adults' behaviour during the period 1991 - 1995. Nests were measured with callipers either during the laying phase or the 1 - 4 first days of incubation in order to avoid deformations produced as incubation progresses (Slagsvold 1989b). We measured nest weight, inner diameter (*ID*), outer diameter (*OD*), and inner nest-cup depth (*ND*). In Short-toed Lark nests, the cover of the lining layer made of materials other than grass stems was estimated as the percentage of the total inner surface of the nest cup covered by the lining layer. Nest edge thickness was calculated as $(OD-ID) / 2$. Nest weight was measured once nestlings had already fledged or after a predation event. Before weighing, excrements were removed and nests were dried up to constant weight, and weighed on a 0.1 g error balance. All field and laboratory measures were made by the same researcher.

The geographical orientation of each nest entrance was recorded using a compass, and the horizontal percentage of the nest's surface covered by the shrub or plant-tuft under which nests are normally found was visually estimated. Clutch size, and date of laying of the first egg were also recorded. For nests found during the first days of the incubation period, clutch size was considered as the maximum number of eggs found in the nest. The date of laying of the first egg was estimated in both species considering a 1 egg / day rate, and an 11 day incubation period, which is the modal value for both species in our populations (own unpubl. data). The final number of nests considered was 127 for the Skylark and 179 for the Short-toed Lark, although it was not possible to measure all variables in all cases. Therefore, sample sizes are specified in each analysis.

Data treatment and analysis

In order to compare nest weight and dimensions between species, female body weight was used to standardise the size of both species. Mean body weights (*BW*) were transformed to a one-dimensional variable (body weight index, *WE*), assum-

ing that the body of birds approaches a sphere of a radius *s* and calculating the diameter of that sphere (Slagsvold 1989a):

$$(4/3) s^3 = BW$$

$$WE = 1.24^3 BW$$

Nest weight and the different nest measures were divided by *WE* (Slagsvold 1989a). Between-species differences in these variables were tested by means of one-factor ANOVAs and a chi-square test in the case of nest orientation. We used type III General Linear Models (GLM) to analyse the correlation of nest measures with different factors. Dependent variables used were nest weight, inner diameter, nest edge thickness, nest depth and percentage of lining layer cover. Year was included in all analyses as a random factor. Provided that nests in the study area are preferentially oriented to NE, other orientations being marginal (Yanes *et al.* 1997), orientation was grouped in two classes: 0° - 90° and > 90° (70.8 % and 29.2% of nests, respectively, *n* = 236). Nest orientation and clutch size were considered as fixed factors. Laying date and shrub cover were included as covariates. In all GLM analyses the interaction terms were tested and removed when non-significant.

The relationship between nest weight and inner diameter (a linear dimension related to how eggs fit in the nest-cup, and thus to their degree of exposure to air temperature) was used to assess the investment of larks in nest thermal insulation. A type III GLM analysis was conducted to study the variation of regression residuals of nest weight over inner diameter with environmental temperature immediately previous to clutch laying, while controlling for the effect of clutch size. The same kind of analysis was carried out using the residuals of weight over nest outer diameter to assess the potential role of sexual selection in determining nest dimensions. Temperatures considered were the average of daily means corresponding to the seven days previous to the laying of each clutch. Temperatures were obtained from the closest meteorological station.

We analysed the potential effect of outer diameter, weight and shrub cover on each nest's probability of being depredated or not by means of a general binomial logistic regression model (Cox 1970) in which clutch size was included as a factor, along with the species in order to compare between both larks. Laying date was included as an additional continuous predictor in order to account for its potential effect on nest dimensions, and the fact that predation probability may show a seasonal pattern. We removed the species term to compare between nests of the same species. To compare seasonal changes in nest weight and nest edge thickness between species, these measures were standardised for each species through the use of the equation:

$$Xi' = (Xmax - Xi) / x$$

where Xi is the value of either weight or edge thickness of nest i , $Xmax$ the maximum value of those measures, and x the average value for all nests. The frequency comparisons were made by means of χ^2 - tests. Percentages were arcsine-transformed when required by parametrical tests. All analyses were performed with SPSS 11.0 (SPSS Inc. 2001). We used two-tailed tests and a significance level of $P = 0.05$. Variation intervals are always reported as mean \pm standard deviation.

RESULTS

After standardising weight and dimensions of Skylark and Short-toed Lark nests (Table 1) with female body weight (WE, Slagsvold 1989a), nest

weight did not differ between species ($F = 0.24$, $df = 1$, $P = 0.628$, $n = 131$), although inner diameter, nest-cup depth, and nest edge thickness were all larger in the Short-toed Lark ($F = 5.94$, 19.82 and 8.48 , $df = 1$, $P = 0.016$, < 0.001 and 0.040 , $n = 78$ in the Skylark, 118 in the Short-toed). Nest orientation was similar in both species (NW, Skylark, 65.6% of 160 nests, Short-toed Lark, 69.7% of 76 nests, $\chi^2 = 0.394$, $df = 1$, $P = 0.555$), and so was the percentage of surface covered by the shrub under which they are placed ($F = 0.03$, $df = 1$, $P = 0.872$, Skylark and Short-toed Lark, $n = 79$ and 129 ; Table 1). No lining layer was found in Skylark nests, whereas percentage of lining layer cover was highly variable among Short-toed Lark nests (Table 1).

Skylark nest weight and edge thickness were negatively correlated with laying date (Table 2, only variables with significance values of $P < 0.1$ are presented), whereas the inner diameter was positively correlated with shrub cover (Table 2, Fig. 1). Nest weight progressively decreased to around 14 g from first to last clutches, which represents a 65% reduction (Fig. 1). Nest edge thickness decreased in a similar manner and order of magnitude (1.5 cm, a 68% reduction, Fig. 1). Nest-cup depth showed no correlation with any of the factors considered. Year and orientation did not correlate with any of the Skylark nest measurements studied.

Short-toed Lark nest weight and edge thickness were negatively correlated with laying date. This factor was also negatively correlated with percentage of lining cover, but it showed a significantly positive relationship with inner diameter (Table 2). Short-toed Lark nests lost about 8 g

Table 1. Mean and standard deviation of Skylark and Short-toed Lark nest measurements.

Variable	Skylark	<i>n</i>	Short-toed Lark	<i>n</i>
Weight (g)	15.2 \pm 5.7	62	11.7 \pm 3.7	70
Inner diameter (cm)	7.0 \pm 0.6	78	5.7 \pm 0.5	118
Nest edge thickness (cm)	1.6 \pm 0.5	78	1.4 \pm 0.4	118
Nest-cup depth (cm)	4.7 \pm 0.8	78	4.1 \pm 0.6	118
Lining layer (%)	-		44.1 \pm 40.4	127
Shrub cover (%)	49.1 \pm 30.0	92	48.1 \pm 27.0	145

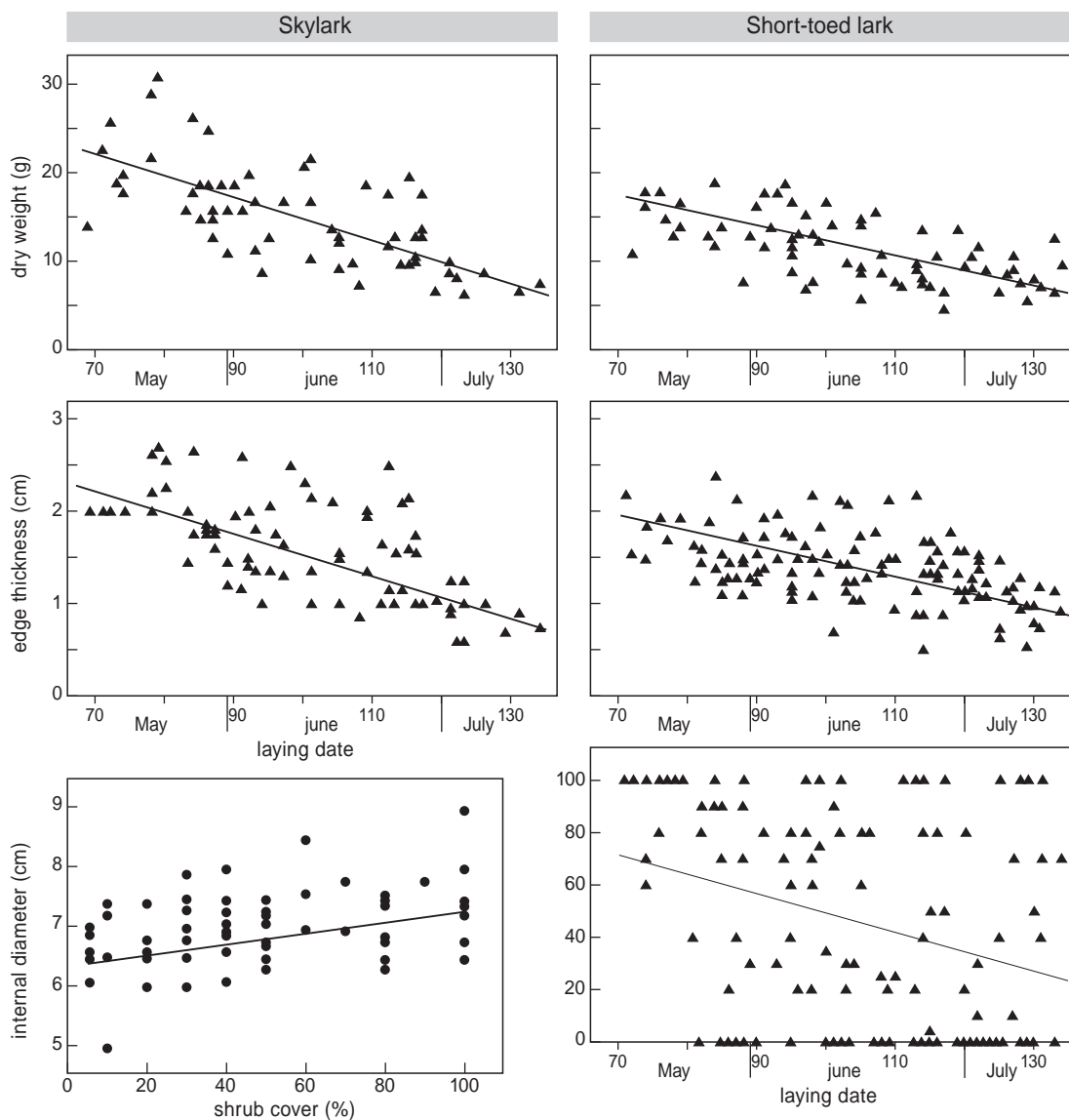


Fig. 1. Significant variation of Skylark and Short-toed Lark nest measures in relation to laying date (1/5: May 1st, 1/6: June 1st, 1/7: July 1st). Variation of inner diameter Skylark nests in relation to shrub cover is also shown.

(50%, Fig. 1) from first to last clutches, while the average loss in edge thickness, considering nests from all years of study, was 0.5 cm (30%, Fig. 1). Inner diameter was the nest measure correlated with laying date in the smallest degree, growing 0.3 cm in average (5%). None of the remaining nest measurements varied with laying date. In this

species inner diameter, nest edge thickness and nest-cup depth varied with year. Nest-cup depth was also correlated with orientation: nests oriented to the NE were significantly deeper than those oriented otherwise (4.17 ± 0.68 cm, $n = 73$ vs. 3.92 ± 0.61 cm, $n = 38$). The standardised nest weight loss rate was larger among Skylarks than

Table 2. Results of the GLM analysis of nest weight and measurements in relation to laying date, shrub cover, year, orientation and clutch size. Only those relationships in which $p < 0.1$ were included.

Species	Nest measure	Factor	Quadratic mean	df	F	P	<i>n</i>
Skylark	Weight	Laying date	442.50	1	23.70	< 0.001	48
	Inner diameter	Shrub cover	1.10	1	4.47	0.041	63
	Edge thickness	Laying date	4.00	1	21.04	< 0.001	63
	Inner nest-cup depth	Clutch size	1.39	3	3.32	0.054	63
Short-toed Lark	Weight	Laying date	265.818		35.486	< 0.001	62
		Shrub cover	19.90	1	2.87	0.097	103
	Inner diameter	Laying date	1.02	1	4.04	0.047	103
		Year	0.73	4	2.90	0.026	5
	Edge thickness	Laying date	2.45	1	27.60	< 0.001	103
		Year	0.49	4	5.54	< 0.001	5
	Inner nest-cup depth	Year	2.42	4	6.52	< 0.001	103
		Orientation	1.78	1	4.78	0.031	103
% Lining layer cover	Laying date	13546.60	1	9.04	0.003	110	

among Short-toed larks ($F = 46.94$, $df = 1$, $P < 0.01$, $n = 62$ for Skylarks, 70 for Short-toed Larks), while that of nest edge thickness was similar in both species ($F = 0.14$, $df = 1$, $P = 0.70$, $n = 78$ for Skylarks, $n = 118$ for Short-toed Larks). Finally, clutch size did not correlate with any of the nest parameters studied in the two species.

Regression residuals of nest weight on inner nest diameter were significantly and negatively correlated with the average value of daily mean temperatures of the seven days previous to clutch laying both in Skylarks and Short-toed Larks ($F = 16.52$, $df = 1$, $P < 0.001$ and $F = 11.82$, $df = 1$, $P < 0.005$, respectively), while no relationship with clutch size was found ($F = 0.36$, $df = 3$, $P = 0.77$ and $F = 0.70$, $df = 2$, $P = 0.5$, respectively). Similar results were obtained for residuals of weight on outer diameter: they were negatively correlated with temperature in both species (Skylark: $F = 5.14$, $df = 1$, $P < 0.05$; Short-toed lark: $F = 8.53$, $df = 1$, $P < 0.01$), but no significant effect of clutch size was found (Skylark: $F = 1.03$, $df = 3$, $P = 0.38$; Short-toed lark $F = 0.25$, $df = 2$, $P = 0.77$).

Nest probability of predation did not differ between species (Table 3). Overall, no relationship was found between nest predation probability, laying date and clutch size. No relationship

was found either between nest predation probability and those variables within species ($P > 0.1$ in all cases, Skylark, $n = 57$; Short-toed Lark, $n = 95$). None of the continuous nest variables considered showed a significant effect on nest predation probability (Table 3).

Table 3. Results of the logistic regression model analysing the effect of the species, year, clutch size, laying date, nest outer diameter, and nest shrub cover on each nest's probability of being predated ($-2 \log$ likelihood = 192.53, Cox and Snell $R^2 = 0.053$, Nagelkerke $R^2 = 0.071$)

Variable	Wald	df	<i>P</i>
Species	0.66	1	0.4
Year	3.48	4	0.5
Clutch size	2.68	3	0.5
Laying date	0.001	1	1.0
Outer diameter	0.42	1	0.5
Shrub cover	0.31	1	0.6

DISCUSSION

Laying date was negatively associated in both larks with all nest measurements related with insulation, that is, weight and edge thickness in both species, and percentage of lining layer cover

in the Short-toed Lark. The significant relationship of residuals of weight on inner diameter with temperatures immediately previous to clutch laying also suggests the importance of insulation on nest size and structure. Nest predation rate was not correlated in any of the study species with outer diameter or weight. These variables were not significant either when comparing the species. However, other nest dimension factors did differ between species. For example, shrub cover was correlated with inner diameter of Skylark nests, although it was not significant in the Short-toed Lark. Year was associated with variation in edge thickness, nest-cup depth, and inner diameter in the Short-toed Lark, but not in the Skylark. In addition, geographical orientation was correlated only with nest-cup depth in the Short-toed Lark. The three groups of hypotheses presented in the introduction may, therefore, be evaluated on the basis of these results.

Hypotheses based on thermoregulation and past reproductive parental investment

The effect of laying date on the variables related to nest insulation found in the two species supports the hypothesis of thermoregulation (Hoi *et al.* 1994) and the accumulated cost of successive clutches (Lens *et al.* 1994). These two processes could not be completely separated in the present study, and they might in fact be working simultaneously. In fact, in multi-brooded species with high nest predation rates (75 - 90% of nests, Yanes & Suárez 1996a), the number of replacement or successive clutches is limited by the duration of the breeding period, so that the time invested in nest construction must be minimised in order to increase the probability of laying another clutch (Slagsvold 1982a; Yanes & Suárez 1996b). This is supported in the case of our study species by the short time taken by females to build a nest, always two days in both species, which did not differ between early and late clutches ($n = 9$ females, J. Herranz pers. com.). The time interval between the end of nest construction and the first egg laid was also fairly constant between early and late clutches (grouped data from both larks: 1.3 ± 0.6 days, $n = 6$ vs $1.4 \pm$

0.5 days, $n = 8$). Investment in nest construction in relation to investments in other nesting stages is considered small in most birds (Collias & Collias 1984; but see Moreno *et al.* 1994; Soler *et al.* 1996).

Although nest composition (in terms of the kind of materials used) did not change, both nest weight and percentage of lining layer cover (in the case of the Short-toed Lark) decreased over the season. In addition, the significant relationship of nest weight-inner diameter residuals with temperature variation supports the influence of temperature on female investment in nest insulation, and the priority of this process in determining nest dimensions as compared with clutch size (see below). Consequently, it is reasonable to conclude that the improvement of weather conditions over the nesting season affects the investment of females in nest insulation, which decreases as the season progresses (Møller 1987), thus supporting thermal insulation as main determinant of nest size and structure.

Finally, individual and environmental factors may also constrain the bird's investment in nest building, for example female age (although no data from the study species are available, young females are likely to make less elaborate nests, Hansell 2000), or availability of nesting material. In relation to the latter, small sticks and wool fibres are always abundant in the daily sheep-grazed woody shrub-steppes of the study area, so that their availability can be considered constant throughout the breeding season.

Hypotheses based on predation

In species with high predation rates such as those studied here, selection may have favoured a reduction of the investment, in terms of materials gathered and, therefore, of the energy effort devoted to nest building, regardless of the total time consumed. This selection pressure may also be responsible for the similar time devoted to nest building by both species, since both are exposed to similar predation rates (Yanes & Suárez 1996a). Our results do not support the predation hypothesis (Slagsvold 1982a) in these larks. Neither the different nest size of each species, nor the varia-

tion in size of individual nests was associated with nest predation rate. The main nest predators of Mediterranean larks are mostly nocturnal, and find the nests by olfactory cues (Yanes & Suárez 1996a). Consequently, variation in outer nest diameter and weight should not be significantly correlated with predation rates, as found in the present study and contrarily to what can be expected in species whose main predators use mainly visual cues.

Hypotheses based on sexual selection and clutch size

Many Palearctic larks add ornaments to nests such as small pebbles, sticks and even excrements, thus forming a more or less marked nest rim (De Juana *et al.* 2004). In the two species studied, however, the nest rim is small (own unpubl. data), while edge thickness (and percentage of lining layer cover in the Short-toed Lark) decreased markedly with laying date. This supports the hypothesis of a reduction of the birds investment in nest building and insulation rather than the existence of a potential, sexually selected, investment in nest ornamentation (Soler *et al.* 1998). In fact, the significant effect of temperature on residuals of weight over outer diameter suggests that female investment in exterior parts is probably more related to insulation than to sexual selection.

Our results are not consistent either with the clutch size hypothesis. Nest and clutch size have been found to be positively related in some hole-nesting species (i.e. Murphy & Haukioja 1986), but also in some species with open or domed cup-shaped nests (Snow 1978; Møller 1982; Soler *et al.* 2001). In the lark species studied here, however, no relationship between weight or any nest measurement with clutch size was found. Moreover, variation of residuals of nest weight on both inner and outer diameter was independent of clutch size in the two species. The reproductive parameters of these larks are very different from those found in the above mentioned species. Clutch sizes show little variation in both species (3-4 eggs per clutch, rarely 2 or 5, own unpubl. data), nests suffer high predation rates, and most reproductive

features result from their adaptation, at the family taxonomic level, to climatic aridity (Tieleman *et al.* 2004; De Juana *et al.* 2004). Provided that the sample size used in the present study is large enough to detect evolutionary trends (Møller & Jennions 2002), our results suggest that nest size does not depend on clutch size in these ground nesting passerines.

Between species differences

Some factors act differently in the two species, for example shrub cover, which was positively related to inner nest diameter in the Skylark. In tree or bush nesting species, larger nests present larger clutch size (Soler *et al.* 2001) or higher nesting success (Slagsvold 1982b), though they normally suffer larger predation rates (Møller 1990). In ground nesting birds, however, nesting success should rather depend on factors such as shelter from unfavourable environmental conditions and visibility (Yanes *et al.* 1995). High shrub cover probably provides a more stable, and thus more favourable, microclimate for Skylark eggs, thus increasing their potential hatching success. This strategy is not found, however, in the Short-toed Lark, in which females seem to make a greater investment in nest insulation while selecting shrub cover patches similar in size to those used by the Skylark. In the case of the Short-toed Lark, nest edge thickness, inner diameter and cup depth vary between years. The latter measure is also influenced by geographical orientation. Short-toed Lark nests are more elaborate, and in relation to female weight, larger and heavier than those of Skylark. Consequently, Short-toed Lark females seem to make a comparatively larger investment in nest construction than Skylark females, and therefore the former species can be expected to better adjust nest elaboration to each year's environmental conditions (e.g. Møller, 1987). Additionally, those Short-toed Lark nests receiving a lower amount of solar radiation as a result of their location and orientation are deeper and, therefore, better sheltered from cold in the short periods during which females leave their nests to feed. Since there is considerable variation in nest structure among lark species (De Juana *et*

al. 2004), and provided that Skylark and Short-toed Lark belong to different genera, the different specific nest building strategies found in our study area are possibly a general rule based on phylogenetic differences.

Conclusion

The investments of time and energy in incubation and chick rearing has been considered, along with predation, as key selection pressures in the evolution of nesting strategies in birds (Hansell 2000). Surprisingly, however, the seasonal variation of energy investments in nest building has been often neglected. Our results support thermal insulation as the main factor determining nest size and structure in two open cup, ground nesters, the Skylark and Short-toed Lark, suggesting that phylogenetically closely related species may use different parental investment strategies for nest building during the breeding season, and may be helpful in the design of future experimental studies aimed at determining the exact contribution of environmental conditions and accumulated reproductive effort.

ACKNOWLEDGEMENTS

We are thankful to P.F. Donald and two anonymous referees for their valuable comments on previous versions of the manuscript. We are also grateful to the shepherds and country people of Layna (Soria). This study was conducted without any official funding.

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SAMENVATTING

De auteurs vergelijken de bouw van nesten van Veldleeuwerik *Alauda arvensis* en Kortteenleeuwerik *Calandrella brachydactyla*, gemeten en verzameld in de periode 1991-1995 in een steppegebied in Spanje, en analyseren vervolgens de verandering van een aantal nesteigenschappen in de loop van een broedseizoen. Ze testen welk van drie verschillende hypothesen het best de variatie verklaart in nesteigenschappen, zoals gewicht van het nestmateriaal, doorsnee van het nest, dikte van de nestrand, diepte van de nestkom en hoe-

veelheid bekleding met zacht grasmateriaal. De hypothesen zijn gebaseerd op (1) thermoregulatie en verleden van ouderlijke investering, (2) nestpredatie en (3) legselgrootte. Deze hypothesen zijn in het verleden onderzocht voor holenbroeders en voor soorten die in bomen of op muren broeden, maar informatie voor grondbroedende soorten, zoals Veld- en Kortteenleeuwerik, is relatief gebrekkig. Nestgewicht en dikte van de nestrand namen af in de loop van het broedseizoen bij beide leeuwerikensoorten. De hoeveelheid zacht nestmateriaal in de nestkom nam in de nesten van de Kortteenleeuwerik eveneens af in de loop van het seizoen (Veldleeuweriken gebruiken dat soort bekleding van de nestkom niet). Nestpredatie en legselgrootte waren niet gerelateerd aan nesteigenschappen. De conclusie is dan ook dat isolatie waarschijnlijk de belangrijkste factor is die de nesteigenschappen bepaalt. In de loop van het seizoen wordt het warmer en investeren beide leeuwerikensoorten minder in de bouw van een goed geïsoleerd nest. (IT)

Received 24 June 2004, accepted 2 October 2004