

Notes on the Breeding Biology, Food and Weight of the Singing Bush-Lark *Mirafra javanica* in Northern Senegal

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Summary

Studies on the breeding and feeding biology of the Singing Bush-Lark *Mirafra javanica* were conducted during 1989 in the savannah of the NW Ferlo, northern Senegal. Average densities of singing males were 22–37 birds per 10 ha at the start of the rainy season. Singing activity decreased rapidly after the rains stopped, and most birds had left the area when the study was terminated at the beginning of October. The probability of a single egg laid producing a fledgling was calculated to be 7–13% (max. 19%); most losses were caused by predation during incubation. Grasshoppers, mainly early instars of the locally abundant *Oedaleus senegalensis*, were the main prey item present in gizzards; both in adults and in recently fledged birds they made up 87–88% of the food items tallied. Weights of males and females were not significantly different.

Résumé

Des recherches sur l'écologie de l'Alouette chanteuse *Mirafra javanica* ont été menées au cours de 1989 dans la savane au nord-ouest de Ferlo, dans le nord du Sénégal. Au début de la saison des pluies, la densité moyenne des mâles chanteurs était de 22–37 oiseaux par 10 ha. L'activité de chant décrivait rapidement après les pluies, et la plupart des oiseaux avaient quitté la zone étudiée à la fin de notre séjour, début octobre. La probabilité qu'un œuf de produire un poussin à l'envol a été calculée: elle est de 7–13% (maximum 19%). La plupart des pertes étaient occasionnées par des prédateurs au cours de l'incubation. Les sauterelles, en grande partie les larves de *Oedaleus senegalensis*, constituent l'essentiel des restes de proies fournis par les gésiers.

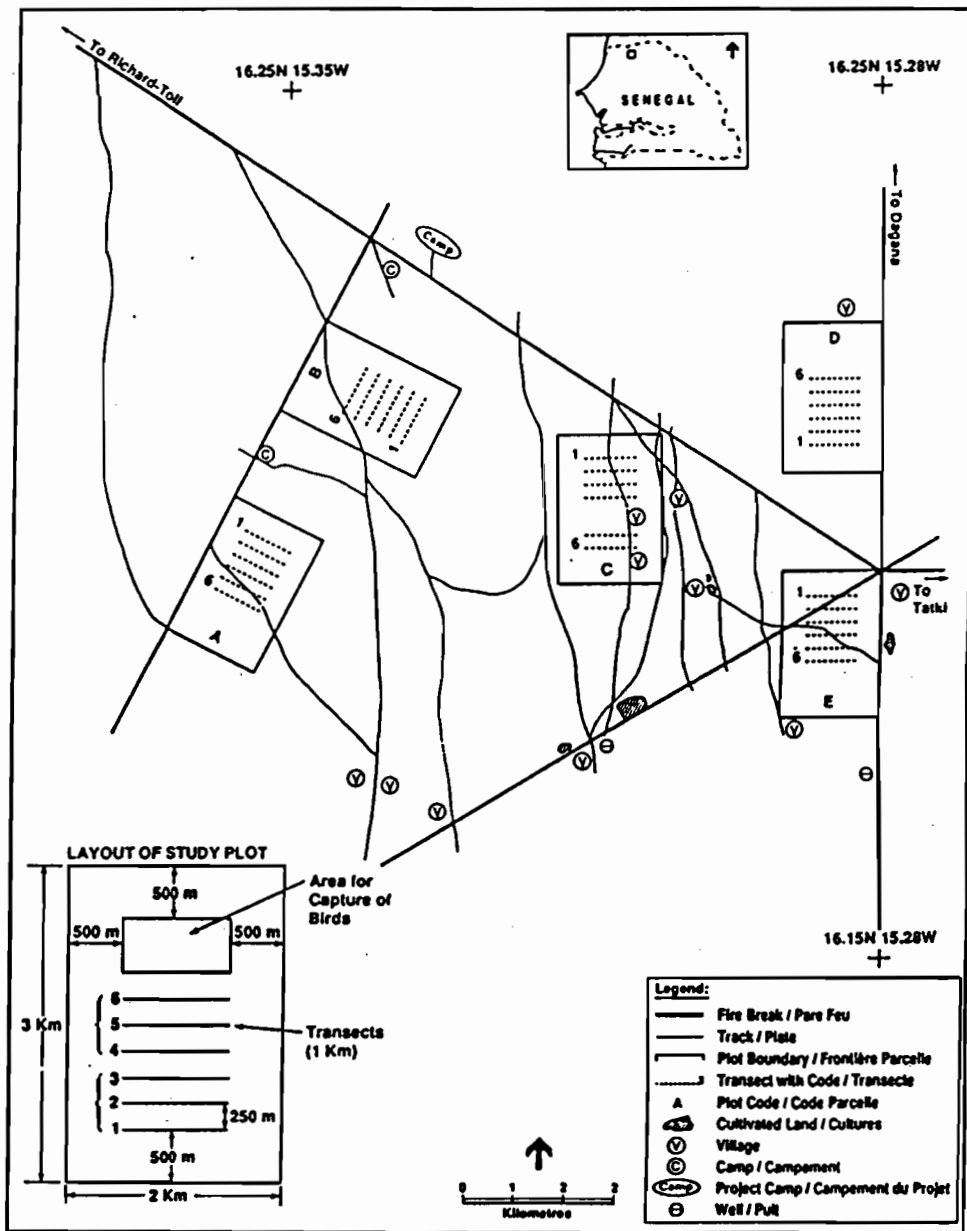


Figure 1. Layout of experimental plots for the study of environmental effects of chemical locust and grasshopper control in the savanna of northern Senegal, 10–30 km south of Richard-Toll and Dagana.

à raison de 87–88% des échantillons, tant chez les adultes que chez les jeunes volants. Aucune différence significative n'a été trouvée entre les poids des mâles et ceux des femelles.

Introduction

The Singing Bush-Lark *Mirafra javanica* is widely distributed in sub-Saharan Africa (Mackworth-Praed & Grant 1970), parts of the Arabian peninsula, such as Oman (Gallagher & Woodcock 1980), and the former North Yemen (Brooks *et al.* 1987). It also occurs in large areas of S and SE Asia (Ali & Ripley 1987), and in Indonesia (Mackinnon 1988) and Australia (Blakers *et al.* 1984).

In Africa, at least a part of the population is migratory, moving north with the Inter-Tropical Convergence Zone (ITCZ) to breed in the rains (Elgood 1981, Lamarche 1987, Lewis & Pomeroy 1989), but movements are not yet fully understood. The main breeding grounds appear to be in the Sahel zone where average annual (summer) rainfall is in the range of 200–400 mm. Resident populations may occur in parts of Sudan (Nikolaus 1987) and Senegal (Morel 1968). However, in a later study, Morel & Morel (1972) considered the status in Senegal to be uncertain. Despite its wide distribution, little appears to have been published on this species' biology.

The present study was part of investigations on the ecological impact of Desert Locust *Schistocerca gregaria* control, under experimental conditions, in northern Senegal (Everts 1990). The Singing Bush-Lark was selected as a potential indicator for side-effects of pesticide use in savanna habitat: they were abundant, widely distributed, breeding in the area, feeding on epigeal arthropods, and likely to be exposed to pesticides used for locust control.

The impact of the insecticides tested (chlorpyrifos and fenitrothion) on the numbers and food habits of birds was presented by Keith & Mullié (1990). In this paper we report more fully on the breeding and feeding biology of Singing Bush-Lark under natural conditions. Unless otherwise stated, all information is based on observations made in areas either not treated, or before they were treated with pesticides, i.e. before 5 Sep 1989.

Study Area

Plots and treatments

A large area (400 km²), some 15 km south of the Senegal River near Richard-Toll and Dagana, in the NW Ferlo, Senegal, was selected in late June 1989 for study of the effects of locust insecticides on terrestrial organisms (Fig. 1). Five, 2 x 3 km study plots, separated by at least 2 km from each other, were established within this study area to evaluate effects of five individual treatments. These consisted of fenitrothion at 485 g/ha (Plot A; recommended rate for Desert Locust control is 500 g/ha),

fenitrothion at 825 g/ha (Plot B), an untreated control (Plot C), chlorpyrifos at 270 g/ha (Plot D; recommended rate for Desert Locust control is 240 g/ha), and chlorpyrifos at 387 g/ha (Plot E) (Courshee 1990). Insecticides were aerially applied to plots in Ultra Low Volume (ULV; less than 5 l/ha) formulations between 5 and 12 September (Courshee 1990).

Vegetation

The semi-arid thornbush savanna of the northern Sahel is characterised by short trees, bushes, and annual grasses, such as *Aristida* spp., *Cenchrus biflorus*, and *Schoenefeldia gracilis* and common dominant herbs such as *Zornia glochidiata* and *Cassia* spp. In the northern Ferlo of Senegal, this vegetation has been termed Mimosaceae thorn scrub (Le Houérou 1989).

Counts on 4–10 ha along a representative transect (see Methods) within each of our five study plots indicated *Boscia senegalensis*, *Balanites aegyptiaca*, and *Acacia* spp. (including *A. senegal*, *A. tortilis*, and *A. seyal*) made up 97% of the trees present. Total tree density ranged from 51 to 84 trees per ha; tree density and species richness was highest in plot A. Of trees counted, 57% were shorter than 2.5 m in height. Baobabs *Adansonia digitata* were widely but thinly distributed and occurred on all study plots (estimated density, 5–10 trees per 1,000 ha).

Large herds of cattle, goats, and sheep grazed the study area. These animals belonged to local villagers and to semi-nomadic Peulh herdsmen and nomadic Mauritians who use the area each year during the rainy season.

There were numerous shallow depressions scattered throughout the study area, ranging from 0.25 to 1 ha or more in size. Water and sediments tended to drain into depressions during the short, intense rain-storms that are typical for the area. The higher soil moisture in depressions supported a greater diversity and biomass of vegetation and usually twice the number of trees as in the surrounding savanna (Bille & Poupon 1972). After rains began, annual and perennial herbs in depressions responded immediately and grew tall and dense, in striking contrast to the shorter grasses in the savanna.

Rainfall

Large local differences in rainfall were often observed, even over distances of only a few km. This is illustrated by rainfall data from 16 stations in the sugarcane plantation of the Compagnie Sucrière Sénégalaise, immediately north of our study area, where total rainfall for the rainy season (June–October) ranged from 183.5 to 313.9 mm (average 235.5 mm, $N = 16$).

Long-term rainfall in the region has averaged 319 ± 39 mm (Morel & Morel 1980). Thus, 1989 had slightly less than average precipitation, but was the second year with good rains, after drought from 1983 to 1987.

Methods

Bird counts on transects

Six 1-km transects were established 250 m apart in each of the five study plots (Fig. 1). Along each transect, a tree or shrub was marked with white paint every 100 m. Bird counts were taken on most transects and plots each week between 24 July and 7 October (Table 1).

Plots were visited in about the same sequence each week. During counts on a plot, each of two observers recorded birds on three transects; one observer visited transects 1–3, the other transects 4–6 (Fig. 1). counts were begun at 07.00 and completed at about 10.00 each day. During 50 min. on each transect, all birds heard or seen within 50 m of the transect were tallied. A constant pace was maintained by covering each 100 m of the transect in 5 min. On the three transects counted by the first author, singing males of the Singing Bush-Lark were noted separately for each 100-m stretch; calculations of densities presented in this paper are based on these counts only.

Densities calculated from bird counts can severely underestimate the number of breeding pairs actually present because only a part of the breeding population is detected at each visit (e.g. Ralph & Scott 1981, Hustings *et al.* 1985). Therefore, average maximum densities of breeding pairs on each of our plots, assuming that each singing male represented a breeding pair, were calculated by using maximum numbers of singing males recorded along each 100 m stretch prior to the start of spraying in week 7, adding the ten maximum values per transect of 1 km (10 ha), and averaging totals for the three transects per plot on which such data were obtained.

Evaluation of nesting performance

Singing Bush-Larks bred throughout the study area during the period of our investigations. Singing males were one of the most common birds seen on transects as they hovered above breeding territories and nests located within grasslands. Nests were found during counts on transects and during searches conducted to discover additional nests. To reduce nest detection by predators, we did not approach closer than 1 m while marking nests with stakes and checking them to determine the number of eggs, young, and fledglings.

Additional information on the breeding cycle was gathered when possible. Complete records on the whole breeding cycle could be gathered for only a few nests. Therefore, the Mayfield method (Mayfield 1961) was employed to calculate the success of nests recorded during only part of the breeding cycle.

Specimen handling

For ecotoxicological studies, some larks were trapped with mist nets or shot with a 4.5 mm airgun. Birds were collected in plots treated with insecticides and, for comparison, in areas not treated (control areas). Weights of live or freshly dead specimens were taken using spring scales with a precision of 0.3% and rounded to the nearest 0.5 g. During dissection birds were sexed and aged. The size of gonads, and other

information on breeding condition, including presence of a brood patch, was noted. The gizzard was removed, and the contents or the complete gizzard were stored in ethanol (96%). Information on the amount of food was noted and gizzards that were completely empty were discarded.

Voucher specimens were labelled and stored as flat skins or preserved in 96% ethanol for deposition in the Field Museum of Natural History, Chicago, U.S.A. In the museum, tentative identifications were verified, and juveniles were determined by the presence of a bursa fabricii.

Gizzard contents analysis

Gizzard contents were identified to Order using a 7–40x binocular microscope; often particular remains were used for identification and calculating the number of prey items present (e.g. Orthoptera jaws and Coleoptera head-parts). Remains of some taxa, such as *Oedaleus senegalensis*, could be identified to the species level. The presence of grit was also noted.

Results

Breeding biology

Densities:— Average densities of singing males, which we assume to represent the number of breeding pairs, were greatest in July and August, when they were in the range of 22–37 singing males per 10 ha (Table 1).

In the second half of September singing activity decreased rapidly in all plots, either treated or control, and in the first week of October only one un-paired male still sang. The treatments, particularly by fenitrothion, significantly affected Bush-Lark numbers on transects (Keith & Mullié 1990).

Nesting performance:— Twenty-eight lark nests were located during searches. All had the entrance facing a northerly direction, between NW and NE, often under grasses that were depressed by the wind in the same direction. Information on lark nests was gathered in unsprayed areas or in plots to be treated, before the start of the actual spraying programme. However, one nest containing 4 nestlings (nest 20 in Appendix 1) was found in Plot D during treatment with chlorpyrifos, just within the sprayed area. The nestlings were still alive when the nest was checked again after five days, and the information was used in the calculation of nestling survival.

The average size of complete clutches was 3.6 ($N = 10$: Appendix 1). Records for the complete nesting cycle were obtained for eight nests, designated with ² in Appendix 1. In these eight nests 26 eggs were laid of which 21 hatched and at least 11 young fledged. This suggests a nesting success of 42%. However, many nests, on which only information during a part of the breeding cycle was obtained, were less successful. Using Mayfield's (1961) method the probabilities for nest, egg, and nestling survival were calculated based on the number of days each nest was under observation

Table 1. Numbers of singing male Bush-Larks on transect counts. Maximum numbers of singing birds counted per transect on a single day are in bold. Plots other than C treated with insecticide in week 7 (A,D,E) and 8 (B) (see text for treatment details).

Transect code ¹	Max No. of different singing males ²	July		August				September				Oct
		23	30	6	13	20	27	3	10	17	24	1
		Count no.:	1	2	3	4	5	6	7	8	9	10
A4	28	25	9	16	17	20	13	NC ³	0	2	0	0
A5	19	11	11	13	8	10	10	NC	2	1	0	0
A6	19	13	17	12	2	8	4	NC	0	1	0	0
average A: 22												
B1	25	15	10	6	19	20	12	2	NC	0	0	0
B2	28	16	10	10	18	24	16	2	NC	3	1	0
B3	36	25	12	11	23	31	21	7	NC	6	0	0
average B: 30												
C4	42	41	26	25	34	33	24	17	13	15	0	0
C5	35	31	23	16	21	25	21	8	10	13	0	0
C6	35	30	21	13	20	19	26	9	9	8	0	0
average C: 37												
D1	34	18	18	27	28	18	18	NC	12	12	11	1
D2	34	13	12	29	25	18	14	NC	15	9	14	0
D3	30	18	14	22	27	19	8	NC	7	8	6	0
average D: 33												
E4	40	31	26	20	32	22	26	NC	3	15	9	0
E5	33	25	19	17	23	13	18	NC	3	6	12	0
E6	32	27	23	19	23	15	15	NC	1	5	7	0
average E: 35												

¹See Figure 1

²Based on birds counted separately per 100 m of transect; see text for explanation

³NC = No count due to spraying programme

(exposure), producing a probability of a single egg producing a fledgling of 7–13% (Appendix 1). Even when the most optimistic figures are used, and it is assumed that nests in which no eggs were detected were not used for laying, the probability of

fledging was only 19%. It is not known whether our activities, despite our precautions, contributed to this low breeding success.

The overall figure for nesting success is broken down as follows (details in Appendix 1). The probability of nest survival during the incubation period was 16–24% (4 nests destroyed by predators; 2 nests deserted; in 5 new nests, no eggs detected despite the observation of birds on the nests). The probability of nest survival during the nestling period was calculated to be 53–59%, with 3–5 nests destroyed by predators. Egg survival within a surviving nest was 94–100%, and nestling survival appeared to be 92–93%.

Table 2. Gizzard contents of Singing Bush-Larks in areas not treated with insecticides. Data are total number of items in all gizzards and (in brackets) percentage occurrence of items in contents.

	n	Grass-hoppers (larvae)	Wind-scorpions	beetles	caterpillars	seeds	grit
ad	14	67 (88.1)		5 (6.6)		4 (5.3)	
juv	3	40 (87.0)	1 (2.2)	3 (6.5)	2 (4.3)		10 (-)

Gizzard contents

The analysis of Singing Bush-Lark gizzard contents, based on numbers of food items, is shown in Table 2. It should be noted that using numbers of food items as a basis for determining food habits tends to bias results in favour of the small, numerous items. There were no great differences between adults and fledglings. Grasshoppers, predominantly early instars of *Oedaleus senegalensis*, were the main prey item present in the gizzards. All fledglings but no adults had grit in their gizzard.

Body weights

There were no significant differences in weights of adult birds from each of the five plots (4 treated, 1 control; single classification ANOVA). Therefore, all adult weights, from both treated and control areas, but separated for sex, were combined to calculate average adult weights. Weights of adult males ($N = 24$, $x = 18.6 \pm \text{S.D. } 1.5$ g) and females ($N = 9$, $x = 18.8 \pm 1.4$ g), tested in a single classification ANOVA, were not significantly different from one another. A similar test for fledglings, followed by a Duncan multiple range test (SAS 1985) showed that fledgling larks from the untreated control area ($x = 17.2$; $N = 3$) were significantly heavier than fledglings from each of the treated areas, collected after treatment ($x = 13.2$; $N = 28$) ($F = 3.45$; $P = 0.0217$) (Table 3). There were no indications that birds from the untreated control areas were older than those from treated plots. However, there is evidence that weight differences were caused by poisoning of fledgling larks by the insecticides used (Keith & Mullié 1990).

Table 3. Weights of juvenile Singing Bush-Larks.

Plot	n x (\pm SD)	weight (g)	significance ¹
treated			
A	2	12.25 (0.35)	a
B	14	13.39 (1.23)	a
D	8	13.44 (2.48)	a
E	4	12.25 (2.63)	a
control			
C	3	17.17 (2.25)	b

¹Weights followed by the same letter did not show significant differences in a Duncan multiple range test.

Discussion

Our figures show that displaying male Singing Bush-Larks occurred at high densities when we commenced transect counts. Based on the assumptions given in Appendix 1, it was calculated that building of the first nest that we found was started around 11 July. Several authors have noticed the Bush-Lark's immediate response to the first significant rains of the season by commencing display flights and nest-building behaviour (Smith 1979, Morel 1981). The first significant rains of 1989, as measured near Richard-Toll, were on 27 June (average 12.5 mm) and 11 July (average 39.9 mm). However, local differences in rainfall were pronounced in the area and it is likely that we missed that actual onset of the breeding season in the general area. Rain as the principal *Zeitgeber* for breeding in Alaudidae has previously been shown for eight species of lark in the Kalahari sandveld (MacLean 1970), and for five additional species in the central Namib Desert (Willoughby 1971).

The decrease in bird numbers towards October, both in control and treated plots (Table 1), indicates that many birds had left the area, although some redistribution within the area may have been partially responsible for the decline in numbers. In one of the study plots we noticed in early October a clustering of Bush-Larks into one of the depressions where feeding conditions probably remained favourable for a longer period than in the savanna.

The average densities which we estimated (22–37 singing males per 10 ha; Table 1) are high for Alaudidae. Only Short-toed Larks *Calandrella brachydactyla*, with 20–30 pairs per 10 ha (occasionally up to 40–50) in optimum habitats, have comparable densities (Glutz von Blotzheim 1985, Cramp 1988).

The only other larks breeding in the study area were Chestnut-backed Finch-Larks *Eremopterix leucotis*, White-fronted Finch-Larks *E. nigriceps*, and rarely Kordofan Bush-Larks *Mirafra cordofanica* (Morel & Morel 1972, 1984). The finch-larks inhabit eroded or bare areas or where bush fires have destroyed the grass cover, and they breed

predominantly in the dry season. The Singing Bush-Lark, a rainy season breeder, prefers dense stands of grasses, not affected by fire (Morel & Morel 1984). We found nests only in dry stands of grasses.

All nest entrances faced between north-west and north-east. The entrances of Chestnut-backed Finch-Lark and White-fronted Finch-Lark nests in the same area faced between east and north-east (Morel & Morel 1984). Nest entrances facing predominantly between north-west and east were seen in two species of meadowlark *Sturnella magna* and *S. neglecta* in Wisconsin ((Lanyon 1957), and in the Short-toed Lark (*N*) and Crested Lark *Galerida cristata* (*N-NE*) in the Palaearctic (Glutz von Blotzheim 1985). Protection from the heat is generally considered to be the main reason.

A probability of 7–13% (or maximum 19%) for an egg to produce a fledgling is low, but not exceptionally so compared to larks breeding under arid conditions elsewhere in Africa. Eighty-two percent of all eggs laid failed to produce fledglings for seven species of lark in the Kalahari (MacLean 1970). In temperate regions of Europe the success to fledging of Skylarks *Alauda arvensis* in five different studies was 18–46% (average 33%) (Schläpfer 1988), but survival to independence in two of these studies was only 8–10% (Delius 1965, Jenny 1984). Losses were mainly due to predators. The percentage of eggs which hatched in the studies reviewed by Schläpfer (1988) was 38–71% and the survival of hatched nestlings to fledging 48–67%. In our study the hatching success was 15–24% (BxC in Appendix 1), while survival to fledging was 49–55% (DxE in Appendix 1). Appendix 1 reveals that nest survival during incubation (16–24%) can be considered as the "critical phase".

Most nests observed in our study area were in Plot C. Compared to the other plots there was much human activity (herds of cattle, goats and sheep, and two villages) and this activity probably attracted ground predators, such as Jackals *Canis aureus*, which were observed occasionally. One dropping, possibly of Jackal, collected close to a predated nest, contained the remains of a Black Bush-Robin *Cercotrichas podobe* (S.M. Goodman, pers. comm.), which shows that these predators take terrestrial foraging birds. Four large mammalian carnivores (*C. aureus*, *Felis lybica*, *Genetta genetta* and *Vulpes pallidus*) occur in the NW Ferlo in densities of 0.4–3.1 individuals per km², whereas smaller carnivores such as *Ichneumia albicauda*, *Mellivora capensis* and *Zorilla striatus* are relatively common in the region (Grenot & Le Houérou 1989). Reptiles are likely to be another important group of predators. The egg-eating snake *Dasyplectis scabra* and the monitor *Varanus exanthematicus* were both captured in the study area.

Singing Bush-Lark gizzards contained predominantly invertebrate remains. Approximately 90% of the prey items identified in the gizzard contents consisted of grasshoppers. Most were early instars of *Oedaleus senegalensis*. In the NW Ferlo this species was believed to have reached the threshold for economic damage to agriculture, and an aerial chemical treatment was performed in the areas immediately bordering our study area (Müller, pers. comm.). Only two gizzards out of 17 (11%) contained a few seeds. Gizzard contents of Bush-Larks taken in experimental plots

after spraying with chlorpyrifos and fenitrothion contained seeds in 17 out of 38 gizzards (45%) Keith & Mullié 1990), suggesting that a lack of insect prey forced them to feed on seeds.

There were no apparent differences in the selection of invertebrate prey between adults and fledglings. There was, however, a marked difference in the presence of grit in gizzards between adults and juveniles. Combining data presented here with those from the pesticide treated plots (Keith & Mullié 1990), 16 of 25 gizzards (64%) from juvenile birds contained 1–25 small stones (maximum weight 0.25 g per gizzard), while in adult birds only four out of 33 birds contained grit in the gizzard.

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Appendix 1.

Calculation of Singing Bush-Lark nesting success following Mayfield (1961).

A. Basic information on nests of Singing Bush-Lark

no. of nest	plot	no. of eggs laid	no. of nest days	no. of eggs hatched	no. of nest days	no. of young fledged	fate of nest
1 ^{1,2}	B	4	7	4	11	4	fledged successfully
2 ^{1,2}	C	2	1	2	9.5	0-2	predation (?)
3 ^{1,2}	C	4	2	4	8.5	0	predation
4 ^{1,2}	C	4	3.5	0		0	predation
5 ^{1,2}	C	3	7	3	7	0	predation/rain (?)
6	C	2	6	0		0	no complete record
7	E	2	3.5	0		0	no complete record
8 ^{1,2}	C	4	1	4	11	3	fledged successfully
9 ²	B	1	4.5	0		0	predation
10	C	1	3.5	0		0	nest desertion
11	B	0	(1-8)	0		0	no eggs laid
12	E	?		2	3.5	(0)	no complete record
13	E	?		?		?	empty, used nest
14	E	0	(1-4)	0		0	no eggs laid
15	C	0	(1-5)	0		0	no eggs laid
16	C	0	(1-5)	0		0	no eggs laid
17	C	2	3	0		0	nest desertion
18 ^{1,2}	A	4	8	4	11	4	fledged successfully
19	C	0	(1)	0		0	no eggs laid
20 ³	D	(4)		4	5	?	no complete record
21	D	(0)		?		?	no complete record
22	D	?		?		?	empty, used nest
23	S	?		?		?	empty, used nest
24	D	?		?		?	empty, used nest
25 ¹	D	3		2-3		?	no complete record
26	E	(3)		3		?	no complete record
27 ¹	C	4	4	3	3	?	no complete record
28 ¹	D	4		?		?	no complete record
total			54 (59-77)		69.5		

¹Complete clutch, used for calculation of clutch size²Clutch used for calculation of nesting success (see text)³Nest with 4 nestlings found just within sprayed area, after treatment with chlorpyrifos (see text).⁴Outside plot boundary, in unsprayed area

B. Probability of nest survival during incubation

1. If nests in which no eggs were detected are omitted from calculations:

Mortality rate: 6 nests lost/54 nest days observation time = 0.111

$$1 - 0.111 = 0.888^{13} = 0.216 \text{ (if incubation time is 13 days as in Short-toed Lark).}$$

$$1 - 0.111 = 0.888^{10} = 0.308 \text{ (if incubation time is 10 days as calculated from data in Morel (1981)).}$$

2. If nests in which no eggs were detected existed only one day with eggs:

Mortality rate: 11 nests lost/59 nest days observation time = 0.186

$$1 - 0.186 = 0.814^{13} = 0.069$$

$$1 - 0.186 = 0.814^{10} = 0.128$$

3. If nests in which no eggs were detected existed the number of days between two subsequent controls minus one:

Mortality rate: 11 nests lost/77 nest days observation time = 0.143

$$1 - 0.143 = 0.857^{13} = 0.135$$

$$1 - 0.143 = 0.857^{10} = 0.214$$

Based on the figures and assumptions presented under 1-3, the probability of nest survival during the incubation period can be calculated to be between 0.16 (incubation time of 10 days) and 0.24 (incubation time of 13 days).

C. Probability of egg survival during incubation

The egg survival is approximately equivalent to nest survival and ranges from 33/35 = 0.94 to 21/21 = 1.00.

D. Probability of nest survival during nestling period

4. 3 nests lost/69.5 nest days observation time = 0.043

$$1 - 0.043 = 0.957^{11} = 0.615 \text{ (if nestling time is 11 days)}$$

$$1 - 0.043 = 0.957^9 = 0.673 \text{ (if nestling time is 9 days)}$$

5. 5 nests lost/69.5 nest days observation time = 0.072

$$1 - 0.072 = 0.928^{11} = 0.439$$

$$1 - 0.072 = 0.928^9 = 0.510$$

Based on the figures and assumptions presented under 4 and 5, the probability of nest survival during the nestling period is between 0.53 (if nestling time is 11 days) and 0.59 (if nestling period is 9 days).

E. Probability of nestling survival

Nestling survival ranged from 11 fledged/12 hatched = 0.92 to 13 fledged/14 hatched = 0.93.

The nesting success can be calculated as follows:

minimum: $0.16 \times 0.94 \times 0.53 \times 0.92 = 0.07$

maximum: $0.24 \times 1.00 \times 0.59 \times 0.93 = 0.13$

(maximum reliable estimate (product of bold figures under B-E): $0.308 \times 1.00 \times 0.673 \times 0.93 = 0.19$)

This implies that the probability of a single egg laid producing a fledgling is only 7–13%. In other words, of every 100 eggs laid only 7–13 fledglings are produced. Even if the most optimistic figures are used, the probability is only 19%.



Spur-winged Plover—Vanneau éperonné—*Vanellus spinosus*
(Photo: P. Blasdale)