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The Behaviour of Skylarks

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Translation and Update of

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Summary

A population of individually marked skylarks was studied by J. D. D. over four breeding seasons in Ravenglass, Cumbria, England. The spring *arrival* of the skylarks in the study area is described. The females arrived one month after the males. Their precise arrival dates were weather-dependant. During the breeding season the skylark pairs restricted their activity to *territories* whose characteristics are described. The relationship between territory size and population density is discussed. The skylarks' tendency to return to previous territories is quantitatively described. The one-year-old skylarks tended to settle in the neighbourhood of their birthplace, but about 10% of them remained without territories. Three types of *song* are described: the aerial song, uttered while circling over the territory, the ground song, given in a number of postures, and the pursuit song. The yearly cycle of song is discussed. The frequency and length of the aerial song of the males was greater during pair formation and during the incubation by the females; length and frequency did not vary by time of day. It is probable that the frequency of ground song showed peaks in the morning and in the evening. Weather affected song production. The relationship between the duration of aerial song bouts and the pauses between them is described. The females only sang occasionally during the pairing and the nestbuilding phase.

The skylarks had a number of *agonistic postures* and these were mainly used in territorial fights. Those that are predominantly aggressive were partially ritualized, those associated with a high escape tendency less so. The fights did not lead to serious injuries. The tendency to attack and to flee was largely determined by the proximity of the own territory. The agonistic behaviour fits in with Moynihan's (1955) motivation scheme if an additional dimension is added, that is, the tendency to fly. The males were involved in about four times as many fights as the females. Both sexes tended to attack birds of their own sex preferentially. The skylarks only very occasionally engaged in interspecific fights, although their territories usually overlapped with those of other songbirds. But when *interspecific fights* did occur, the skylark behaviour was similar to that shown in intraspecific fights. Birds of prey flying overhead caused the skylarks to freeze or to crouch, but some males in song flight only climbed higher. Only birds incubating or caring for young reacted to crows approaching the nest while they foraged. Predatory mammals and sitting/perched birds of prey were mobbed communally by the skylarks. Incubating or brooding females showed distraction displays.

Pair formation, which took place during the first 10 days after the arrival of the females, is described. It consisted mainly of the females settling in the territories of the males. The apparent loyalty to a mate mainly seemed to depend on the yearly return to the same territory. Monogamy was usual. Skylarks without a territory remained unpaired but they sometimes paired up later in the season with widowed males. The males showed a variety of courtship displays towards the females, whereas the females had only one, the copulation-soliciting posture. With the exception of the fluffed posture, all courtship displays of the males were predominantly shown to their mates. The courtship activity of the males varied with the time of day and was heightened during pair formation and the nestbuilding phase. There was a positive correlation between courtship frequency and agonistic activity. The copulation-soliciting posture of the females was strictly linked to the nestbuilding. Between the members of a pair there was no dominance relationship. Amongst other things, the closeness of the females and the time of day influenced the crest raising of the males. *Nests* were only built by the females and occurred mostly in the morning. By means of a series of temporally linked patterns, the females deepened natural hollows and lined them with grass. The building of the first nest of the season showed a different temporal pattern from that of the following nests. Nest material preference changed during the course of nestbuilding. I describe a characteristic behaviour shown by the males while the females were nestbuilding. *Oviposition* took place in the early morning at 24-hourly intervals. The average clutch size was 3.6 eggs. Each season a female laid an average of 2.7 clutches, the clutch size changing in the course of the season. Each female had a typical clutch size range. The laying date of the first clutch of the season depended on the air temperature. The females of a group tended to lay in the same order from year to year. Young females laid later than old ones. The laying date of later clutches depended on the fate of earlier broods. *Incubation*, which was confined to the females, started after the laying of the penultimate egg and lasted 11 days. Incubation bouts and pauses showed daily fluctuations. The former were negatively, and the latter positively correlated with air temperature. The incubation rhythm changed as the season advanced, and the incubation performance improved in the course of the incubation phase of any one clutch. During incubation the females possessed well developed brood patches and showed egg retrieval behaviour. I describe the behaviour of incubating females and analyse quantitative relationships with the incubation rhythm.

The *young* hatched synchronously and unaided by the females. The eggshells were carried away by the parents. I describe experiments in which the stimuli eliciting the eggshell removal were investigated. At hatching the incubation behaviour of the females changed suddenly to brooding behaviour. Both the males and females showed a rapid increase in the feeding activities they had already been showing during the late incubation phase and started to remove the chicks' faeces. The covering performance had a morning and an evening maximum and decreased with the increasing age of the young, while the feeding rate increased. The amount of food and the size of the prey brought was adapted to the age of the young. I report on the food gathering technique of the parents and the food-begging behaviour of the young. Optical and acoustical stimuli evoked gaping. The females' share of feeding and faeces removal was greater than that of the males. At the beginning, faeces were eaten, later they were carried away. When the young were 8 days old, they left the nest. Normally the males took up an increasing share in the care of the young from the time they left the nest until they became independent a month later. The young moved over a large area and their begging call helped the parents to locate them. When the young were about 14 days old they started to fly. In July, the skylarks began to *flock*, merely keeping up short inter-individual distances and the pair bonds breaking up. The flocks left the study area in August, returning the following spring. Finally, I survey the different songs and calls of skylarks before ending with an outlook on the need for conversation efforts.

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Introduction

The precursor paper in German (J. D. Delius, 1963) was one partial result of 15 months of field work that I carried out in 1958–1961 under the supervision of Prof. Niko Tinbergen, Oxford University. Its aim was broadly conceived: collecting materials for a biology of the skylark, *Alauda arvensis*, especially their behaviour. The choice of the subject was more or less coincidental; however, ground-nesting songbirds had been largely neglected in similar studies until then. Results on the population dynamics and the non-reproductive behaviour of skylarks were not considered in this paper as they were separately treated in two other papers (Delius, 1965, 1969). The immediate aim was to create a comprehensive inventory of their behaviour. At some points I tried to gain insights into the behavioural structure with statistical methods. Comparative remarks were largely limited to a few other lark species; those to a wider range of species were mainly omitted to avoid a too cumbersome publication. The paper was originally written in German because it first served as a doctoral thesis presented to the Faculty of Biology at the University of Göttingen, Germany (a PhD without a preceding B.Sc. was not feasible at Oxford, but at the time, it was quite usual at universities in Germany, where I had previously studied). This English text is a translation of a reprint of the German publication (Delius, 1963) that I had annotated by hand over the years. It was prepared because of the relatively minor attention that the German original has received. Please consult the original (full text available at http://nbn-resolving.de/urn:nbn:de:bsz:352-205917) if you have any doubt about the precision of the translation.

We have not translated the original figures. Where the labels are in German (printed green in brackets), we offer suitable English translations in the corresponding captions. The translation was prepared in 2020 by J. D. D., assisted by an automatic translation program, and it was revised and formatted by J. A. M. Delius in 2021. It has been updated at several points with information taken from the more recent skylark literature. Newer behavioural data from the books by Pätzold (1983), *Die Feldlerche,* and Donald (2004), *The Skylark*, are reported too whenever we felt that this usefully supplements the earlier account. However, note that both books are markedly more ecologically oriented than my own paper, which mainly addresses the skylark's reproductive behaviour. Pérez Granados et al. (2016), a recent Spanish monograph on the skylark, is quoted frequently. I also recommend it to the reader more generally. Suárez, Hervás, and Herranz (2009) present a very thorough study of the eight species of Iberian larks, including the skylark. I cite this report somewhat less often but also strongly recommend it as it provides informative tables and figures on a number of relevant issues.

Location and methods

In 1958–1961, the investigation area was a largely arbitrarily delimited patch of coastal dunes of approximately 25 ha within the Drigg Dunes and Gullery, a nature reserve then better known as Ravenglass Gullery, located at 54° 21'15" North and 30 25'05" West at Ravenglass, Cumbria, in England (Figure 1). The heavily eroded dune landscape protrudes into the Irish Sea as a peninsula. occupied by a breeding colony of about 30,000 black-headed gulls, *Larus ridibundus* in the summer months. This colony disappeared towards 1985, probably because of an increased predation by foxes, *Vulpes vulpes* (Anderson, 1990; Lowe, 1991) which began about 1960 (Kruuk, 1964). After the black-headed gulls, the skylarks, *Alauda arvensis,* were the most common breeding birds with about 250 pairs densely populating the more protected and vegetation-rich, gull-free dune valleys; the skylarks still populate the area in similar densities today (2020).

Methods. For individual identification I trapped the skylarks that settled in the observation area, either at the nest with a funnel-trap, or at poppy-seed feeding stations with a clap-trap, some of them also with a clap-trap baited with a stuffed skylark (it was fought or mated!). I took young

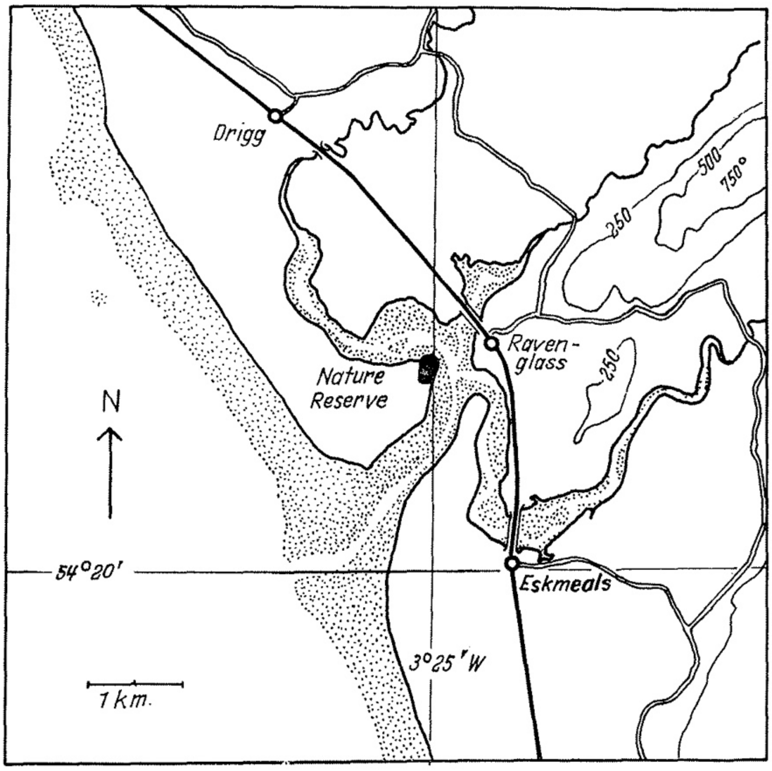

Figure 1. Location of the study area (marked in black). Approximate contour lines in feet above sea level.

larks out of the nest around their 5th day of life. To mark the adults, I employed two celluloid colour leg-rings in individually different combinations. The young received one such combination per brood; if they settled in the observation area later, they were caught again and re-ringed individually. The eight colour ring variants used proved to be sufficiently colour-fast and no ring losses were recorded within the four years. From 1959 onwards I additionally provided all birds with an official British Museum aluminium ring. In 1960 and 1961 I dyed plumage parts of some birds with alcohol-soluble pigments (Boyd, 1950/51). Furthermore, I affixed adhesive tape of different colours around the aluminium rings of brood siblings, so that they could be temporarily distinguished individually. I determined the sex of the adults by measuring their wings (average length 112 mm for males, 101 mm for females; Figure 2) and then re-checked this sexing by observing their behaviour.

It was not possible to determine the age of adult larks, one-year-olds could not be distinguished from older ones, as I found out from recaptures. For the behavioural observations I relied as far as possible on the animals marked in this way, but exceptionally also on those that were individually recognizable by natural, sometimes temporary plumage peculiarities. The only difference in behaviour between marked and unmarked larks I noticed was that the newly ringed ones passingly pecked at their legs a little more frequently. In 1958 I watched the larks 4–5 hours a day (10 March to 30 July), in 1959, 1960, and 1961 8–10 hours a day (5 March to 15 August 1959, 5 February to 30 June 1960 and 14 to 30 April 1961), practically all

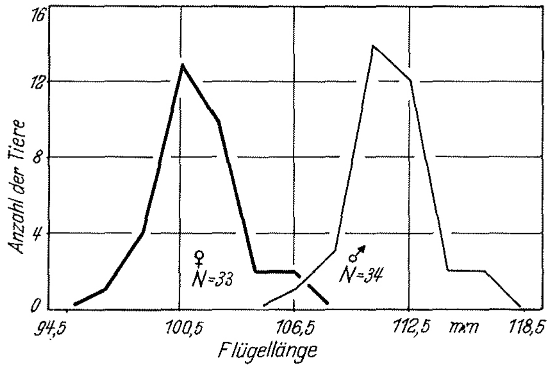

Figure 2. Wing length [Flügellänge] of male and female skylarks. Ordinate: number of birds [Anzahl der Tiere].

through 10 × 50 binoculars mounted on the articulated head of a light metal tripod. With a few exceptions, I took notes immediately. The larks quickly got used to the observer and let me approach up to 10–15 m. From elevated observation posts I could keep an eye on individual birds in the sparse vegetation for as long as I liked. For some special observations at the feeding place and for all at the nest, I used hides that were gradually moved closer by up to 3–4 m over several days. Every day I spent about half of the watching time on one of 2 or 3 preferred pairs with favourable territorial conditions; in the remaining time I controlled the other 15–20 pairs and also took notes about their behaviour. I thus saw all pairs of the observation area about every 2–3 days.

Statistical evaluations. For the evaluation of quantitative data, I mostly used non-parametric statistical methods (Siegel, 1956) in addition to the classical parametric methods (Weber, 1961). The former had the advantage that they do not impose too restrictive requirements on the data quality, are independent of the normality of the distributions and are simple to calculate. The test used and the calculated probability p is indicated everywhere; if p was greater than 0.05, it was labelled 'not significant'. Valid statistical testing requires samples independent of those that led to the hypothesis formation. If this requirement is not met, the calculated probabilities p were distorted to an uncertain extent. This is often overlooked, and in practice it is almost unavoidable. In this paper all p's that are afflicted by this are marked with an asterisk *.

Arrival

In autumn and winter, the larks did not stay in the study area (see *Swarm behaviour* chapter towards the end). Their arrival there in spring was only observed in 1961. Males and females arrived separately (Figure 3).

The mean arrival day of the males (20 February) was about 10 days earlier than that of the females since some—at least 5 of 16 males—were already there on 3 February before the start of orderly observations on 5 February, but were only properly re-recorded when returning after an intervening bad weather spell. Nevertheless, the difference in arrival between males and females (mean arrival day 3 March) is highly significant (partition at median date, chi^2, $p<0.001$). The factor causing this difference cannot be securely identified due to the limited data available; however, in addition to gender-specific thresholds for daylight hours, the temperature, which was about 3° C higher when the females arrived, could also play a role (Figure 4).

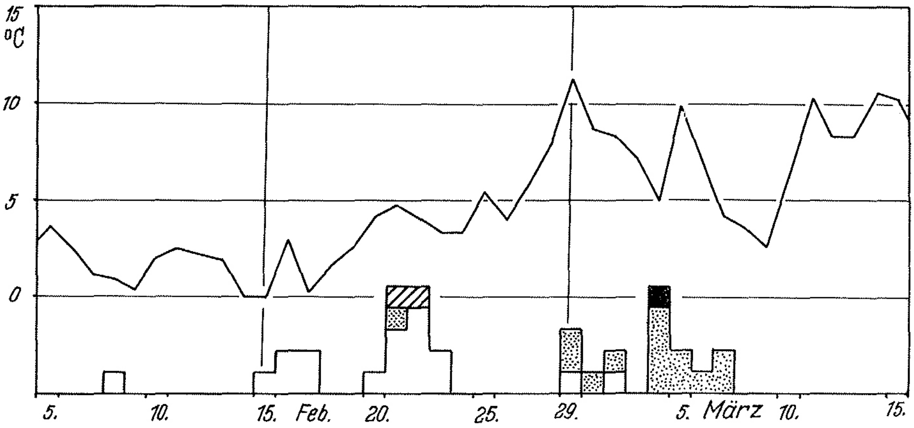

Figure 3. Arrival dates of skylarks in the observation area in 1961 [März = March]. A square represents the arrival of an individual: empty, old males; striped, one-year-old males; spotted, old females; black, one-year-old female. Upper line, air temperature (in °C).

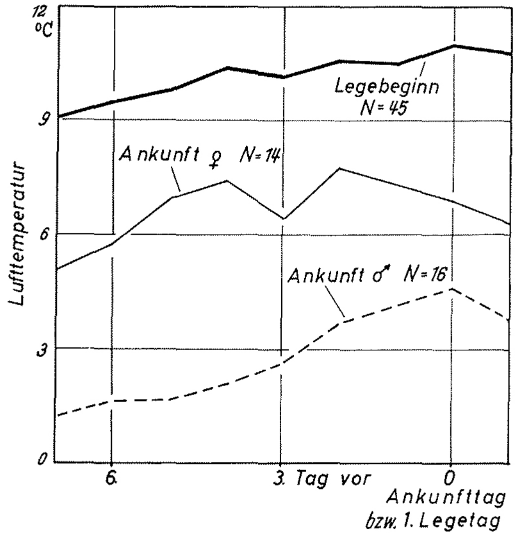

Figure 4. Average air temperatures [Lufttemperatur] around dates of arrival [Ankunfttag] and of beginning egg-laying [Legebeginn]. The different individual days of arrival or laying begin have been synchronized. *N* = number of cases.

In general, they arrived on fine days, no single weather parameter seemed to be decisive, but only a combination of them. The males appeared in groups of 10–20, mixed with those that moved on, sometimes after a short rest and upon being chased away by the local males. After a few minutes of communal foraging, some males suddenly became aggressive and showed clear-cut territorial behaviour, mostly in the mornings; around noon, or whenever the weather turned bad, they often fell back into a swarm behaviour; then they left the observation area and came back the next fine day. The arrival of the females was basically similar, but somewhat more complicated, since the occupation of the territory coincided with the pairing-up behaviour. The numbers are too small to statistically confirm any age-dependent differences in the arrival data (Figure 3). If one considers all new settlers as being one-year-olds, which has some justification, they probably arrived somewhat later: six arrived at least simultaneously, three perhaps, and three certainly later than the ringed older ones. In Russia (strongly continental climate) the skylarks generally arrive later, in southern Germany (comparatively more temperate maritime climate) earlier (Pätzold, 1983, p. 82).

Territorial behaviour

Once settled in the breeding area, about 90% of the larks of the population very soon restrict their activity to a limited individual area, not tolerating, except temporarily, any conspecifics in this territory besides their partner and their young.

Description. Compared to the area they occupied in the winter swarm by maintaining individual distances, the breeding territory of adults was larger by a factor of about 10^4 and is also pronouncedly stationary (cf. Hinde, 1961). The average size of 41 territories in the observation area was about 5,000 m^2; (the extremes were 8,000 and 2,500 m^2) (Figure 5).

However, these data should not be generalized: in a neighbouring sheep grazing area, for example, three skylark territories averaged about 15,000 m^2, and a single, isolated male skylark in the nearby Lake District sang over an area of about 200,000 square meters. A territory can be considered as the area where the owners search for food, which they defend against conspecific intruders and in which they sing. In the observation area all three coincided to a large extent, but in the nearby area the foraging areas were considerably smaller than the 1.5 hectares in which the territory owners sang. The same was true for the single lark, that did not experience intruders either, as it was completely isolated from neighbouring peers. The defended territory, which mostly coincides with the territory sung over, is the larger, the lower the population density, and vice versa. It is unclear which of the two variables is the cause, and which the effect: a minimum size of the territory that cannot be undercut probably limits the population densities upwards (Huxley, 1934; compare Pérez-Granados & López-Ibarra, 2015, on Dupont's lark, *Chersophilus duponti*). On the other hand, in the sparsely populated neighbouring areas, the sizes of the territories seemed to passively match the annual density fluctuations. The territorial boundaries were either directly indicated by minor ground irregularities or they were defined by the repeated locations of conflicts with neighbours. These were based on the fact that the larks did not include larger areas in their territories that were ecologically worthless for them, such as sand, water, or tall overgrown areas. These were by no means linked with repeated fights, but tied to ground markings over the course of the breeding season, so that they were usually not exceeded, even in the temporary absence of the corresponding neighbour. The more specific the guiding ground accidents such as dune ridges or vegetation micro-boundaries were, the better defined the territorial limits. Since all territory boundaries were ultimately primarily or secondarily tied to ground details, the layout of some territories was surprisingly constant over several years, even after intervening changes of the owning larks. Apart from that, the smaller the territory areas were, in other words, the more densely populated the area was, the more precisely and strongly defined the territory borders were.

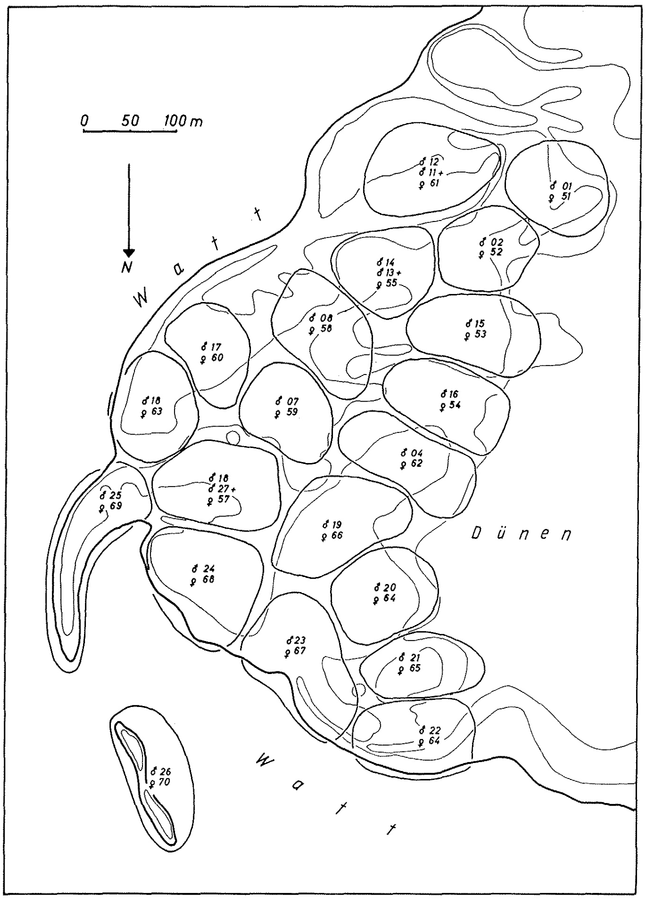

Figure 5. The skylark territories in 1959. Thick line: coast at spring tide, medium lines: territorial boundaries; thin lines: approximate contour lines in feet [Dünen = Dunes, Watt = Beach]. For territories in 1960, see Delius (1965).

Site tenacity. Breeding territories of skylarks arise through the concurrence of to two factors: the site tenacity that they exhibit and the behavioural intolerance that they exhibit against conspecifics (Tinbergen, 1957, see later *Agonistic behaviour* chapter). Of about 100 cases in which territory owners were observed over an average of three months within the breeding season, only two moved or even switched their territory: a female trapped on just laid eggs and an unpaired male. All others only shifted their territory borders slightly at most (compare Pickwell, 1931, horned lark, *Otocoris alpestris*). Five larks (3 males, 2 females) were back in their territories within a few minutes after being released upon being experimentally transported up to about 1 km away (meadows above Ravenglass village or alternatively, Drigg railway station).

Two territories outside the study area, one within a cornfield, the other within a fern stand, were already abandoned in June, about one month early, clearly because the increasingly denser and taller vegetation made them uninhabitable for larks. In general, in agriculturally used areas, the habitat of skylarks can be considerably reduced by the consequent biotope changes. The spraying of a variety of agrochemicals also seems to curtail the habitability of fields (own observations, southern Germany, 1980). In the Ravenglass study area, one territory silted up over winter and was not re-occupied afterwards.

Skylarks show a tendency to remain in the same location (territory) from one breeding season to the next; for example, Makowski (1954) found an albino skylark breeding in the same place two years in succession. Of my 101 returning skylarks, 57 (56%) settled in the previous year's territory, while the remaining 44 (44%) settled at an average distance of 130 m, at most 380 m away from their previous territory. It must be remarked that a likely extra border strip of about 1 km width around the study area was also checked for my colour-ringed birds (Figure 6). Two birds returned to their first-year territories on the third year by resettling twice, 10 out of 18 larks retained their

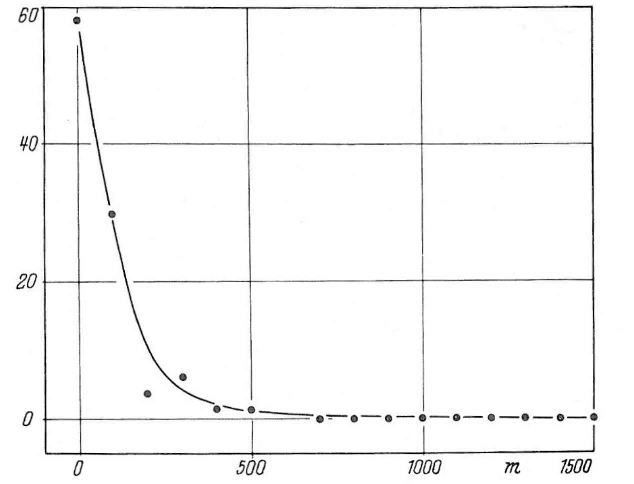

Figure 6. Skylarks' year-to-year resettlement distances (abscissa, in meters). Ordinate: number of cases.

same territory for 3 breeding seasons, 3 out of 12 for 4 seasons, and 1 out of 3 for 5 breeding seasons in succession.

Of seven more precisely observed freshly resettled male larks, four could be definitely identified as having tried to settle in the previous year's territory, but that they had found it already firmly occupied by another male. In two further cases, this was less clear. The somewhat higher resettling rate and mean distance of the females, as compared to the males, were not statistically significant.

One-year-old skylarks showed birthplace fidelity: 11 ringed as nestlings in the observation area—out of an estimated 25 possible (surviving) ones—were again seen in the observation area and its periphery; of these, 6 settled in the actual study area and 4 in its peripheral area, that is, at most 1.5 km away from their birthplace. Donald (2004, p. 92) reports ring recoveries that generally support this statement; that is even so in continental Europe where skylarks show a regular autumn/winter long-distance migration to the southwest. The location fidelity of the breeding birds did not change with their age, small trendless variations in my data were all non-significant. For information about the relationship between location fidelity and pairing fidelity, see *Pair loyalty* section in *Sexual behaviour* chapter below. Site fidelity is widespread in birds, for woodlarks, *Lulula arborea,* it has been documented by Koch (1936) and Koffan (1948/51). Donald (2004) calls attention to the fact that in skylarks breeding on agricultural land, the sex ratio may be uneven, males being at a numerical advantage (Schläpfer, 1988; Jenny, 1990; Daunicht, 1998; cf. Eraud et al., 2006).

Site fidelity involved three processes: a juvenile imprinting on (= memorizing of) the locality of hatching and growing up, a tendency to return to it, and an ability to orient themselves appropriately (Kramer, 1961). In the first months of their life, skylarks bound themselves to the place where they grew up (compare Löhrl, 1959; Mauersberger, 1957). In the second phase—their first breeding season—they settled in a circumscribed territory nearby and, if at all feasible, stuck to it in the following years, but in later breeding seasons, they could also bind themselves to new, neighbouring territories. It is uncertain by which criteria the larks came to prefer a given place in these later seasons. Apart from proximity to the place where they grew up (birthplace loyalty), ecological value, that is, the feeding and nesting possibilities it offers, the non-occupancy by same-sex larks, and the presence of a still available male partner in the case of the females, sometimes also of a female partner in the case of males, certainly played a role. In addition, general areas that were already occupied by larks were more attractive to those seeking a territory than areas that were not (that is, a certain colony-forming tendency). In the case of resettlements, a proximity to the earlier territory probably counted additionally.

An *incompatibility* expressed itself in the exchange of agonistic behaviours between the territory owners and intruders, mostly nearby neighbours: in one's own territory, on this side of the border of it, the willingness of the first to attack predominated, on the other side of the border of it, that is, mostly in a neighbouring territory, the tendency to flee was stronger in the same birds; both tendencies were about equally strong at the precise boundary of the territories. This explains the frequent and often rapid changes of roles of the attacker and the fleeing bird among the same two neighbours (Pickwell, 1931; Tinbergen, 1939b). Further factors (see *Agonistic behaviour* chapter below) can modify the dominance relationships so that some shifts in territory boundaries over time were possible.

Before pair formation, females were mostly not considered intruders by the males owning a territory, but after that, only the own female was fully tolerated. Own young were tolerated, and even occasionally defended until they became independent (see *Care of young* chapter below). For information about the defence of territories against other bird species, see *Behaviour towards other species* chapter; for information on the proportion of the two sexes' participation in territorial defence, see *Agonistic behaviour* chapter. Under certain circumstances females had own territories independently of males, e.g., the two females of a bigamous male (two cases). To a certain degree, pair formation consisted in the settlement of the female in the territory of the male, the pairing thus largely consisted in the coincidence of the territories of both partners (see *Pair formation* chapter below).

The territorial behaviour did not remain constant over the whole breeding season, but rather changed steadily. The males every now and then still fell back into the winterly swarm behaviour in February and early March, the females even did so at the beginning of April, whenever bad weather broke in. Also, later on, territorial behaviour, more especially the incompatibility between neighbouring larks, was clearly still influenced by the weather. But in the course of May, June, and July, independent of the weather, the incompatibility behaviour decreased steadily, so that in July there was hardly any evidence of territories. In mid-August, after the plumage moult, the territorial behaviour re-awakened temporarily in some of the male skylarks.

Larks without territories. As already mentioned at the beginning of this section, about 10% of the larks in the Ravenglass Dunes population remained non-territorial. They seemed to roam freely over larger areas, but mostly conspicuously alone, not in any swarm. Both sexes were represented; the apparent predominance of males may have been due to biases of observation occasioned by their more conspicuous behaviour. Why they did not have territories is uncertain: some males may not have been able to find a habitat-wise fitting foothold anywhere, some females may not have found a territory-owning partner, further males may have given up their territories because they did not find a female partner—one such case was well observed—others may have been physiologically immature. Three roaming larks began to show territorial behaviour midseason when they took over from territory-owning conspecifics that had died.

Song

Both males and female skylarks sing, but males do so much more often. With the exception of the last section in this chapter, I only address the males' singing here.

Description. In males three different types of singing could be distinguished: flight, ground, and pursuit songs. The most striking of these was the flight song performed aerially (Figure 7a). After a silent take-off, the bird rises steeply with short wing strokes and a very spread tail, if needed flying facing the wind, singing continuously. Ten flight songs (3 males) measured by rough triangulation (two observers) reached an average height of 50 m, but it is estimated that the more general average height may have been about 80 m. Pickwell (1931) mentions 150 m for the horned lark (*Octocoris alpestris*). This is followed by a phase in which the male remains at about the same height without noticeable changes in flight and song style; often he circles slowly over the territory (Howard, 1929) whereas horned larks do not keep strictly to territorial boundaries during their song flights according to Pickwell (1931). This phase usually takes up most of the time of a song flight, on average about 2.5 minutes (ranging between a few seconds up to 9 min, but see Alexander, 1941; Rollin, 1942). In strong wind, the bird exhibits the periodic wing closures typical of the songbird's bolt flight in this and the preceding phase, which then clearly clip the singing sound. Then slowly, with almost motionless, fully spread wings, the bird sails down, now weaving in extended flute-like sounds. Either the singer glides down in this way until landing, or he steeply

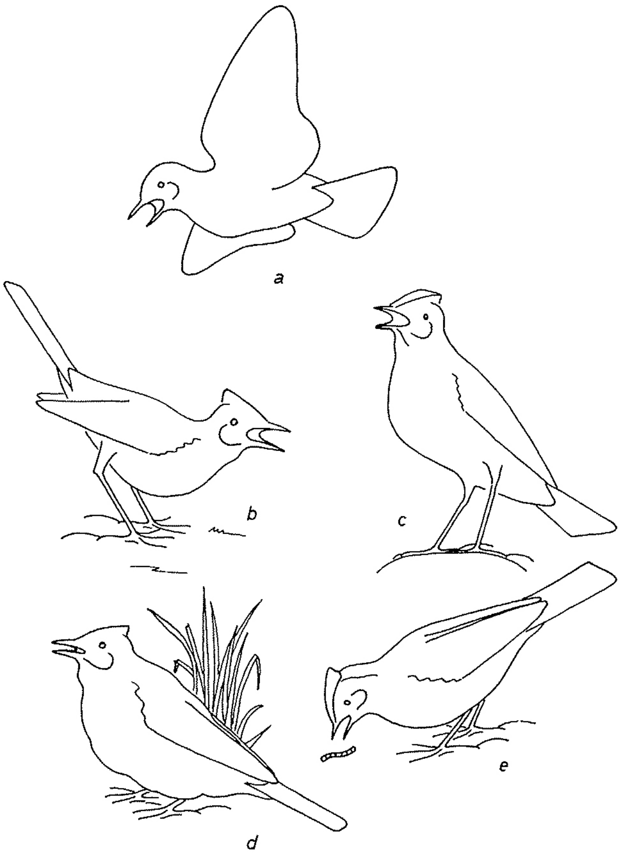

Figure 7. Singing skylarks: (a) song flight, (b) courting, (c) impressing/showing-off, (d) resting, (e) foraging.

plunges down silently from a height of 10–15 m, with half-folded wings and the body bent over (Pätzold, 1983, Fig. 10) catching himself up by spreading his wings shortly before landing. Donald (2004, p. 74) reproduces a spectrogram of a song recorded in France and Brackenbury (1978) provides a discussion of the song's structuring. The ground singing, is basically similar to the flight song acoustically, but much more variable in every respect. It is not tied to any particular posture or motions and is more interrupted, quieter and more melodious than the flight song. Calm, puffed-up males sitting on the ground sing it softly; foraging males interrupt it whenever they peck at something; courting males standing upright on a ground elevation sing it loudly with their beaks wide open and their throats rhythmically inflated so that more of the white of the gular (= throat) feathers (Pätzold, 1983, p. 37) become visible, sometimes nearly non-stop for up to 15 minutes (Figure 7b). In all cases, the throat bulges out more or less to the rhythm of the song notes' loudness. This makes the lighter feather bases visible, and the throat glows-up white. Gerss (1989a, 1989b) measured an average song length of a little more than 2 min in Germany, the daily modulation being rather weak. The very early-morning beginning of singing, before sunrise, is underlined by Donald (1983, p. 84).

The pursuit song, which sounds like a pressed, broken-up flight-song, is produced in males' wild flights chasing females (see *Sexual behaviour* chapter below), as far as the sexes of the participants could be determined; this behaviour pattern was comparatively rare. Cresswell's (1994) suggestion that an aerial pursuit song could serve the skylarks as a behaviour to deter merlins (*Falco columbarius*) seems unlikely to me.

Seasonal variations. Donald (2004, p. 75) points out the frequent imitations of wader calls by skylarks (see also Fefelov, 1997; Jenny, 1990). Flight songs were rarely heard in August and early September (moulting), but they resumed by the end of September, although not as strongly as during the breeding season. In November there was a renewed break again, which ended at the end of January (Alexander & Alexander, 1908; Rollin, 1931; Cox, 1944; Lange, 1951). The ground song was also interrupted in August, but then it restarted somewhat earlier in autumn than the flight song. Whether there is a total winter break in song is unknown. At the beginning of February, the ground song became frequent. These fluctuations are undoubtedly related to fluctuations in gonadal activity; androgens, especially testosterone, having a song-promoting effect (Eisner, 1960). The August break coincided with Marshall's (1961) gonadal regeneration phase and with the only annual moult of skylarks (Witherby, 1916). The autumn singing coincided with the so-called acceleration phase, which is temporarily suppressed by external factors in winter and resumes its course in spring. It is perhaps worth mentioning that experiments showed that the regeneration

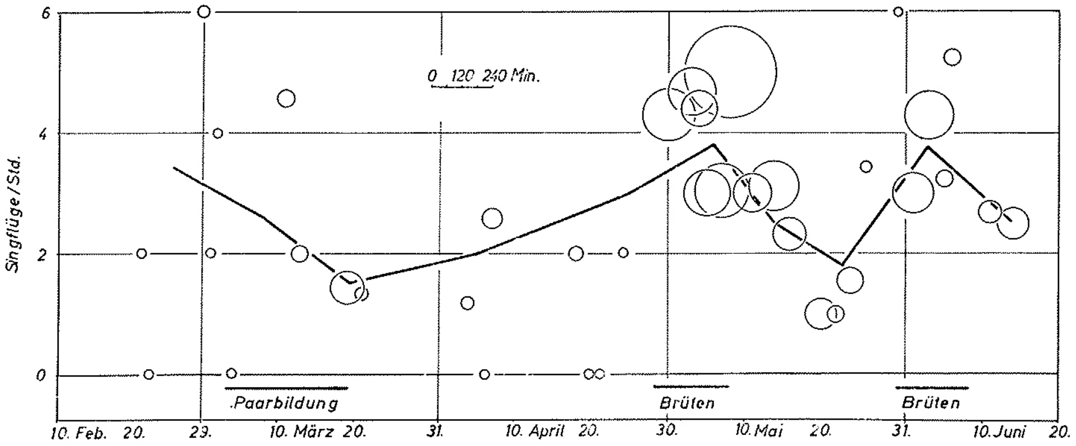

Figure 8. Song-flight frequency per hour [Singflüge/Std.] across the breeding season. The diameters of the circles indicate the duration of the various observations. Total observation time 59 hours, mainly of one male. Balanced 15-day (February–April) or 10-day (May–June) average. Pair formation [Paarbildung], brooding [Brüten].

phase of songbirds is barely influenced by outside factors, as is the onset of the acceleration phase, the further course of which can, however, be very much influenced by weather variables. This makes it understandable why the duration of the autumn singing and the onset of the spring singing in skylarks was so variable.

Even within the proper breeding season, the productivity of songs fluctuated (Cox, 1944; Clark, 1947; Lange, 1951; Koch, 1936; Pickwell, 1931). Figure 8 shows three peaks in the song-flight activity of a male: one peak before pair formation and two during egg incubation by his female. Donaldson (2004, p. 81) calls attention to Møller's (1991) assertion that the wing loading (= wing surface) of the skylark males has an effect on song-flight duration (confirmed by Nussbaumer, 1992; Lüps et al., 1993; Hedenström, 1995). The song-flight activity of the males thereby presumably promotes pair-bonding and territorial integrity at an early stage, and later, the female's incubation activity. The peak recorded before pair formation was not quite statistically significant, but the incubating phase maxima were (Table 1, Mann Whitney, $p^* < 0.001$). Obviously, the actual presence of females inhibited the males' song-flight activity and their absence encouraged it, but the rhythmicity of their song-flights was not noticeably affected by whether the female was present or absent from the territory for short periods. Pätzold (1983, p. 93) presents a song-flight duration table from Radig (1914), which broadly agrees with my data. The latter observer also documented year-to-year variations within the monthly averages, however without ascribing them to any specific cause. Too little was known about hormonal fluctuation of male birds within the breeding season at the time (cf. Eisner, 1960) to determine whether the variations in song frequency were effected via nervous or neurohumoral paths. The length of the individual songs seemed to be similarly determined as their frequency of occurrence (Table 2). According to Lange (1951), the length increases during the breeding season, but Rollin (1931) found it to be constant. The poor quantifiability of the ground song prevented me from finding out whether the same factors operated on it.

Further factors. As shown in Figure 9, the frequency and length of flight songs remained the same across the day. Lange (1951), who heard longer flight songs produced in the morning than in the afternoon, contradicts some of Rollin's (1943, 1956) data for the length of the songs, but then he measured the average minutes of song per time unit (hour), which might have confused Donald (2004, p. 87). However, since I am certain of the diurnal variation changes during the breeding season, at least for flight song frequency, these contradictions are explainable, since the data in Figure 9 only apply to males whose females were incubating from late April to early May. In February and April, the flight-song activity had a clear morning maximum. In April/May, the flight-

Table 1. Frequency of song flight before and after, or during the incubating phase.

Songs flights / 30 min	Before and after incubating phase	During incubating phase
0	9	1
1	15	13
2	9	27
3	4	12
4	0	2

Table 2. Variation of song length during the breeding season.

	Territory occupation and pairing	Incubation I First clutch	Feeding I First brood	Incubation II Second clutch	Feeding II Second brood
Average length (min)	3.4	2.4	1.3	2.1	2.0
Number	$N = 11$	$N = 84$	$N = 34$	$N = 26$	$N = 9$

Kruskal Wallis test, $p^* < 0.001$.

song activity began at about 3.30 am. When the curve in Figure 9 is suitably extended, a phase shift of approximately –1 hour against the local diurnal light cycle becomes apparent (see Aschoff & Wever, 1962).

As far as their poor quantifiability allowed a judgement, the ground songs (Figure 9c), showed a main maximum in the morning and a secondary maximum in the evening (Naumann, 1900; Lange, 1951; cf. Bourke, 1947, Horsfield's bush lark, *Mirafra javanica*). Low temperature, heavy rain, heavy clouds, fog and strong winds inhibited the singing activity, good weather generally promoted it. Sudden marked changes of weather had a phasic effect. If sunshine suddenly set in after heavy rain, the flight-song frequency increased abruptly and dropped back to normal levels after about 15 minutes. The intrusion of the observer into the station triggered flight singing by the owner male, which in turn encouraged his neighbours to sing. But for most of the singing flights, I could not identify an eliciting stimulus. Flight song was followed by an inhibition phase (Figure 10), the distribution of the singing pause lengths deviates clearly from the random exponential distribution (chi^2, $p < 0.01$; Hinde, 1958). The duration of this inhibition phase depended on the duration of the preceding song, as shown in Figure 11 ($r_s = +0.40$, $p < 0.001$). The regression curves are approximately exponential.

Conversely, no significant correlation was found between song length and the preceding pause in singing ($r_s = +0.12$, $p < 0.2$). The distribution of vocal lengths is approximately exponential (Rollin, 1942); a small but significant deviation (chi^2, $p < 0.001$) indicates self-promotion during the first 3 or 4 minutes. There is at most a slight correlation between air and ground vocal frequency ($r_s = +0.20$, $p^* > 0.05$). Although males carrying food in their beak could sing normally loudly without noticeable hindrance, the feeding and singing frequencies were probably negatively correlated

($r_s = -0.32$, $p^* < 0.05$); the regression curves being near-hyperbolical. By the way, Poulson (1996) reports that hand-reared skylark chicks taken from the nest early do not exhibit proper skylark song later as adults but rather a hodgepodge of imitations: producing a regular skylark song requires it to have been heard by the very young birds.

Singing by females. In the bird fanciers' literature there are records of singing caged females (for example, Gerber, 1954). It sounds quieter than that of males, more monotonous and quite choppy, and is much rarer than in males. All of my about 15 field observations of such song fell into the phases of territory occupation or pair formation and those of sexual readiness. In both situations the females sang both in flight and on the ground, several times also while they were soliciting the male to copulate with them.

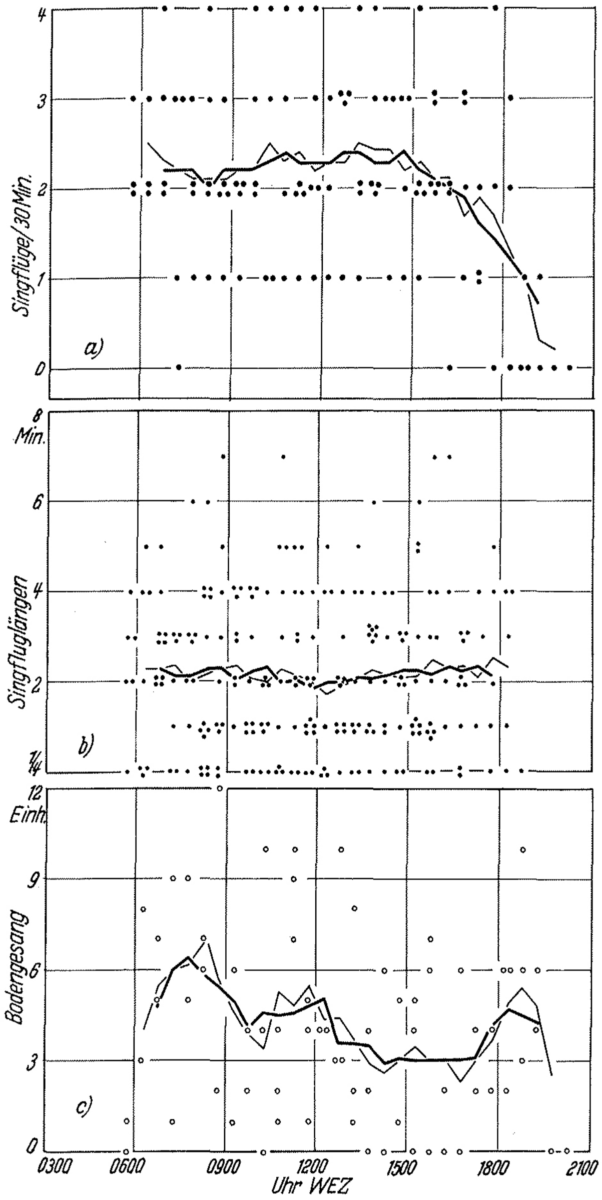

Figure 9. Singing flight frequency [Singflüge] (a), singing flight duration [Singfluglängen] (b), and ground singing [Bodengesang] (c) depending on the time of day, Greenwich Mean Time (GMT) [Uhr WEZ]. In (a) and (c) each point corresponds to a 30-minute observation, points in (b) represent the length of a flight song. (a and b) Observations on three males whose females were incubating (17 April to 8 May), (c) observation on two males, the ground song was measured in arbitrary units that record both song intensity and duration. Moving averages over 90 and 150 minutes.

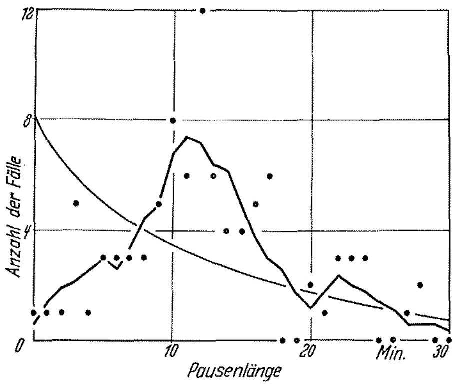

Figure 10. Pause durations between the singing flights. Solid line: calculated exponential random distribution. Moving average over 5 minutes. Ordinate: number of cases [Anzahl der Fälle], abscissa: pause durations [Pausenlänge] (in minutes).

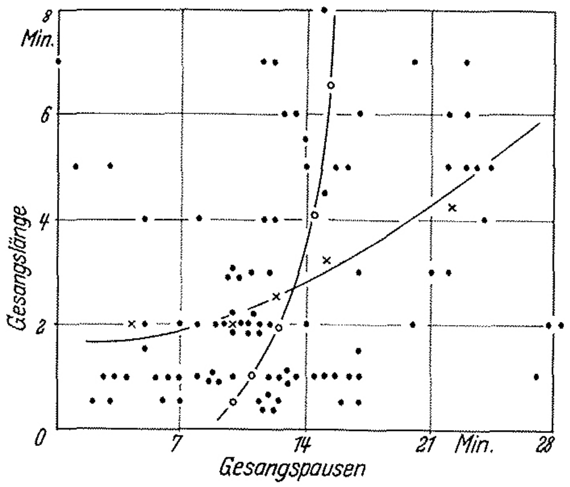

Figure 11. The length of the pauses between song flights as a function of the previous song flight durations. Ordinate: song duration [Gesangslänge] (in minutes), abscissa: song pauses [Gesangspausen] (in minutes).

Agonistic behaviour

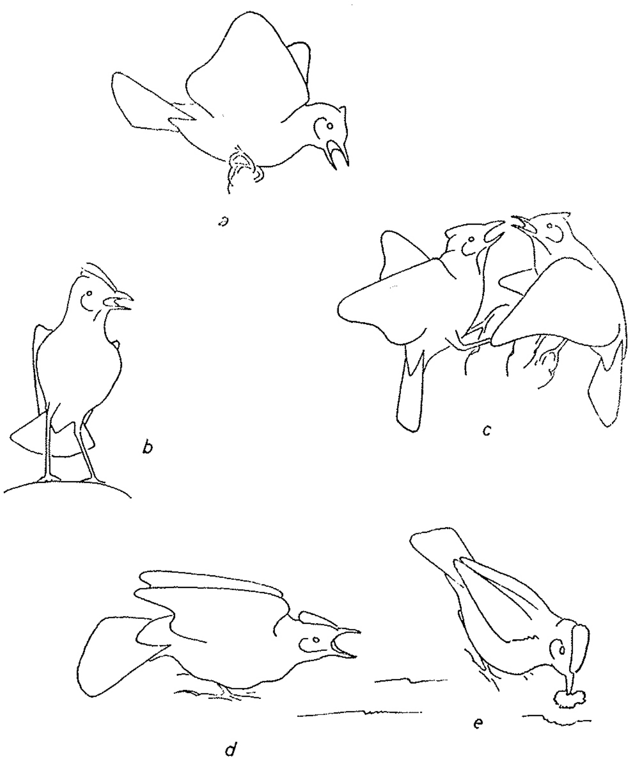

Figure 12. Agonistic behaviours: (a) threat flight, (b) impressing posture, (c) air combat, (d) threat posture, (e) grass-plucking response.

Description. The agonistic behaviours were quite variable: they appeared in very different completeness and merged from one into the other, and behavioural elements of other functional complexes were also woven in. The most frequent variants are described here and possible modifications are indicated. The mere presence of the territory owner had an intimidating effect on intruders, especially if he showed the impressing posture (Figure 12b). In this case, he mostly stood on a local elevation, upright and with puffed-up, more brightly shining breast feathers; the middle section of these feathers being lighter than their tips (Pätzold, 1983, Fig. 29). The carpal joints were slightly angled out laterally (Pätzold, 1983, Fig. 18), the wing tips somewhat drooped down, the tail was spread out, and the crest was erected. He stood like this motionless and mute, sometimes for minutes, or he uttered the attack call at intervals: a quickly repeated *tchirr,*

tchirr (Pätzold, 1983, Fig. 6, *Melanocorypha calander*). Whether a similar posture, in which the males ground-sing loudly, is homologous, remains uncertain. The impressing posture devolves in its variations from a simple securing posture—a stretching-up and visual fixating—over into a slim, fearful looking-out posture. While the mutually impressing males kept a distance of several meters, they faced each other at less than a meter when actually threatening each other (Figure 12d). They ducked down and stretched forward, slightly puffing up their plumage, lifted their crests somewhat, folded out their wings and fanned their tail in a twitching manner, usually batting it down, but sometimes up, at the same time. With their beaks wide open they emitted the hate call, a hoarse, easy to overhear expiratory *gch, gch*, or more rarely the attack call. The bird threatened its rivals frontally or broadside; the latter probably when it was ready to stop the threatening. Either the larks stayed at their place, or they ran forwards with their wings spread wide open, and wobbling them about. Donald (2004, p. 95f.) describes and illustrates this posturing. If the birds threatened an overflying lark, this posture took on an upward orientation. Incomplete forms of threatening were frequent: running forward uttering the hate call, which is reminiscent of the keeping of individual distances in winter flocks, furthermore a tail-spreading with attack calls, wing-bow angling-out alone, and other variants. In addition, there were all the transitions to the escape responses described further below. When the territorial bird flew towards an intruder, usually with attack calls, just before reaching him he switched over to a threatening flight (Figure 12a), a sequence of short, arching, upward going gliding flights with widely spread, slightly upwardly bent wings, interrupted by brief wing flutterings, reminiscent of butterfly flutters (Pätzold, 1983, Fig. 9, but on p. 84 he notes that he never observed them fully developed). Attack calls rarely accompanied this action; whether the hate call was regularly associated with these threatening flights, I could not fully ascertain.

The arc flights are probably just as intimidating: while attack-calling, the skylark flew in an arc towards the intruder and landed near him. Transitions between threatening flights and chase flights were frequent. Only the aerial combats (Figure 12c) where the two rivals faced each other on the ground and flew up at each other at the same time, involved true bodily fighting. Flying larks rarely switched over to aerial body fights directly without landing before and facing up against each other on the ground. During these aerial combats they fluttered 23 m up and down belly to belly, trying to bite, claw, and probably also to deal wing beats. Almost always they separated before landing, only 2 or 3 times (out of hundreds of encounters) did I observe them continuing the fight on the ground after landing. Only very rarely did one of the rivals fly up for the combat without the other following suit. Donald (2004, p. 89) says that the participants regularly sing during these encounters but like me, Clark (1948) apparently did not observe this. I think Donald (2004) might have confused the aerial combats between two males with the pursuit-song flights of males after females, which are in fact regularly accompanied by song. Except for occasionally losing feathers during the fights, the rivals did not seem to injure each other (Selous,1901; cf. Darling, 1950, horned lark). All in all, I observed only two permanently and two temporarily injured larks, but their wounds probably had not arisen from fights but rather from having suffered unsuccessful predation attempts or accidents. During chase flights, male (rarely female) larks chased away their rival in fast flight with repeated attack calls. All escape responses were very little ritualized and make a description unnecessary: jumping away, running away, flying way. Much as the impressing posture signalled readiness to attack, a fear-vigilant posture, that is, standing very upright with sleek feathers, indicated a readiness to flee (Pätzold, 1983, Fig. 8). Intermediate postures from an impressing, over to a simple securing posture, were common. Apart from a turning and a running-away response, larks that had just threatened but were ready to flee, showed a grass-plucking (Figure 12e) behaviour. The bird, very deliberately, plucked grass or moss and threw it away sidewards; this can, however, be reduced to a mere pecking at the ground; the equivalent motions shown during foraging and nest building are much less 'pronouncedly', or 'pointedly' executed. Tinbergen (1939b) called this behaviour 'displacement foraging' (cf. Delius, 1967, 1970). Note that Pätzold (1983) slightly differs in his description of the occurrence of this behaviour. Finally, the tail-up and more rarely the hopping response were shown several times, even by females ready to fight. Fleeing larks often interrupted their flight and crouched: they pressed themselves flat into a ground depression and kept a close eye on their rivals (which then often desisted from confronting them further). Donald (1993) is less concerned about the details of the agonistic behaviour, though he illustrates the threat posture (p. 96), but more concerned about its main consequence: the territory sizes that various studies report; I understand that he works out that the main factor is the height of the local vegetation (cf. p. 95).

Influencing factors. Different types of behaviour belonging to the one functional ensemble do not necessarily have to have a common causal basis. With the skylark's agonistic behaviours described here, however, this seems to be the case. These behaviours all occurred with marked temporal coincidence, probably because they were all reactions to a singular stimulus complex, and the frequencies of their occurrence per 30-minute period correlated consistently and positively ($r_s = +0.40$, $p < 0.05$). It is reasonable to suppose that these behaviours arise from the interaction of two variables, the readiness to flee and the readiness to attack. Each behaviour corresponds to a cluster of a set of strength ratios between the two tendencies (Moynihan, 1955). In the case of the skylarks, a third variable is whether the bird is flying or on the ground, since, as described above, the various agonistic responses appear to be shown in parallel air and ground versions. How far these three variables correspond to actual physiological causal processes could not be decided here (but see Blurton Jones, 1968). Within this schema, the grass-plucking response is fully likely to be a displacement activity. For discussion of the dependence of both types of readiness on whether the bird was inside or outside his territory, see the earlier *Site tenacity* section. The assured demeanour of an intruder could intimidate a territory owner. The intruder's willingness to attack could be enhanced by the proximity of his nest, his partner, or his young. Personal acquaintance with old neighbours inhibited the attack tendency: newcomers (3 observed cases) that settled in territories of deceased skylarks, were unusually violently attacked by neighbours, and even skylarks from more distant territories harassed these newcomers, even though they had to fly over several other territories. On the other hand, these newcomers were also particularly ready to attack, and they obviously could withstand the dominance they faced. The behaviour of one rival could obviously influence that of the other directly, without affecting the latter's attack or escape tendencies, when one rival always flew up for air combat when the other did. At most, the agonistic activity had a weak, non-significant, morning peak (Figure 13, chi^2, $p > 0.05$). During the breeding season, the frequency of the fights fluctuated (Figure 14). In this individual male, it increased from his arrival in early April and then decreased continuously. In July, hardly any fighting could be observed. The initial increase was probably due to the spring weather improvement: bad weather like rain, cold, or storm lowered males' willingness to attack.

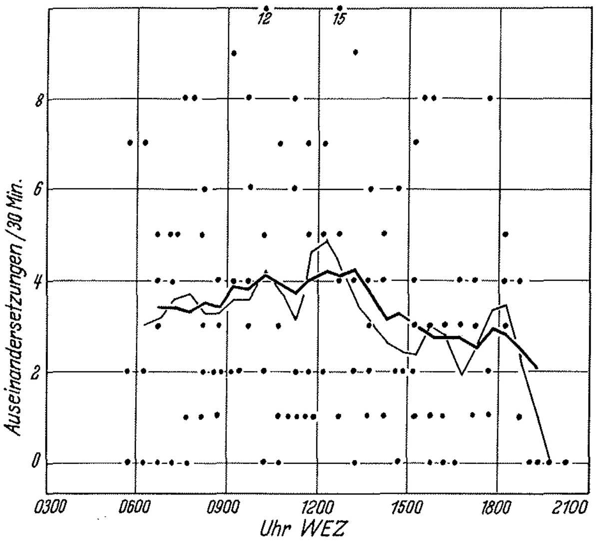

Figure 13. Frequency of agonistic encounters depending on the time of day. Threat posture, threat flight, and air combat combined. Each point represents 30 minutes of observation, 3 males. Moving averages over 90 and 150 minutes. Ordinate: agonistic encounters [Auseinandersetzungen]/30 min, Abscissa: GMT [Uhr WEZ].

Sex differences. The males were more aggression-prone than the females: over 59 observation hours, a male was involved in fights on average 4 times/hour, several

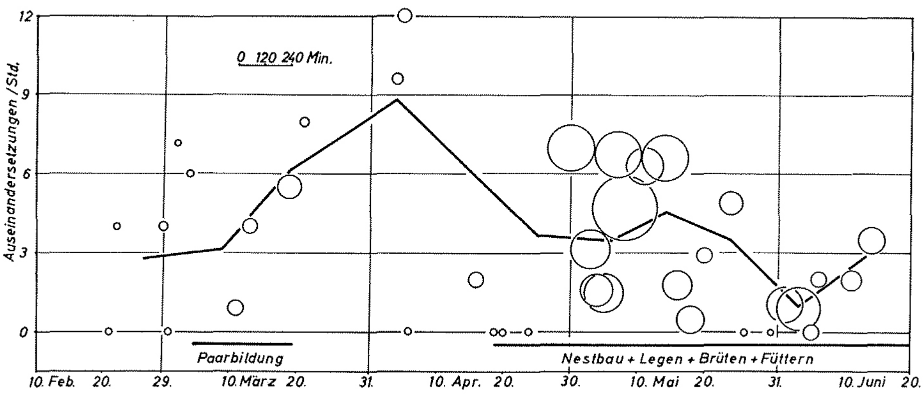

Figure 14. Frequency of agonistic encounters of during the breeding season. Threatening, threat flights, and aerial combats combined per hour. The circle diameters indicate the duration of the individual observations, total observation time 59 hours, mainly of one male. Balanced 15-day (February–April), respectively 10-day (May–June) average. Ordinate: agonistic encounters per hour [Auseinandersetzungen/Std.], Abscissa: dates (10 Feb.–20 June). Labels: pair formation [Paarbildung], nestbuilding, laying, incubating and feeding [Nestbau + Legen + Brüten + Füttern].

females in 39 similarly distributed observation hours less than once/hour. The partners of a pair did not necessarily attack every intruder, but preferentially those of their own sex. Within 21 hours one male attacked male intruders 54 times and female intruders 21 times (chi^2, $p < 0.001$). His females attacked male larks 8 times and female larks 17 times within 30 hours (Kolmogorov-Smirnov, $p < 0.05$). For females the selectivity may be lower, for males higher than the numbers reflect, because males were less likely to invade foreign territories than females. Unfortunately, I did not adequately quantify this latter difference. When females had fights with intruders, their males often stepped in for them; the opposite was rarely the case, except when males attacked other females: then their own females usually attacked these quite violently too.

Behaviour towards other species

Two kinds of alien species could be distinguished: habitat competitors and outright enemies, as well as of course, species which were neither, that is, largely indifferent.

Habitat competitors. Skylarks showed the same agonistic behaviours towards these species as towards conspecifics. Wheatears and meadow pipits also nested in the observation area: their territories completely overlapped those of skylarks. The meadow pipit, *Anthus pratensis,* was frequently attacked by the larks and regularly fled without any resistance. But often they were ignored for long periods. In any case, the pipits did not avoid the larks or their territories; even if they had just been chased away repeatedly, they seemed to seek their loose company (augmented anti-predatory vigilance?). The physically stronger northern wheatears, *Oenanthe oenanthe,* were attacked less frequently, rather, they attacked the skylarks, but again a peaceful coexistence was rather the rule. The function of this agonistic behaviour is uncertain, it might have contributed weakly to a mutual population thinning. Its motivation might be the same as for the agonistic reactions toward conspecifics: the alien birds may have represented incomplete releasing stimuli, which were only reacted to when other aggression-promoting factors were strong. Some of the attacks on meadow pipits may have been due to a redirection taking effect (Moynihan, 1955), that is, skylarks which had lost territorial fights with conspecifics then tended to attack the weaker meadow-pipits instead. Other birds that occurred, such as linnets, *Linaria cannabina*, starlings, *Sturnus vulgaris*, gulls, *Larus,* and waders, *Limicolae*, passed apparently unnoticed.

Enemies. When some of these appeared, the skylarks exhibited special behaviour. When a merlin, *Falco columbarius*, peregrine, *Falco peregrinus*, Eurasian hobby, *Falco subbuteo* (Liebe, 1893), or even a kestrel, *Falco tinnunculus,* flew over the area, skylarks wandering about on the ground, pressed themselves flat on the ground and froze motionless while they monocularly fixated the bird of prey, or else they slowly sought cover among higher vegetation (e.g., marram-grass tufts) and then ducked down. A few skylarks that were late in noticing the appearance of the bird of prey 'froze' in a ready-for-take-off posture. Several times I heard an accompanying soft-sounding warning call. After the bird of prey had disappeared, they slowly 'thawed' again. Gulls, *Larus ridibundus,* flying overhead were enough to make them freeze again (a threshold-lowering effect!). A female skylark on the ground, at which the merlin dove, flew away at the last moment with a shrill fear call; the least frightening of the falcons around was the kestrel. Flight-singing males did not interrupt their song, but only seemed to rise higher upon merlin attacks (see Pätzold, 1983, p. 69; Radford, 1986). Liebe (1893) reported a similar incident, adding that larks flying around would otherwise dive to the ground and take cover there. N. Tinbergen (personal communication) saw a flying male skylark dodge a merlin diving at him several times with own short plunging flights; they likewise dodged young gulls, which often dove playfully after them. According to Montfort (1949), a skylark fled from a goshawk, *Accipiter gentilis,* into a well; Radeck (1929) reported a skylark taking refuge from a sparrowhawk, *Accipter nisus,* among a group of people (see also Taylor, 1986, merlin). Several larks were observed mobbing a merlin gorging on a lark. Incubating or feeding larks only took notice of crows, *Corvus corone,* when they came near the larks' nest or young: they pressed themselves onto the ground and/or issued their warning calls. A cuckoo, *Cuculus canorus,* was in one instance pursued in flight by a skylark and two meadow pipits together (compare Smith & Hosking, 1955, regarding woodlarks). A red-backed shrike, *Lanius collurio,* was similarly pursued according to Homeyer (1893). Weasels, *Mustelis nivalis*, ermines, *Mustelis erminea,* and hedgehogs, *Erinaceus europaeus,* were mobbed by the skylarks: several pursued the predatory mammals together with meadow pipits and wheatears, fluttering in a swarm low over them, landing close to them and flying up again without respecting territorial boundaries, mostly silent, only occasionally emitting soft warning calls. Surprisingly, they sometimes did not react to these predatory mammals at all, certainly not because they had not seen them: was it that the skylarks judged them as not being hungry or not in a hunting mood? The skylarks fluttered at sheep, *Ovis aries,* and rabbits, *Oryctolagus cuniculus,* coming near their nests, sometimes even pecking at rabbits, but otherwise ignored them. Humans, *Homo sapiens,* caused the larks to flee or squeeze themselves on the ground, the latter being more often observed in females than in males. If one approached them at 2–3 m, they suddenly flew up. Outside the time when they had young, the larks rarely warned, mostly the males standing still and upright, emitting repeated warning calls, while their tail twitched up and down with fine strokes. When I approached females incubating eggs or brooding their young, they usually left the nest with the luring-away behaviour. Larks captured with a clap-net trap sometimes gave off a shrill fear call. Those I hand-held after trapping made sudden attempts to escape but did not peck or bite and remained silent. Dathe (1955) notes that scared skylarks can on occasion show a fright moult reaction (i.e., a generalized feather loss when nearly caught by a predator or a clap-trap closed over them).

Pair formation

In the winter swarm, there are probably no subsisting pair bonds. They must be largely formed anew at the beginning of each breeding season.

Description. When the females arrived, all eligible males already had stable territories; if these gave them up temporarily, they also no longer showed an interest in females. The females behaved differently depending on whether they had already been paired-up and had a territory in the previous year, or not. If they had had a territory at that time, they returned to it and carried on with the resident male if he was not yet paired-up, otherwise they were chased away by his meanwhile new female. In this case, the rejected females, much as the newly settling females, wandered singly, from territory to territory, that is from male to male, until she was paired with one of the territory-owning males.

The females proposed themselves by landing a few meters—typically 3.5 m—away from the male, initially seeking cover and assuming a fearful securing posture. At the latest the male approached her when she began feeding some minutes later and mostly went straight into courtship behaviour (see *Sexual behaviour* chapter below); only in 4 out of 20 such observed instances did they attack them. Nevertheless, most of the females left their territory at this stage and continued to roam about the neighbourhood males. If they stayed, they began to linger closer to the male, who courted her ever more frequently. If the female now flew away, the male flew behind her and began to chase her, thereby trying to drive her back to his territory (chase flight). If they moved out of the male's territory in the process, neighbouring males sometimes also joined in in the hunt flight. Sometimes, however, the male would turn back at the border of his territory and slowly fly back to its centre. This sometimes encouraged the female to follow him. If a female left the male in spite of everything, he would repeatedly utter the lure call during the next quarter of an hour or so. The longer a female stayed in the territory of a given male, the stronger the bond between the two became and the more likely it was that they would end up paired together. If a given female was seen together with a male for a few hours, her firm pairing with him was to be expected; if such a paired male then tried to attract further females, the first female began to show unmistakable territorial behaviour and attacked these invading females, and occasionally even intruding males, quite violently. If the partner of a pair died during the breeding season, the remaining partner usually paired up anew. Roaming, females without a territory then behaved much as described above; the aforementioned roaming males without a territory, on the other hand, seemed to pair up simply by taking over the orphaned territory including the widowed female, mostly within a day or so.

Influencing factors. Most of the roaming females were seen in the area during the mornings (16 out of 17 cases, binomial-test, $p < 0.001$); in the afternoon they usually gathered together in swarms and on occasions even left the study area. The males did not bother about such females, at the most they attacked them. Of 37 pair formations that were closely observed, 30 could be considered completed before March 15 (that is, 10 days after the average arrival of the females), and only 7 were completed later than that. Old females may have paired up somewhat earlier and faster than newly settling ones, but I am not certain about that. A similar kind of difference among males was certainly not significant. Prompt recognition of the gender of the participants played a major role in pair formation. At first sight, it was not possible for the human observer to detect differences between the sexes, but with experience one learned to tell them apart by the simultaneous appraisal of behaviour, size, plumage patterning, length of the hind toes, and other characteristics. It is not known how skylarks distinguish the sexes; as could be deduced from their behaviour, they were able to from a distance of up to 50 m. In any case, the firm pair bond required a solid individual acquaintanceship. With time, I too succeeded in recognizing individual skylarks, and the skylarks certainly did much better. As their behaviour showed, they recognized their partner optically very well at a distance of 30 m, acoustically perhaps from even further away. Artificial colouring (yellow, red) of larger feather patches that we applied to some larks for easy recognition did not seem to appreciably impair their mutual recognition.

Pair loyalty. Of 44 pairs observed over three months after pair formation, 43 remained together. The exception was a pair whose female I trap-caught on just laid eggs: thereupon she left the egg and her partner. Out of 30 pairs in one breeding season, 16 remained together in the next, all of which stayed in their previous year's territories, only one moved its boundaries slightly. In the 14 males that were not pair-loyal, both partners moved their territory in 6 cases, the females in 5 cases and the males in 3 cases. According to this, location fidelity is the crucial factor for the pair fidelity. In no single case did a previous year's pair relocate without separating, although this would have been possible in two cases where the just arrived, relevant females actually visited their still unpaired ex-male partners in their new territories. Thus, the actual pair bonds seem to play hardly any role from one year to the next; in one case however, it was observed that a female that was mated with a new male in her previous year's territory showed a rather persistent interest in her previous year's male mate that had moved to a neighbouring territory.

Polygamy. Not a single case of polyandry was detected, not even a temporary one, and only 2 cases of bigamy among 93 monogamous pairs: a mated male took over a widowed neighbouring female and her territory and soon neglected his first female so that she did not proceed to a second brood. In the following year, the male was again monogamously mated with the previously neglected female. The emergence of the other bigamy case was not closely observed. Although I obtained no evidence of outside-pair copulations in skylarks in my study, they clearly do occur according to genetic analysis of broods (Sánchez et al., 2004; Hutchinson & Griffith, 2007). These studies have shown that even the members of a single brood can be of different fathers; several show that such copulations can thus have preceded a female's laying of a single egg clutch.

Unpaired larks. All males without a territory remained unpaired. Some of these males, however, must have been ready for pairing up: two widowed females including their territories were taken over by such males within a few days in mid-breeding-season. A territory-owning male that had been abandoned by its female (see above) remained partner-less for 2 months and then abandoned its territory; the following year it was normally paired up with a different female. A small proportion of females also remained unpaired, some probably because they did not find any unpaired territory owners as they arrived late, others perhaps because of some physiological immaturity. In any case, one such female was able to successfully replace a paired female that perished midseason.

Sexual behaviour

All behaviours shown between the sexes that are described here were largely restricted to the partners of the pair.

Pérez-Granadoz et al. (2016, p. 21), who apparently followed Clark (1948) on this, recognized four types of courting, with the pursuit flights being essential. Another element was the hopping performance of the males that Pérez-Granadoz et al. regarded as part of the pair formation process, but also occurred before copulation according to them: Here the male positioned himself in front of the female with his crest raised and his body stretched upwards, and performed 5–10 vertical jumps of 1–2 cm height. A further kind of courting often occurred after these jumps, in which the male let the tips of his wings fall and displayed his raised tail to the female. The fourth type, mostly observed together with the second or third, consisted of a series of wing openings close to the female, sometimes even touching her.

Behaviour of the male skylarks. The most conspicuous courtship action was the hopping display, already noticed by Selous (1901) and also described and illustrated by Donald (2004, p. 91). His figure, though not his text, suggests that they sing while performing it but that is not the case, they are silent. As is well known, skylarks otherwise only exhibit a walking gait (Took, 1947; Pätzold, 1983, Fig. 41), with each single step some 70–100 mm (mean 85 mm) long, going from a fast trot to a slow pacing. The male produced the hopping display when about 20 cm away from the female, frontally orientated, stretched upright with sleek plumage, jumping several times up to 1–2 cm high, while not moving much from the spot, or more often while jumping somewhat nearer towards the female (Figure 15c). Apart from this clear hopping, all intermediate stages from hopping intention motions occurred, starting from a mere brief raising of the head; transitions to a tail-up posture were also frequent. The male showed the tail-up display (Figure 15b) a few centimetres to several meters away from the female, while turning or moving away from her. He kept his head bowed down, so that the mostly angled-up tail pointed diagonally upwards; this angling-up of the tail

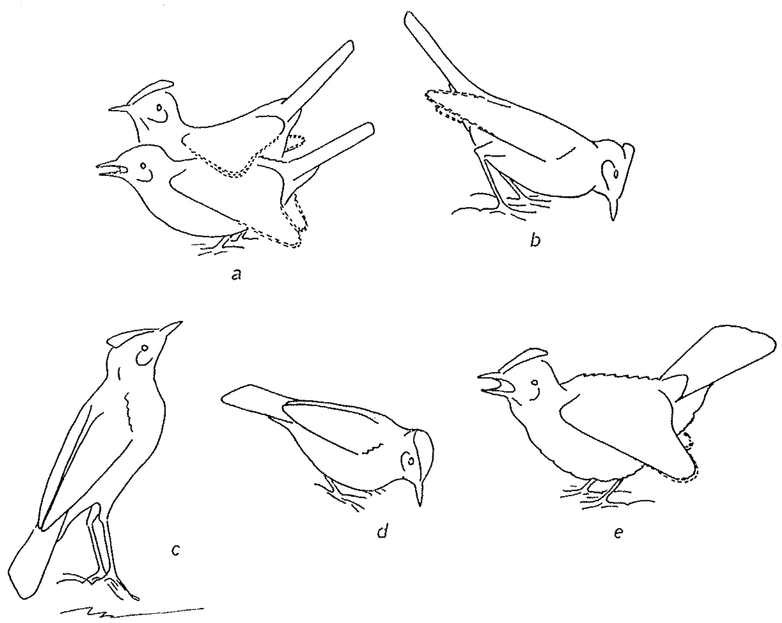

Figure 15. Sexual behaviour: (a) Female in front, soliciting copulation from the male at the back, with him tickling her back with a vibrating wing, (b) male showing the tail-up display, (c) male showing the hopping display, (d) female in normal feeding attitude, (e) male showing the tank display; note the varying orientations of the male with respect to the females under (a) and (d).

displayed his somewhat swollen pale-feathered anal opening to the female. Pätzold (1983, p. 108) reports having seen a pair of skylarks (male & female?) displaying the tail-up mutually. During the tail-up posturing, but also sometimes by itself, a small-amplitude vibration of the wings was fairly regularly displayed. The wing next to the female was often angled out and executed more extensive fluttering motions (Rose, 1924; Pätzold, 1983, Fig. 86, p. 95). During this tail-up and wing trembling display, males could continue to forage or preen, thereby both displays could last for several minutes in that combination. Suffern (1951) described that in higher groundcover vegetation, skylarks created a kind of courting patch by locally flattening the vegetation by trampling repeatedly around a particular spot but neither I nor Pätzold or Donald observed such behaviour; could Suffern have been confounded by the earlier described hopping display?

The pursuit flights were comparatively rare. Either sex—mostly the males however—started it by flying up towards their females, inciting her to fly up too. Thus, it was usually the male that chased after the female—though the roles were sometimes reversed—in fast flight, doing all turns after her and singing strenuously while doing so. After one minute at the most, both landed: the female went back to her usual activity, the male, however, showed a conspicuous cooling behaviour: with sleek plumage and angled wings, he panted for a few seconds in an upright position. This cooling behaviour must be ritualized as the female never showed it, although her flight performance during the chasing flight was just as effortful (compare Tinbergen, 1939a). I am not sure whether these pursuit flights are homologous with the hunt flights described earlier in the *Pair formation* chapter (see also Clark, 1948). Approach runs were not very salient: while both were looking for food, the male every now and then ran up to the female and pecked for food directly under her beak.

The contact call was a quickly repeated *chrr*, which could sometimes sound quite similar to the attack call; when one partner uttered the contact call, however, the other usually answered. The luring call is a pitiful sounding stretched-out *yuuu*, repeated at intervals; I heard it almost only from males that had been abandoned by their firm or prospective female partner, and only 4 or 5 times from incubating or brooding female skylarks.

When showing the tank courtship display (Figure 15e) the male skylark fluffed up its plumage and retracted his neck; the body was held approximately horizontal, the tail was slightly fanned and held obliquely upwards, the wing tips hung low down and trembled, the one directed to the female being somewhat more angled-up. With short steps the male walked around the female and sang loudly with its beak wide open. Stresemann's (1956) description of the skylark's courtship display probably refers to this (see also Pätzold, 1983, p. 105; cf. Gengler, 1903; Barret et al., 1948; Rokitansky & Aschenbrenner, 1956; Stresemann, 1957, crested lark).

Behaviour of the females. Apart from the sexual acts shared with the males and described above (run ups, contact calls, and chasing flights), females had only one display of their own: the copulation soliciting posture (Figure 15a): The female ran towards the male, crouched with her body horizontal, slightly ruffled-up, especially the back plumage, the tail angled upwards, the neck retracted, with drooping wings that trembled finely. During that display I often heard them singing softly; whether they always did so while soliciting I do not know for certain.

Copulation. The female approached the male in the manner just described, soliciting him to copulate with her. The male hopped closer to her and stood beside the now immobile female and touched her back with a vibrating wing-tip (Figure 15a). Then the male jumped up, keeping his balance in an upright position by wing-beating, and folded his tail under that of the female, and she facilitated this with lateral movements of her own tail. I failed to ascertain whether any 'handedness' (cf. Güntürkün et al., 1988) was involved in this act. After briefly coupling the female's cloaca with his own cloaca the male jumped off and moved away quickly, while the female maintained her copulation posture for a few seconds before resuming her previous nestbuilding/feeding/preening activity (cf. Howard, 1929). Donald (2004, p. 91) also briefly describes the skylarks' copulation act. Pérez-Granadoz et al. (2016, p. 21) seem to rely on Simms (1992) concerning copulation of the pair, which is said to occur in the morning, 3–4 days before the laying of a clutch begins; one copulation suffices for the insemination of all eggs of the clutch. Their description of the act closely coincides with my observations.

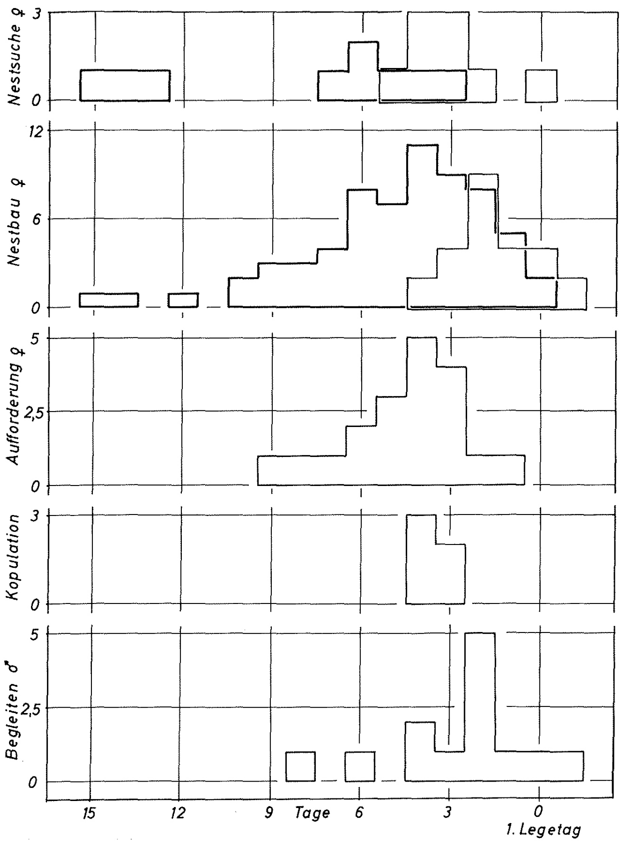

Figure 16. Frequency of different behaviours synchronised to the first day of egg-laying. Ordinate: number of observations during nest finding [Nestsuche] and nestbuilding [Nestbau]; thick line: first nests; thin line: second nests. Soliciting female [Aufforderung], copulation [Kopulation], accompanying male [Begleiten]. Abscissae: days [Tage] before first egg laying [1. Legetag].

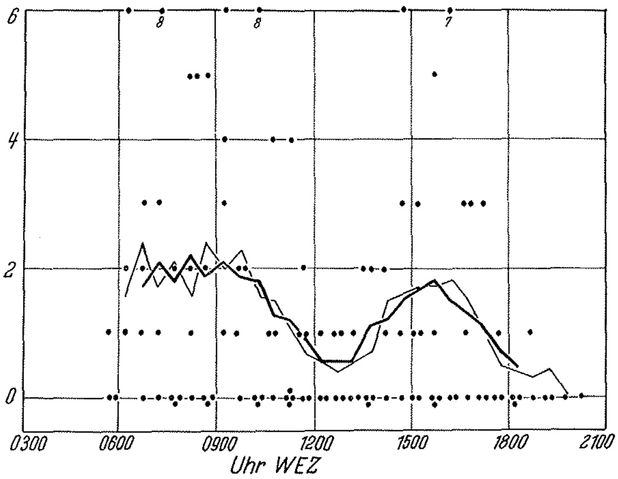

Figure 17. Dependence of the frequency of courtship displays (tail-ups and hoppings summed) on the time of day. Each point represents 30 minutes of observation on 3 males. Moving averages across 90 and 150 min. Ordinate: tail-up and hopping [Schwanzhoch und Hüpfen]. Abscissa: GMT [Uhr WEZ].

Influencing factors. Hopping and tail-up, the two most common courtship displays of the males, were closely linked temporally: out of 38 hopping sequences, the tail-up up was shown within the same minute in 30 instances, and within 2 minutes in 3 further instances. In 28 of the cases the hopping preceded the tail-up display. The tail-up display was about three times more frequently shown than the hopping display, so that it also occurred on its own: in 33 occasions, it was associated with hopping, and 60 times it was not. The linkage was probably due to the fact that both displays were reactions to the same stimulus: proximity of the female, regardless of whether the male ran up to her or she ran up to him. The female's copulation-soliciting display was temporally closely linked with the nestbuilding activity: the cases observed were chronologically similarly distributed to those of nestbuilding activity relative to the laying of the first egg: the most frequent occurrence of both patterns was 4 days before egg laying began (Figure 16), but they also co-occurred within a finer time frame of about 5 minutes. The males' courtship activity fluctuated over the day. Figure 17 shows a morning and evening maximum (chi^2, $p^* < 0.01$). The females mainly solicited copulations in the mornings (in 19 instances and only once in the afternoon (Kolgomorov-Smirnov, $p^* < 0.001$). The males' courtship activity also varied over the breeding season (Figure 18), being maximal during the pair-formation and the nestbuilding

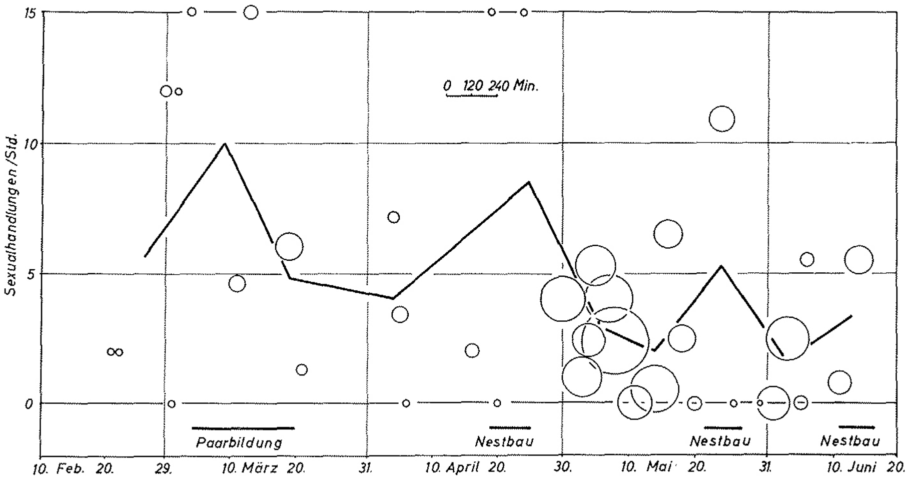

Figure 18. Frequency of courtship displays, tail-ups and hoppings summed across the breeding season. The circle diameters indicate the durations of the individual observations, total observation time 59 hours. Observations of one male. Balanced 15-day (February–April) or 10-day (May–June) average. Ordinate: courtship acts / h [Sexualhandlungen/Std.]. Abscissa: dates (10 Feb.–20 June). Labels: pair formation [Paarbildung], nestbuilding [Nestbau].

phases. The sexual behaviour of the females was restricted to the nestbuilding, pre-egg laying phases (Figure 16).

There was a positive correlation between the 30-minute frequencies of agonistic and courtship behaviours (rs = +0.47, $p < 0.01$); at the time the reason was unknown, but today it is clear that the common hormonal background is the cause!). Most of the courtship acts of the males were directed towards their own females; foreign females were attacked, or less frequently greeted with the tank display (extra-pair copulation attempts?). Of 25 observed tank displays, only 4 were addressed at the own female, all 21 remaining were addressed at foreign females (binomial against the 1:1 zero hypothesis, $p < 0.01$). Only rarely did the males court foreign females normally (as they did their own female, see earlier); if they did so for a moment, they usually soon followed it up with a tank display. More often however, the tank display was associated with aggressive behaviour. The similarity of the tank display of males with the copulation-soliciting posture of females is striking (compare Marler, 1956). The function of this male behaviour is unclear: the females did not react, or actually fled; I did not observe that they ever copulated with males courting in this manner. Hutchinson and Griffith (2007, skylarks) and Sánchez et al. (2004, *Calandrella sp.*) have however reported polyandry even within single broods. As far as my observations go, copulations were by the own male and were restricted to the 3rd and 4th day before the first egg of a brood was laid (Figure 16). According to my observations, a single successful copulation seemed to be sufficient to inseminate all eggs of a given clutch. Besides their own females soliciting copulation, males occasionally tried to copulate with their females when they were bathing in the sand or, more rarely, preening their plumage. Fluffed plumage and a horizontal-body stationarity of the female appeared to be the essential triggering stimuli, an observation that was backed by own experiments with a stuffed skin of a lark (compare Rittinghaus, 1956). Since males occasionally did not take any notice of the soliciting females for days, there must be an inner readiness in the males for the above-mentioned stimuli to trigger the copulation. But since the date of laying the eggs depended centrally on the females (see later) and the date was closely related to the datum of copulation, the males had to follow the females' soliciting behaviour within 2 or 3 days.

In the description of the sexual behaviour of the males, the raising of their crest was mentioned several times (however, see also *Agonistic behaviour* chapter). The closer the male was to the female, the more his crest was erected (Figure 19, $r_s = -0.45$, $p < 0.001$). Also, the closer a rival was, the higher the male's crest rose. The connection between crest lift and an escape tendency, which Andrew (1956) considered probable in finches (*Emberiza* sp.), was not observed in the skylarks: on average, attacking and fleeing larks erected their crests to about equal degrees. Furthermore, the securing-posturing males exhibited an erect crest. As Figure 20 shows, males erected their crests more in the mornings than in the afternoons (chi^2, $p < 0.01$). The crest-rise seemed to be a function of arousal (= reactability, Delius, 1970).

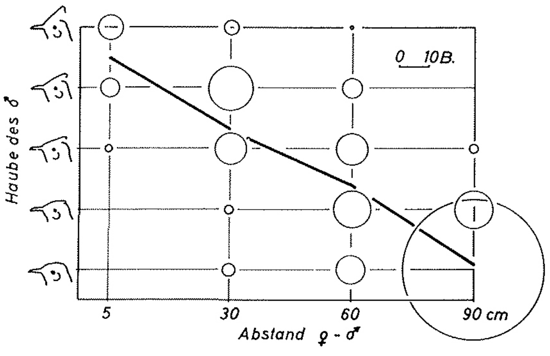

Figure 19. The male's crest raising depended on the extant distance from his female. The diameters of the circles represent the number of observations for each point. A pair of larks, observation at intervals of 15 seconds. Ordinate: crest of male [Haube des Männchens]. Abscissa: distance between male and female [Abstand].

Agonistic behaviour between the partners. Agonistic conflicts between the members of a pair were rare. Most of them were limited to a short, incomplete threatening act: an opening of the beak with an uttering of the threat call. It occurred when the courting male approached the female too closely, when she urged the unwilling male to copulate, or when both were seeking to peck-up precisely the same food morsel. If the female landed in foreign territory, she was usually flown at and chased back (chase flight) by her own male, sometimes after the owner of the territory had already chased her away. Sometimes there was no apparent reason for the always short agonistic encounters between partner males and females. There was no stable hierarchy between the partners, their dominance relationship often changed within minutes.

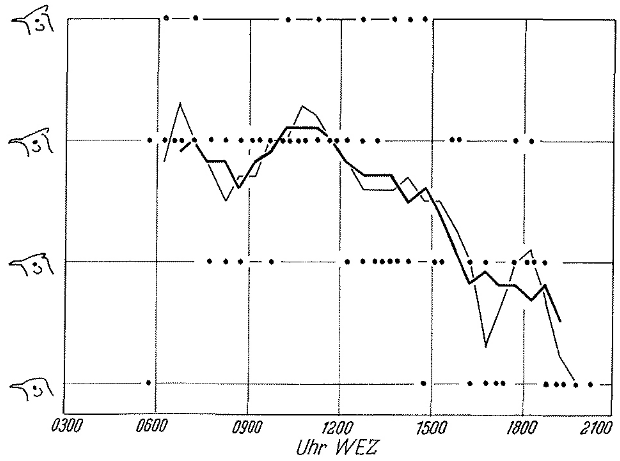

Figure 20. The male's crest erection as a function of the time of day. Each point indicates the average crest erection during a 30-minute observation of two males. Moving averages over 90 and 150 minutes. Abscissa: GMT [Uhr WEZ].

Nestbuilding

Only the female skylarks build nests (Lebeurier & Rabine, 1935; Pätzold, 1983, pp. 107–112; the same applies to the wood lark: Koffan, 1960; Wadewitz, 1953; the crested lark: Löhrl, 1944; the horned lark: Sutton, 1932; Pickwell, 1942; the short-toed lark: Dathe, 1952).

Description. The females interrupted their search for food or other activities and began to walk around in the more densely overgrown parts of the territory, crawling through the taller vegetation here and there, often stopping and showing the securing posture for prolonged periods. Some females noticeably increased their flying activity while engaged in this. They were obviously searching for ground hollows in bouts of a few minutes to up to about half an hour. Donald (1993, p. 100) reports that females visited up to 20 ground hollows and brought nest material to several of them before focusing on one of them. By and large they seemed to prefer vegetation no taller than 20 cm, but in some circumstances, their nests ended up in vegetations as tall as 55 cm! He presents studies reporting that the average inter-nest distances of a pair could be as short as 10 m and as l large as 250 m, clearly depending on population density that the particular habitat could support.

The collecting of nest material (Figure 21a) consisted in plucking-up, rarely in only picking-up nesting material. The female skylarks grabbed one or more grass stalks or moss bundles with their beaks and tore them off with up to 10 repeated jerky upward head and neck movements, without dropping what they had already collected before (Figure 21a). They seemed to move the bundles into the corner of their beak gape with their tongue. Sometimes, however, they dropped everything, shaking their heads, and did not take it up again. This collecting behaviour could vary in degrees of completeness, so that in extreme cases it could not be distinguished from the grass or moss plucking to uncover prey or seeds, which was occasionally exhibited during foraging.

When carrying the material to the nest (Figure 21b), the female flew or ran to the nest with the bundle and simply dropped it over the nest hollow. This sequence could be interrupted at any point by her dropping the nest material prematurely. The kicking motions (Figure 21c), as all the now following actions, were initiated by the female stepping into the nest; if the nest hollow was already several centimetres deep, they jumped into it. The lark then snuggled down into it, bowing her body downwards, placing her neck and head flat on the edge of the hollow, the tail pointing diagonally upwards; then the rear body mostly jerked somewhat upwards about 10 times in quick succession,

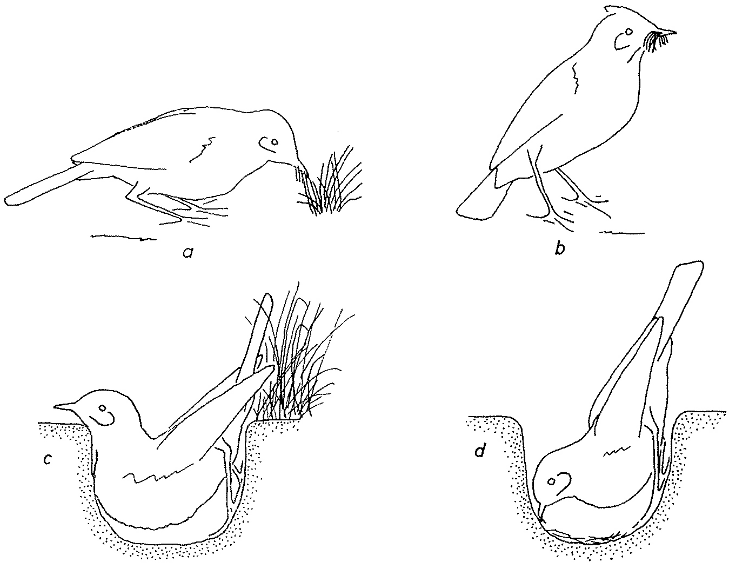

Figure 21. Nestbuilding behaviours: (a) collecting nest material, (b) carrying nest material to the nest, (c) kicking motion, and (d) steep-up activity.

obviously because the legs alternately kicked backwards or scraped upwards depending on the nature of the nest wall (sand, earth, pebbles). This inference is supported by the form of the movements, the condition of the nest hollows after the kicking actions and the fact that soil or sand was seen sometimes to fly out backwards when she kicked in shallow hollows. Also, from the form of movement and the state of the breast feathers of frequently kicking females I concluded that the breast was being pressed hard against the nest wall. The breathing frequency increased from about 60 to 90 per minute or more; when the weather was warm the bird panted for a while after kicking (see Atkinson 1951; Suffern, 1951). The turning activity consisted of a change of the female's cardinal body orientation while standing in the nest: she turned by a large angle, on average about 50° at a time, without any lateral preference. In the steep-up action (Figure 21d) the female rose from the squatting position, stretched her legs, bent forward so far that her head and neck almost disappeared in the nest hollow, and made small head movements to the side or upwards. As I observed with the help of a mirror placed above a nest, she wove the tips of grass stalks into the nest wall or pulled up stalks, which she then sometimes deposited on the nest edge. After some minutes of such steep-up activity the skylark female always got out of the nest and ran or flew away.

Nestbuilding process. Skylark females built a new nest for each of their successive broods. The construction of the first nest took longer than that of the later nests in the same breeding season (Labitte, 1957a, crested lark). The import of nest material lasted 8 to 10 days during the construction of the first nests and only 4 to 5 days for the second nests (Mann Whitney, $p < 0.001$). This could also be deduced from the time the females needed to pad up the nest hollows (Table 3). Also, the distributions of searching and collecting were closer together during the second nestbuilding than during the first nest building, and both distributions moved closer to the laying day (Figure 16, mean searching day for first nests: 8th day before laying; for second nests: 3rd day before laying (Mann Whitney, $p < 0.01$); collecting likewise, 5th and 1.5 day (t-test, $p < 0.001$) before laying). The shortened building times for second nests was due to faster construction activity (more numerous

Table 3. Padding-up of first and second nests.

	1st nests	2nd nests
Longer than 3.5 days	7	1
Shorter than 3.5 days	1	8

Fisher's test < 0.005

building activities per time unit), fewer unfinished activities and the longer summer than spring days. Nevertheless, on average the finished second nests contained less building material than the first nests; functionally this was not disadvantageous, as the mean air temperature naturally increased during the breeding season. Differences between early and late second nest construction times of a season could not be detected. Searching and collecting always started on about the same day, but both were only weakly linked minute-by-minute at the beginning, they became more strongly linked over the following days; however, searching reached its peak earlier than collecting (Figure 16: differences in the distribution of searching and collecting, $p < 0.05$ first nests and, $p < 0.005$ second nests were Mann Whitney-test significant). Collecting was increasingly followed by importing, with the importing/collection ratio peaking at about the same time as the collecting activity (Table 4).

Kickings, turnings and steep-ups were linked in time with the hollow searching at the beginning and later with the importing of nest material. These actions were then always preceded by importings: after 40 importings, 13 in-nest activities followed, and these were followed by an average 13 kickings, 12 turnings, and 5 steep-ups. They probably reached their peak frequency at the same point of time as the importing activity. The choice of nest materials also changed during the construction process. If all the days in which I observed females collecting moss were synchronized, 10 days of nestbuilding had preceded while another 33 of them followed. Similarly, for grass-blade collecting I noted 32 preceding and 23 following nestbuilding days (chi^2, $p^* < 0.001$). Table 5 furthermore shows that less moss was collected overall than grass. In fact, only a few shreds of moss were found in the nests (compare Hinde & Steel, 1962). The nestbuilding activity was clearly daytime dependent with a distinct morning peak. In 13 of 17 cases nest building females were observed in the morning, in 4 cases in the afternoon with an almost evenly distributed observation time (binomial-test, $p < 0.05$).

As described earlier, the search activity was concentrated on the more densely overgrown areas of the territories. Here the females preferentially headed for dense grass tufts (anti-predator cover!) or depressions in the ground, where she snuggled down, kicked backwards, turned and showed the steep-up motion. At the beginning, each female visited many such hollows: I counted up to about 20 different ones; later they limited themselves to a few, and then usually entered only 4 or 5, and finally only one was built into. Also, the collecting of nest material was often limited to a few places in the territory, even if suitable places could be found in many places; for instance, on one occasion a female collected material very close to one and the same place 22 times in a row, i.e., she remembered it for at least some 20 min.

Nest. The hollows found during searching were rarely deep enough to accommodate the nest without further ado: usually the females deepened them with a scraping action with the legs

Table 4. The ratio of collecting to incorporating while nestbuilding.

	Before the collection peak	During the collection peak	After the collection peak	Total
Collecting	86	169	71	326
Incorporating	40	132	33	205
Ratio in %	46.5	78	46.5	63

The collection peak falls on the 4th and 5th day before laying in first nests and on the 1st and 2nd day before laying in second nests (Figure 16). Ratio difference significant at $p < 0.001$ (chi^2).

Table 5. The incorporation/collection ratio.

	Collected	Incorporated	Ratio in %
Moss bundles	24	3	12.5
Grass blades	40	28	82.5
Total	58	31	54.0

Ratio differences are significant at p >0.01 (chi^2). The figures for moss bundles and grass blades were collected within the same observation periods.

(Chappell, 1946; cf. Pickwell, 1942, horned lark; Koffan, 1960, wood lark). It is unknown which factors determine the final nest location choice of location. There are probably many, since even a single female built its nests in very different microbiotopes. However, all of the nests were located in the same own territory, but without any preference for the centre and without there being any discernible relationship between the locations of the successive within-season nests of a female; Donald (2004, p. 103) attributes the quite variable inter-nest distances that have been reported as being due to the very variable territory sizes (largely a consequence of the variable population densities). The clear width of the nests was quite constantly 6 cm, the depth fluctuated considerably around 5.5 cm. The 0.5 cm (late) to 1 cm (early in the season) thick padding consisted of some moss, thin and coarse grass, and occasionally also lichens; a particular female wove a few feathers into several of her nests. Pätzold (1983, Fig. 89) exemplarily illustrates the structure of a typical skylark's nest. I did not see the little stone thresholds (could they be stones scraped up while deepening the hollow?) described by Congreve (1950) at any of 'my' nests (but compare Jourdain, 1927, desert lark; Pickwell, 1931, horned lark; Engelbrecht & Mashao, 2019, reported 'domed' nests for Sabota lark, *Calendulauda sabota*). Suárez et al. (2009, p. 82) describe that some of the Iberic lark species decorate their nests with strange objects (among them sheep excrement!) and some add a kind of entrance hall, but not the skylark? In the hot Iberic climate the orientation of the 'entrance' seems to play a role (Yanes et al., 1997; Suárez et al., 2009, p. 83) (as insulation?) but I found no preferential orientation in my study area.

Nestbuilding and other behaviours. Information on the close coupling of the nestbuilding and copulation behaviour of females, and indirectly with that of males, is shown in Figure 16; information on female song during this phase is provided in the earlier *Song* chapter. Feeding young does not stop females' nestbuilding behaviour: building and feeding can alternate within 5 minutes. This circumstance makes so-called telescoped broods possible. Females still brooding young, however, were never observed searching for a nest location or nestbuilding. The laying of eggs only partially inhibited nestbuilding (see Figure 16, compare also Löhrl, 1944, crested lark; Koffan, 1960, wood lark). In three cases in which their nests were destroyed before/while they laid eggs, females built a completely new nest during laying. In one instance a clutch of eggs was totally overbuilt; what circumstance occasioned this remained obscure. If I prematurely put (foreign) eggs into the nest, the females continued to build.

Behaviour of the males. They did not participate in nestbuilding, but some males followed the nestbuilding female at every step and turn, fluttering above them when they entered the nest or standing perched on a higher plant near the nest and keeping balance with their wings and singing loudly. Other males, however, showed no such intense interest (in contrast, Donald (2004, p. 102) opines that all males showed such behaviour). Koffan (1960) interpreted similar behaviour by male wood larks as a nest-pointing response; however, this functional interpretation does not apply to the skylarks, as the males only performed it in late stages of nestbuilding, when the nest location had been already been firmly chosen by the females. In any case, males always followed the females, but never the other way around. The behaviour just described did not appear to be closely related to the sexual activity, which is noticeably increased in males at this time (see Figure 16).

Egg laying

Behaviour. The females stepped into the nest and for about 10 minutes behaved as when incubating. Then they stood up a little while with fluffed plumage, made 5 to 10 pressing-down movements with their abdomen, stood there motionless breathing heavily for a few seconds with sleek plumage and then sat down again. This sequence took about 5 minutes. After about another 15 minutes of sham incubating, the bird left the nest. Some females, but not all, showed a bout of resting behaviour for some minutes afterwards by remaining sitting in the nest or crouched quietly somewhere within their territory.

The eggs were laid in the early morning hours, usually between 5:00 and 8:00 h (Figure 22). The laying intervals were almost exactly 24 hours; I could not detect any significant deviations from this, but they may occur sporadically (see Labitte, 1958). Clutches of 5, 4, 3, or 2 eggs were found in Ravenglass, but the latter ones were certainly partial clutches plundered by crows or other predators. The mean clutch size was 3.64 eggs ($N = 112$) (Wörner, 1931; Brown, 1946). Each female produced an average of 2.73 clutches per breeding season, varying from 1 to 4. Accordingly, on average a female laid some 10 eggs per year.

Clutch size. Factors influencing the clutch size are only briefly discussed here, as that has been done in detail elsewhere (Delius, 1965). The clutch size varies across the season (von Kalitsch, 1930; Haun, 1931; Verwey, 1931; Labitte, 1957b; Donald, 2004, p. 106). Probably, however, the changes in clutch size do not depend directly on the season, but on the sequence of clutches laid by each female. But there are also differences between the breeding seasons, which surprisingly can be followed over the whole breeding season. The females had an individual clutch size (intraindividual variance = 0.208, interindividual variance = 0.693, F-test, $p < 0.01$, compare Curio 1959a). An influence of the female's age on the clutch size could not be detected (new settlers being considered as one-year-olds (t-test, $p > 0.05$). With regard to the size of the second clutches, there was no relationship to the pre-history, that is, there was no influence of the stage at which the preceding clutch was lost. Donald (2004, p. 108) presents a comparative table of the average clutch size found in a number of different studies, but he does not succeed in attributing the variations to definite variables.

There has been some doubt whether skylarks are 'determinate' or 'indeterminate' layers (Stresemann, 1927/34): Chappell (1947) induced a skylark to lay a total of 10 eggs one after the other by repeatedly removing the 4th egg (= indeterminate). When I removed the eggs from the first onwards, as they were laid, the female stopped laying after the 4th egg (= determinate layer). Attempts to stop the laying prematurely by adding artificial eggs failed in 2 cases (compare Weidmann, 1956, *Larus ridibundus*). More recently the skylarks were independently affirmed to be determinate layers (Kennedy, 1991).

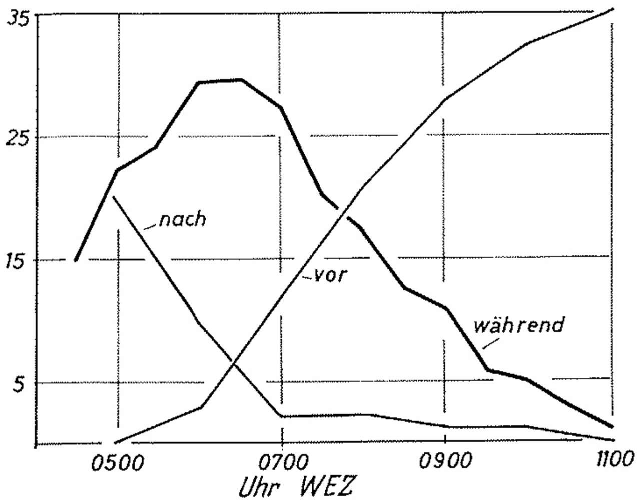

Figure 22. Time of egg laying. Thick line: half-hourly frequency of the periods during which an egg was laid. Thin lines: Number of cases where eggs were laid before or after a given time. Abscissa: GMT [Uhr WEZ].

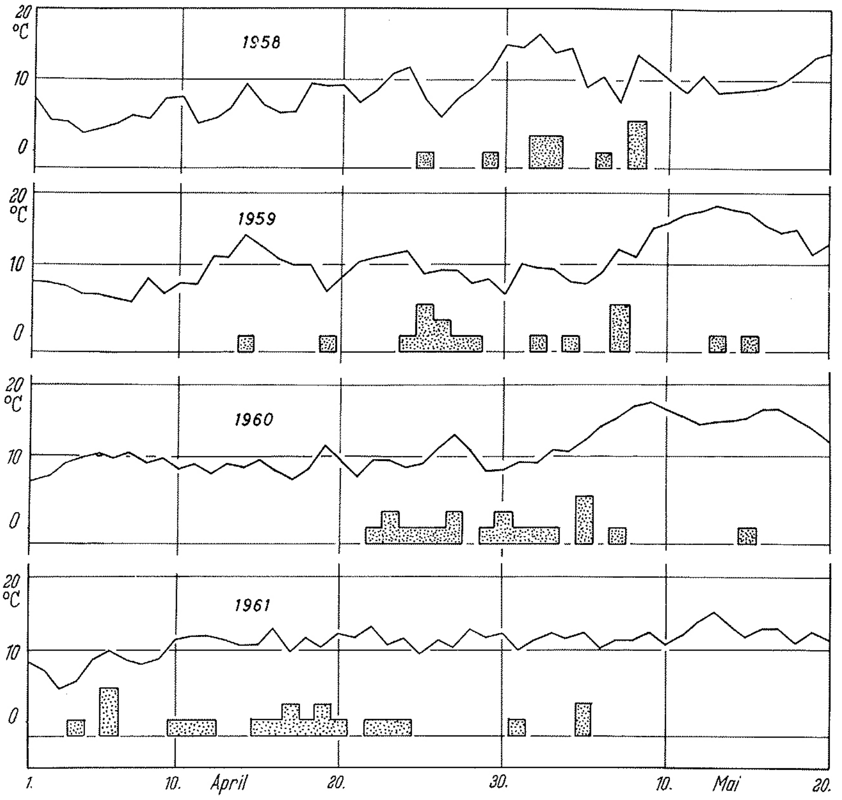

Figure 23. Start of laying of first clutches in 1958–1961 and average daily temperature. Each square represents a different clutch of eggs. Ordinates: degrees centigrade (°C), Abscissae: date (1 April – 20 May).

Time of laying. The timings of the first laying in a breeding season differed (Figure 23). Apparently, several factors worked together (Marshall, 1961), including air temperature: in the warm spring of 1957 egg-laying started particularly early (Goodacre & Lack, 1959; C. Beer, oral communication, 1958). This relationship can also be seen in Figure 23 (see also Figure 4); the mean daytime temperature had to rise to about 10° C for the larks to start laying. Again, there were individual differences: certain females were quite regularly either early, average, or late layers (Figure 24, Kendall's r for 1958–1959 = 0.76, $p < 0.01$; for 1959–1960 = 0.72, $p < 0.001$; for 1960–1961 = 0.68, $p < 0.001$). Even over 3 years this consistency of sequence could be detected: Kendall's W = 0.77, $p < 0.01$. The males had little influence on this at best; females paired with their old or a new partner yielded the same correlation coefficient (Kendall's tau = 0.73, $p < 0.028$). Males that changed females did not seem to impose any order on them (Kendall's tau = 0.07, $p > 0.5$). Thus, this may be due to the fact that females have individually different thresholds to the factors that trigger laying. One-year-old females laid their first eggs on average one week later than older females (t-test, $p < 0.001$, newly settling females considered as being one-year-olds).

The start of laying of the second clutches does not depend on the air temperature, which is usually well above 10° C in the later breeding season anyway. Incubation of the first clutch as well as feeding the young of the preceding clutch clearly inhibits the development of the oocytes of the next clutch (Figure 25, distributions significantly different at $p < 0.01$, Mann-Whitney). It remains to be seen to what extent oocyte growth is interrupted in the females that were disturbed during the laying of the clutch and when they began a new laying cycle. How the end of the breeding season was regulated I did not find out; grossly, but not directly, it seemed linked to the begin of the plumage moult (cf. Marshall, 1961). Instances of skylarks laying eggs during winter typically coincided with abnormally warm periods (Hary, 1939; Thorburn, 1954; see also Hachisuka, 1924,

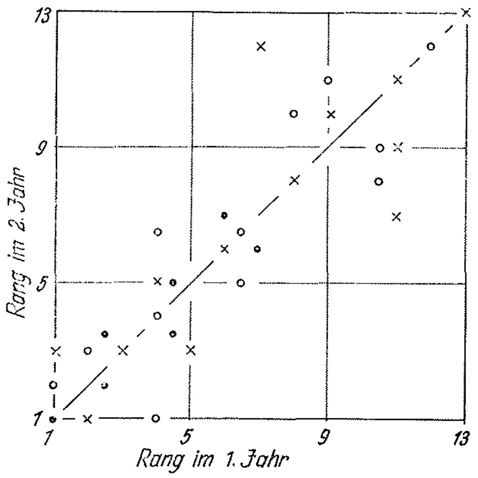

Figure 24. Order of first laying of three female collectives in two successive breeding seasons. Full points: 7 females 1958/1959; empty circles: 12 females 1959/1960; crosses: 13 females 1960/1961. Ordinate: rank in 2nd year [Rang im 2. Jahr], Abscissa: rank in 1st year.

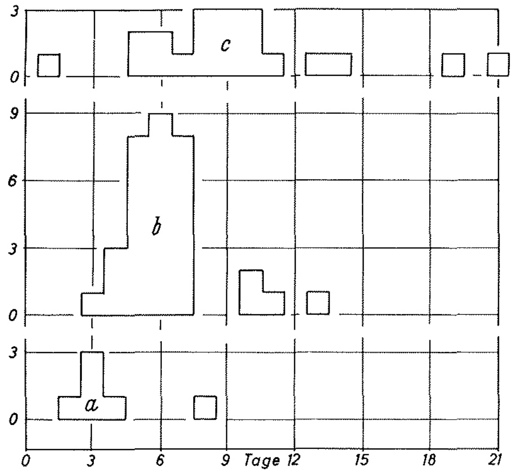

Figure 25. Laying time of the second clutch. Abscissa: days after loss of the preceding clutch during laying (a); after loss of the preceding clutch during the incubation or of nestlings during brooding (b), or after the young left the nest (c). Ordinates: number of clutches/broods. Abscissae: days 0 to 21 [Tage].

Alaemon alaudipes). These must probably be regarded as premature clutches of the following breeding season (Marshall, 1961).

Incubation

Only the females incubated (Koch, 1930; Verheyen, 1957; crested lark: Liebe, 1878; Haun, 1930; Hartley, 1946; wood lark: Koch, 1936; Steinfatt, 1939; horned lark: Pickwell, 1942; Barth & Haftorn, 1948; Sutton & Parmelee, 1955; Drury, 1961; note that Bourke, 1947, mentions incubating Horsfield's bush lark males, *Mirafra javanica*; the current Wikipedia, 2021article on this species reaffirms this). The following statements refer to females unless otherwise noted. Some behaviours mentioned in the following passages but not described here were already presented in some detail in the previous *Nestbuilding* chapter.

Description. The female landed a few meters away from the nest, never in the nest itself, walked up to it, jumped in and turned around so that she came to face the nest ‘entrance’ before settling down. Donald (2004, p. 110) rightly stresses the furtiveness and stealth with which the female approached and left the nest in this phase. She settled down on the eggs with a loose plumage, especially on her belly, after a few seconds of oscillating around the longitudinal axis, which is probably due to a kicking with her legs. As the bird sank into the bottom of the nest, the frequency of the rocking movement increased while the amplitude decreased, and the plumage sleeked again. The brooding patch presumably came to rest exactly on the eggs. But the bird also showed occasional rocking episodes when she was sitting on the eggs continuously; a light standing-up preceded it.

Mostly the sitting female just remained still; Donald (2004, p. 109) points out their occasional pecking at passing insect and the occasional preening of an accessible body area. But mostly they dozed, intermittently closing one or the other eye for seconds at a time with their head drooping a little. But the females did not sleep properly during the day, that is, they did not place their head behind the wing with a brief head shuddering, as they did regularly at the setting in of night while incubating. Dozing females tended to yawn: they somewhat retracted their heads and briefly opened their beaks widely, the tongue curling up. During incubation they occasionally peered, that is, they visually fixated a nearby bit of a grass blade, a grain of sand, a dewdrop or passing ants binocularly and occasionally pecked at these items (as to binocular viewing of more distant objects while outside nest, see Pätzold, 1983, Fig. 56); they also preened their plumage as far as they could reach it while steadily sitting firm. Every now and then they took up a securing posture: a neck stretch with monocular fixation in the distance, occasionally sleeking the plumage, raising their crest, and retracting the hyoid bone (= tongue). Mandibulating was a quick opening and closing of the beak, probably accompanied by tongue movements; they otherwise also panted with an open beak and fluffed-up plumage, or else they contact-called.

Only during the tail-up motion did the females rise completely from their eggs. In addition to occasionally showing the movements described during nestbuilding, the female now also showed an egg turning response (Figure 26a). As could be seen with a mirror above the nest, the skylark rolled the individual eggs with the underside of her beak and side-to-side trembling head-withdrawal movements. Sometimes she then preened her belly plumage while she stood quite high-up in the nest. From time to time the stand-high was interrupted by egg turning. A nest leaving began with a stretching of the neck, a plumage sleeking, and a retraction of the hyoid bone. Then the female rose from the nest and usually flew up a few steps away from it. A special behaviour was the retrieval of eggs from outside of the nest, when the skylark females moved eggs that had come to lie beyond the edge of the nest—where they occasionally landed due to predator activity, a response that Poulsen (1953) did not describe. The incubating female stood up in the nest, stretched her neck and put her beak in front of the egg outside the nest (Figure 26b). Then she rolled it towards her breast by retracting her neck with added fine lateral head movements. This led to the egg gliding down gently between her breast plumage and the nest wall to the nest floor. If the females were surprised by enemies, including humans, while incubating, they either left the nest as described above, or they first ducked down into it and, then when the enemy approached closely, suddenly flew up directly from the nest, thus startling him so as to distract him from the nest. This could occasionally lead to an egg or two landing outside the nest. Often, they then also lured away from the nest: they landed close to the nest and then ran away from the nest for a short distance (Figure 26c), crouched and bent over with their bodies, while they intermittently executed short fluttering-away flights. If they were pursued by the predator, they showed this behaviour until they

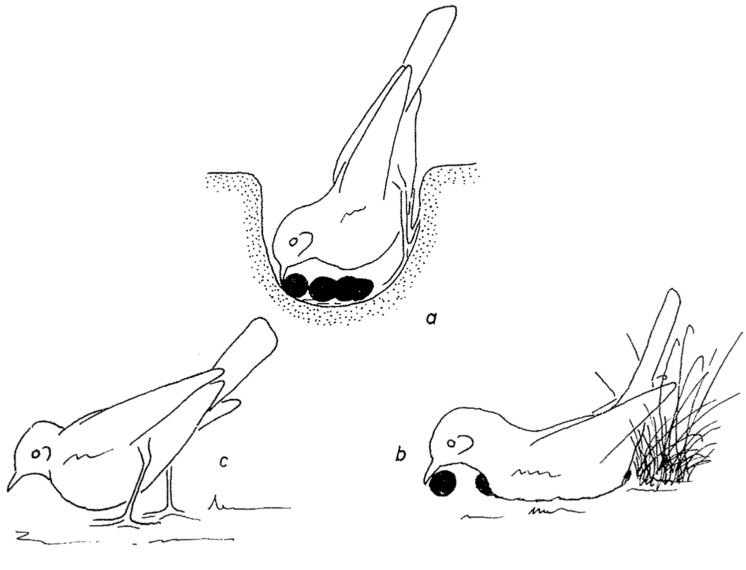

Figure 26. Incubation period behaviour: (a) turning eggs in the nest, (b) egg retrieval from outside the nest, (c) luring away from the nest.

were several meters away from the nest. During the brooding pauses, the female eagerly searched for food, very often securing in erect posture in the direction of the nest and if the access to the nest was blocked—perhaps due to the obtrusive presence of the observer—, she often flew up and fluttered near to the nest's location.

Begin of incubation. In all broods ($N = 50$), females incubated at a steady rhythm from as soon as the last egg of the clutch had been laid. Probably all of them already began to incubate after laying the penultimate egg (as it was the case in 11 more closely observed clutches), but initially with an as yet incomplete brooding rhythm. Some individual females slept on the eggs the night before laying the penultimate one, but all of them slept on them the following night. Short nest visits lasting up to 5 minutes occurred during the whole laying period, some still coupled with continued nestbuilding. The statement by Brown (1924a) that incubation begins before laying must be based on a misinterpretation of his observations.

The virtually synchronous hatching of the young of a clutch indicates that any incubation prior to the deposition of the last egg of the clutch was not fully effective; the brood patches were probably not yet fully developed: one week before laying, nothing special was observed on the ventral feather apteria of the females. A female caught on the nest on the 4th day after laying had an already well-developed brood patch: the ventral apteria appeared oedematous, swollen and dark red (= richly blood irrigated). Incubating females captured later showed the same picture. In females caught 3 days after hatching the young, the brood patch was already pale and wrinkled throughout. Also, when the females were prematurely given young instead of eggs, the brood-patch regression began. This indicates that the presence of the brood patch requires continuous contact of the eggs with the ventral apteria. It is therefore probable that incubation before the laying of the last egg was not fully effective because the brood patch was not yet properly developed.

Incubation rhythm. During incubation, sitting periods and pauses by the females alternate; their lengths fluctuate daily (Figure 27). The U-like progression of the sitting period durations is significant with $p < 0.001$ (chi^2) and fits a parabola $y = 0.00016\ x^2 - 0.208\ x + 76.12$ between 5:00 and 19.00 h (x = time in minutes, y = sitting time duration). The curve probably more correctly corresponds to a fraction of a sinusoid with a period of 24 hours, which was phase-shifted forward by about 1 hour (= 15°) against the lighting rhythm (Aschoff & Wever, 1962; see also *Song* chapter). The less pronounced diurnal fluctuations of the sitting pauses seem to have two peaks and three valleys, but these could not be statistically confirmed. At night, if not disturbed, the females appeared to incubate (while sleeping) for several hours without interruption.

Figure 28 shows the daily rhythm of the incubation performance, which is the time in minutes per hour that the female incubates. It jointly summarizes the sitting time and sitting pause rhythms (Curio, 1959b, pied flycatcher, *Ficedula hypoleuca*). The obvious assumption that the daily temperature pattern was responsible for the rhythm of the sitting times through a negative correlation was probably at least partially correct, because the deviations of the sitting times from the mean values in Figure 27 correlated positively with the corresponding deviations of the temperature from the average daily temperature pattern ($r_s = -0.42$, $p < 0.001$). However, temperature cannot be the only factor, because the minimum of the daily sitting period curve is reached at about 11:00 h, while the mean daily temperature peak occurs at about 13:00 h. There was a positive correlation, albeit weaker one, between the deviations of the sitting pauses and those of the daytime temperature ($r_s = +0.21$, $p < 0.02$. The deviations of the successive sitting times and sitting pauses however showed no relationship to each other ($r_s = \pm 0.10$, $p > 0.05$). This indicates that both were independently influenced by various factors, so that the functionally important incubation performance must have been regulated in a correspondingly complex manner. As the brood progressed, the incubation performance (Figure 29, chi^2, $p < 0.02$) increased, mainly due to

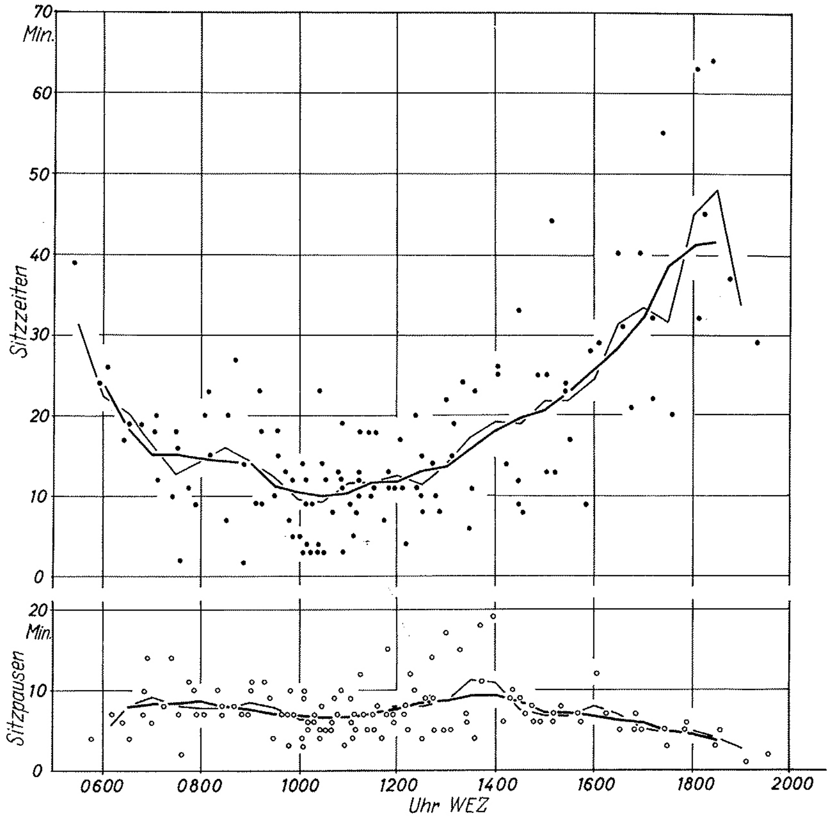

Figure 27. Daytime variation in sitting times and pause lengths. 56 hours of observation on a female (25 April – 5 May). Moving averages across 60 and 120 minutes. Ordinates: incubation periods [Sitzzeiten] and pauses [Sitzpausen] in minutes. Abscissae: GMT [Uhr WEZ].

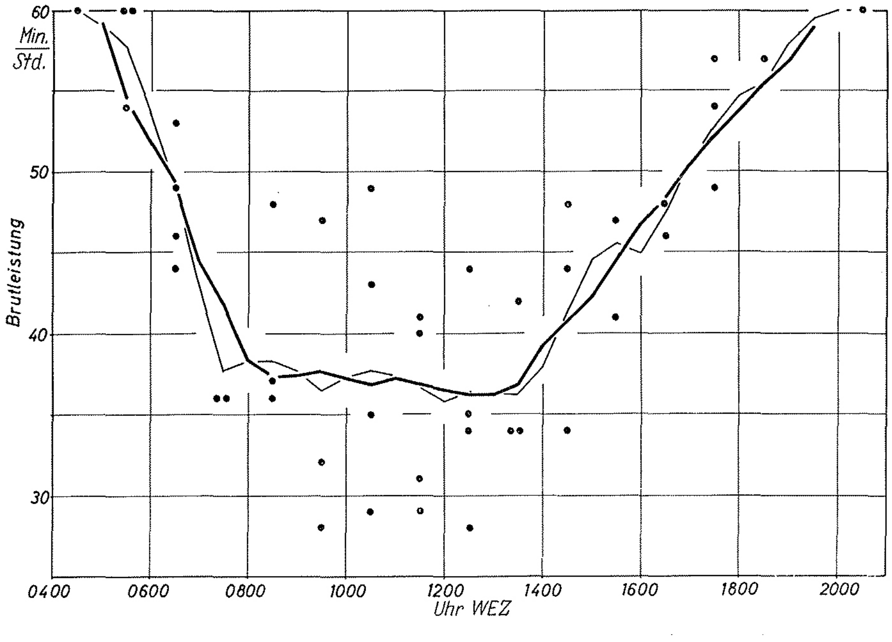

Figure 28. Incubation performance [Brutleistung] depending on the time of day. Each dot represents a 60-minute observation of a female (25 April – 5 May). Moving averages across 60 and 120 minutes.

the shorter sitting pauses; the sitting periods were only extended slightly. The greater incubation performance variability, which was noticeable between about 9:00 and 11:00 h, was probably due

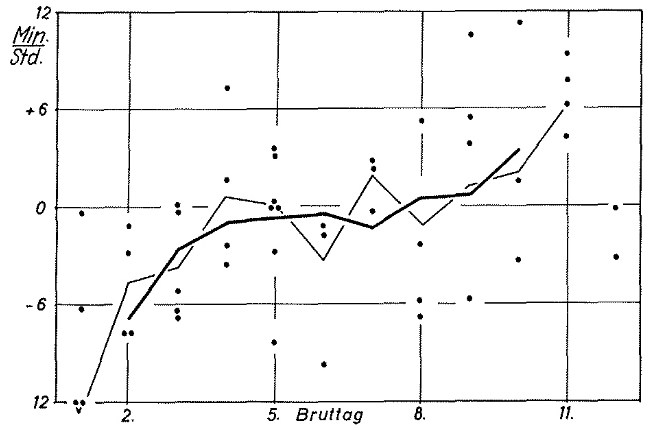

Figure 29. Incubation performance increase during the course of the breeding season. Ordinate: deviation of incubation performance from 120-min curve in Figure 28. Daily average and moving average across 3 days. Abscissa: incubation day [Bruttag].

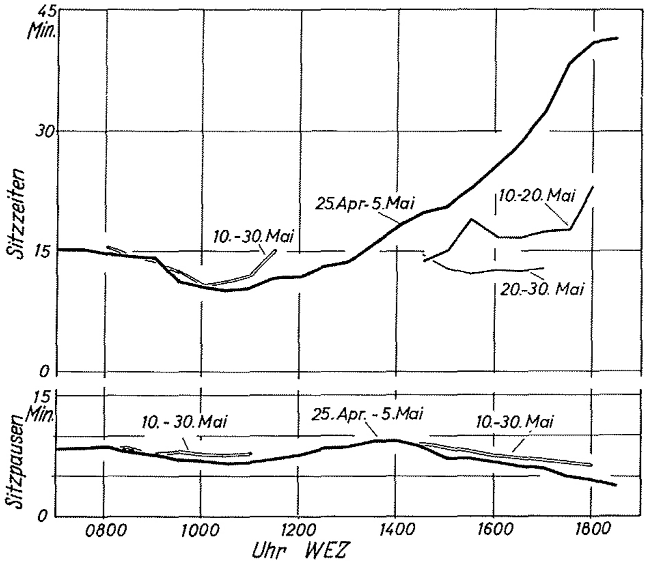

Figure 30. Seasonal changes of the daily rhythms of sitting periods [Sitzzeiten] and pauses [Sitzpausen]. 25 April – 5 May from Figure 27, 10 May – 30 May from 39 hours of observation of two females. Moving averages across 120 minutes.

to the interference of the hunger-influenced foraging activities at that time of day.

The parabola describing the sitting periods seemed to flatten more and more during the course of the breeding season without the location of the apex changing, while the pause times generally lengthened somewhat. For the sitting periods the differences were statistically supported (modified median procedure, chi^2, $p^* < 0.001$ (Figure 30). Donald (2004, p. 110) indeed indicates that the incubation periods shorten from 12 days to 10 days across the succeeding clutches of a season, presumably because the rising ambient temperature aids the incubation. In the same context, he mentions that on a few rare occasions he saw males bringing food to incubating females; I made no such observations and only saw a few rare male visits of their incubating females with empty beaks. Surprisingly, Donald (p. 109) also found that three-egg clutches required longer incubation periods than four-egg clutches, but might that not be because the former were more frequently early in the season, while the latter more often occurred later in the season?

A female whose clutch was replaced by natural-looking wooden eggs continued to brood normally without being disturbed by the eggs' thermal property differences. However, when this artificial clutch of eggs was exchanged for egg-coloured cylinders of egg-like size, her sitting times were significantly reduced from an average of 17 to 6.3 minutes (median procedure, Fisher's exact test, $p < 0.025$); the sitting pauses were also shorter, but the drop from an average of 9.2 to 6.1 minutes was not statistically significant.

Factors influencing incubation behaviour. The frequencies of the different behaviours during incubation in no instance correlated significantly with the progression of the incubation period. For two behaviours where the opposite seemed to apply, it cannot be excluded that my quantification criteria were not stable enough. Within the sitting periods, the occurrence of yawning, preening, and mandibulating was evenly distributed; but rocking was more frequent than average during the first 3–5 min of the sitting periods (chi^2, $p < 0.001$). Turning, however, was practically limited to the first minute after the start of the sitting periods. The contact call also occurred preferentially towards the beginning of the sitting period and was probably connected with the nest-entry action, because a synchronizing with the beginning of the sitting periods resulted in a stronger association than a synchronizing with their end (Figure 31, chi^2 = 32.4, $p^* < 0.001$ and chi^2 = 11.1, $p^* < 0.01$). Peering, on the other hand, became much more frequent towards the end of the sitting periods and probably actually presaged the leaving of the nest (Figure 32, $r_s = +0.28$, $p > 0.05$ and $r_s = -0.58$, $p < 0.001$).

The behaviour of the incubating female correlated variously with the duration of the sitting periods. As expected, most of the high-ups, dozings, mandibulations, contact calls, and peerings (Figure 33) showed a positive relationship when the numbers of their occurrences were plotted against the durations of the sitting periods and no relationship when their frequency (occurrences per minute) was plotted against the end of the sitting periods. In contrast, rocking showed a positive correlation in the first instance and a negative correlation in the second instance (Figure 34). The explanation for this is the aforementioned accumulation of rocking in the first 5 min of the sitting periods, obviously independently of whether these were short or long. This was similarly the case with turning. Yawning (Figure 35) and preening correlated positively in both instances, the reason being that their daily rhythms were similar to that of the sitting periods (see later).

The contact call stimulated the partner to answer. In about 33 hours of observation, 74 of 238 calls of the female were answered by the male: if the calls had coincided by chance in the given order within 15 s, the expected number would have only been 5 (chi^2, $p < 0.001$). Twelve calls by the

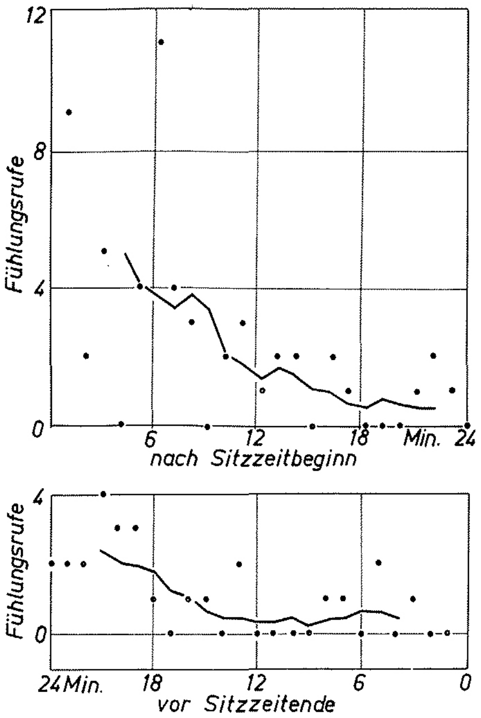

Figure 31. Number and frequency of contact calls after the beginning and before the end of the sitting periods. Synchronization of 20 sitting periods longer than 24 minutes. Ordinates: number of contact calls [Fühlungsrufe] per minute. Upper abscissa: minutes after start of sitting period [Minuten nach Sitzzeitbeginn]. Lower abscissa: minutes before end of sitting period [vor Sitzzeitende]. Moving average across 7 minutes.

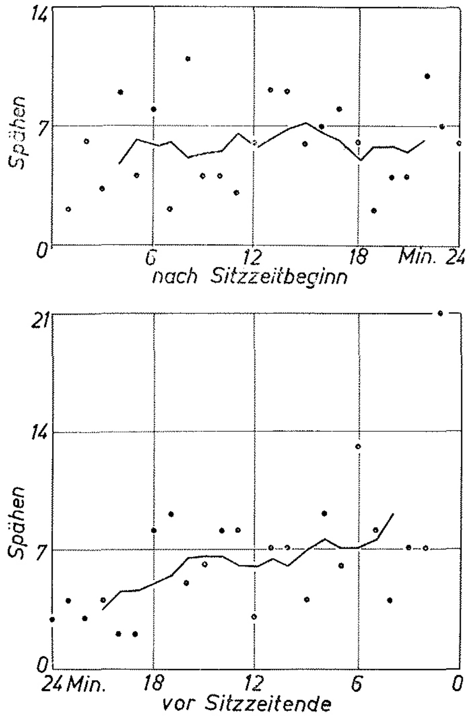

Figure 32. Number and frequency of (visual) peering episodes after the beginning and before the end of the sitting periods. Synchronization of 20 sitting periods longer than 24 minutes. Ordinates: number of peering episodes per minute [Spähen]. Moving average across 7 minutes. Abscissae: see Figure 31.

female were obviously responses to their mate's song flight, further ones were certainly responses to his contact calls, still others responses to a sighting of the male. Panting was most likely caused by high temperature, I only saw it between 11:00 and 13:00 h; in 17 of the 21 instances, the temperature was then above the average for the time of day (binomial, $p < 0.01$). Yawning and preening occurred especially in the early morning and late evening hours and probably indicated sleepiness. On average, the females incubating at the beginning of May fell asleep, that is, they put their head under their wings, at 20:00 h ($N = 4$, extremes 19:00–21:00 h [moonlight!]). On average they woke up again at 6:30 h (N = 3, extremes 6:25–6:45 h).

Eggs silted up in the nest by sandstorms were freed up by the females as long as they could still see something of them, with the behaviour described earlier as egg turning. If the nest became disordered, they were able to repair the damage without endangering the eggs or the young by turning, rocking, and weaving away and pulling up straws in the steep-upright position. A renewed importing of nest material was never observed in this situation. Egg retrieval could be elicited throughout the whole incubating phase, fastest when all eggs were removed from the nest hollow; however, compared with gulls, this reaction was harder to elicit in skylarks; eggs outside the nest are a normally far rarer situation in skylarks than in gulls due to deep versus shallow nests. Donald (2004, p. 109) has me wrongly describing an 'egg-rolling' response by the skylark females to temporarily remove their eggs from their nest to carry out nest repairs, but in fact, I did not observe anything of the kind (see also Suárez et al., 2009, p. 101).

Luring-away behaviour in reaction to potential predators could also be induced throughout the incubating phase, perhaps more readily as the incubation phase progressed, if one (or, on several occasions, a stoat or a weasel) approached the incubating female suddenly enough. The response

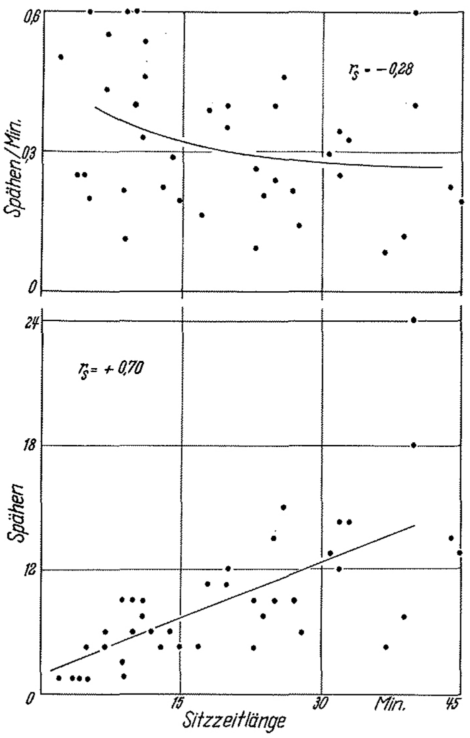

Figure 33. Dependence of the number of peering episodes ([Spähen], bottom, $r_s = +0.70$) and their frequency (top, $r_s = -0.28$) on the length of sitting periods. Approximate regression curves. Abscissae: duration of sitting periods [Sitzzeitlänge], in minutes.

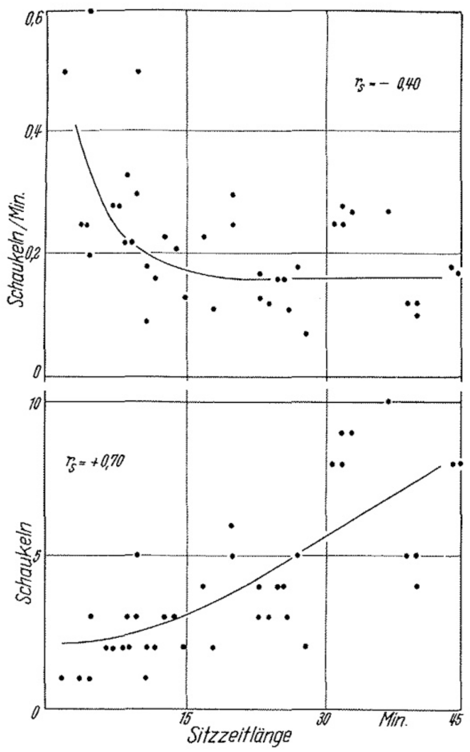

Figure 34. Dependence of the number of rockings [Schaukeln], bottom, rs = +0.70) and the frequency of rockings [Schaukeln/Min], top, rs = -0.40) on the duration of sitting periods. Approximate regression curves. Abscissae as in Figure 33.

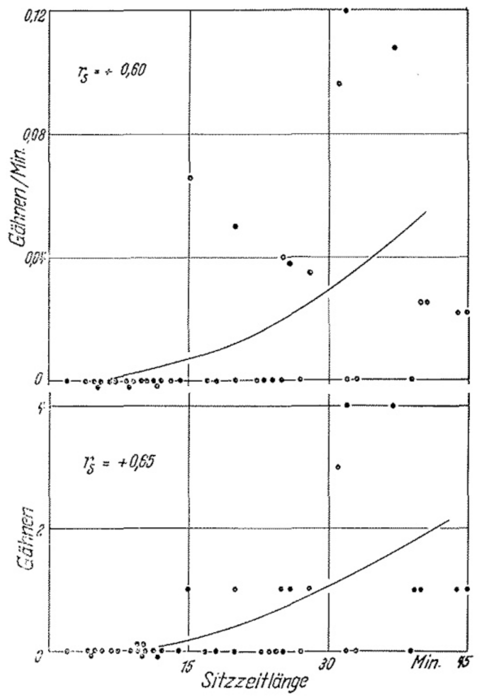

Figure 35. Dependence of the number of yawns ([Gähnen], bottom, $r_s = +0.65$, and their frequency [Gähnen/Min], top, $r_s = +0.60$, on the duration of the sitting periods [Sitzlänge]. Approximate regression curves.

threshold to these stimuli seemed to be individually different and probably also dependent on whether one approached the bird shortly after the beginning or towards the end of a sitting period, the threshold being lower in the first case than in the second. Females who had access to their nest blocked by a funnel trap, or who were afraid to enter the nest because foreign objects were close to it, often pecked at the ground without taking in food (displacement activity, see earlier), and snuggled down on the flat ground for some seconds as if incubating.

Incubation phase duration. From the day of laying the last egg to the day of egg hatching, both included, an average of 11.1 days elapsed for 32 broods. Since incubation begins on the day of laying the penultimate egg, but the hatching day counts as only half a day of incubating, this time period corresponds to the effective incubating time. Rare deviations (10 or 12 days) remain unexplained. If the egg clutch was removed prematurely, all incubating behaviour ceased after about 1 hour and could not be rekindled again by putting the eggs back into the nest. Experimental shorter-term removals of the eggs did not sustainably change the female's behaviour. When two females had their egg clutches, which had already been incubated for several days, exchanged for un-incubated eggs, they both incubated for a total of 14 days and only then gave up. This response normally prevents an overlong incubation of infertile or dead eggs.

Care of the young

Hatching. In 10 more closely observed broods, the hatching of all eggs took 4–15 hours, on average, it happened within 8 hours. Further 25 broods hatched within a maximum of 24 hours, none needed more. The young hatched approximately in the laying order of the eggs, but deviations from this were not rare. Hours after the appearance of fine cracks in the egg shell, the egg tooth of the hatchling broke through, and in less than 1 hour the blunt half of the egg-shell was broken off along the shell-equator. The chick, now sitting in the pointed shell cap/half, freed herself/himself of it within the next half hour. I could not hear any sounds emanating from the hatchlings (but ultrasound ones could not be ruled out). In 5 cases, 1–3 hours passed from the first peck opening of the eggshell to the complete hatching of the young. The incubating/brooding female did not help with the eclosion process. A few eggs did not hatch but were left in the nest. Donald (2004, p. 111) estimated that about a 5% average of eggs were infertile or the embryo within had died of unknown causes whereas Suárez et al. (2009) only reported 1,5% such instances. The eggshells were carried away by the female in its beak, occasionally also by the male, and were dropped some 10–20 m away from the nest. Smaller eggshell fragments were eaten by the female. The rarely occurring unhatched eggs were left in the nest.

Eggshell removal was releasable throughout the incubating and brooding phases; according to Koffan (1960) this response is also already triggerable during the wood lark's nestbuilding phase. With the exception of nest material, objects resembling eggshells or young nestlings, everything conceivable was carried away: roots and gross straw bits, feathers, lichens, little stones, pieces of

Table 6a. Removal of different eggshell models. In N experiments, the various models were removed by the female n+ times, percentages %, and not removed n– times.

Model type	n+	%	n–	*N*
Eggshell	38	100	0	38
Egg angle	21	91	2	23
White angle	25	61	16	41
White shell	12	60	8	20
Shell angle	7	39	11	18
Cylinder	9	50	9	18

Table 6b. Significance of the results in Table 6a (chi^2 and Fisher's test).

	Egg angle	White angle	White shell	Shell angle	Cylinder
Eggshell	n.s.	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Egg angle		$p < 0.01$	$p < 0.05$	$p < 0.001$	$p < 0.01$
White angle			n.s.	n.s.	n.s.
White shell				n.s.	n.s.
Shell angle					n.s.

Eggshell: 0.5 cm^2 piece of a black-headed gull's eggshell, the colouring of which was grossly similar to that of the larks. Egg angle: sheet metal angle of similar size, covered with seagull eggshell. White angle: sheet metal angle as above, but painted with white oil paint. White shell: Irregular pieces of sheet metal of 0.5 cm^2 painted with white oil paint. Cylinder: Unpainted wooden cylinder of egg size.

paper, bottle tops, wood pieces, mussel shells, a stuffed mouse skin, and other things that I placed in the nest or at its edge. The discrimination against eggs proper was good, because approximately egg-shaped pebbles, empty egg shells with a hole of about 1 mm, and egg-sized and -coloured cylinders were carried away from the nest. Since these things were left lying for different lengths of time before being carried away, it was possible to examine the response-releasing strength of some eggshell models. In four series of experiments, I placed four eggshell models arranged in a Latin square on the edge of four different nests, 5 cm outside the nest, and 30 min later I checked which models had been carried away (Table 6). The number of experiments for the different models differs because some were used in more experiments than others. Deviations in the number of trials from the multiple of four numbers expected were due to the abandonment of some nests due to predation during the experiments. Only the differences between the eggshell and egg angle group, between the white angle and white shell group, and the shell angle and cylinder group are significant in the table. This indicates that the colour or colouring pattern and perhaps the texture were probably important triggering factors.

Table 7. Eggshell removal during the incubation and brooding phases.

	Incubating days			Brooding days
	1–5	6–8	9–12	1–8
Carried away	9 (36%)	16 (57%)	18 (58%)	20 (95%)
Not carried away	16 (64%)	12 (43%)	13 (42%)	1 (5%)
Trials	25 (100%)	28 (100%)	31 (100%)	21 (100%)

chi^2, $p < 0.01$

Surprisingly, the reaction to the white models, admittedly not as blob-shaped as faeces, was relatively low when compared with the white faeces (see later), which were carried away so promptly during the corresponding phase. Table 7 shows that carrying-away responses increased very strongly after hatching—white angle, white shell, shell angle, and cylinder are pooled here–, probably because the male also visited the nest during the brooding-of-the-young phase and showed the carrying-away reaction. But possibly the reaction threshold was additionally reduced in the female.

The carrying-away response seemed resistant to habituation: in two experiments the incubating females removed 10 or 20 pieces of paper in less than 20 minutes; and once, when an eggshell model was firmly pinned down on the nest edge, the frequency of the female's attempts to carry the model away did not decrease over the course of 2 hours. No signs of reaction fatigue could be detected in the aforementioned series of experiments either (cf. Tinbergen, Broekhuysen et al., 1962, gulls). Individual differences in the preparedness to carry away egg shells are likely: in 13 trials one female carried away the same eggshell models 12 times (92%), another female only 6 times in 15 trials (40%). As already commented, the discrimination of the eggshell against egg models was very good. One female, however, incubated the wooden cylinder in one experiment and carried it away in the next. One of the earlier mentioned cylinders was once rolled-in instead of being carried away. Wooden eggs of natural shape, size, and colouring were incubated without any ado (cf. Tinbergen, Kruuk et al., 1962, gulls). In the literature, there are reports of dead and even living chicks being carried away (Hesse, 1917; Mountfort, 1940; Lewis, 1959; Donald, 2004, p. 119), but my own two experiments with a dead chick were negative. The subject of skylark nest parasitism by cuckoos is treated in Donald (2004, p. 107; see also Hegemann & Voesten, 2011), who concludes that they somehow seem to be able to resist it rather well. I saw no instance of it in Ravenglass, but then the appearance of cuckoos in the study area was quite exceptional in any case.

Brooding. As soon as the first young had hatched, the female's behaviour changed. The incubation rhythm switched abruptly into the brooding rhythm (Figure 36). The stimuli triggering the transition were obviously the sight of the hatched young and their tactile presence. Two incubating females into whose nest I put young 2 days prematurely, changed their behaviour similarly suddenly. The brooding times were shorter than the sitting times and fluctuated only slightly during the day (Figure 37). On average, the brooding pauses were just as long as the sitting pauses, but scattered more amply, as the female now had to gather food for her young, an undertaking of chancy duration. Variations depending on the time of day could not be detected (Figure 37). There was no significant correlation between the lengths of the subsequent and preceding brooding pauses and brooding times. The brooding performance (Figure 38) showed two maxima depending on the time of day, which were only barely significant as they were accompanied by a simultaneous variability peaks, $p^* < 0.05$ (chi^2). On average they were lower than the incubation performance peaks. They

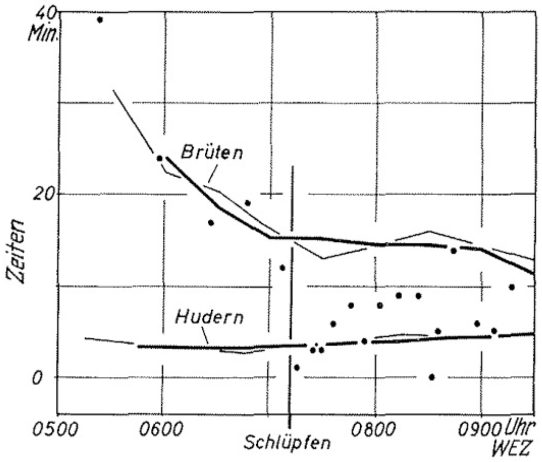

Figure 36. Switch from incubation rhythm to brooding rhythm upon hatching [Schlüpfen]. Curves from Figures 27 and 37 respectively. Dots show sitting [Brüten] or brooding [Hudern] times respectively on the day of hatching.

decreased in the course of the brooding phase, i.e., the pauses become longer and longer, the brooding times shorter and shorter, and under normal weather conditions the female did not brood the young at all from their 5th day of life onwards (Figure 39) (chi^2, $p < 0.01$). Rain and perhaps low air temperatures were able to increase brooding performance or reactivate the brooding altogether (Table 8). The brooding behaviour was not very different from that of incubation: the female sat a little looser and egg turning, or rather "young turning", was not shown. Willford (1925) observed the retrieval of nestlings, but I did not. He also reported a shading of the young in strong sunshine: the female stood panting with puffed-out plumage over the nest hollow containing the young. Typical for the phase of caring for the young is the warning call of the parents—especially the females'—that causes the young, once they are older than 4 days, to duck down in the nest, keeping still. They also do so if they are suddenly shaded by a bird of prey, a gull, or by a mere singing male skylark flying overhead; and later when they are 5 days or older, if an unusual object approaches them or when they hear the alarm calls of other local birds (wheatears, *Oenanthe oenanthe*, pipets, *Anthus trivialis*, or black-headed gulls, *Larus ridibundus*).

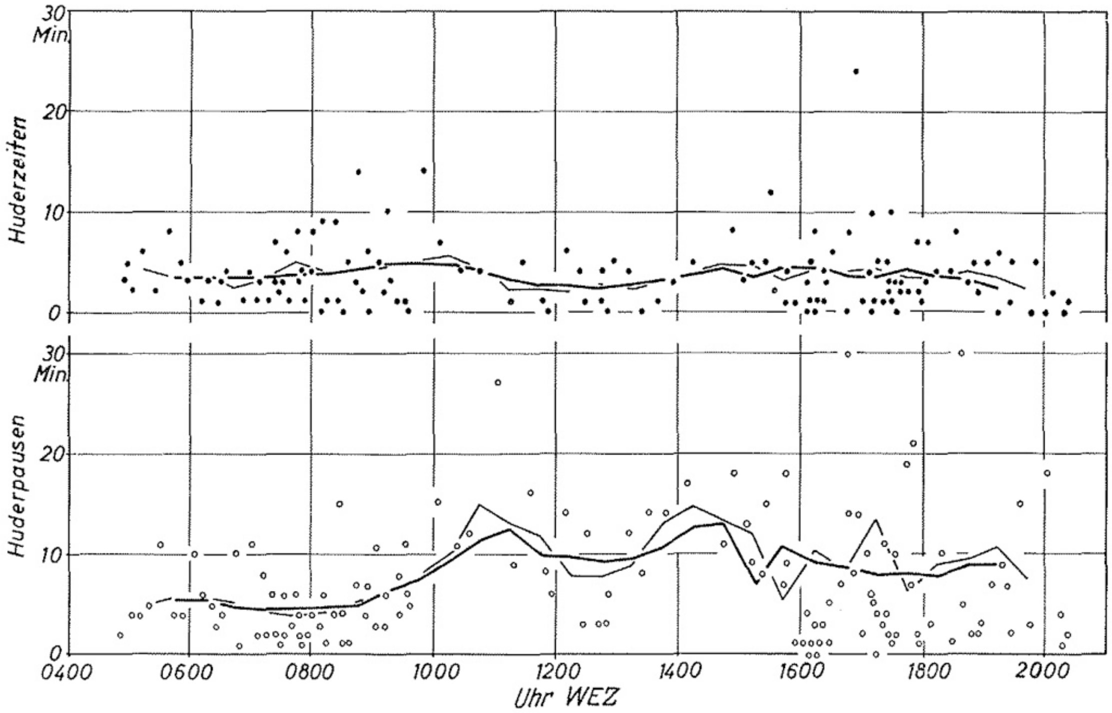

Figure 37. Brooding times [Huderzeiten] and pauses [Huderpausen] depending on the time of day. 48 hours of observation of one female. Moving averages across 90 and 150 minutes.

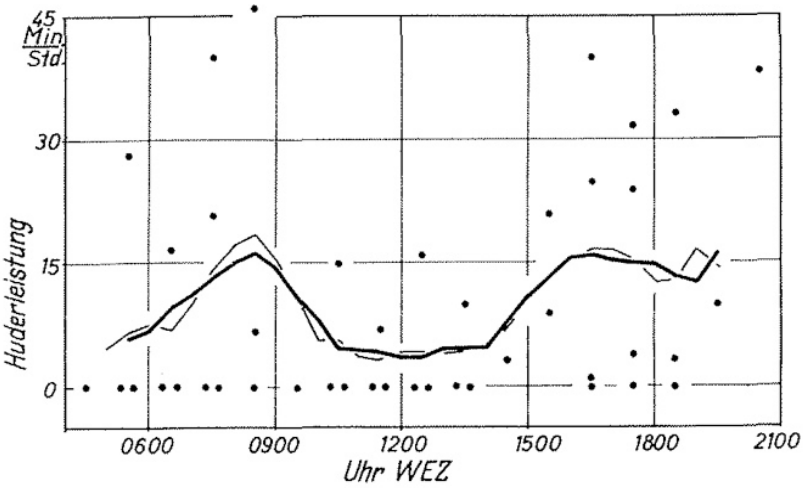

Figure 38. Changes of brooding performance [Huderleistung] depending on time of day, GMT [Uhr WEZ]. Each dot represents a 60-minute observation period of one female. Moving averages across 120 and 180 minutes.

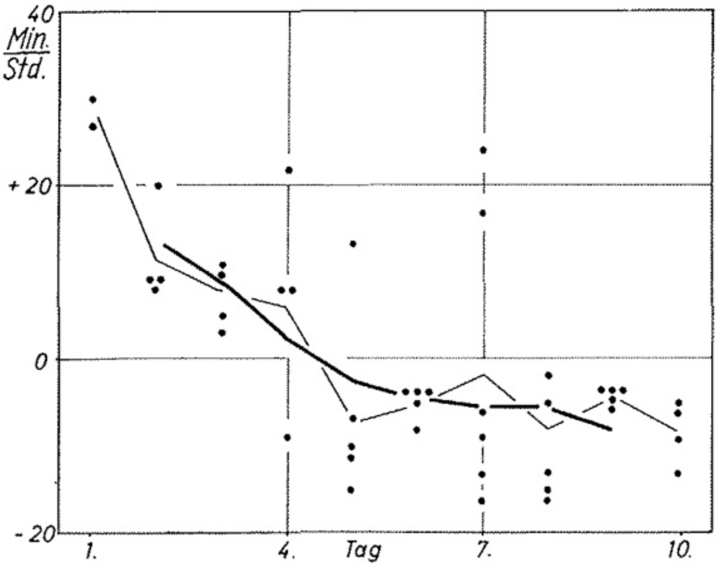

Figure 39. Decrease of brooding performance with increasing age of chicks in days [Tag]. Ordinate: deviation of brooding performance in minutes per hour [Min/Std.] from 180-minute curve in Figure 38.

Feeding young. A few minutes after the first young hatched, the female began to feed. Minutes to hours later, the male also started to feed. Even sooner though, just after the beginning of egg incubation, the male came to the nest with food in his beak and uttered the feeding call, a repeated soft *tju tju*. These occasional visits became more frequent towards the hatching date (Figure 40). The females behaved similarly, but much less frequently in this way. Both males and females swallowed what they had brought along after looking into the nest. Never did the male feed the brooding female, but the latter left the nest hastily as soon as the male approached, or later if she was brooding. Conversely, the feeding male hurriedly left the nest as soon as the female approached with food.

Table 8. Brooding performance on 3 days during 4 30-minute periods at the same times of the day.

Chicks' age	Day 5	Day 7	Day 8
Weather	Dry	Rain	Dry
Brooding performance in min. per 30 min. of observation	0	18	0
	1	12	0
	3	25	0
	1	1	0

Mann Whitney, $p = 0.002$

The hatched young, especially their beg-gaping, promoted the feeding behaviour in the female, as they suddenly came to the nest with food far more often after hatching than before. In the male, the female's feeding behaviour had a facilitating effect, as did the presence of the young after first feedings, since the male then also brought food much more frequently. When I exchanged a female's eggs for young from another brood 4 days before hatching, the female began to feed immediately, and the male with about the usual latency.

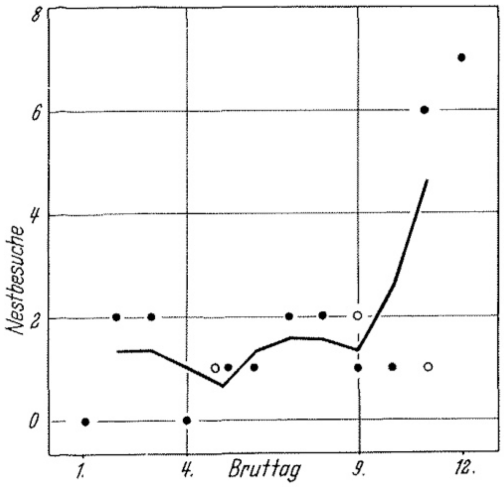

Figure 40. Frequency of nest visits [Nestbesuche] by the male (filled dots) and the female (empty dots) with food or feeding calls during the brooding phase [Bruttage]. Each dot represents a 5-hour observation, 0 visits by female left out. Moving averages over 3 days.

When skylarks with some food in their beaks proceeded to pick up or hunt for further prey, they first laid their bundle on the ground, gathered new food, and then always found and picked up the earlier bundle again. This was repeated several times until they had gathered enough food to carry it to the young (Ashford, 1915; Turner, 1915). Pätzold (1983, p. 81) reports that skylarks occasionally pursue insects on the wing for short distances; I saw this too but not regularly: mostly they picked them up while walking. Once near the nest, they uttered the feeding call, especially during the first days, when the young were still blind. Then they fed the food to one of the begging young, rarely to several. The feeding frequency did not show a definable daily cycle (Figure 41), but increased with the age of the nestlings (Figure 42, median procedure, chi^2, $p < 0.001$). In addition, the amount of food also increased as the larks caught increasingly larger prey. If younger nestlings were exchanged for older ones and vice versa ($N = 4$), the feeding larks adapted the prey size and food quantity they brought very quickly. The proportions of male and female feeding seem to change over time (Figure 43). The male certainly fed less frequently than the female during the period when the young were in the nest; if the female proceeded to a further brood, the male was exclusively in charge of feeding the young outside the nest from the earlier brood. Generally, it appeared to the author that the parents preferentially fed insects to the young and fewer seeds or small grains. They took quite some proportion of the latter for themselves even during the breeding season (about 1/3 of seeds and grains).

For more on skylark feeding generally, see Pätzold (1983, pp. 76ff.). Donald (2004, p. 121) reports the mean distance flown by the parents from the provisioning site to the nest as amounting to 75 m, with some flights even reaching up to just over 350 m. Incidentally, Pätzold (1983, p. 76), Donald (2004, pp. 120 & 156), and Pérez Granados et al. (2016, p.18) have much to say about the diet of skylarks in general, and particularly about what they feed their young (see also Jeromin, 2002).

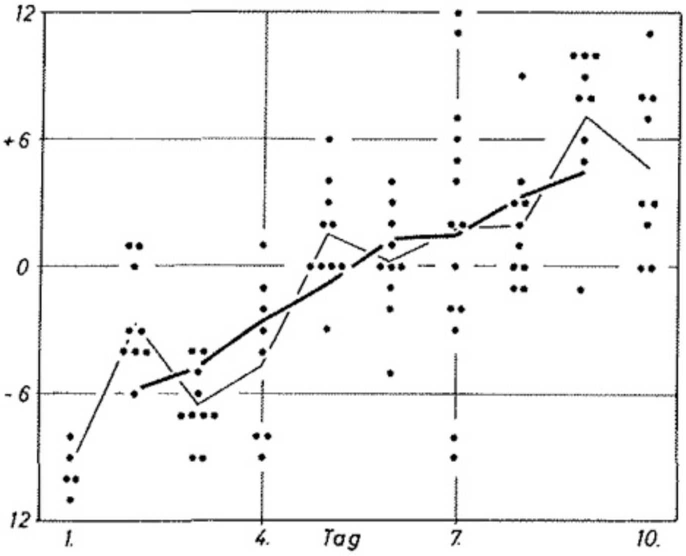

Figure 41. Variation of feeding frequency [Fütterungen/30 Min] during the day. Each dot represents a 30-minute observation of a pair with four young. Moving averages across 90 and 150 minutes. Abscissa: GMT [Uhr WEZ].

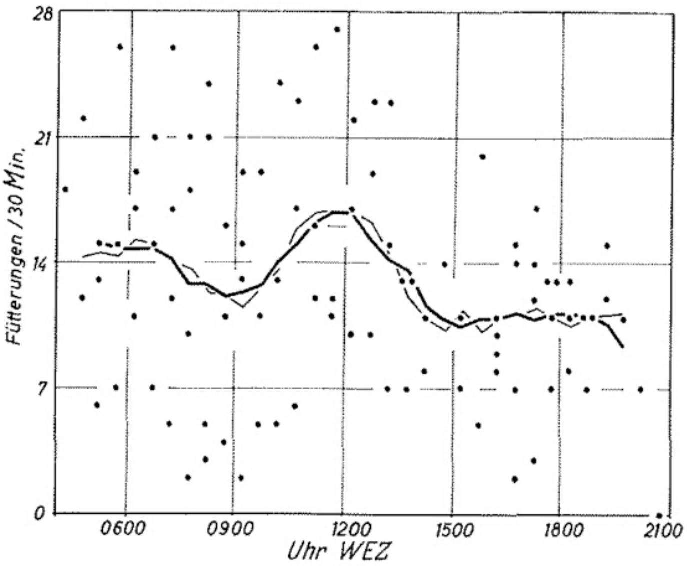

Figure 42. Feeding increase with the aging of the young. Ordinate: deviations of the feeding frequency from the 150-minute curve in Figure 41. Daily average and moving average over 3 days. Abscissa: day [Tag].

Gaping behaviour of the young. Initially, as long as they were blind, the young only gaped upon acoustic stimuli. High pitch sounds were more effective than low pitch sounds. When gaping, they raised their heads in an undirected, slightly swinging movement and opened their very conspicuous black and yellow patterned pharynx wide. In the course of the 4th day of life they opened their eyes, and about 1 hour later practically every object moving near the nest already triggered gaping. At this time, they also began to produce a hoarse gaping sound. In the course of the 5th day of life,

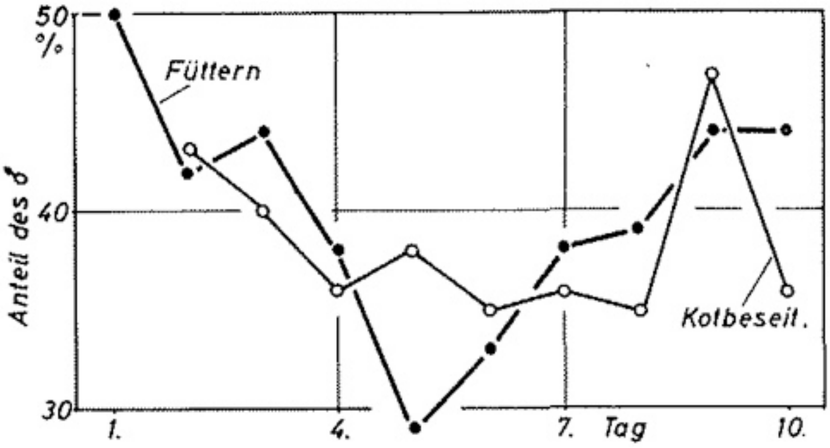

Figure 43. Fluctuations in the contribution of the male contributions to feeding [Füttern] and faeces removal [Kotbeseit.(igung)] with increasing age of the young in days [Tag]. One pair, 1222 feedings and 275 defecations. Ordinate: contribution [Anteil] of male, %.

the throat began to be directed towards the releasing object. At the same time, the optical reaction became more specific, until they finally gaped only at the parents. Similarly, at this age, the initially unspecific acoustic triggering became more focused, so that finally only the parents' feeding call was effective. They did not react to ground vibrations, and only rarely did they react to touch of their beak bulges or other body parts.

Optical and acoustic stimuli were additive, i.e., when presented simultaneously, two individual heteromodal stimuli pushed each other up over the threshold to release the gaping. Furthermore, I could detect a reaction-specific initial friction and a corresponding later fatigue, both independent of which of the two stimuli were used and of their order. In addition, however, a stimulus-specific fatigue could be observed; if one stimulus was repeated often enough not to be responded to, the other still remained fully effective. This applied not only to stimuli of different modalities, i.e., optical and acoustic, but also to different stimuli of the same modality. A persistence of the reactions after the end of stimulation was occasionally observed, i.e., after a series of stimulus tests individual young gaped spontaneously once or twice (compare Prechtl, 1953). In addition to threshold lowering, hunger also had the effect of yielding a behavioural regression: older young began to gape again when they were very hungry, as during their earlier nesting period; such a regression to earlier behaviour was also typical of sick young. Touching the base of the tongue already triggered strong swallowing in just hatched young (Dewar, 1908). During begging, salivary secretion seemed to be much augmented. Young birds that had left the nest occasionally showed a synchronous, fast whirring of the wings during beg gaping.

Nest cleaning. The faeces of the nestlings were swallowed or carried away by the parents, almost always immediately after feeding. They picked up them up directly from the young's cloaca, or later from the floor or the sides of the nest, where the older young deposited them with an appropriate movement. I could not detect any action by parents that specifically enticed them to defecate, their simple presence seemed to suffice. They ate the excrement on the spot. Later, they carried the bales away in their beak, mostly flying, in 75% of the cases dropping them only after landing, often at the same place in their territory repeatedly, when they cleaning their beak on the ground. Initially, all excrement bales were eaten, later, when they were more firmly skinned, less so, probably because they were then easier to carry away (Figure 44). During the already mentioned exchange of differently aged young, the larks changed their excrement disposal behaviour in the according ways. The faeces removal rate did not vary by time of day (Figure 45) and also not with the increasing age of the young (Figure 46). They seemed to cope with the increased feeding by increasing the size of the faeces bales. In fact, at the end of the in-nest period, the droppings bales were about 10 to 15 times larger than the first ones. The partners' participation in the feeding and faeces removal seem to have co-varied (Figure 43). That is to be expected because the more often one feeds, the more excrement is produced. It is likely that the removal of both droppings and eggshells by carrying them away is based on the same behavioural mechanism.

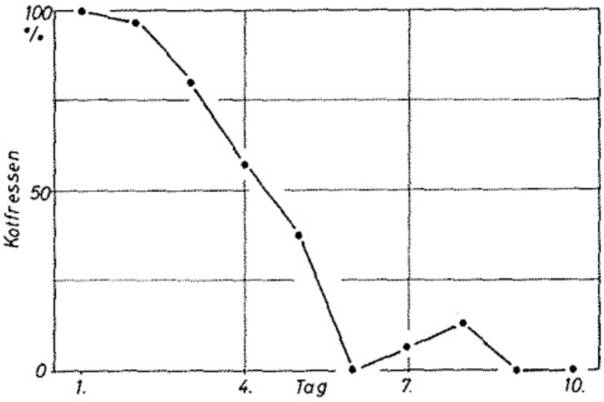

Figure 44. Percentage of faeces bales eaten [Kotfressen] rather than carried away depending on the age of the young in days [Tag]. One pair, 275 defecations.

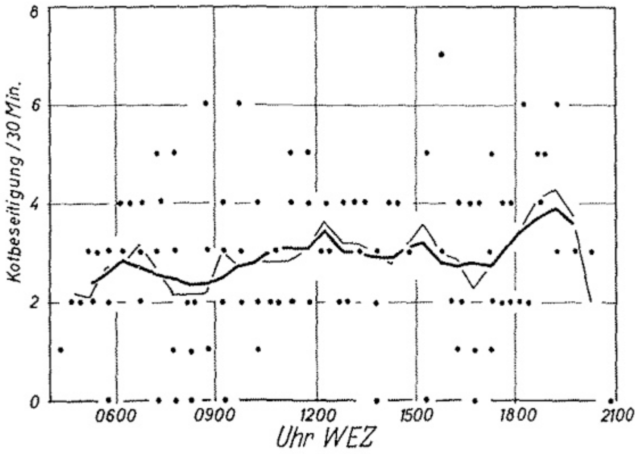

Figure 45. Variations in the rates of faeces disposal [Kotbeseitigung/30 min] depending on time of day (GMT [Uhr WEZ]). Each point represents a 30-minute observation of a pair with a brood of 4 young. Moving averages across 90 and 150 minutes.

Donald (2004, p. 113) noted the colourful gape of the young and wondered whether this helps the parents to locate them in nests in darker locations (e.g., in higher vegetation?). Another hypothesis is that the brightness of the individual gape colorations signals the healthiness of the various young and may influence the rates of feeding them (Ayala et al., 2007) but neither Donald nor I have relevant data on that particular issue. The next issue that Donald rightly stresses (p. 115) is the extraordinary growth of skylark chicks, particularly of their legs—only 8 days later they are able to move away from the nest, in some cases for quite considerable distances (see below).

Nest leaving. The young of a sample of 32 broods remained in the nest for 7 to 11, mostly 8, on average 8.5 days. On the 6th day they jumped out of the nest to meet their feeding parents, but returned to the nest. On the 7th day they often stayed outside longer and hid somewhere close to the nest, but at least hopped back to the nest for the night. On the 8th day they behaved similarly,

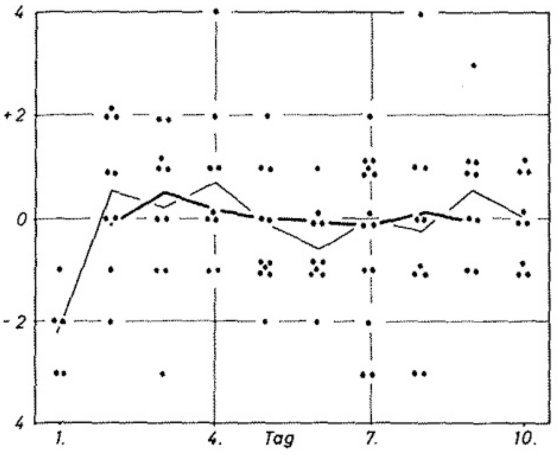

Figure 46. Faeces disposal depending on the age of the young in days [Tag]. Ordinate: deviations of the faeces disposal frequency from the 150-minute curve in Figure 45. Daily average and 3-day moving average.

but hopped and ran further away from the nest and begged *iuiu, iuiu*, which can be easily distinguished from the beg-gaping call. As described above, leaving the nest is an active performance of the young. In some instances, however, it was observed that the parents actually lured the young away from the nest with food in their beaks (Gröbbels, 1940). The young of a brood definitely left the nest surprisingly simultaneously; in 10 more precisely observed cases, all had gone within 4 hours at most.

Care of the nidifugous young. Until they became fully independent on about their 30th day of life, the young birds continued to be cared for by their parents outside the nest. After leaving the nest, the feeding rate did not increase significantly. On the 15th day, the young, which had just become fully fledged, started with their first independent food uptake, and on the 19th day they were already constantly searching for food. Probably the parents were paying them less and less attention since they became fledged, from the 12th to the 15th day of life. In any case, the parents attended them less and less often; often the young had to wait 1–2 hours. They followed the feeding parent bird over longer distances, and the parent would then push each little bit of food it picked up into their throats one by one. Afterwards the chicks went back to cover or started to look for food themselves.

The male’s share of feeding normally increased sharply: on the 10th day after nest leaving, it was 64%, on the 16th day 82%, and on the 24th day 100%. Deviations from this were possible if the female did not move on to produce the next clutch. I did not observe incubating females feeding, but I could see nestbuilding females doing so—they were able to import nesting material and feed their young within the same 5 minutes without confusion. If both partners fed, they seemed to limit themselves to certain young by the hour or so: that is, the male fed the young A and B, the female the young C. The next day the distribution could already be quite different. The chicks—presumably particularly when they were hungry—often called out the previously mentioned begging sound during this phase, which obviously helped the parents to find them. The young moved very widely across the terrain on foot and could travel up to 50 m in less than 15 minutes before they became airborne. Mostly they followed their feeding parent, who obviously remembered where the young were at each stage, because they were able to locate them unerringly, even if they did not call. From time to time, the young changed their location, either on their own, or because they were frightened by something without their parents noticing. Then the feeding parents were obviously at a loss until they heard the easily localizable begging call of the young; this was also demonstrated by several young-transporting trials. The described movements of the young were by no means restricted to the parental territory; in neighbouring territories they were apparently not noticed or ignored; only once did I see a territory owner attack such a foreign young bird. It needs to be remembered, that by the time the first chicks left their nest, the skylarks' territorial behaviour had already diminished considerably. Nevertheless, the parents that tried to feed their young in a foreign territory were still attacked from time to time. Since the parents clearly preferred to feed in their own territory, their young tended to stay there. I could never observe a feeding of foreign young, although some males seemed to find themselves in such a situation. It is not clear how the parents distinguished between their own and others' young; but individual variations of their begging calls may have played a role.

Carrying away excrement was only sporadic in the first days after nest leaving, when the young kept hiding in the same place for a longer period of time. When the young were about 28 days old, they were suddenly attacked now and then, mostly by their male parent, but were then mostly fed again by him shortly afterwards. Thus, on about the 30th to 32nd day of life, the young finally separated from their parents and joined together in smaller groups of skylarks that then roamed around in the immediate vicinity. They were extremely shy, behaved inconspicuously, and were difficult to observe. The adults did not take notice of them. These young seemed to leave the observation area before the adults. Notably, one 10-week-old still in its juvenile plumage was already observed ground-singing (see also Pätzold, 1983, p. 129).

Swarm behaviour

In July, the territories began to dissolve; the now no longer breeding larks joined together in small troops of 3 to 5 individuals. By the beginning of August these had grown into flocks of 20 to 30 skylarks that did not only consist of local (= ringed) birds. Their attachment to the breeding area was then already very loose. By mid-August I could only observe a few skylarks in Ravenglass. Some of them, which had moulted at an earlier stage, seemed to show some interest in their territories again at this time when the weather was fine. Within the flocks I did not see any signs of continuing pair bonds, instead the partners of a pair often joined different flocks (see also Busche, 1982). Whether there was a separation of males and females within the groups could not be clearly determined, but it is possible. The birds in the flocks had very long flight distances, which made it very difficult to observe them. They spent most of their time eagerly foraging. They kept individual distances among themselves (Tinbergen, 1957; cf. Simmons, 1952, desert larks, *Ammomanes deserti*) by briefly threatening other larks that came too close, which then always avoided them; I did not see any 'bodily' fights. Thus, small "movable territories" of about 30 cm in diameter developed (Gerber, 1949, crested lark). I could not hear any particular calls except the flight call *tschirit* from the swarm birds; they uttered it in flight or just before flying up. Often, they sang softly (subsong?) during their search for food. From the end of August until the arrival of the breeding birds in spring, no skylarks were seen in the area according to Ravenglass and Drigg village residents. Ring recoveries and observations (W. R. P. Bourne, verbal communication) indicated that although British skylarks do not migrate regularly in winter, they do roam extensively throughout the British Isles (cf. Hegemann et al., 2010, Netherlands). Donald (2004) treats the swarm, migration, and winter behaviour of skylarks quite extensively, we refer the reader to his chapters 9 and 10.

Vocalizations

In this chapter, I briefly review the vocalizations of the skylarks mentioned in the various chapters in a unified context (for information on the flight, ground, and pursuit singing, see the earlier *Song* chapter). Note again the great inter-individual differences among the flight songs and the pronounced intra-individual variations of the ground song. Flight-song sonograms are presented and richly commented by Pätzold (1983, Fig. 63, pp. 90ff.) and Donald (2004, p. 74f.), but the only one of diverse calls is illustrated with a sonogram by Donald (p. 160). I could quite reliably recognize several individual males by their flight song (see Briefer et al., 2008, 2010). In their song the skylarks wove in elements that strongly reminded me of some their own calls, especially of their contact call and their luring call; often they intercalated sounds that strongly reminded me of the calls of locally occurring waders (dunlins, ringed plovers; see also Poulsen, 1996) and wheatears (Brown, 1924b; Lloyd, 1948; see also Pérez Granados et al., 2016, p. 15, who remarked that skylarks even pick up song elements from species that they can only have heard during winter). Skylarks are known to lovers of caged birds as excellent imitators (Perzina, 1892). Young birds can produce a well-developed ground song at the age of two and a half months (Naumann, 1900). The attack call (see *Agonistic behaviour* chapter) was often not easy to distinguish from the contact call, neither by the sound nor by the situation in which it was heard (see *Sexual behaviour* and *Incubation* chapters): the former sounds harsher and harder like *tschrr, tschrr*, the latter softer and more melodious like *chrr, chrr*. It seems to me that these calls are really graded variations of a single call: all intermediate variations occurred, and perhaps even in a third variation, which could be called escape call according to the situation in which it is emitted. Only sound recordings and spectrograms are likely to be able to solve these questions. Pätzold (1983, pp. 87–92) reviews the skylark's vocal behaviour, but only shows sonograms of the song (which are indeed complexly variable!) and not of the calls. Cramp (1988) recognizes a contact call, *sker, sker, titeesker,* a courtship call, a liquid *tchirrup,* and some further call variations, a *tit, terr, reep,* a *where,* and a dry *trrt* or *trt.*

The hate call (*gjj gjj*, see *Agonistic behavior* chapter) is surprisingly similar to the begging call of the young (*ch ch ch*, see *Care of the young* chapter), perhaps because both calls are produced out of the wide-open beak. Several times I observed young skylarks begging from their siblings, probably aggressively. Thus, by changing its function the begging call might have developed into the hate call. Likewise, the luring call (*juu juu*, see *Sexual behaviour* chapter) may have developed from the feeding call by the young (*iuu iuu*, see *Care of the young* chapter); the change of function would in this case have been minor as the purpose of both calls was similar anyway.

The shrill fear call (see *Behaviour towards other species* chapter) was emitted by both old and young birds when they were suddenly attacked by a predator (merlin, stoat). The warning call (*tluituitui tluituitui*, also described in that chapter) was typical for the phase of caring for the young, as was the feeding call *(tju tju*, see *Care of the young* chapter), which served as an acoustic trigger for the chicks'begging. The flight call (*tschirit tschirit,* see previous *Swarm behaviour* chapter) was presented by members of a skylark flock only outside the breeding season and seemed to promote their staying together during take-off. The following sounds were uttered almost exclusively by the males: all three types of singing, and less pronouncedly so the warning call; all others belonged to both sexes, only that the males were generally more vocal.

Conservation

Sadly, this paper on the behaviour of the skylark may soon have to be classed as a palaeontological one in as far as it might soon be on the behaviour of an extinct species (Donald et al., 2001)! Judging by J. D. D.'s local experience (in the Lake Constance area) alone, skylark numbers are in vertiginous decline. Ten years ago, when opening the window of my study in spring I could hear the song of two different males above a nearby field. Now they are gone, as skylarks have generally become a rare species in the wider area (cf. Schlager et al., 2020). Several factors related to agricultural intensification seem to have contributed to this decline: reduced crop diversity, predominance of autumn-sown crops, the increased use of fertilisers and insecticides (European Commission, 2007), increase of energy crops (such as silage maize; Csikos & Szilassi, 2020), greater sward height (Kolecek et al., 2015), reduction of grazing land (Mischenko et al., 2019), farming tramlines as linear structures in fields that are dangerous nesting sites (Püttmanns et al., 2021), but also more wind turbines (Erickson et al., 2014) and predators at field edges (Morris &

Gilroy, 2008)—taken together, the general deterioration of the agricultural landscape as a habitat for skylarks (Chamberlain et al., 1999; cf. Guette et al., 2016). Thankfully, manifold efforts are underway to improve the situation (e.g., Brodier et al., 2014; Buckingham et al., 2015; Lovasz et al., 2021), but much work remains to be done (Naturschutzbund Deutschland, 2019), not only to protect the skylark, but also biodiversity in general (European Commission, 2020).

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Useful websites

Xeno-canto: Sharing bird sounds from around the world. Xeno-canto Foundation. https://www.xeno-canto.org/species/Alauda-arvensis

Animal sound archive. Museum für Naturkunde Berlin. https://www.animalsoundarchive.org

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