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On song post selection and the timing of song in the Corn Bunting *(Miliaria calandra)*

Zur Wahl der Singwarte und zum zeitlichen Ablauf des Gesanges bei der Grauammer *(Miliaria calandra)*

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Key words: *Miliaria calandra*

Summary

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Song post use and the timing of song was studied in the promiscuous Corn Bunting. Preferred song posts (overhead wires, windbreaks) had a large extension in territories occupied for many years. More preferred song post types were present in territories which were frequently occupied. Song post utilization changed during the study years, perhaps because of habitat changes. Sound transmission was maximized by choosing high song posts in winter, fences in spring and higher song posts again in mid and late summer. High song posts were used during the middle of the day and lower ones in the morning and the evening. In winter males sang during thaw in weather with high visibility, whereas days with frost or fog were avoided for singing. It is suggested that particular song posts are chosen, and that song is timed partly, in order to maximize attraction of females.

Zusammenfassung

MØLLER, A.P. (1986): Zur Wahl der Singwarte und zum zeitlichen Ablauf des Gesanges bei der Grauammer *(Miliaria calandra)*. Ökol. Vögel 8: 57-66.

Die Singwartenwahl und der zeitliche Ablauf des Gesanges bei der promiskuiden Grauammer wurde untersucht. Die bevorzugten Singwarten wie Überlandleitungen und Hecken waren in den langjährig besetzten Revieren weit verbreitet. Häufig besetzte Reviere enthielten besonders beliebte Singwarten. Die Bevorzugung von bestimmten Singwarten änderte sich über die Jahre — möglicherweise in Zusammenhang mit Biotopänderungen. Die Vögel versuchten die Reichweite des Gesanges im Winter durch Singen von erhöhten Plätzen, im Frühjahr von Zäunen und im Sommer und Spätsommer wieder von erhöhten Plätzen zu optimieren. Hohe Singwarten wurden zur Mittagszeit, niederigere am Morgen und Abend bevorzugt. Im Winter sangen die Männchen wenn es getaut hatte besonders bei klarem Wetter, nicht jedoch an Tagen mit Frost oder Nebel.

Es wird angenommen, daß die Männchen versuchen, durch die Wahl bestimmter Singwarten und ein zeitliches Abstimmen des Gesanges die Anlockung der Weibchen zu maximieren.

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1. Introduction

Environmental conditions put selection pressures on song patterns, song morphology, and choice of song posts (e.g. KONISHI 1970, CHAPPUIS 1971, JILKA and LEISLER 1974, HUNTER & KREBS 1979, HUNTER 1980). Song may be broadcasted to optimize transmission towards conspecifics of importance (SCHLEIDT 1973, LEMON et al. 1981). In monogamous bird species this will usually be the mate, the nearest neighbours, and young within or outside the nest. In polygynous or promiscuous species sound transmission is expected to be maximized in order to attract many females.

Males of the promiscuous Corn Bunting *(Miliaria calandra)* (HEGELBACH & ZISWILER 1979) occupy territories and sing frequently from late March through mid August (MØLLER 1983a). Territories occupied for several years (apparently by different males in different years due to a high mortality rate) are smaller than other territories, and males inhabiting these territories sing more frequently than others (MØLLER 1983a). Furthermore, females are observed more often in territories frequently used by males, and the breeding success is higher in these territories than in those rarely occupied (MØLLER 1983a). Male Corn Buntings may thus attract females by means of song.

Female attraction may be optimized by choosing appropriate song posts with optimal sound transmission possibilities. Furthermore, the timing of song in relation to sound propagation may act to optimize attraction of potential mates. The temporal and spatial distribution of song has been investigated in this paper.

2. Study area

The study was conducted at Kraghede (57°12'N, 10°00'E), N Jutland, Denmark. A total of 14,66 km^2 arable land with few coniferous plantations and a number of houses and farms were investigated. A detailed description of the study area is given in MØLLER (1983b) with comments on habitat alterations during the study period.

3. Methods

The Corn Bunting was censused during the breeding seasons 1972 and 1978-1982. I made censuses on bicycle following roads and paths on 10 occasions in 1972, 21 in 1978, 20 in 1979, 11 in 1980, 22 in 1981, and 149 in 1982. Birds were mapped during each census. Song posts were recorded especially in later years, whereas some detailed records of song posts in the early years are lacking, thus the varying sample sizes. Censuses took place between late March and early August and with regular censuses during the winter period (October to mid March). Most observations were made during maximum song activity in the morning.

Territories were mapped from the total number of censuses each year. The numbers of territories were 50, 49, 43, 36, 55 and 51 in the years 1972 and 1978-82. If two territories overlapped during two different years they were recorded as the same territory being occupied for two years. If there was overlap with more than a single territory, then the territory with maximum overlap during two years was considered occupied. Territory use was calculated as the number of years with male Corn Buntings holding the territory; thus, duration ranged from 1 to 6 years. The length of the three main song post types (overhead wires [height: 6-8 m], windbreaks [height: 2-5 m] and fences [height: 0,75-1 m]) within territories was measured on a map to the nearest 25 m. Song post preferences were calculated for the 1982 territories using the Jacobs index:

$$P_i = \frac{X_i/X \div Y_i/Y}{X_i X + Y_i/Y}$$

where P_i is the preference index for habitat i, X_i is the number of times a male is recorded in habitat i, X is the total number of records, Y_i is the length of habitat i and Y is total length of overhead wires, windbreaks and fences (a few rare song post types were excluded from the calculations) (JACOBS 1974). Values range from ÷ 1 (avoidance) to + 1 (preference).

Daily song activity was measured as the frequency of territories with song during the period 10 April to 31 July 1978 and 1979. For each hour at least 5 censuses took place along a 4.55 km route with 20 territories within the study area. Song frequency is expressed as the fraction of territories with singing males during each hour for all censuses combined. Seasonal changes in song activity are small during the period mid April to late July (MØLLER 1983a).

Statistics were used in accordance with BISHOP et al. (1975) and SOKAL & ROHLF (1981).

4. Results

4.1 Song post occurrence

The territories occupied many of the years contained more overhead wires and windbreaks than territories occupied for fewer years by a male (Figs. 1-2). The length of fences, however, did not vary with territory use ($r=0.07$, $t_{(103)}=0.7$, n.s.).

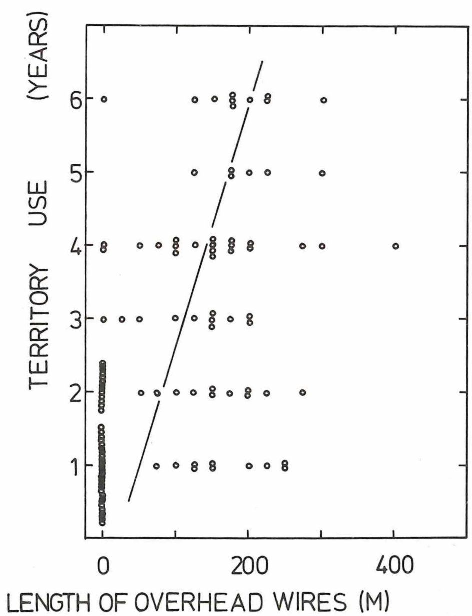

Fig. 1. Territory use (no. of years occupied) in relation to the length of overhead wires within Corn Bunting territories. $Y=0.03\,X \div 0.61$, $r_{(105)}=0.52$, $t_{(103)}=6.18$, $P<0.001$.
Abb. 1. Reviernutzung (Nutzungsdauer in Jahren) in Abhängigkeit zur Länge von Stromleitungen innerhalb der Grauammer-Reviere ($Y=0.03\,X \div 0.61$, $r_{(105)}=0.52$, $t_{(103)}=6.18$, $p<0.001$).

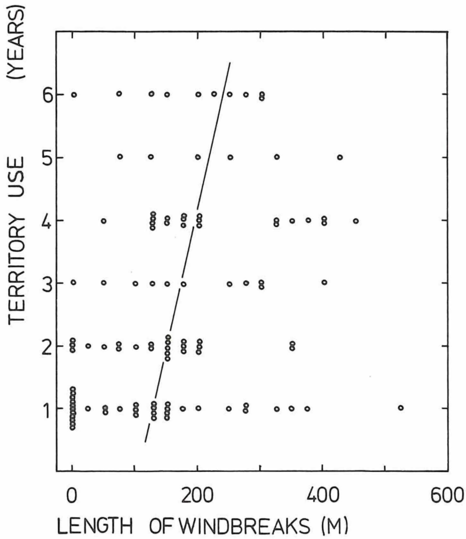

Fig. 2. Territory use (no. of years occupied) in relation to the length of windbreaks within Corn Bunting territories. Y=0.05 X ÷ 4.86, r=0.30, $t_{(103)}$=3.19, P <0.01.
Abb. 2. Reviernutzung (Nutzungsdauer in Jahren) in Abhängigkeit von der Länge von Windhecken innerhalb der Grauammer-Reviere (Y=0.05 X ÷ 4.86, r=0.30, $t_{(103)}$=3.19, p<0.01).

Table 1. Territory use (no. of years occupied) in relation to song post availability in Corn Bunting territories.
Tab. 1. Reviernutzung (Nutzungsdauer in Jahren) in Abhängigkeit von der Zahl der Singwarten in Grauammer-Revieren.

Territory use (years)	Song post type	Song post availability (No. of territories) Song post present	Song post absent	Total
1–3	Overhead wires	32 (46%)	37 (54%)	69
	Windbreaks	40 (58%)	29 (42%)	69
	Fences	54 (78%)	15 (22%)	69
		126	81	207
4–6	Overhead wires	32 (89%)	4 (11%)	36
	Windbreaks	20 (56%)	16 (44%)	36
	Fences	35 (97%)	1 (3%)	36
		87	21	108
Total		213	102	315

The availability of song post types affected length of territory occupation (Tab. 1; G=13.97, df=2, P<0.001). Thus, presence of overhead wires and fences increased with territory use. Similarly, the number of song post types increased with territory use, all types generally being present in permanently occupied territories (Tab. 2). A test for quasi symmetry (Bishop et al. 1975, pp. 286-293) fitted the data well indicating partial symmetry between duration of occupation and number of song post types present (Tab. 2).

Table 2. Number of song post types in Corn Bunting territories used for different numbers of years. A quasi symmetric model fitted the data (G=0.98, df=1, n.s.). Expected numbers in parentheses.
Tab. 2. Anzahl der Singwartentypen die im Laufe der Jahre genutzt wurden. Ein quasi-symmetrisches Modell wurde angepaßt (G=0.98, df=1, n.s.). Erwartete Anzahl in Klammern.

No. of song post types in territory	Territory use (years) 1–2	3–4	5–6	Total
1	26 (26)	2 (2.6)	1 (0.4)	29
2	24 (23.4)	16 (16)	4 (4.6)	44
3	8 (8.6)	13 (12.4)	11 (11)	32
Total	58	31	16	105

4.2 Song post preferences

When song post utilization is compared with the occurence of the various types in territories overhead wires (Jacobs index median +0.32, range +0.66 to ÷0.44) are preferred over windbreaks (median ÷ 0.01, range + 1.00 to ÷ 0.95) which again are preferred over fences (median ÷1.00, range ÷0.03 to ÷1.00, 39 territories).

A similar result with preference for overhead wires and avoidance of fences as song posts was seen in Corn Bunting territories whether they were used for few or many years (Tab. 3).

Table 3. Distribution of song post observations in relation to territory use. The two variables were not independent (G=613.62, df=10, P<0.001).
Tab. 3. Verteilung der Singwartenbeobachtungen in Abhängigkeit zur Reviernutzung. Die beiden Variablen waren nicht unabhängig (G=613.62, df=10, p<0.001).

Territory use (years)	Overhead wires	Windbreaks	Fences	Total
1	18	24	7	49
2	31	30	10	71
3	123	101	5	229
4	296	216	20	532
5	74	58	13	145
6	224	65	47	336
Total	766	494	102	1362

4.3 Temperal pattern of song post utilization

The use of windbreaks increased during the study period, while Corn Buntings sang less frequently from fences during the later part of the study period (Fig. 3). These changes may have been due to alterations of the habitat. Decrease in use of low song posts as soil and fences and increase in windbreak use may be due to vegetational alterations. High cereals may compared with grass increase attenuation from low song posts leading to a shift to higher posts.

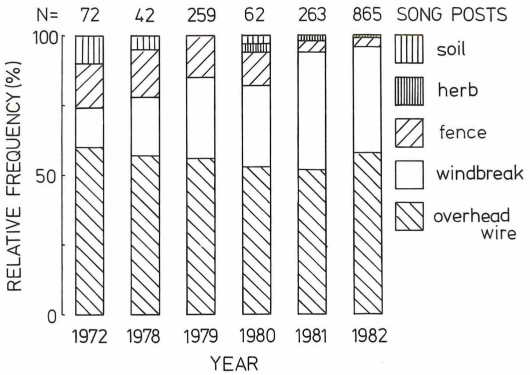

Fig. 3. Between-year variation in song post use of Corn Buntings. N=sample size.
Abb. 3. Jahr zu Jahr-Variation der Nutzung von Singwarten bei der Grauammer. N=Stichprobengröße.

The Corn Bunting sings nearly yearround allowing an analysis of seasonal alterations of song post use. The only marked temporal change except from the difference between summer (March-August) and winter (October-February) song posts (see below) was a frequent use of fences during the spring period (Fig. 4). During winter Corn Buntings sang nearly exclusively from overhead wires whereas fences and especially windbreaks were utilized to an increasing extent in summer (G=72.6, df=2, P<0.001).

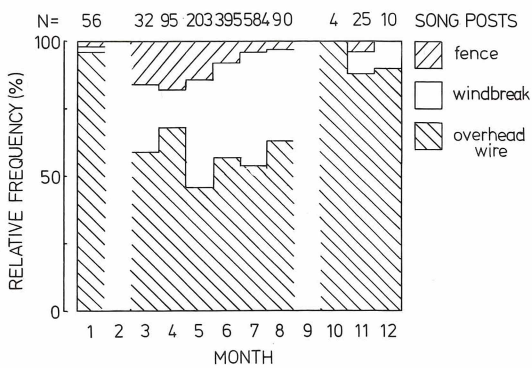

Fig. 4. Annual variation in song post use by the Corn Bunting. N=sample size.
Abb. 4. Jahreszeitliche Variation der Singwartennutzung bei der Grauammer. N=Stichprobengröße.

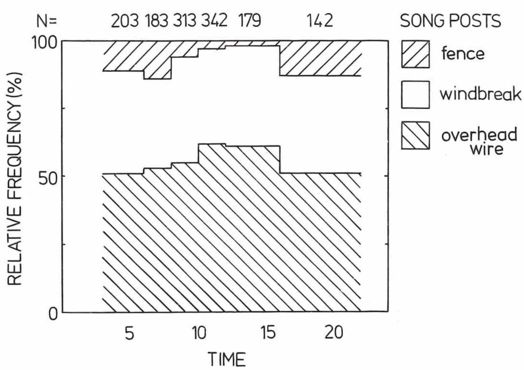

Fig. 5. Diurnal variation in song post use by Corn Buntings. N=sample size.
Abb. 5. Tageszeitliche Variation der Singwartennutzung bei der Grauammer. N=Stichprobengröße.

The daily pattern of song post use showed an increased utilization of high song posts and a concomitant decreased use of low song posts during the middle of the day (Fig. 5). Daily changes in song post use were highly significant (G=24.47, df=6, P<0.001). However, daily changes in song post use did not correlate with territory use (G=6.96, df=4, n.s.).

4.4 Timing of song

Corn Buntings sing irregularly in winter, but mild weather with good visibility is a reliable predictor of song occurrence (Tab. 4).

Table 4. Winter song in relation to weather conditions. Data from October to February. On each day the study area was searched for singing males.
Tab. 4. Wintergesang in Abhängigkeit von Wetterbedingungen; Oktober bis Februar. Das Gebiet wurde täglich nach singenden Männchen abgesucht.

	Weather conditions (No. of days) Frost	Thaw	Total
Days with song	3	30	30
Days without song	144	116	260
Total	147	146	293
	G=28.66, df=1, P<0.001		

	Visibility during thaw (No. of days) Below 500 m	Above 500 m	Total
Days with song	0	30	30
Days without song	51	65	116
Total	51	95	146
	χ^2=18.38, df=1, P<0.001		

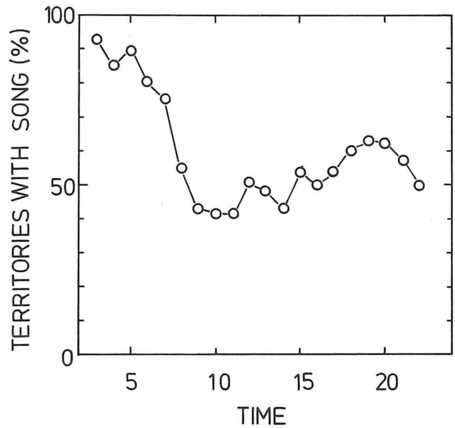

Fig. 6. Daily variation in Corn Bunting song activity shown as the fraction of territories with a singing male. 20 territories were censused 5 to 13 times during each hour.
Abb. 6. Tageszeitliche Änderung der Gesangsaktivität dargestellt als relativer Anteil der mit singenden Männchen besetzten Reviere. 20 Reviere wurden stündlich 5-13 mal kontrolliert.

During the breeding season maximal song activity is reached in April and lasts until July (MøLLER 1983a). The daily maximum in song activity occurs in the morning (Fig. 6). A slight peak in activity is recorded during the hours preceeding sunset. Even during the middle part of the day nearly half the males are recorded singing (Fig. 6).

5. Discussion

5.1 Song posts as a territory resource

Male Corn Buntings may attract females by means of song output (MøLLER 1983a). If this is so, than song posts become important resources for female attraction. Overhead wires were the most preferred song posts and fences the least preferred ones with windbreaks taking an intermediate position. Territory use increased with lengths of overhead wires and windbreaks indicating their significance as a territorial resource. An increased amount of preferred song posts was found in frequently used territories, even if these territories were smaller than less frequently used ones (MøLLER 1983a). The more overhead wires and windbreaks in territories used for many years may be due to causes other than song post utilization, e.g. feeding or nesting purposes. Actually windbreaks were preferred foraging habitats together with road-sides and field-boundaries, but only windbreak area increased with territory use (MøLLER 1983a). Overhead wires are, however, used exclusively for singing and resting purposes. Corn Bunting nests were placed in dense vegetation on the ground, frequently on road-sides or in cereal fields (A. P. MøLLER unpubl.). These habitats did not occur more frequently with increasing amount of song posts (overhead wires, windbreaks). Song posts thus seemed to be important territory resources per se. Preferred song post types were lacking more frequently than expected from territories occupied for few years, and there seemed to be a direct proportionality between the number of song post types and territory use.

5.2 Functional aspects of song post use and timing of song

If a part of the male Corn Bunting song is devoted to maximize female attraction this will have certain consequences for the choice of song posts and for the timing of song. Song posts should be chosen to allow for maximum sound transmission taking temporally variable microclimatic, and vegetational conditions into account.

Even if the Corn Bunting uses various song post types singing generally takes place from the highest possible point of the song post (e.g. SCHERRER 1972, own obs.). Overhead wire song posts consist of several wires with a distance of appr. 10 cm, but males were always recorded sitting on the uppermost wire on all occasions during the present study!

The choice of overhead wires as song posts in winter may partly be due to the restriction of song activity to males in frequently used territories (MøLLER 1983a), where this song post type is common, and partly due to the effects of humidity and temperature gradients (Tab. 4). Sound is transmitted furthest away if high song posts and moist microclimatic situations are chosen (MICHELSEN 1978, WILEY & RICHARDS 1978). As copulations are restricted to the period May to August territoriality and vocal activity in winter and early spring may be the necessary costs of holding a superior territory with nest sites, song posts and other resourses (MØLLER 1983a).

In spring and summer (March-August) low song posts on fences were utilized during March to late May with a decrease until July-August when air temperatures reach maximum values. Higher song posts in windbreaks and on overhead wires were used to an increasing extent during March to August. Ground attenuation is negligible for bird song frequencies if the signaler is situated above 1 m from the ground level (MICHELSEN & NOCKE 1974). Thus, this holds for overhead wires and windbreaks.

Propagation possibilities of song change daily. During the middle of the day when temperature and humidity gradients are marked and thus influence song especially from low song posts (WILEY & RICHARDS 1978) high song posts were chosen over lower ones, and the opposite situation was seen during morning and evening (Fig. 5). Wind is generally strongest in the middle part of the day and some effects due to increased wind strength may occur (e.g. MICHELSEN 1978, WILEY & RICHARDS 1978). However, wind turbulence effects can hardly be counteracted by responses in song post choice.

Singing males expose themselves to predators, especially so if conspicuous song posts are chosen (SCHERRER 1972, BAKER & PARKER 1979). The Corn Bunting may not expose itself to predators by choosing elevated song posts as potential predators can be seen when at a distance. Plumage variation in Corn Buntings seems rather to fit the status signaling hypothesis (ROHWER 1975) than the predator hypothesis (BAKER & PARKER 1979) (A. P. MØLLER in prep.).

Communication may except from alterations of song post choice be maximized through temporal changes in song output. During winter (October-February) song was only heard on days with temperatures generally above the freezing point (Tab. 4). Relative humidities are high, air temperatures are low, but ground temperatures are frequently lower than air temperatures. On days with frost and thus dry air or on days with fog and thus strong attenuation effects and high predation risks (predators can only be spotted at a close range) song is only rarely heard.

During summer (March-August) most song activity is recorded during favourable sound transmission conditions, i.e. during morning and evening. At these times of the day wind turbulence effects, the sound attenuation effects of dry air, and the effects of ground temperatures being higher than air temperatures are avoided. However, contrary to the common song pattern among most other birds (e.g. the monogamous Yellowhammer *Emberiza citrinella*) song activity during the middle part of the day has a relatively high level in the Corn Bunting (Fig. 6). The mating system of Corn Buntings may account for this interspecific difference.

Song may serve other purposes than mate attraction. During the non-breeding season it may be used for territory maintenance, and this may be an additional effect at least during territory establishment in spring. The lack of maximization of song transmission among birds (LEMON et al. 1981) may suggest that the choice of optimal song posts for long-distance sound transmission in the Corn Bunting is due to mate attraction. Territorial song should be directed towards nearby neighbours rather than distant males (LEMON et al. 1981). A significant function of Corn Bunting song post choice and song production thus seems to be mate attraction.

In conclusion, song posts seem to be chosen in order to maximize sound transmission, and varied and preferred song post types occur as a significant resource in preferred Corn Bunting territories.

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