

Seasonal and diel patterns in the song of the Thrush Nightingale *Luscinia luscinia* in SE Finland

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The song of the Thrush Nightingale was studied during five years at Parikkala, SE Finland. It began in the first half of May and ended at the end of June. Breeding males ceased singing when the young hatched in the first half of June. The peak of singing is at midnight but song may be heard at any time of the day. The frequency of singing correlates best with light intensity. The commencement of the nocturnal song did not follow the time of sunset exactly: at the beginning and end of the song period the males started to sing after sunset but in the middle of the period they began before. Two types of song were distinguished: territorial song and courtship song. The phrases of the territorial song were perfect at night and followed each other very closely, but in daytime the phrases were incomplete and the intervals longer. The courtship song was not so loud and the sections of the phrases were less fixed in form; it was heard just before laying.

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Introduction

Studying night-singing birds has become very popular in Finland during the last decade, and annual counts of singing males have been performed, especially in Päijät-Häme and North Karelia. However, only a small number of papers pay attention to the ecology of the night-singers; for the Thrush Nightingale *Luscinia luscinia* see SOTAVALTA (1956), PIIPARINEN & TOIVARI (1958) and SORJONEN (1974 a, b); for the Grasshopper Warbler *Locustella naevia*, HOLOPAINEN et al. (1967); for the River Warbler *L. fluviatilis* SORJONEN (1975); for the Marsh Warbler *Acrocephalus palustris*, TOIVARI & LINDQVIST (1962), ERIKSSON (1969a, b) and SORJONEN & TASIHIIN (1976); and for Blyth's Reed Warbler *A. dumetorum*, TOIVARI & LINDQVIST (1962),

ERIKSSON (1969a, b), TOIVARI et al. (1969) and SORJONEN & TASIHIIN (1976).

Knowledge of the relation between song intensity and the breeding period, so necessary for such work as density estimates, is still very incomplete. In the case of the Thrush Nightingale, there are papers on the subject by STEINFATT (1939) and SORJONEN (1974a, b) and a publication on song activity by PIIPARINEN & TOIVARI (1958).

The aim of the present study is to relate the song intensity of old and young males to light intensity and breeding period, in order to discover the best time of the day and summer for counting the males.

Material and methods

The field studies were carried out in

TABLE 1. The numbers of singing male Thrush Nightingales and newly arrived males at Parikkala in 1968—70.

5-day periods	6—10 May	11—15 May	16—20 May	21—25 May	26—31 May	1—5 June	6—10 June	11—15 June	16—20 June	21—25 June	26—30 June
Singing	4	27	63	80	81	75	56	37	16	6	1
Newly arrived	4	23	36	17	1	—	—	—	—	—	—

Parikkala commune, SE Finland, in 1968—75, being most intensive in 1969—70. The Thrush Nightingales bred in greatest number around Siikalahti ($61^{\circ}33'N$, $29^{\circ}33'E$), a eutrophic 5-km-long arm of Lake Simpele. Four small islands in Siikalahti and the shores of the lake carry dense *Alnus incana*, *Betula verrucosa*, *Prunus padus* and *Salix* spp.. The birds were observed throughout the day but least work was done between 2.00 and 5.00. The age of trapped birds was determined and they were colour-ringed.

The song activity of each of four males was recorded for one day, and that of one male for two days, all the phrases being counted during periods of 15 minutes throughout the day and the following night. Temperature and relative humidity were measured with a thermohygrograph placed under the main singing tree of the male. Light intensity was measured under the open sky at intervals of 15 min with a LUNASIX exposure meter, whose scale ran from 1 to 22, covering ca. 0.12 to 350 000 lux. These LUNASIX records were used in the statistical treatment of light intensity. The time of sunset in May and June is given according to data from Imatra, about 65 km SW of Parikkala.

The length of the song phrases of 19 males and the song intervals of 13 males were measured with an accuracy of 0.1 sec in the field or from tape recordings.

Results

Seasonal singing pattern. In 1968—72 singing was first heard at Siikalahti between 8 and 13 May. All these males were old ones (at least 2 years). The first young singing male (1 year) was heard on 17 May. Every year, the first song was heard before the leafing of the trees, but the greatest number of males was not heard until the trees were in leaf. The song period lasted until the end of June (Table 1), the last singers being non-breeding birds. The singing of the breeding males became less intense when incubation started towards the beginning of June, and singing ceased completely when the young hatched on 7—20 June (SORJONEN 1974b). One male stopped singing one day before laying, when his singing period had lasted only 12 days. Males may sometimes sing fragmentarily between feeding, but this song is not nocturnal. When singing by feeding males is included, the duration of the longest song period was 45 days. Table 2 shows the mean song period of old and young males in relation to laying and hatching.

Diel singing pattern. Singing was most intense at midnight, but it was heard throughout the 24 hours (Fig. 1). In the early part of the song period (8—25 May), males could be divided into three classes according to their diel singing pattern: (1) Males that regularly stopped singing at the darkest time of the night, when light intensity

TABLE 2. Start, end and duration of the song period of breeding and non-breeding males and mean laying and hatching times. Sample size in parentheses.

	Song period			Laying	Hatching
	Start \pm S.D.	End \pm S.D.	Duration \pm S.D.		
Breeding	15 \pm 3.3 May (46)	10 \pm 6.9 June (25)	26 \pm 7.6 (25)	30 May (32)	14 June (52)
Non-breeding	22 \pm 4.5 May (10)	22 \pm 3.8 June (10)	32 \pm 8.2 (10)	—	—

was below 3–5 lux (Fig. 2a), (2) males that occasionally stopped singing at the darkest time of the night, and (3) males that always continued singing even at the darkest time of the night (Fig. 2 b–c).

After 25 May when the nights remained light (Fig. 2 d–f), none of the singers paused in their song. Of the 194 males studied in 1969–72, 45 belonged to class (1) and 48 to (3).

In the daytime, singing was often very occasional and some males of class (3) were not heard singing at all. Other males, mostly belonging to class (1), sang frequently in the daytime as well, especially at the beginning of the song period. Non-breeding males sang very often in the day, even at the end of the song period.

At the beginning of the song period, the night song began shortly after sunset (Fig. 3); between 14 and 20 May 1972, it started when the light intensity sank to ca. 490 lux (LUNASIX records 12.41 ± 0.21 (S.E.), $N = 25$). But later, between 21 May and 10 June, it started at intensities as high as ca. 1120 lux (LUNASIX records 13.65 ± 0.15 , $N = 32$). The difference in light intensity between the two periods was highly significant ($t = 4.97$, $P < 0.001$). It was difficult to determine the exact time of the beginning of the night song for singers of class (1), because they sang a great deal in the daytime, but its

commencement was generally very noticeable in singers of class (3).

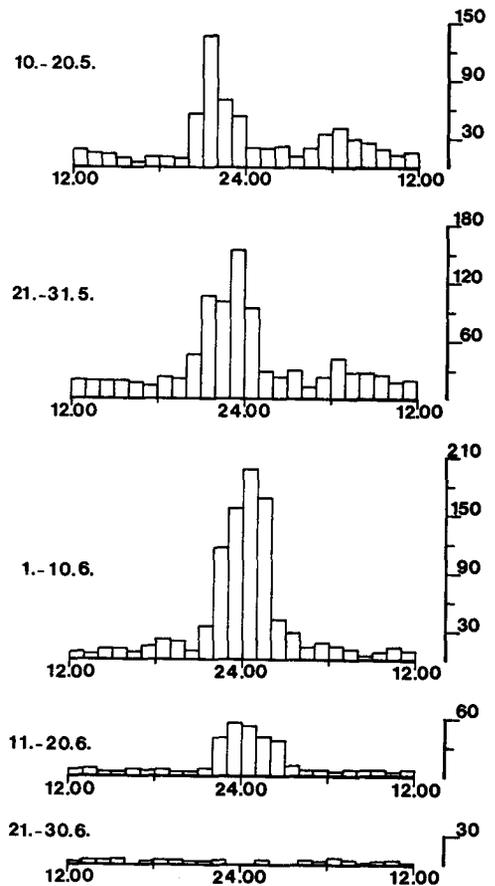


FIG. 1. The numbers of singing male Thrush Nightingales (y-axis) heard per hour at different times of summers 1968–72 at Parikkala.

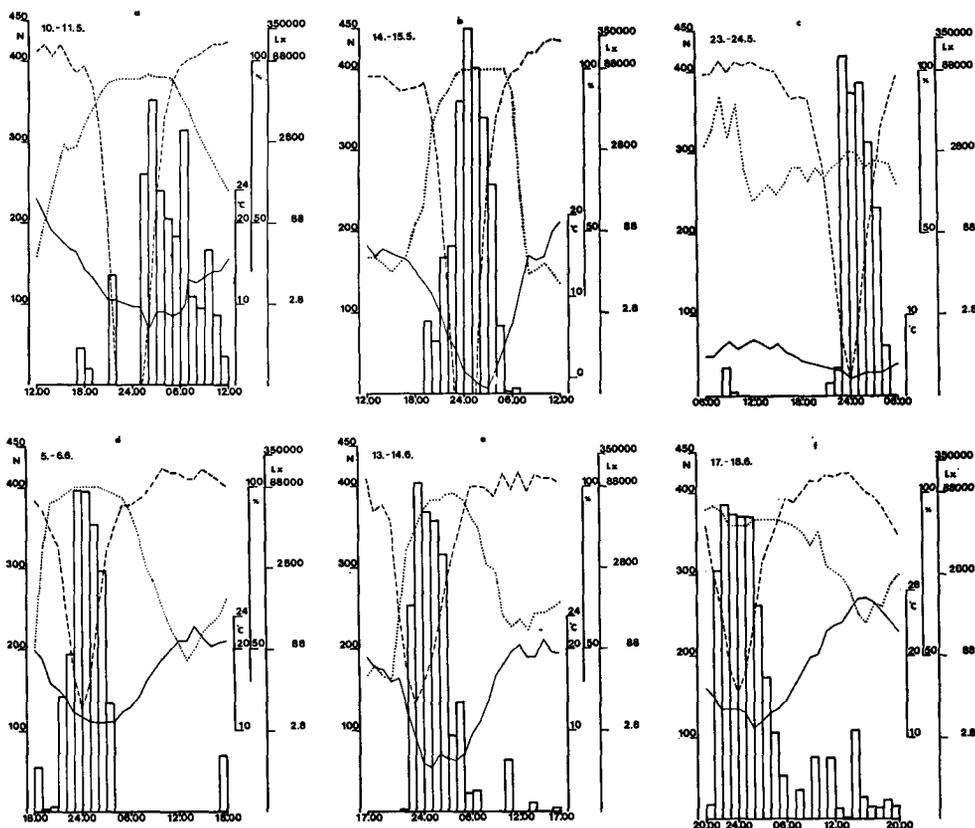


FIG. 2. The number of phrases sung by one Thrush Nightingale per hour during 24 hours. Solid line = temperature, broken line = light intensity, dotted line = relative humidity, columns = number of phrases per hour.

a. Male singing on 10—11 May 1969

b. Male singing on 14—15 May 1969

c. Male singing on 23—24 May 1969 (same as in b)

d. Male singing on 5—6 June 1968

e. Male singing on 13—14 June 1969

f. Male singing on 17—18 June 1968

Territorial song. The song was classified as territorial or courtship song, according to its structure and the manner of singing.

The species is a typical phrase-singer, who repeats several different phrases at short intervals. A phrase usually consists of eight sections (SORJONEN 1974a), and each section consists of one figure, which may be single or repeated a few times.

The territorial song is very loud and distinct. At midnight the song phrases

were 6.70 ± 0.07 sec long ($N = 744$), the intervals between phrases being 1.93 ± 0.04 sec ($N = 649$). In the daytime and in the evenings just before the intense night song, the phrases lasted 4.99 ± 0.07 sec ($N = 470$) and the intervals 4.94 ± 1.15 sec ($N = 262$). The difference in phrase length between the night and day is highly significant ($t = 15.84$, $P < 0.001$), as is also the difference in intervals ($t = 4.13$, $P < 0.001$). In the daytime, some sections of the phrases are repeated less

often or not at all. In the day song, 23 % ($N = 118$) of the phrases are abbreviated (the last sections lacking), in the night song only 12 % ($N = 224$), the difference being statistically significant ($\chi^2 = 6.06$, $P < 0.025$).

Courtship song. This song is not loud and distinct as the territorial song. It is more intense and the intervals between phrases may sometimes be difficult to distinguish. The length of the phrases changes much more than in territorial song (6.21 ± 0.25 sec, $N = 153$). The phrases consist of the same sections as the phrases in the territorial song, but the order of the sections is different and their form less fixed (SORJONEN 1974b).

The courtship song is sung in dense bushes near the ground. At times it ends with the pursuit of the female, or the male begins territorial song from a somewhat higher bush. The courtship song is given many times a day, usually before noon, ten to five days before

incubation (SORJONEN 1974b), and was heard between 19 and 28 May.

Discussion

It is not known whether the males begin to sing immediately after their arrival. The first Thrush Nightingales observed in spring were usually singing males, but there are observations of singing migrants and of males who did not start to sing until a few days after their arrival (DEMENTEV & GLADKOV 1968, HILPRECHT 1965). One male arrived at Siikalahti on 8 May but began singing on 11 May. POPOV (in DEMENTEV & GLADKOV 1968) maintains that singing does not usually begin until the trees are covered with foliage. Singing commences before the trees are in leaf at Siikalahti, but the reasons why some early males do not begin singing at once may be some other feature of the habitat, perhaps the absence of com-

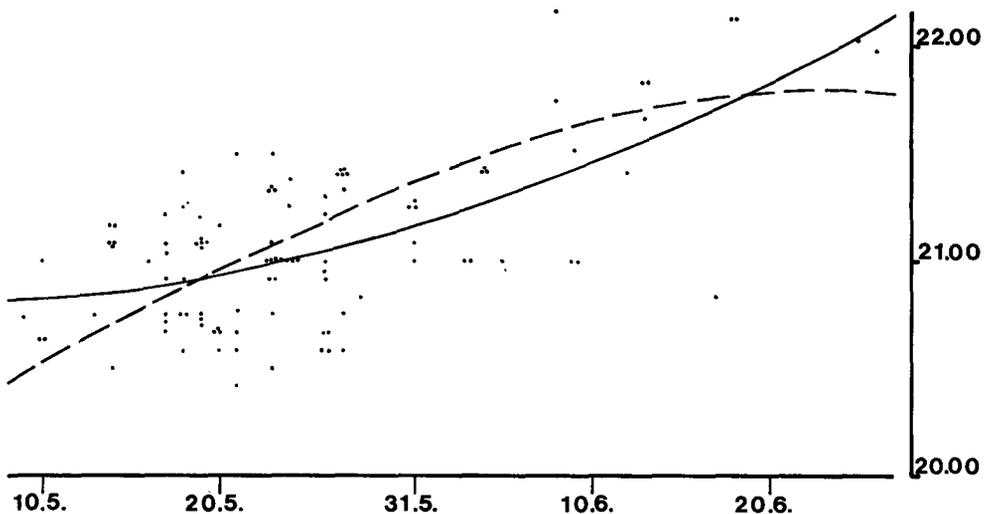


FIG. 3. The beginning of nocturnal song in 1968—74 at Parikkala. Broken line = the time of sunset at Imatra, solid line = curve of regression ($y = 48.478x^2 + 0.360x + 0.025$) of the beginning of nocturnal song on time during the song period, dots = recorded times of the beginning of nocturnal song on which the regression curve is based.

petitors or poor development of the herb layer.

At Siikalahahti the song period began about two weeks earlier than in the Lahti district (KOLUNEN 1970) and SW Finland. The age composition of the populations seems to be very different at Parikkala and in SW Finland. Of the birds trapped by me at Parikkala in 1971—73, 42 were old (at least 2 years) and 11 young (1 year), whereas birds trapped at Vihti and Tammisaari (SW Finland) in 1972 consisted of five old and six young specimens. This difference is significant ($\chi^2 = 7.21$, $P < 0.01$). It seems likely that the song period begins earlier in the old breeding range of the Thrush Nightingale, where old birds predominate.

The song period seems to end at the same time everywhere (v. HAARTMAN et al. 1963—72, DEMENTEV & GLADKOV 1968, KOLUNEN 1970). The observations of STEINFATT (1939) on cessation of singing in breeding males are very similar to mine. According to DEMENTEV & GLADKOV (1968), however, some males are still singing in the middle or end of July. I have never heard song in July. The fledgelings sometimes sing outside the actual song period in August (DEMENTEV & GLADKOV 1968, HILPRECHT 1965); I have heard birds singing twice outside the song period, on 6 August, but could not determine their age.

Since song intensity reaches its peak at midnight and singing begins near sunset, the Thrush Nightingale may be considered a night-singer, although the song is also an essential part of its diurnal activity (cf. PIIPARINEN & TOIVARI 1958 and v. HAARTMAN et al. 1963—72). Singing has been reported to be mainly restricted to the night, except in cloudy weather (HORTLING 1929, SEPÄ 1951, HUDÉN & LINKOLA 1955, SOTAVALTA 1956). This is more

or less true of singers of my class (3), but HILPRECHT (1965) considers that singers of this type are exceptional. According to DEMENTEV & GLADKOV (1968), singing is nocturnal only at the beginning of the song period, but at Siikalahahti day song is frequent at the beginning of the period (Fig. 1).

The song intensity correlates fairly well with light intensity (Fig. 2), as does also that of the Grasshopper Warbler (HOLOPAINEN et al. 1967). TOIVARI & LINDQVIST (1962) assume that the increasing song intensity of the Marsh Warbler at night is correlated with increasing relative humidity, but they did not check the influence of light. To me it seems likely that light intensity is the chief factor determining the song time of nocturnal singers, but an increase in humidity and perhaps decrease in temperature may contribute to initiate singing. The song of other males also triggers and intensifies singing; if one male begins to sing, others join in. This effect was clearly demonstrated with my taperecorder and was presumably the reason why males generally began to sing before sunset in the middle of the song period (Fig. 3), when the number of males was at its peak.

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Selostus: Satakielen laulun vuodenai- kais- ja vuorokausirytmikka Parikka- lassa

Satakielen laulukäyttäytymistä on tutkittu Parikkalassa viitenä vuonna. Laulavien koiraiden ja uusien muuttajien määrät on esitetty taulukossa 1. Laulu on alkanut toukokuun alkupuolella (vanhat koiraat), noin 2 viikkoa aikaisemmin kuin Lah-

dezza, ja päättynyt kesäkuun lopulla (pesimättömät koiraat; aineisto taulukossa 2). Pesivät koiraat ovat lopettaneet laulunsa poikasten kuoriutumisen aikoihin kesäkuun alkupuolella. Paras laulu aika vuorokaudessa on keskiyö, mutta laulua voi kuulua minä vuorokauden aikana hyvänsä (kuva 1). Kuvassa 2 on esitetty 6 koiraan säkeiden lukumäärät tunneittain yhden vuorokauden aikana (yhtenäinen viiva = lämpötila, katkoviiva = valaistus, pisteviiva = suhteellinen kosteus). Laulukauden on todettu korreloivan parhaiten valaistuksen kanssa ja yölaulun alku on siirtynyt myöhäisemmäksi kevään edistyessä. Yölaulun alkaminen ei kuitenkaan seuraa tarkalleen auringon laskua, vaan laulu alkaa laulukauden alussa ja lopussa sen jälkeen, mutta keskivaiheilla hieman ennen sitä (kuva 3). Satakielen laulu on jaettu kahteen eri laulutyyppiin: reviiirilaulu ja kosintalaulu. Reviiirilaulu on etenkin yöllä hyvin kaavamaisista, säkeet ovat täysimittaisia ja lähes samanpituisia sekä tauot niiden välissä hyvin lyhyitä. Päivällä säkeet ovat usein vaillinaisia ja säkeiden väliset tauot ovat yöllisiä pitempiä. Kosintalaulu ei ole yhtä kuuluvaa kuin reviiirilaulu ja säkeissä olevilla aiheilla ei ole mitään tiettyä järjestystä. Soidinlaulua kuuluu juuri munintaa edeltävänä aikana.

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