WHY MATED DUSKY WARBLERS SING SO MUCH: TERRITORY GUARDING AND MALE QUALITY ANNOUNCEMENT

by

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Summary

The fertility announcement hypothesis states that males sing most intensively during the period of female fertility in order to assure their paternity, as females would prefer to sexually mate with males singing at a high rate. The dusky warbler (*Phylloscopus fuscatus*) is one of the species in which singing intensity clearly peaks when females are fertile. As a test of the fertility announcement hypothesis, we study why males of this species sing so much after pairing. Dusky warblers have two distinct kinds of song, an individually specific, stereotype song type (S-song) and a highly variable song type (V-song). S-song is used as an individually recognisable signature to mark the claimed territory area. Playback experiments indicate that males can even memorise their neighbours from the previous breeding season. S-song is used while patrolling over the territory area, presumably to ward off intruding males.

Males do not guard fertile females, but intensity of S-song peaks when a male's partner is fertile. In contrast, V-song appears to advertise male quality, functioning to attract females for copulation. This song type is used at the highest rate when any female, the own or the neighbouring, is fertile. Our study clearly supports the idea that song can function as a paternity guard. However, analysis of extra-pair paternity (shown elsewhere) revealed that females choose copulation partners on the basis of the quality of their V-song, but not on the quantity of song. This means that the fertility announcement hypothesis does not apply to the dusky warbler, as the presumed mechanism — selection on song rate — is not given. We discuss what selective pressures may favour and maintain such ways of paternity assurance.

Introduction

It is generally accepted that male birds sing in order to acquire a mate and to defend a territory and its resources (Searcy & Andersson, 1986; Catchpole & Slater, 1995). In some species males cease from singing once they are paired with a female (*e.g.* Catchpole, 1973), while in some other species males also sing intensively after pairing (*e.g.* Møller, 1988). Greig-Smith (1982) suggested that song after social pairing might function to assure within-pair paternity ('mate retention') and/or to attract neighbouring females to perform extra-pair copulations. Studying the great tit, Mace (1987) demonstrated that singing was most intense during the period when females were laying eggs, supporting the idea that song may function as a paternity guard. Møller (1991) carried this field one step further by suggesting a mechanism that could allow song to act as a paternity guard. If the rate of singing was a condition dependent trait, and thereby a reliable indicator of male quality, females might prefer to copulate with males singing at high rate. Given this female preference, intensive singing could, on the one hand, prevent the own female from being unfaithful, and, on the other hand, attract neighbouring females for extra-pair copulations. Simultaneously, singing at high rate would help to discourage neighbouring males from intruding into the territory, as females paired to males singing at a high rate would tend to remain faithful to their mates. Møller claimed that for these reasons a majority of bird species would reach a peak of singing intensity during the period of female fertility. As neighbouring males may use male singing intensity as a cue to recognise a female's fertile period, this hypothesis was named the fertility announcement hypothesis. We feel that this term is unfortunate, because it emphasises

an unintentional by-product of singing (*i.e.* revealing a female's fertile period) rather than the presumed purpose of singing (*i.e.* advertising a male's quality). The fertility announcement hypothesis might better be named something like 'male quality announcement hypothesis', because it suggests that males sing to advertise their quality by displaying at a higher rate than their neighbours. According to Møller (1991), this would help to assure paternity, given that there is a female preference to copulate with males that sing at the highest rate.

Over the past decade quite a few studies have challenged Møller's hypothesis by analysing temporal patterns of singing intensity (reviewed by Gil *et al.*, 1999). In most species males sang more intensively before pairing than during the period of female fertility, thus leading to a rejection of the fertility announcement hypothesis (Gil *et al.*, 1999). Some studies describe puzzling cases, where singing is most intense in the fertile and especially in the post-fertile period (Rodrigues, 1996; Currie *et al.*, 1998). Finally, there are some studies showing a clear positive temporal relationship between male singing activity and female fertility (Mace, 1987; Møller 1988; Welling *et al.*, 1997; Pinxten & Eens, 1998). It can be summarised that the fertility announcement hypothesis may apply at best to a restricted number of species. However, the question of why males of some species still sing intensively after pairing, has not yet been answered satisfactorily. Most seriously, the mechanism underlying Møller's model (*i.e.* a female preference for high song rates) remains to be tested.

Preliminary observations on the dusky warbler (*Phylloscopus fuscatus*) suggested that this species might be a potential candidate for the fertility announcement hypothesis, as dusky warbler males sing intensively after pairing (*e.g.* Johansen, 1954). By looking at the dusky warbler, we try to answer the question of why mated males sing so much, which is equivalent to testing the fertility announcement hypothesis. We do this by analysing various aspects of song use that may shed some light on the functions of song. Specifically, we take the following steps:

(1) We describe and characterise the song of the dusky warbler, which has not yet been done in sufficient detail (see Glutz von Blotzheim & Bauer, 1991; Cramp, 1992). It is known that the species has two very distinct kinds of song (Bergmann, 1996): an individually specific, stereotype song type (S-song) and a highly variable song type (V-song). The individual distinctiveness of S-song suggests that it may

serve to facilitate individual recognition. We test this hypothesis experimentally by looking at a male's reaction towards playback of the song of a familiar versus unfamiliar male. To gain insights into the functions of the variable V-song we estimate the size of a male's repertoire and its similarity to the repertoires of neighbouring males.

(2) We study spatial and temporal patterns of use of the two song types. In several passerine species stereotype songs appear to be territorial signals directed towards males, while more complex songs often address females (Catchpole, 1980, 1982, 1983; Slater, 1981; Groschupf, 1985; Catchpole & Leisler, 1989, 1996; Fessl & Hoi, 1996). It might be hypothesised that, in the dusky warbler, stereotype song functions as a territory defence, while variable song advertises for copulations to both, the own and neighbouring females. This produces testable predictions on temporal patterns of song-type use: S-song should be used most intensively during fertility of the own female, to prevent other males from intruding the territory. V-song should be used at a high rate as long as any female in the neighbourhood, including the own, is receptive. Like Lemon *et al.* (1987) we try to obtain further insights into the functions of the two song types by looking at the spatial distribution and vegetation structure of song perches that are used for broadcasting either of the two song types.

Methods

The study was conducted in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan, in the Russian Far East (154°14′E; 59°51′N). Here dusky warblers breed in high density in bushlands of varying coverage and height, located in the transition from inland taiga forests to coastal tundra. We studied this population over three consecutive breeding seasons between 1997 and 1999. The dusky warbler is an insectivorous long-distance migrant passerine and it has a sexually monomorphic dull brown plumage. The species is present in the study area from the last days of May to the first days of September. We followed the birds for the duration of the summer season, which comprises a single brood (replacement clutches do occur) and a postnuptial, pre-migratory moult.

All territorial males and most of the females (84%) were colour ringed. The birds were observed daily and nests were checked frequently in order to obtain dates of settlement, pairing, egg-laying and hatching. The exact date of pairing proved to be difficult to determine. In all cases where we managed to do this, the first egg was laid either 7 or 8 days later ($N = 1$ and $N = 5$ respectively). As a result of brevity of the breeding season females are constrained

to start the clutch as soon as possible, and we assume that an interval of 7 or 8 days is the minimal time span required for nest building (only the female builds) and egg formation. We therefore define the date of female settlement as being 8 days before deposition of the first egg of the first clutch.

The song of dusky warblers consists of short strophes (typically of 1-2 s duration) with pauses of typically 3-5 s between strophes (Fig. 1). There are two distinct kinds of song type (stereotype song type = 'S-song' and a variable song type = 'V-song'), that can easily be distinguished in the field. In 1997 we observed the use of song posts and song types for 14 territorial males nearly every day and plotted them to the nearest 5 m on a detailed map (scale 1 : 1000) that was obtained from own distance measurements. To illustrate spatial and temporal patterns of song-type use on a typical example, we conducted a 18 h focal observation of a territorial male, that was selected for its territory being spatially isolated from other territories, in order to minimise direct influences from neighbouring males. Each minute we recorded song type and singing location of the male to the nearest 10 m.

For each of 14 territorial males of 1997 we took measurements of vegetation structure at the five or six most frequently used song perches. Within a 20×20 m square area around the perch we estimated cover of bush vegetation in five layers (0-0.5 m, 0.5-1 m, 1-1.5 m, 1.5-2 m, >2 m above the ground). Using 0 m height for parts of the square without any bush cover we calculated a value of mean vegetation height for the square area around a perch. This measurement reflects both, the average height of bushes and the total coverage of the area by bushes.

In 1998 we measured song rate for 16 males holding a territory in the same area as studied in 1997. For each male we performed 10 min focal observations once per day between 04:30-10:00 h. These observations were carried out almost daily between male settlement and hatching of nestlings and sporadically after that period. Focal observations were started at predetermined times, irrespective of whether the male was singing or not. In order to decrease systematic biases caused by between-male differences in time of day at observation we randomised male observation order to the extent allowed by constraints of observers travelling distances. During this 10 min period we recorded the number of strophes of each song type and for each minute separately. For most of the analyses we used song rates per minute (mean number of strophes per minute). To quantify the relative share of the two song types (irrespective of song rate) we discarded all minutes without song (38% of 6, 240 min) and those during which both song types have been recorded (3%). From the remainder we calculated the share of minutes with only S-song and only V-song.

For statistical analysis we defined three discrete phases to allow pair-wise testing: (1) The nest-building phase is from day -8 to -2, with day 0 being the day when the first egg is laid. (2) The peak-fertility phase comprises all those days after which an egg was laid, reflecting the period with highest chances of fertilising eggs (Howarth, 1974; Colegrave *et al.*, 1996). (3) The post-fertility phase is from the day of deposition of the last egg to day $+12$. Note that other authors have defined the fertile period differently, partly because they could use a pre-fertile period as a reference (*e.g.* days -39 to -9 in non-migratory European robins, *Erithacus rubecula*; Tobias & Seddon, 2000). We expect an increasing intensity of sperm competition over the course of the nest-building phase, but sperm competition should be strongest in the second phase, when the chances of fertilisation are highest. For each male we calculated mean song rates for each phase.

Tape recordings of songs were made with a Nagra SN recorder and a Sennheiser MKH 815T directional microphone in 1997, a Sony TCM-459V recorder and a Shure Prologue

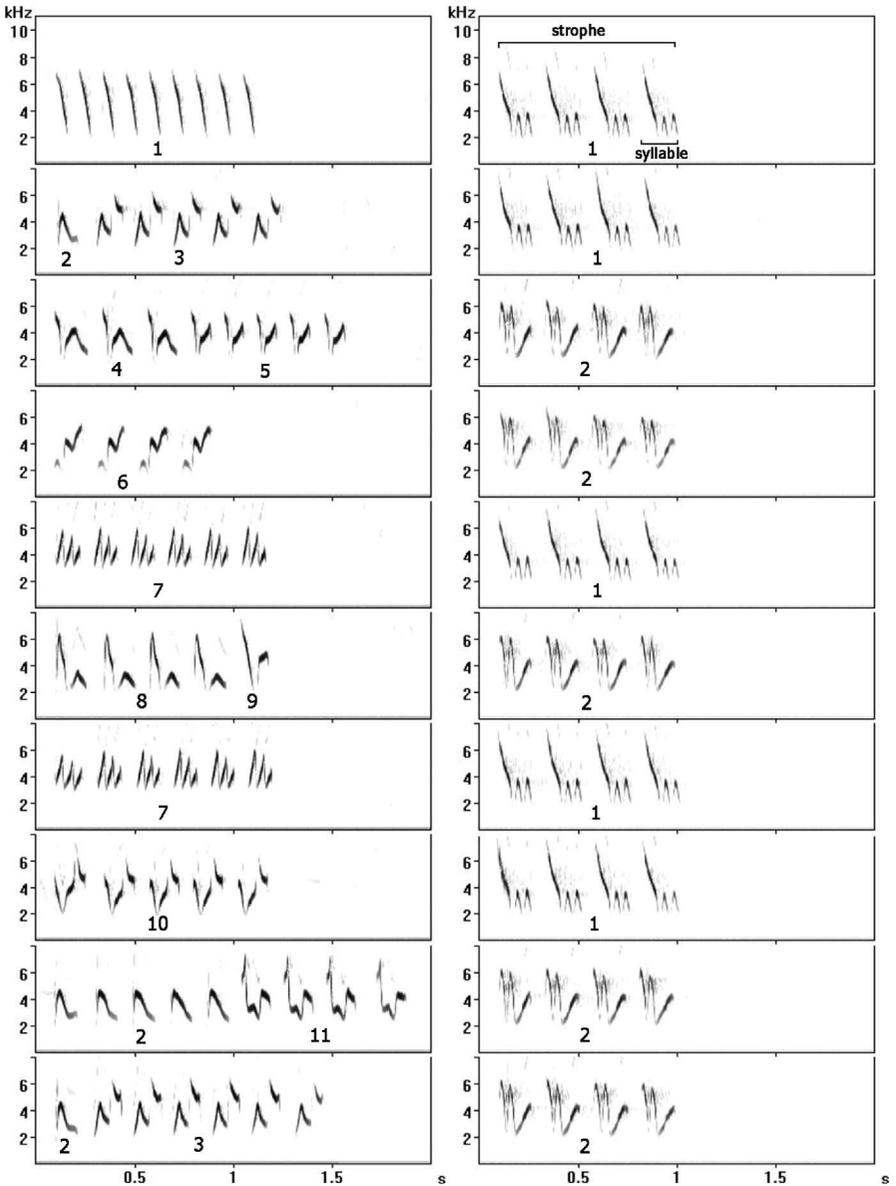Fig. 1. Spectrograms of 10 continuous strophes of variable song-type (V-song, left side) and 10 continuous strophes of stereotype song-type (S-song, right side) of a single male (Bandwidth 111 Hz, time resolution 5.8 ms). The total duration, including pauses, of the 10 V-song strophes was 54 s, of the 10 S-song strophes 74 s. Numbers reflect the classification of different syllable types (1-11 in V-song and 1-2 in S-song).

16AM microphone in 1998, a Sony TC-D5 PRO II recorder and a Sennheiser K6-M67 microphone in 1999. Recordings of S-songs were obtained from a total of 85 males (including 18 individuals recorded in more than one season). A small sample of S-song strophes per individual was sufficient to obtain the full repertoire of syllable types used (maximally three syllable types). We sampled a small number of V-song recordings from most of the males in each breeding season. Recordings of 100 continuous strophes (approx. 10 min) were often difficult to obtain, so most analyses are based on recordings of 30 strophes. All song recordings were analysed with Avisoft SASLab Pro (sampling frequency 22.050 Hz, 16 bit, time resolution 5.8 ms, bandwidth 111 Hz). Syllable types were categorised by visual inspection of printed spectrograms, all done by the same person (WF) to ensure the consistency of classifications (see Fig. 1).

Getting a precise measure of the full V-song repertoire of an individual dusky warbler male proved a virtually impossible task, as new syllable types (rarely used types) continue to turn up throughout even the longest recordings. We used the computer program EstimateS (Version 5.0.1, R.K. Colwell, http://viceroy.eeb.uconn.edu/estimates), to make extrapolations on the full repertoire sizes. Although this program is designed to obtain statistical estimators of true species richness from repeated censuses, it is highly suitable for our purposes. Simple capture-recapture techniques (mentioned by Catchpole & Slater, 1995) assume that all syllable types are used at equal rate. This leads to an underestimation of repertoire size if some syllable types are much more frequently used than others (see also Garamszegi *et al.*, in press). This problem is analogous to the fact that species communities contain both, abundant and rare species, and EstimateS is designed to cope with this. Note that this program is inappropriate for species with strong sequentiality of syllable-type delivery. Recordings of 25 continuous strophes were used as the unit of survey (like one census of a species community), with syllable types representing the species. Abundances were defined as the number of strophes in which a syllable type was found (theoretically varying from 0 to 25). We always entered data from four recordings for each male (4×25 strophes), and let the program calculate several different estimators of the true number of syllable types, i.e. what is expected to be found in an infinite number of recordings of that male. In this paper we present mean estimates, averaged among eight different estimators (namely ACE, ICE, Chao 1, Chao 2, Jack 1, Jack 2, MMRuns, MMMean), all of which produced fairly similar results.

In order to make comparisons between two repertoires (obtained from 30 strophes) we calculated a coefficient of syllable type sharing (Sörensen index; see McGregor & Krebs, 1982) as $2*C/(R_1 + R_2)$, where R_1 and R_2 are the numbers of syllable types found in repertoire 1 and repertoire 2, respectively, and C is the number of syllable types that the two repertoires have in common. We used this measure to determine whether neighbouring males shared more syllable types than males located 0.5-3 km apart from each other.

In 1999 we performed a playback experiment to determine whether males discriminate between S-songs of individuals they are familiar with and S-songs of presumably unfamiliar males. Males that had just established territories in early spring of 1999 at the same site they had occupied the previous year, received playback of the S-song of the nearest neighbour from the previous year (given that this individual had not yet arrived) and, as a control, the S-song of a randomly selected other male, that had bred at least 1 km apart in 1998. The two playbacks (presentation of familiar and unfamiliar song) took place at least 24 h apart and the order of treatment was randomised. Playbacks were done with a Sony TCM-459V recorder and a Sony SRS-A60 active loudspeaker. Tapes used for playback were prepared from recordings obtained in 1998 and were standardised for song rate (8 strophes per min),

duration (1 min) and volume using the Avisoft SASLab Pro. In the field, sound pressure was adjusted and fixed at a natural output level. We made sure that bush vegetation allowed a more or less continuous approach by birds, not being hindered by gaps in the vegetation. We measured the intensity of male response to playback as the minimal distance of approach to the loudspeaker while singing. We decided to use this as the sole measure of aggressive response to playback, as previous playback experiments in 1997 and 1998 showed a high repeatability and a strong relationship between closest approach and male age reflecting confidence of territory ownership (unpubl. data). Additional parameters of male reaction were not recorded to avoid the problem of multiple testing.

Results

Song type characteristics

Spectrograms of ten consecutive V-song strophes and ten consecutive S-song strophes of a single male are shown in Fig. 1. The main differences between the two song types are summarised in Table 1, based on V-songs recorded from 30 males and S-songs from 85 males.

S-songs are characterised by a small individual but a large population repertoire. Of the 85 males analysed, 56 used only one syllable type, 23 males used two syllable types (as the example in Fig. 1) and 6 males used three different types. This population of 85 males used 40 different syllable

TABLE 1. *Characteristics of stereotype song type (S-song) and variable song type (V-song)*

	S-song mean ± SD (range)	sample size	V-song mean ± SD (range)	sample size
Song rate (strophes/min)	4.74 ± 2.33 (1-16)	1937 min (16 males)	7.81 ± 4.25 (1-19)	1350 min (16 males)
Number of syllables per strophe	3.69 ± 0.66 (3-6)	120 strophes (85 males)	6.01 ± 1.84 (1-13)	120 strophes (30 males)
Versatility (syllable types per strophe)	1.00 ± 0.00 (1)	120 strophes (85 males)	1.63 ± 0.83 (1-5)	120 strophes (30 males)
Individual repertoire (30 strophes)	1.41 ± 0.62 (1-3)	85 males	18.62 ± 3.87 (9-27)	30 males
Population repertoire (32 males, 60 strophes each)	30		205	

All differences in means and standard deviations are highly significant ($p < 0.0001$).

types altogether, allowing us to recognise most males individually by their S-song syllable type. All males using two or three syllable types had a unique combination of syllable types. We estimated that an average male using only one syllable type will, statistically speaking, find exactly one twin male (using the same syllable type) within a sample of 42 males. Experienced human listeners can learn to recognise individual males by their S-songs with reasonable confidence, suggesting that S-songs may signal individual identity. Circumstantial evidence suggests that young males learn the S-song from tutors other than the social father, and that they may compile their individual S-song repertoire from different tutors. As a rule, individual S-song repertoires are kept throughout an individual's live. Only one out of 18 males observed in more than one season had exchanged one of his two syllable types to a new one between his very first and the following breeding season.

V-song differs from S-song by the following characteristics (see Table 1 and Fig. 1): (1) V-song is, on average, produced at a higher rate per minute compared to S-song. (2) In V-song, pauses between strophes may contain series of short calls (the 'drrr'-call depicted in Glutz von Blotzheim & Bauer, 1991). These calls were present in 50% of 107 V-song recordings, but were never heard in S-song. (3) V-song strophes, on average, are longer than S-song strophes, and contain more and a more variable number of syllables. (4) V-song regularly shows syllable-type switches within strophes, that do not occur in S-song. (5) V-song comprises large individual repertoires.

Individual V-song repertoires found in 100 continuous strophes comprised an average of mean $\pm$ SD $= 33.9 \pm 7.1$ (range: 22-42, $N = 10$ males) syllable types. We split these recordings into 4 parts, each of 25 strophes. From these 4 samples we calculated estimates of full repertoire sizes of males, using the EstimateS program: mean $\pm$ SD $= 44.9 \pm 12.0$ (range: 28-61). For comparison, we did the same for 10 other males where we had 4 different recordings (each of 25 strophes) that had been taken over the whole breeding season (one recording per week). The repertoires found in these samples of 100 strophes were not significantly larger (mean $\pm$ SD $= 38.5 \pm 6.5$, range: 22-46) than those mentioned above (T-test, $T_{18} = 1.5$, $p = 0.15$), but the estimates of full repertoire sizes were considerably higher (mean $\pm$ SD $= 61.4 \pm 13.1$, range: 30-75; T-test, $T_{18} = 3.0$, $p = 0.009$). The fact that this latter method yielded higher estimates of full repertoire size is a result of a higher turn-over of syllable types between recordings

when these are taken at one-week intervals. The repertoire sizes found within 25-strophe bouts did not differ between the two groups of males (18.7 *vs* 19.0, T-test, $T_{18} = 0.2$, $p = 0.81$). This indicates that males do not make use of their full repertoire at a given time and/or continuously learn new syllable types from their neighbours. The latter hypothesis is confirmed by the finding that males have a significantly higher coefficient of syllable-type sharing with their nearest neighbour (mean $\pm$ SE $= 0.35 \pm 0.05$, $N = 13$) than with a randomly selected male from 0.5-3 km distance (mean $\pm$ SE $= 0.15 \pm 0.02$, paired t-test, $T_{12} = 4.0$, $p = 0.002$). Part of the variation in syllable-type sharing between neighbours is explicable by the seasonal changes. Repeated measurements of syllable-type sharing on the same pairs of neighbours ($N = 8$ pairs) show that repertoire sharing increases with the time they spend as neighbours (ANCOVA; effect of pair: $F_{7,16} = 7.5$, $p = 0.0004$; effect of date: $F_{1,16} = 7.3$, $p = 0.016$; effect of number of days between the paired recordings: $F_{1,16} = 3.9$, $p = 0.067$; the latter variable varied between 0-5 days, mean $= 1.7$). Single cases indicate that males may rebuild nearly their whole repertoire within a few weeks, and adopt new or at least a more frequent use of syllable types that were present in the repertoires of their neighbours already at the beginning of the season.

Spatial use of song types

The great majority of males defending established territories use only one or sometimes two selected bushes or groups of bushes from which they exclusively display their V-song ('V-song perch'). In all of the remaining territory area only S-songs are used. Figure 2 illustrates this pattern on the example of a typically behaving male observed over a full day period. Only 1.7% of 1,937 observations of song-type and perch use from 14 males in 1997 did not comply with the rule of spatial separation. There are two main sources of deviation: (1) Males moving through their territory area and singing S-song, will generally switch to V-song if they encounter and evict an intruding male. (2) Males intending to leave the V-song perch rarely produce a single S-song strophe just before leaving. In contrast to these rules, males that have no established territory or are just starting to establish one, often do not show a clear distinction between a V-song perch and the territory area.

Birds select the location of the V-song perch on the basis of vegetation structure (Fig. 3). In all of 14 territories studied in 1997, V-song perches
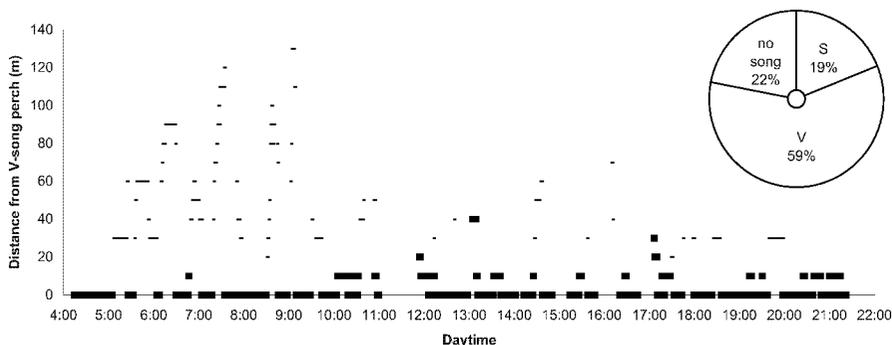
Fig. 2.   Spatial and diurnal use of two different song types (V-song in bold squares, S-song in dots) by an individual male. The male was observed on 20th of June 1997, the day when its own female laid the fifth of six eggs. As a rule, S-song was used all over the territory area, more than 20 m away from the V-song perch, whereas V-song was used close to that perch. Each of 1,029 minutes was assigned to either V-song, S-song or pause (lack of any symbol indicates a pause). The pie-chart shows the proportions of minutes assigned to either category.
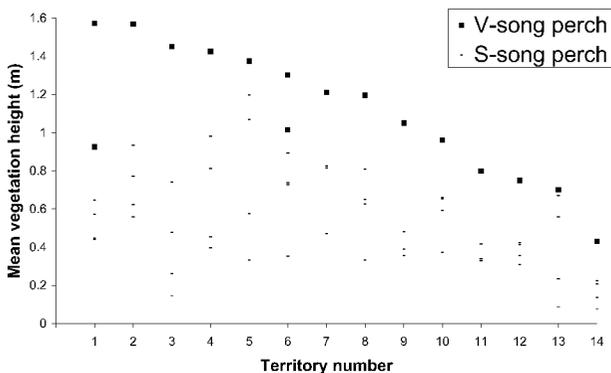

Fig. 3.   Vegetation height at song perches for each of 14 territories. Measurements were taken at all perches regularly used for V-song (12×1 and 2×2) and the four most frequently used perches for S-song. Mean vegetation height is estimated within a square of 20×20 m around the centre of the perch and reflects both the height and coverage of bush vegetation (as height of 0 was entered for the proportion of area lacking bush cover).

showed a greater mean vegetation height than the four most frequently used S-song perches in the territories (paired t-test of means, $T_{13} = 9.7$; $p < 0.0001$). As the measure of vegetation height shown in Fig. 2 reflects both, the coverage and height of bushes, it appears that males seek to have a maximally large volume of dense bush vegetation underneath, when singing

V-song. If males face the choice between dense bushes and a tall tree lacking bushes below, they prefer the bushes. Therefore, not the height of the singing perch, but the volume of bush appears to be of importance. New males settling in this area in 1998 and 1999 ($N = 14$) chose identical V-song perches as their predecessors, with one minor exception.

Temporal use of song types

The population-wide amount of V-song and S-song use varied greatly throughout the season (Fig. 4). Daily means of the proportion of V-song relative to total song (derived from song rate measurements on 16 males) are shown for 1998. Very similar overall patterns were observed in 1997 and 1999 (not shown). During times when only males but no females are present in the study area (before female arrival in early June and after female departure in late August, when males are still defending territories) both song types are used in approximately equal proportion. When females start to
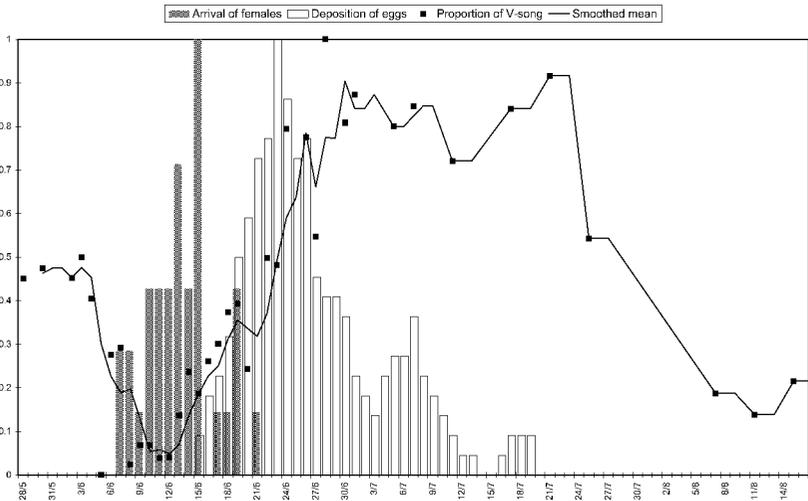

Fig. 4.   Seasonal patterns of population-wide song-type use, arrival of females and egg-laying. Squares indicate the proportion of V-song use relative to total song, measured for 16 males in the centre of the study area. The solid line shows the smoothed mean of the proportion of V-song (3-day averages). Bars indicate daily numbers of newly arriving females ($N = 35$) in the whole study area (the highest value of seven females was set to 1 on the y-axis) and daily numbers of eggs laid ($N = 245$) in the whole population (the highest value of 21 eggs was set to 1 on the y-axis). All eggs laid after July 2nd were from replacement clutches.

arrive in the breeding area, males use S-song almost exclusively. As soon as females start to lay eggs, the proportion of V-song increases and remains very high until the start of incubation of the latest replacement clutches. Notice that the arrival of females ($N = 35$) and deposition of eggs ($N = 245$) indicated in Fig. 4 reflect patterns from the overall study area, while song rate data are from 16 males from the central part of the study area. This is justified by the fact that arriving females were seen to move through the whole area.

A finer temporal resolution of singing patterns is reached when looking at singing intensity of individual males (Fig. 5). Three of the 16 males surveyed in 1998 remained unmated, another one lost its female probably due to predation. Ten of the remaining 12 were mated monogamously, two males were polygynous. Singing intensity of these 12 males is shown in relation to season, measured in days before and after the monogamous or primary female laid the first egg (Fig. 5). As mentioned in the Methods, pairing takes place roughly eight days before the start of egg-laying. The last egg was laid 3-6 days after the first. Total singing intensity clearly peaks during
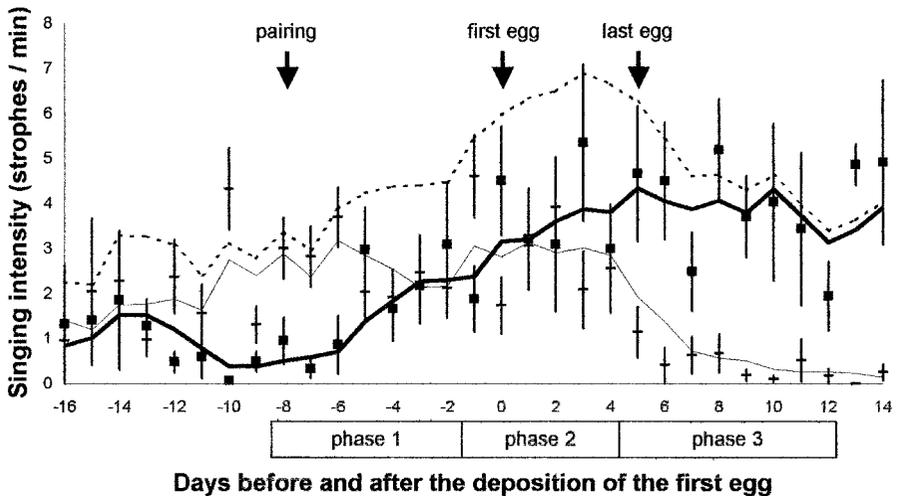

Fig. 5. Mean song activity (mean ± SE; averaged among 12 males) of V-song (bold squares) and S-song (bars) in relation to the reproductive cycle. Curves show smoothed means (3-day averages) of V-song (bold line), S-song (tiny line) and total song (sum of S-song and V-song; hatched line). The date of the last egg varied between 3-6 days after the first egg (2×3, 3×4, 6×5, 1×6 days), whereas the date of pairing almost invariably occurred 8 days prior to the start of egg-laying. For statistical analyses we use a division into three phases (see text).

the egg-laying period, fitting with the expectations derived from the fertility announcement hypothesis. S-song is used at a constantly high level from mate attraction to the end of egg-laying but hardly thereafter. The intensity of V-song increases during the period of female fertility and remains very high during incubation.

Overall singing intensity in the peak-fertility phase was significantly higher than in the nest-building phase (paired t-test: $T_{11} = 7.1$, $p < 0.0001$) and almost significantly higher than in the post-fertility phase (paired t-test: $T_{11} = 2.2$, $p = 0.051$). Intensity of S-song in the peak-fertility phase tended to be higher than in the nest-building phase (paired t-test: $T_{11} = 2.0$, $p = 0.076$) and was significantly higher than in the post-fertility phase (paired t-test: $T_{11} = 5.7$, $p = 0.0001$). Intensity of V-song was significantly higher in the peak-fertility phase than in the nest-building phase (paired t-test: $T_{11} = 4.2$, $p = 0.002$) and was even higher, but not significantly, in the post-fertility phase (paired t-test: $T_{11} = 1.0$, $p = 0.35$). The three males that remained unmated showed very similar patterns. Singing intensity (S-song and V-song considered separately) averaged among these three males differed by less than one SD (measuring between-individual variation) from the mean of the 12 mated males for the two first phases. During phase 3, however, S-song was more frequent in unmated than in mated males ($T_{13} = 2.4$, $p = 0.034$).

During the phase of highest female fertility males spend most of the daytime singing. The 12 males sang during 497 of 620 minutes of observation (80%) between 4:30-10:00 h in phase 2. The male shown in Fig. 2 sang 78% of the 1,029 min it was observed, while we could not observe any encounters between this male and its female during that day. Mate guarding, in the sense of a male following its fertile social female, was hardly ever witnessed in any breeding pair. Conservatively speaking, males spend less than 10% of the time during the fertile period in close vicinity (<20 m) of the female.

Discrimination of S-songs

All seven experimental males reacted to playback by approaching and singing V-song, as this is typically observed in aggressive male encounters. Playbacks of S-song of nearest neighbours from the previous season elicited significantly stronger responses than S-song of males having had no prior ownership in this area (paired t-test on $\log_{10}$-transformed distances of closed approach: $T_6 = 6.2$, $p = 0.001$).

Discussion

Testing the fertility announcement hypothesis

The present study demonstrates that, in the dusky warbler, singing intensity reaches its seasonal peak when females are fertile. This is remarkable, as males of most other passerine species start to sing less once they are mated (Gil *et al.*, 1999). Therefore, the dusky warbler offers a very good system to study the applicability of the fertility announcement hypothesis (Møller, 1991) to species which do sing intensively after pairing. The fertility announcement hypothesis states that males should try to sing as much as they can, because this will increase their attractiveness to females. This idea is based on the assumption that females prefer to copulate with males singing at high rate. However, a study on extra-pair paternity in the dusky warbler (Forstmeier *et al.*, subm.) does not support this assumption. The paternity analysis showed that: (1) Nearly half of the offspring were sired by males from nearby territories. (2) Females consistently preferred males with high-quality V-songs as copulation partners. (3) The measure of V-song quality that was strongly correlated with paternity patterns, was unrelated to song rate (Pearson correlation: $r = -0.31$, $N = 15$, $p = 0.27$). As song rate *per se* was not under sexual selection, the fertility announcement hypothesis is unlikely to apply to our system.

If females do not prefer males with a high song rate, why should males then sing intensively during female fertility? We suggest that males display their V-song during that period because females base their choice of copulation partners on the quality (not quantity) of that song type. We argue that there is no need to invoke intersexual selection on song rate — female preference for song quality might be sufficient — in order to obtain a peak of singing activity when females are fertile.

Individual recognition

Using a playback experiment we were able to show that, when re-establishing their last-year territory shortly after spring arrival, males react stronger to the S-song of a last-year neighbour (that has not yet arrived) than to the S-song of an unfamiliar male. At first sight, the strong reaction towards the previous neighbour may seem to contradict the 'dear-enemy effect' (Fisher, 1954; Ydenberg *et al.*, 1988), which suggests that territorial males react less towards the song of an already established neighbour than towards the song

of a newcomer. However, in the present case, the territory-establishing male should perceive males with prior territory ownership in the area as a greater threat than other males. This is because the prior territory owner should have strong intentions to settle in this place, and prior ownership is an important factor in determining success in territory establishment (Forstmeier, 2002). In conclusion, the experiment indicates that males discriminate between familiar and unfamiliar S-song types, which supports the idea that S-song may facilitate individual recognition.

Functions of the two song types

We tried to get deeper insights into song functions by looking at how the two song types are being used by singing males. Other studies of song-type functions in relation to song complexity (Catchpole, 1980, 1982, 1983; Slater, 1981; Groschupf, 1985; Catchpole & Leisler 1989, 1996; Fessl & Hoi, 1996) led us to the hypothesis that the S-song might be used as a territorial signal, while the much more complex V-song might signal male quality.

The first part of this hypothesis is supported by the following findings: (1) As predicted, S-song was used at high intensity when a male's social partner was fertile, the period when it is most crucial to keep out intruding males. (2) S-song is used while the male is patrolling through the territory area. Periods with much S-song are therefore the periods of high patrolling activity and male intruders are best discovered when patrolling. Observations of male intrusions suggest that these may lead to secretive extra-pair copulations. Increased territorial defence by males during female fertility was also found in European robins, *Erithacus rubecula* (Tobias & Seddon, 2000). (3) The individuality of S-song strengthens the idea that this song type serves to mark the claimed area by using a kind of individual signature.

Our results also support the idea that V-song may advertise male quality: (1) Males use V-song most intensively when their own female is fertile and also after this period, when neighbouring females are still laying eggs (late females, secondary females and females making replacement clutches). (2) V-song is presented only from a certain group of bushes, the interior of which provides maximal protection from view by others. Our observations strongly suggest that females visit males at these song perches and that extra-pair copulations happen inside of these bushes. Although such visits appeared to occur quite regularly (judging from male behaviour),

the density of bush vegetation hindered us from witnessing even a single extra-pair copulation. As social males provide substantial parental care, one should expect extra-pair copulations to happen secretively. Alternatively, the selection of V-song perches may be interpreted as an anti-predator behaviour, but we found no behavioural differences between areas with frequent and very infrequent predator encounters (unpubl. data). (3) Paternity analysis strongly suggests that females choose copulation partners based on the quality of their V-songs (Forstmeier *et al.*, subm.).

Although it may be tempting to deduce that V-song is used to address females and S-song is used to address males, such a conclusion would ignore the following two facts. (1) At the time when females arrive and settle in the area (*i.e.* when social mating takes place) S-song is used almost exclusively. (2) V-song is used extensively in aggressive male-male interactions. We therefore suggest that the two song types do not primarily differ in whom they address (see *e.g.* Kroodsma *et al.*, 1989), they differ in their function. S-song marks a territorial area, while V-song reflects male singing abilities. The importance of these messages may differ between male and female receivers and this should also vary throughout the season:

(1) The fact that males are capable of discriminating between familiar and unfamiliar S-song, as shown by the playback experiment, renders it very likely that females may also be able to individually recognise males that they know from the previous breeding season. Even juvenile females potentially have the possibility to look for future social partners in late summer and early autumn when adult males are still defending territories using both, S-song and V-song. It might be hypothesised that females prefer to mate generally with older males, or specifically with certain males of known identity and quality. Although very few studies have actually shown the existence of such long-term memory (*e.g.* Godard, 1991), there are no indications why individual recognition should not be a common phenomenon (Falls, 1992). In contrast, we found no support for the hypothesis that song rate was correlated with social mating success (see *e.g.* Radesäter *et al.*, 1987). Neither total song rate nor song rate of S-song was negatively correlated with the pairing date of a male ($r = 0.23$, $N = 13$, $p = 0.46$ and $r = 0.16$, $N = 13$, $p = 0.61$) nor were these two measures of song rate lower in males that remained unmated ($T_{15} = 0.82$, $p = 0.42$ and $T_{15} = 1.67$, $p = 0.11$), but all trends were in the opposite direction. We therefore conclude that the

rate of S-song was not important for social pairing. Instead we suggest that individual recognition may play a role in female choice.

(2) The fact that males switch from S-song to V-song when they have aggressive encounters is best understood as signalling arousal. Similar phenomena, such as switching to another song type, increasing the rate of switching between song types or singing more variable songs have been described for many other species (Lemon, 1968; Dixon, 1969; Schroeder & Wiley, 1983; Lemon *et al.*, 1987; Staicer, 1989; Spector, 1991; Luschi & Seppia, 1996). Assuming that females judge male quality by V-songs, what is the significance of large repertoires and syllable-type sharing between neighbours? In the dusky warbler males typically engage in countersinging. Some incidental recordings of countersinging males indicate that syllable-type matching does occur quite regularly. Moreover, our finding that syllable-type sharing is highest between nearest neighbours and even increases with duration of acquaintance (see McGregor & Krebs, 1989; Mountjoy & Lemon, 1995), suggests an important role of matching. Recent studies indicate that syllable-type matching correlates with aggressiveness of male-male interactions (Beecher *et al.*, 2000) and other studies suggest that females may assess potential extra-pair males by eavesdropping on male-male interactions (Otter *et al.*, 1999). We hypothesise that males compete with each other about the quality of their songs (whatever the criterion for quality is; see *e.g.* Forstmeier *et al.*, subm.; Lambrechts & Dhondt, 1987; Lambrechts, 1992) and continuous learning from neighbours is part of this competitive interaction. Such competition would be most intense if females could judge male quality only from direct comparison between males (*i.e.* when these match their syllable types). By introducing new variation (*e.g.* syllable type switches within strophes or new syllable types) birds may try to escape from being matched or challenge their neighbours with something they cannot match.

Are there any likely alternative interpretations of the functions of song-type use after pairing? Rodrigues (1996) studied song in the closely related chiffchaff (*Phylloscopus collybita*) and found a temporal pattern of singing intensity resembling that of the V-song shown in Fig. 5. Song rates during female fertility were roughly twice those around pairing and became higher still in the post-fertile period. Applying our conclusions to the case of the chiffchaff would mean that males probably advertise their quality to attract females for copulations. However, Rodrigues interpreted the late singing

in the chiffchaff as territorial defence and as attracting a new female in anticipation of possible nest predation. We can argue that this at least does not apply to the dusky warbler. The risk to lose a territory is relatively high early in the season as long as new males arrive to the breeding area, but loss of territory never occurred during the breeding period. Similarly the chance of attracting a female strongly declines as soon as there are no more new females arriving. The intensity of song related to these two functions should therefore decline rather than increase over the course of the season.

The lack of mate guarding

Comparing the dusky warbler to congeneric species and other passerines, it is not only very astonishing that paired males sing so much, but also that they do not guard their fertile females. In the well studied European *Phylloscopus* species, males prefer mate guarding over singing in order to maximise their reproductive successes (Arvidsson, 1992; Rodrigues, 1998; Gil *et al.*, 1999). The fact that all dusky warbler males, irrespective of their individual V-song quality, do not guard their mates, demands a general explanation. There is one striking difference between the dusky warbler and its European counterparts that might hypothetically explain this phenomenon. In our study area, dusky warblers suffer heavily from brood parasitism by the oriental cuckoo (*Cuculus saturatus horsfieldi*). Eight out of 40 nests (20%) found prior to the deposition of the first egg were parasitised by cuckoos. Half of these nests were deserted and in the other four cases the cuckoo egg was accepted. In contrast, European cuckoos (*Cuculus canorus*) hardly ever parasitise on European *Phylloscopus* warblers (Glue & Morgan, 1972), and this is probably because these show a very strong and successful rejection behaviour (Moksnes & Röskaft, 1992). As the presence of conspicuously behaving males near the nest increases the risk of parasitism (Banks & Martin, 2001), we suggest that male dusky warblers avoid parasitism by not accompanying their nest-building females. Other studies suggest that mate guarding is not very efficient in reducing cuckoldry by conspecifics (Kempenaers *et al.*, 1995), and a slight increase in the risk of cuckoldry by heterospecifics may render this behaviour maladaptive. The fact that dusky warbler males guard their territories instead of their mates is unusual, but certainly not unique. Robins (*Erithacus rubecula*) guard their mates not very intensively, but increase their territorial aggressiveness when females are

fertile (Tobias & Seddon, 2000). Other studies have described such variation in paternity defence strategies in relation to group composition (Langmore, 1996) or to the overall operational sex ratio (Currie *et al.*, 1998).

Conclusions

When pairing occurs male singing intensity declines in most passerine species (Gil *et al.*, 1999). Territorial defence can be maintained with little song and paternity can be assured through mate guarding by following and/or frequent copulation (Birkhead & Møller, 1992). However, in some species, such as the dusky warbler, song has achieved the function of a paternity guard. The high risk of parasitism by cuckoos may have contributed to the fact that males guard their territories instead of their fertile females. S-song is used during guarding the territory against male intruders and V-song advertises male quality towards females. Obviously, males can simultaneously advertise for both within-pair and extra-pair copulations. This system may originate from the fact that females select copulation partners on the basis of V-song quality.

We agree with Møller (1991) that song can function as a paternity guard. Theoretically this is most easily explained if there is a direct female preference for males singing at high rate (the basic mechanism underlying the fertility announcement hypothesis). However, in the dusky warbler, reality does not match this theoretical explanation. As there is no female preference for males singing at high rate, we have to conclude that a female preference for high song quality can be sufficient to let mated males sing so much.

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