

Song output and reproductive success in the Dartford warbler (*Sylvia undata*)

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ABSTRACT. *Song output and reproductive success in the Dartford warbler (Sylvia undata).*- A study on the Dartford warbler (*Sylvia undata*) in southern England investigated annual song output and reproductive success, as well as other aspects of male and territory quality. Male song output over the year was correlated with the number of young produced. Song output was also correlated with short-term measures of song rate, although song rate itself was not correlated with reproductive success. There was no evidence that song output or reproductive success were related to other aspects of male quality or territory quality. However, song output was correlated with measures of male aggression during territorial disputes. It is suggested that males who sang more throughout the year were more successful in attracting and retaining females for successful breeding.

KEY WORDS. Song, Reproductive success, Dartford warbler, *Sylvia undata*

Introduction

Although it is generally agreed that song functions in both territorial defence and mate attraction, so far there has been greater emphasis upon the quality rather than the quantity of song males produce (Catchpole, 1982, 1987). However, some studies (e.g. Reid, 1987) have shown that singing behaviour is costly and related to the energetic condition of the male. The more food a male obtains the more time and energy he can allocate to singing. If singing is related to territorial defence and mate attraction, males which sing more might be expected to show higher reproductive success. Furthermore, a vigorously singing male might reflect his own superior quality, the quality of

his territory, or both to prospecting females.

A link between territory quality and song rate has been demonstrated by Radesater et al. (1987), who found that male willow warblers *Phylloscopus trochilus* who obtained better territories spent less time searching for food, had a higher singing rate, and attracted females earlier. Radesater and Jakobsson (1989) tested this further by removal experiments, and found a strong correlation between the singing rates of different male willow warblers on the same territories. Alatalo et al. (1990) investigated the relationship between food supply and singing rate experimentally in a population of the pied flycatcher *Ficedula hypoleuca*. Males supplied with extra food sang at twice the rate of controls, and also paired before the controls.

There has been rather less evidence to suggest

that song output is related directly to male quality. The only study so far was by Greig-Smith (1982) on the stonechat *Saxicola torquata*, where two correlations between song rate and male parental behaviour were obtained. Males with high song rates invested more in feeding young and in defending the nest. However Greig-Smith found little evidence to suggest that song rate was correlated with various measures of reproductive success.

Indeed, there has been little direct evidence to show that males who sing more increase their fitness by leaving behind more offspring. Payne & Payne (1977) studied a population of village indigobirds *Vidua chalybeata*, and found that males who obtained more matings at dispersed leks had higher song rates. Møller (1983) measured the amount of seasonal song in corn buntings *Emberiza calandra*. He found that males who sang more intensively were observed with more females and more young in their territories.

The Dartford warbler *Sylvia undata* occurs on lowland heath in southern England and is particularly associated with areas of gorse *Ulex europaeus*. It is a resident species, and sings throughout most of the year. This study attempts to quantify the amount of song produced during the year, and relates this and other relevant variables to male reproductive success. The study also measures reproductive success directly, as the number of young produced by each male during the year.

Methods

The study site

The study site was Holt Heath National Nature Reserve, Dorset, U.K., a 400ha area of lowland

heath in southern England. The heath is dominated by heather *Calluna vulgaris*, and gorse *Ulex europaeus*, and this floristic simplicity makes it ideal for measuring the precise area of the important plant species. Accurate scale maps divided into 100m grids were used to map vegetation, singing males and territory boundaries. Some adults were caught and colour-ringed to permit individual identification. The project was started in January 1989, and the heath was visited on an almost daily basis for the next two years.

Territory quality

Territory boundaries were obtained by plotting the positions of singing and fighting males onto scale maps, and by detailed observations of individual males. By the end of the season, there was little doubt about the location of territory boundaries. The vegetation in each territory was mapped, and precise areas determined using a Quantimet Image Analyser programmed to measure the area of each territory, the area of dominant plant species and the territory perimeter. The following territory quality variables were measured and used in this analysis:

Territory perimeter (m): The total length of the territory boundary.

Territory size (ha): The total area of the territory.

Area of gorse (ha): The total area of gorse within the territory.

Area of heather (ha): The total area of heather within the territory.

Height of gorse (m): The average height of gorse within the territory.

Number of neighbours: The number of surrounding territories whose boundaries were shared at some point.

Nearest neighbour (m): The distance from the centre of the territory to the nearest centre of a neighbouring territory.

Male quality

Once a week throughout the year, each territory was visited in the early morning to collect behavioural data on male quality. The following data were systematically collected in this way:

Song output: A note was made of whether or not each male was heard singing and song output is expressed as the total number of days during the year each male was in song.

Song rate: Dartford warblers sing discrete songs in short bouts, and song rate is expressed as the average number of songs per minute for each male.

Song flights: Song flights were relatively uncommon, and are expressed as the total number of days in the year on which song flighting was observed in each male.

Aggression: Aggressive interactions between rival territorial males were also noted, and are expressed as the total number of days in the year in which each male was observed in such interactions.

Ten males were caught during the study, and the following biometric data was taken and used in a separate analysis:

Weight (g)

Wing length (mm)

Tail length (mm)

Throat patch: Total area of the red throat patch, and the number of white spots on it.

Breast colouration: Hue, value and chroma using Munsell colour cards

Reproductive success

Dartford warblers are resident, monogamous breeders in southern England. The following analysis is restricted to males which maintained a territory all year, and whose reproductive success could be accurately determined by finding nests and young. Male reproductive success is taken as the

total number of young successfully fledged during the year in the territory of each resident male. Dartford warblers nest in dense vegetation such as gorse, and with low nest predation enjoy relatively high breeding success. In both years of the study most pairs raised two broods successfully, but reproductive success showed considerable variation from 0-8 fledged young. Most males produced 5-8 young by raising two consecutive broods, a few produced 1-4 young by raising only one brood, and a very few no young at all. In 1990 for example, 26 out of the 33 males successfully raised two broods. Five males raised only one brood, two because they paired too late to raise a second brood, and three because the female deserted them after raising only one brood. Only two males failed to raise any young at all. In one case the female deserted during a breeding attempt, and in the other case the female deserted before breeding was attempted. Therefore, the main factor affecting reproductive success in males is the ability to attract females early enough, and to retain them throughout the breeding season to raise one or two broods. It seems likely that the ability to sing throughout the season plays an important role in this process.

Statistical analysis

Preliminary analysis revealed that although most variables could be transformed to achieve a normal distribution, this was not so with the number of young produced, which was the key dependent variable. For this reason the non-parametric Spearman rank correlation (Siegel, 1956) has been used throughout. As evidence has consistently indicated the robustness of multivariate analyses to departures from parametric assumptions (e.g. Harris, 1975), multiple regression has also been used in part of the analysis. A conservative two-tailed region of rejection was set for all statistical tests.

TABLE I. Multiple regression of six intercorrelated variables on the number of young produced and song output in male Dartford warblers during 1990.

[Regresión múltiple de seis variables intercorrelacionadas con el número de jóvenes producidos y emisión de sonidos en machos de *Sylvia undata* durante 1990.]

Independent variable	Dependent variables			
	Number of young		Song output	
	B coeff.	P	B coeff.	P
Number of neighbours	-0.08	0.74	-0.06	0.70
Nearest neighbour	-0.30	0.89	-0.01	0.92
Aggression	-0.23	0.43	0.51	0.01**
Song flights	-0.10	0.72	0.32	0.06
Song rate	0.15	0.48	0.16	0.25
Song output	0.62	0.05*	-	-

Results

In 1989, an initial preliminary study provided data from 16 males whose reproductive success (as measured by the number of young produced) was accurately known. Measurements of territory quality (see methods) were taken as well as song output throughout the season. Song output was the only variable which was found to be significantly correlated with the number of young produced ($r_s=0.562$, $n=16$, $p=0.023$). However song output itself was not significantly correlated with any of the territory quality variables.

The 1990 study provided data from a much larger sample of 33 males whose reproductive success was known. As well as territory quality variables and song output, this data set included measurements of three additional male quality variables (song rate, song flights and aggression). Again, only song output was significantly correlated with the number of young produced ($r_s=0.353$, $n=33$, $p=0.044$, fig. 1).

However song output itself was significantly intercorrelated with the five other variables shown in

table I. Males with a high song output also sang at a faster rate, song flighted more, were more aggressive, had more neighbours and were closer to their neighbours. A highly significant correlation

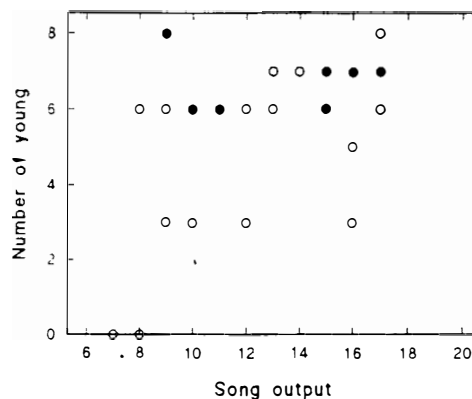


FIGURE 1. The relationship between male song output and the number of young produced in 1990. (Filled circles represent more than one data point).

[Relación entre la emisión de sonidos del macho y el número de jóvenes producidos en 1990.]

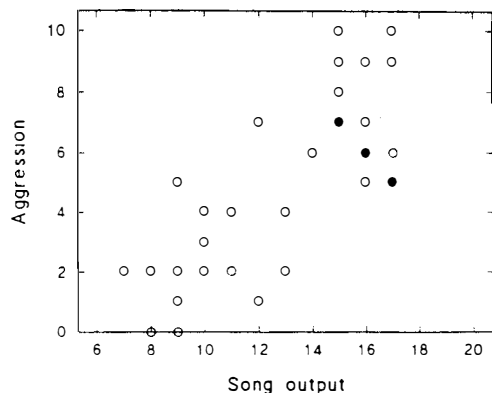


FIGURE 2. The relationship between male song output and territorial aggression in 1990. (Filled circles represent more than one data point).

[Relación entre la emisión de sonidos del macho y la agresión territorial en 1990.]

between song output and song rate ($r_s=0.459$, $n=33$, $p=0.007$) is particularly interesting, suggesting that the short-term measurement of song rate can give a reliable indication of song output throughout the season.

When these six intercorrelated variables were entered into a multiple regression with the number of young as the dependent variable, the analysis confirmed that song output was the only significant variable affecting the number of young produced (table I). When the other five variables were entered, this time with song output as the dependent variable, the analysis shows aggression to be the only significant variable which appears to affect song output (table I). The particularly strong relationship between song output and aggression ($r_s=0.725$, $n=33$, $P=0.001$) is illustrated in figure 2.

Over the two years 10 of the adult males were caught and measured to collect other male quality

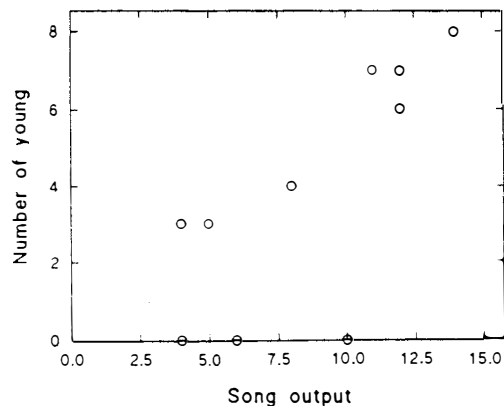


FIGURE 3. The relationship between male song output and the number of young produced in a sample of 10 males for whom detailed biometric data was available.

[Relación entre la emisión del sonidos del macho y el número de jóvenes producidos en una muestra de 10 machos de los que se obtuvieron datos biométricos.]

data such as weight, wing length, tail length and plumage colouration. These data were added to the existing data on song and territory quality for each male. From all the male and territory quality variables now available for analysis, the only relationship to emerge was again a highly significant correlation between song output and the number of young produced ($r_s=0.770$, $n=10$, $p<0.01$, fig. 3).

Discussion

Dartford warblers are resident, and unlike migratory species, there is no sudden arrival and pairing when female choice is readily apparent to the

observer. We therefore have no direct evidence that females are choosing males on the basis of their singing. Pairing date has been used as an indirect correlate of reproductive success with song rate in studies of migratory species such as the pied flycatcher (Gottlander, 1987; Alatalo et al., 1990), where there is also good experimental evidence that females are attracted by male song (Eriksson & Wallin, 1986). There is now considerable experimental evidence that females are stimulated and attracted by quality attributes of male song such as repertoire size (Catchpole, 1987), but rather less suggesting that the amount of song is important. However in the sedge warbler *Acrocephalus schoenobaenus*, high song rate can compensate for lower repertoire size and was found to elicit more response from captive females (Catchpole et al., 1984). Wasserman & Cigliano (1991) have shown that captive female white-throated sparrows *Zonotrichia albicollis*, responded more when song rate and song length are increased.

The main link between song rate and eventual reproductive success seems to be with territory quality and food supply in particular. The evidence here is largely from studies which have shown that increasing food supply increases song rate, which in turn leads to earlier pairing (Radesater et al., 1987; Alatalo et al., 1990). Such a male is not only in better condition, but needs to spend less time foraging and so has more time and energy to allocate to singing. Under more natural conditions, the nature of the link between song output and male or territory quality (or both) is far from clear. A male who is of higher genotypic or phenotypic quality might be expected to have a high song output, but so might a male in a high quality territory. Song output in the present study was not correlated with any of the obvious measurements of territory or male quality, but was correlated with several behavioural measures associated with singing and territorial defence - notably male aggression. But again the link is a tenuous one, there was no

independent correlation between male aggression and reproductive success.

In this study, the exact nature of the link between song output and reproductive success remains elusive. We have no direct evidence that females are even selecting males on the basis of their song output. However, males which sang more throughout the year left behind more young. This is not surprising, as such males would be expected not only to attract females, but to retain them throughout the breeding season, thus eventually producing two broods of young. Some males which sang less attracted females too late to achieve this, and some even lost their females before breeding. Such unmated males in many species of songbird increase song output, but this was not the case in the Dartford warbler. This suggests that song output in the Dartford warbler might act as an honest advertisement of male quality, and that females who select males with a high song output will increase their reproductive success. Although song rate is the most obvious aspect to assess in the short-term, in a resident species the female has considerable time to assess song output, and could certainly become aware of males in the population who are more or less frequent singers.

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Resumen

*Emisión de sonidos y éxito reproductor en la *Curruca rabilarga* (*Sylvia undata*).*

Se estudió la emisión de sonidos y éxitos reproductivos de la curruca rabilarga (*Sylvia undata*) al sur de Inglaterra, así como algunas características del macho y de la calidad del territorio. La emisión de sonidos por el macho durante el año está correlacionado con el número de jóvenes producidos, así como con la proporción de sonidos emitidos a corto plazo, aunque la proporción de sonidos por sí mismo no está correlacionado con el éxito reproductivo. No se encontró evidencias de que la emisión de sonidos o el éxito reproductivo estuviera relacionado con otros aspectos de la calidad del macho o del territorio. Sin embargo, la emisión de sonidos está correlacionada con medidas de la agresión del macho durante las disputas territoriales. Esto sugiere que los machos que cantaron más durante el año tuvieron más éxito atrayendo y reteniendo a las hembras para reproducirse con éxito

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