

Male bird song attracts females – a field experiment

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Summary. The initial stage of pair formation of the pied and the collared flycatcher (*Ficedula hypoleuca* and *F. albicollis*) was simulated in a field experiment. Male dummies positioned near nest boxes and “singing” by means of tape-recorded song from loudspeakers offered prospecting females a nest box combined with an automatic trap. An unequivocal demonstration of female arrival at the male’s territory was obtained by the trapping of the female. Control nest-box traps were provided with silent dummies. Factors other than male song causing female attraction were controlled by a daily switch of the position of “singing” and silent dummies. Nine out of ten females were caught in nest-box traps with “singing” dummies (one-tailed binomial test, $P=0.011$). The result supports the hypothesis that male song functions in mate attraction. This hypothesis has never previously been tested in field experiments although circumstantial evidence for it has been available.

Introduction

Although it is frequently stated that the song of male passerine birds plays a role in attracting females (Howard 1920; Marler 1956), there is so far no experimental evidence to support this assertion (Catchpole 1982). Evidence clearly has been difficult to obtain. It should be based on field experiments designed to prove that the female’s approach to and arrival at the male’s territory is in direct response to his song activity. In this report we present such an experiment.

The species studied were the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*F. albicollis*). These two Palearctic species are closely related and in areas of sympatry actually hybridize

at moderate frequency despite great differences in song and plumage (Alatalo et al. 1982). Both species are tropical migrants that overwinter in west and central Africa, respectively. In central Sweden the males of both species usually arrive at the breeding grounds in the first week of May. These birds breed in three holes but prefer nest boxes if such are available. The first males arrive several days before the first females, and each male defends a small territory consisting of a nest site and its immediate surroundings (Haartman 1956; Curio 1959). The male sings frequently from a perch close to the nest hole, and if a prospecting female approaches he vigorously demonstrates the nest hole by repeated flights to its entrance. During these demonstration flights he also emits a special type of song. The female eventually inspects the nest hole by following the male into it, and stays inside for a short while. If the female accepts the offered nest, the male almost immediately stops singing, and the nest building by the female begins promptly. The fact that in these two species the male abruptly stops singing after acquiring a mate is indirect evidence that song functions primarily to attract females (Wallin 1986).

Methods

To test whether females were attracted by the male’s song, we used special traps in the shape of a nest box. A perch at the nest box entrance functioned as a release mechanism for a spring net which captured females alive as they were inspecting the nest site. In this manner we replaced direct observation with automatic recording of the female’s arrival in order to assess arrival objectively and to increase the number of records of female visits. Nest-box traps were arranged in groups of four, with one trap placed in each corner of a square with sides about 30 m long. To simulate the natural situation, each trap was guarded by a male dummy (about 1 m away from it). Two of the dummies in the group were silent while at the other two traps song was broadcast from a loudspeaker fed

from a cassette player (one battery-operated Sanyo M-G14 stereo cassette player fed signals to two Audio Technica AT-SP5 loudspeakers with a battery-operated amplifier built into each speaker). The sound level of the loudspeakers was adjusted to "natural" with the aid of the level meter of a tape recorder (Sony TC-D5M or Nagra SN) calibrated on live, singing flycatchers. Each cassette player contained a continuous loop with normal pied or collared flycatcher song (1-min sequence on TDK EC-1M endless cassette). Song and dummies of only one of the two species were presented in each group. To control for the possibility that some sites were preferred over others by the females, the positions of singing and silent dummies were switched clockwise each day within each group. Captured birds were usually released within a few min.

In May 1985 seven such trap groups were set up. Three were placed at Horn Nature Reserve (57°10'N/16°58'E) on the island of Öland in the Baltic and four at Lake Hosjön (59°55'N/18°20'E) near Uppsala, central Sweden (trap groups about 150 m apart at each locality). On the island of Öland where both species occur, one trap group of pied and two of collared flycatcher were used. This reflects the local relative abundance of the two species. Pied flycatcher was presented in all four trap groups at Uppsala as only this species occurs there. Experiments were carried out each day from 9 May until 27 May, from sunrise to noon (except for a few days with rainy weather).

Results

Six pied flycatcher females were captured at Uppsala in nest-box traps with "singing" pied flycatcher dummies while no female was obtained in traps with silent dummies at this locality. Three collared flycatcher females were similarly trapped on Öland at "singing" collared flycatcher male dummies, and one pied flycatcher female was trapped at a silent pied flycatcher dummy. All females were banded before they were released; no female entered a nest-box trap more than once.

The close similarity of behaviour in the two species was the basis of the earlier decision to combine them in an analysis of the results of the experiment. Nine out of ten females were caught in traps at which song was broadcast whereas only one was caught in a trap with no song (binomial test, one-tailed probability, $P=0.011$). This result is consistent with the hypothesis that male song functions in mate attraction. At the only locality (Uppsala) where the sample size for a single species was sufficient for testing, the attraction of females by song was also demonstrated ($P=0.016$).

Discussion

In many species of songbirds the male's singing activity drops dramatically after he has acquired a mate, implying that one function of song in these species is female attraction. After removal of the female in pairs of white-throated sparrows (*Zono-*

trichia albicollis), great tits (*Parus major*) and starlings (*Sturnus vulgaris*), a significant increase in the male singing activity was recorded (Wasserman 1977; Krebs et al. 1981; Cuthill and Hindmarsh 1985). Such experiments provide strong but nevertheless indirect evidence for the role of song as a mate-attracting signal (the behaviour of the female was not tested). Circumstantial evidence is also provided in laboratory studies with captive female brown-headed cowbirds (*Molothrus ater*) (King and West 1977) and with female white-crowned sparrows (*Zonotrichia leucophrys*), song sparrows (*Melospiza melodia*) and sedge warblers (*Acrocephalus schoenobaenus*) treated with steroid hormones (Baker et al. 1981; Searcy and Marler 1981; Catchpole et al. 1984). These females perform courtship display when presented with conspecific male song. Such laboratory experiments show that a female responds to song in intersexual interactions, but they do not demonstrate mate attraction (expressed as the female's approach to and arrival at a male's territory). An aversive effect of song upon males has previously been demonstrated in some field experiments (Peek 1972; Göransson et al. 1974; Krebs 1976; Smith 1979).

One of the difficulties associated with standard playback experiments is how to interpret and quantify any response observed (Catchpole 1979). In the course of our experiment we saw some females approaching a "singing" dummy without carrying out nest hole inspection. Consequently, these females were never trapped and are not included in the sample. On these occasions a live male would probably have elicited the female's final nest hole inspection by switching to the courting song and by demonstrative flights to the nest hole. Because pair formation of the pied and collared flycatchers takes place at the nest hole, however, we avoided the problem of interpreting the response by quantifying female behaviour in an objective way. The trapping of the female was the sole criterion for defining her approach to and arrival at the male's territory, and in that respect our test is conservative. We consider the result of the present study to be direct evidence that male bird song may serve as a mate-attracting signal.

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