

Song functions and territoriality in Eurasian Treecreeper *Certhia familiaris* and Short-toed Treecreeper *Certhia brachydactyla*

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Abstract. The study was conducted in Western Poland during three breeding seasons (1996–1998). Spontaneous song rate changes and playback experiments were used to determine functions of the song in two closely related, sympatric species: Eurasian Treecreeper and Short-toed Treecreeper. Substantial differences in spontaneous song rate and reaction to playback between the studied treecreepers were found. On average Short-toed Treecreeper had a two times higher song rate and longer song bouts than Eurasian Treecreeper. Both species reacted stronger to the playback during the prebreeding and egg-laying stages than during the incubation/feeding stage. Therefore, the primary function of the song in these sibling species is to deter rival males from gaining access to the territory and fertile females. We found no evidence that the song was directly related to mate attraction or stimulation. When reacting to the playback the response patterns differed between the two species, but the overall experimental song response was similar. Interspecific differences in the singing pattern can be explained by dissimilar territorial behaviour. Short-toed Treecreeper bred in clusters, leading to frequent and more ritualized countersinging between rival males. Eurasian Treecreeper territories were scattered and separated by unoccupied habitat. This probably explains why the males rarely sing spontaneously, but behave more aggressively when rivals intrude.

Key words: Short-toed Treecreeper, *Certhia brachydactyla*, Eurasian Treecreeper, *Certhia familiaris*, avian song, territoriality, playback experiments

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INTRODUCTION

The passerine song is considered to have evolved under two kinds of sexual selection (Trivers 1972). Firstly, males use songs to establish and defend a territory as a prerequisite for acquiring a female later (intrasexual selection; e.g. Krebs 1977). Secondly, the song itself may be attractive to females and, therefore, increases a singer's mating chances (intersexual selection; Catchpole 1982, Bensch & Hasselquist 1992). These two functions are not mutually exclusive (Armstrong 1973). Some evidence suggests also that in some species male song affects directly female's reproduction (e.g. Wingfield & Farner 1993).

Eurasian Treecreeper *Certhia familiaris*, and Short-toed Treecreeper *Certhia brachydactyla* are sibling species. Their songs are simple and monotypic over large areas (Thielcke 1961, 1965a). The major dimension in which song production varies is song rate, not song structure or length (Thielcke 1961, Cramp & Perrins 1993). The simplicity of song structure and bout organisation (e.g. no switching between song types) suggest that the song has evolved under a strong intrasexual selection in both species (Catchpole & Slater 1995). In the present study song rate changes and playback experiments were used to determine whether the song has a territorial or a female attractant function in these two species. We focused on

quantitative differences in response to playback and their possible origin.

STUDY AREA AND METHODS

The study was conducted in the Wielkopolska National Park of W Poland (52°15'N, 16°50'E), in three breeding seasons, 1996–1998. The study area (ca. 150 ha) consists of a mixture of both pure and mixed forest stands. Most of the Wielkopolska NP is dominated by Scotch Pine *Pinus sylvestris*, but there are also patches dominated by English Oak *Quercus robur*, Norway Spruce *Picea abies*, Beech *Fagus sylvatica* and False Acacia *Robinia pseudoacacia*.

We studied individually recognizable treecreepers, breeding mainly in special nest-boxes. We carried out playback experiments between 06:00 and 12:00 hour local time. Experimental trials were performed during three breeding stages: prebreeding (PRE), egg-laying (EGG), and incubation/feeding (INC). Breeding stages were determined during regular inspections of nest-boxes, and observations of birds. Each bird was tested no more than three times per year, and no more than once in each of the distinguished breeding stages. The tested males were recorded with a Sony DAT TCD-D8 recorder and Sennheiser ME67 shotgun microphone. Recordings were analysed using Avisoft SASLab Pro 3.4d (Specht 1998) and Spectrogram 4.1.12 software. In this study, the recordings were used only when any problems with male identification or call classification occurred during experiment trials.

We located the subject bird before starting each trial. Experiment trials simulated intrusions by a stranger male into the subject's territory, so loudspeaker was placed between the edge and the centre of the subject male's territory. Each trial consisted of a 3 min. test period (playback 1–3), during which the tape was played, followed by a silent 6 min. period (for analysis divided into two 3 min. periods). The songs used in playback experiments were obtained from other males in a population located at least 2 km away, i.e. from non-neighbours. We used four different recordings for each species to avoid pseudoreplication (McGregor 1992, Hopp & Morton 1998). Such a level of multiple stimuli was sufficient because the intrapopu-

lation song variation in both the studied species is very low, and the typical songs do not differ according to the properties coding the species specificity (Thielcke 1961, 1987, Martens & Geduldig 1988; see also Gil 1997 where a similar playback design was used). The problem of pseudoreplication was also minimized because recordings were of a high and similar quality, whereas numbers of song phrases played back, intervals between songs, and song volume corresponded to natural values. The order of males chosen for playback was random. During playbacks we recorded the number of song phrases sang by the test male, distance between the male and the loudspeaker, number of calls of four types uttered in each 15 sec. interval, and presence and behaviour of other treecreeper individuals. Calls were divided into four groups: 1) rival calls, i.e. "tut" calls in Short-toed Treecreeper and "zii" in Eurasian Treecreeper; 2) aggressive calls, i.e. "trill" and "zii + drohtrill", respectively; 3) long-distance calls, i.e. "srih" and "ziah" in Short-toed Treecreeper and "srih" in Eurasian Treecreeper; 4) short-distance calls, i.e. "pit" in both species. For a detailed description and sonograms of calls see Thielcke (1965b, 1971), Bergmann & Helb (1982), Cramp & Perrins (1993), and Glutz von Blotzheim & Bauer (1994).

Data about spontaneous song rate were collected from the same population from March till July of 1996. The study area was visited 43 times by 2–3 observers and singing males were mapped and their song rate counted.

Prior to ANOVA the original data were log-transformed to meet the requirements of parametric tests. Whenever transformation had not given expected results, non-parametric tests were applied using original data.

RESULTS

Generally, Eurasian Treecreepers (0.4–2.5 p/10ha) were more abundant than Short-toed Treecreepers (0.7–1.8 p/10ha) in our study plot (authors unpubl. data). Eurasian Treecreepers bred throughout the Wielkopolska NP rather uniformly, while territories of Short-toed Treecreepers often occurred in clusters of 3–5 territories, especially in deciduous patches (with oaks and/or false acacias – original unpubl. data).

SPONTANEOUS SINGING

The studied species differed in singing intensity. The spontaneous song rate in Short-toed Treecreeper was on average two times higher (3.1 ± 0.94 phrases per minute, $n = 20$ males) than in Eurasian Treecreeper (1.6 ± 0.34 phrases, $n = 13$ males). The difference was significant (Mann-Whitney U-test, $U = 56.0$, $p = 0.005$). The song rate changes during the longest observed, uninterrupted spontaneous bouts showed that Short-toed Treecreepers were more persistent singers (Fig. 1; data from the prebreeding and egg-laying stages, concerning only observations of a single male without accompanying females or rival males singing in the neighbourhood; for both species, the longest 17 spontaneous singing bouts were included). The song bouts were very specific, as male treecreepers usually moved along trunks and branches while singing, and did not cease foraging at all.

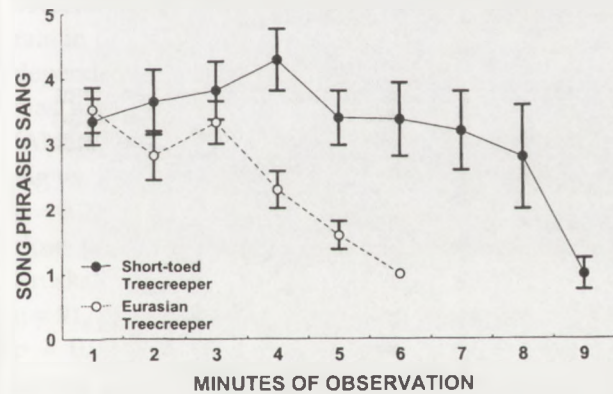


Fig. 1. Number of song phrases (mean ± SE) sang by male treecreepers in consecutive minutes of observation.

PLAYBACK EXPERIMENTS

The numbers of trials carried out during the three breeding stages were 17, 15 and 13 for Eurasian Treecreepers, and 18, 10 and 18 for Short-toed Treecreepers.

Short-toed Treecreeper males decreased their spontaneous song rate just after the playback began (< 2 song phrases per minute) and approached the loudspeaker. After the test period males started to sing more frequently, reaching the highest song rate during the 4th or 5th minute of the trial. Then, the song rate diminished (Fig. 2). Males often came very close (< 5 m) to

the loudspeaker, but generally circled around the loudspeaker at a distance of 10–20 m and flew away just after the test period (Fig. 3).

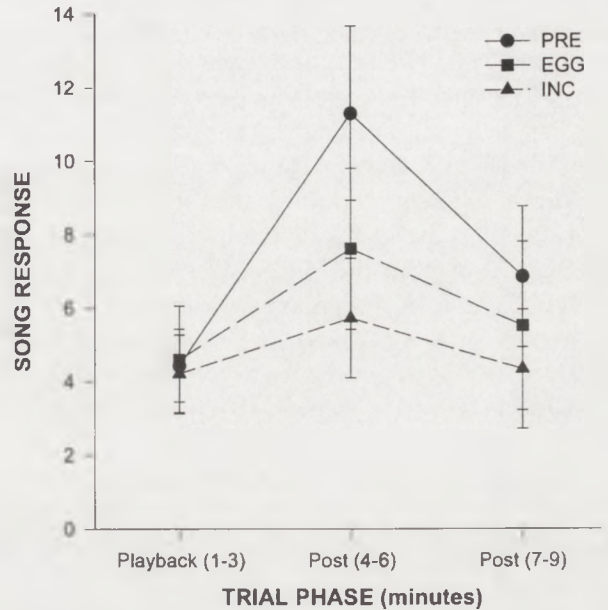


Fig. 2. Song response of the Short-toed Treecreeper to playback (mean number of phrases sang ± SE) during three each 3 min. phases of trials, in three breeding stages: PRE — prebreeding, EGG — egg laying, INC — incubating and nestlings.

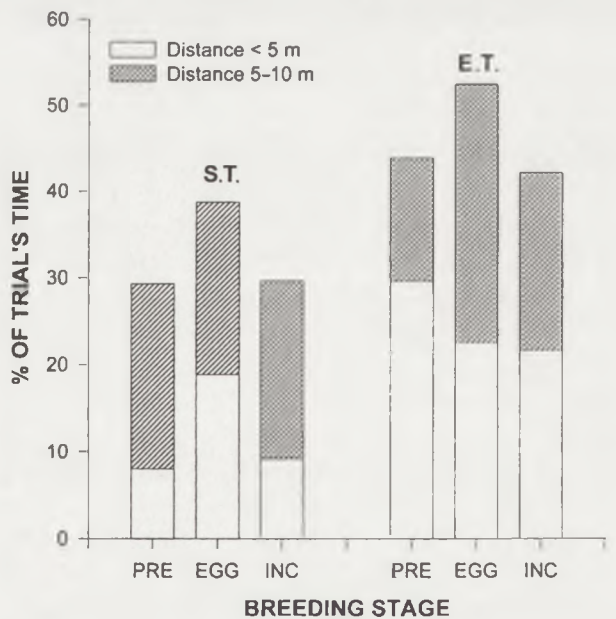


Fig. 3. Mean time spent (%) by the tested Short-toed (S.T.) and Eurasian Treecreeper (E.T.) males at a distance < 5 m and < 10 m from the loudspeaker during trials. Symbols of breeding stages — see Fig. 2.

Short-toed Treecreepers sang significantly more phrases in the first three minutes of the post-playback period in the prebreeding and egg-laying stages than in the incubation/feeding stage (Tukey-HSD, $p = 0.002$ and $p = 0.024$, respectively). The difference in song rate between the first two breeding stages was insignificant (Tukey-HSD, ns). There was no significant difference in song rate between breeding stages during the test period (Tukey-HSD, all ns). Post hoc analysis revealed a significant difference between the prebreeding and incubation/feeding stages in time spent at a distance of less than 10 m from the loudspeaker (Fig. 3, Tukey-HSD, $p = 0.035$), and an almost significant difference between the prebreeding and egg-laying stages (Tukey-HSD, $p = 0.098$). Time spent at a distance of less than 10 m to the loudspeaker depended on the presence of

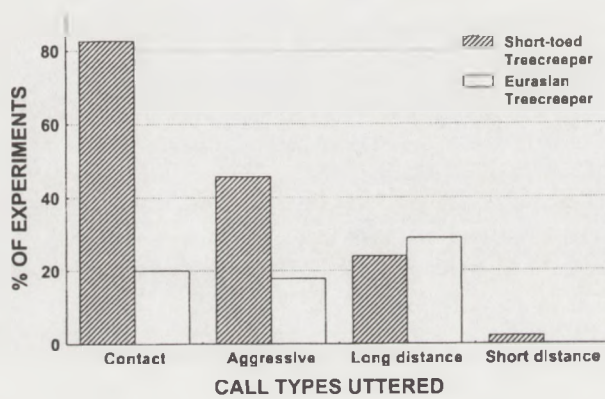


Fig. 4. Percentage of different call types uttered during trials by treecreepers studied.

additional, singing conspecific males during the trial (ANOVA, $F_{1,40} = 4.83$, $p = 0.034$). Almost significant was the interaction between the breeding stage and the presence of an additional male (ANOVA, $F_{1,40} = 2.86$, $p = 0.069$). As a rule, the tested males stayed longer near the loudspeaker if there was another singing male, and during initial breeding stages. Males did not call in all trials (Fig. 4), and called more often in the prebreeding than in the two later stages (Fig. 5, Kruskal-Wallis ANOVA, $H = 6.95$, $n = 46$, $p = 0.031$).

The general pattern of reaction to stimulation was similar in the two sibling species. However, most response measures differed to some extent. Male Eurasian Treecreepers approached the loudspeakers more quickly, and stayed longer near the loudspeaker after the test period than Short-toed Treecreepers (Fig. 3).

Moreover, Eurasian Treecreepers called infrequently in comparison with the other species (Fig. 4). We found no significant difference in total call production in any of the breeding stages (Fig. 5, Kruskal-Wallis ANOVA, $H_2 = 1.42$, $n = 45$, ns).

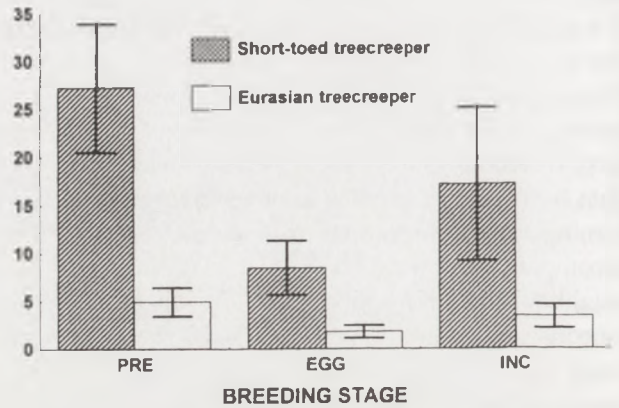


Fig. 5. Mean (\pm SE) number of calls uttered by treecreepers studied during trials in different breeding stages.

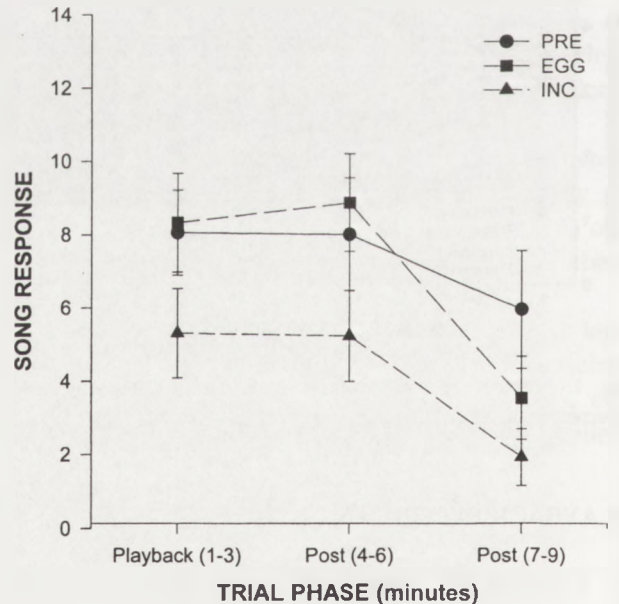


Fig. 6. Song response of the Eurasian Treecreeper to playback (mean number of phrases sang \pm SE) during three min. phases of trials.

Eurasian Treecreepers sang more frequently during the first 3 min. of the post-playback period in the prebreeding and egg-laying stages than in the incubation/feeding stage (Fig. 6). However, these differences were insignificant (Tukey-HSD, both ns). The presence

of conspecific males or females did not have any effect on the distance of the tested male from the loudspeaker during experiments. During the prebreeding stage males uttered more contact calls than in the later stages (Kruskal-Wallis ANOVA, $H_7 = 7.12$, $n = 45$, $p = 0.028$), but no significant difference was observed in the frequency of other call types.

INTERSPECIFIC DIFFERENCES

Overall song production during the trials was similar in both species, but a few striking differences in response to the playback between the studied treecreepers were observed. Eurasian Treecreepers sang more uniformly during the trial, and did not stop or decrease song rate during the test period as did males of the other species (Figs. 2 and 6). Eurasian Treecreepers sang more phrases in test periods than Short-toed Treecreepers (ANOVA, $F_{2,85} = 10.27$, $p = 0.002$). The song rate in the first three minutes after playback (post 3–6) depended on the respective breeding stage only, and was higher in the prebreeding and egg-laying stages (ANOVA, $F_{2,85} = 3.25$, $p = 0.043$, Tukey-HSD, prebreeding vs. incubation $p = 0.055$, egg-laying vs. incubation $p = 0.098$). Secondly, Eurasian Treecreeper males stayed close to the loudspeaker significantly longer (Fig. 3; Kruskal-Wallis ANOVA, at a distance ≤ 5 m: $H_1 = 6.44$, $n = 91$, $p = 0.011$; at distance ≤ 10 m: $H_1 = 4.77$, $n = 91$, $p = 0.029$). Thirdly, Short-toed Treecreepers uttered almost six times more calls than the sibling species (mean call number per trial \pm SD 19.3 ± 28.34 , and 3.4 ± 4.81 , respectively; Mann-Whitney U-test, $U = 459.5$, $n = 91$, $p < 0.001$).

DISCUSSION

Both studied species clearly responded to the playback by approaching, singing and calling. The intensity of reactions ranged widely, but both species reacted stronger before the incubation/feeding stage, which suggests that songs deter rival males in contexts of territory and female defence.

Male treecreepers did not stop responding to the playback after pairing. The decrease in their response was correlated with the start of incubation (i.e. the end

of female receptiveness). We did not observe any increase in song rates during trials in which a female was also present. Therefore, the role of singing as a signal directed to the female after pairing in both species is probably of minor importance. On the other hand, the playback experiment design applied in this study did not allow to distinguish clearly between two song functions before mating: territory defence and attraction of females.

One of the basic differences between the studied species, which possibly explains the differences in singing and reaction patterns, is territoriality. Eurasian Treecreeper territories are spread rather uniformly and are usually separated by "empty zones" (ca. 100 m wide), especially in pure pine stands (Schnebel 1972, Schönfeld 1983). Actually, these zones may be wider than the defended territory. In Short-toed Treecreepers, territories are often clumped, with unoccupied areas found mostly between territory clusters, not between individual territories. Furthermore, the territories of neighbours often partly overlap (Schnebel 1972, authors unpubl. data). In fact, we observed such a territorial pattern in the study area. These differences are probably caused by different habitat preferences. Eurasian Treecreeper is a typical generalist. It has a wide habitat amplitude and forages for food on trees of virtually any species (Kuitunen & Helle 1988, Suhonen & Kuitunen 1991). Short-toed Treecreeper inhabits even small groups of trees with rugged bark, parks, orchards and forest edges — especially broad-leaved and mixed (Schnebel 1972, Schönfeld 1983). In sympatry, Eurasian Treecreeper tends to be confined to coniferous stands, higher altitudes or poorer habitats (Cramp & Perrins 1993).

Because of such a distribution of treecreeper territories in our study area, male Short-toed Treecreepers established and kept territories during permanent contact with many neighbours, which forced them to frequent movements and repelling. Territories of Eurasian Treecreepers were much more isolated from each other, so males of this species had relatively infrequently chances for countersinging. Field observations showed that most Eurasian Treecreeper males sang spontaneously only in a rather small part of the territory around the nest (ca. 50–70 m). It is also known that they show weaker responses to playback outside this zone (Schönfeld 1983). Generally, Eura-

sian Treecreepers are less persistent singers than Short-toed Treecreepers (Cramp & Perrins 1993, Osiejuk & Kuczyński 1997).

When Short-toed Treecreeper males detect singing intruders (or playback), they quickly approach the source of the signal and increase their song rate. If an intruder stops singing (which was simulated in our playback trials), males quickly fly away. Ritualized countersinging is a frequently displayed behaviour in this species. The decreasing song rate or lack of singing during the test period might be connected with an attempt to recognize the intruder: neighbour or stranger (Slater 1981, 1983). The discrepancy between the low spontaneous song rate and a strong response to playback in Eurasian Treecreeper is striking and needs explanation. In this species, intrusions of rival males are less frequent but may have more serious effects, e.g. extra-pair copulations. That is probably why males of this species sang more uniformly during the trials. Territory occupation is obviously stronger in Eurasian Treecreepers, which is supported by the fact that this species behaves generally more aggressively than Short-toed Treecreepers in male-male interactions, and vocal duels escalate more frequently into overt aggression (Thielcke 1959, 1960, Schnebel 1972). Our data also indicate that male Eurasian Treecreepers did not try to recognize rivals (no decrease of song rate during playback).

Our results suggest that the singing strategy in treecreepers is related to the actual territorial pattern and indirectly also to differences in food preferences. Nevertheless, such a correlation may be limited to relatively rich, diversified habitats. Treecreepers utilize a relatively unproductive microhabitat – tree bark (Osiejuk 1998), and this is a probable reason for the exceptionally large size of territories (> 10 ha) of Eurasian Treecreeper in some parts of its range (Kuitunen & Törmälä 1983). At higher latitudes, Eurasian Treecreeper is supposed to suffer more often from food shortages than species belonging to other guilds, even during the breeding season (Kuitunen & Suhonen 1991, Suhonen & Kuitunen 1991). This may involve a higher level of intraspecific competition among males and more intensive singing. For example, in Finland male Eurasian Treecreepers can stay far away from the nest for quite a long time and sing at a distance of up to at least 200 meters from the nest (T. Aho pers. comm.).

Finally, our study shows that the primary function of song in both treecreeper species is to deter rival males, mainly during territory establishing, pairing and female fertility period. However, the species differed both in spontaneous song rate and in response to playback, which is probably due to differences in their territorial systems. If this is true, the species should also differ in recognition of neighbours and non-neighbours.

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STRESZCZENIE

[Funkcje śpiewu i terytorialność pęczacza leśnego i pęczacza ogrodowego]

Badania przeprowadzono w Wielkopolskim Parku Narodowym w ciągu trzech sezonów lęgowych (1996–1998). Ich celem było stwierdzenie różnic w strategiach śpiewu pęczacza leśnego i ogrodowego oraz sformułowanie wyjaśniających je hipotez.

W trakcie badań prowadzono rejestrację częstości śpiewu spontanicznego pęczaczy oraz wykonano eksperymenty, które polegały na odtwarzaniu z głośnika w terytorium samca nagrania śpiewu nieznanego mu osobnika własnego gatunku. W ciągu trzech minut odtwarzania, oraz kolejnych sześciu po zaprzestaniu playbacku notowano szereg zachowań samca poddanego eksperymentowi (m. in. liczbę zaśpiewanych fraz, głosów różnych typów oraz dystans w stosunku do głośnika). Eksperymenty przeprowadzono w trakcie trzech etapów cyklu lęgowego: 1) przedlęgowego — od momentu kiedy samce zaczynają intensywniej śpiewać i zajmować terytorium do czasu łączenia się w pary, 2) składania jaj (płodności samicy), oraz 3) wysiadywania jaj i karmienia piskląt.

Stwierdzono istotne różnice między badanymi gatunkami zarówno w śpiewie spontanicznym, jak i ich w reakcji na głosy odtwarzane. Samce pęczacza ogrodowego śpiewały spontanicznie z częstotliwością wyższą niż samce pęczacza leśnego (odpowiednio 3.1 ± 0.94 i 1.6 ± 0.34 fraz na minutę). Również czas trwania spontanicznych śpiewów pęczacza leśnego był krótszy (Fig. 1). Samce obu gatunków reagowały na playback silniej w okresie przedlęgowym i płodności samicy, niż w późniejszych etapach cyklu reprodukcyjnego, co wskazuje na jego funkcję obrony terytorium i samicy (Fig. 2–6). Nie stwierdziliśmy reakcji na głosy odtwarzane, które można by bezpośrednio powiązać z przywabianiem bądź stymulacją partnerki. Samce pęczacza ogrodowego podczas odtwarzania nagrań zaprzestawały śpiewu bądź znacznie obniżały jego częstość i szybko zbliżały się

do głośnika. Intensywność śpiewu zwiększały dopiero później w 4-ej lub 5-ej minucie eksperymentu, a następnie dość szybko oddalały się i obniżały częstość śpiewu (Fig. 2–3). Pełzacze leśne w czasie odtwarzania nagrania nie zaprzestawały śpiewu i szybko zbliżały się do głośników. Po zakończeniu odtwarzania śpiewały z podobną do początkowej częstością i pozostawały istotnie dłużej w pobliżu głośników niż gatunek bliźniaczy (Fig. 3 i 6). Oba gatunki różniły się również znacząco, jeśli chodzi o reakcję na głosy odtwarzane mierzoną częstością wydawania głosów różnych typów (Fig. 4 i 5).

Stwierdzono rozbieżności między niską aktywnością pełzaczy leśnych w śpiewie spontanicznym i ich silną reakcją na odtwarzanie śpiewu. Są one najprawdopodobniej związane z systemami terytorialnymi badanych gatunków. Pełzacze ogrodowe charakteryzują się większą wybiórczością środowiskową i związane były z bardziej zróżnicowanymi drzewostanami liścia-

stymi i mieszanymi. W konsekwencji ich terytoria występowały skupiskowo, często pokrywając się w znacznym stopniu. Terytoria pełzacza leśnego były rozmieszczone równomiernie, rzadko pokrywały się bądź graniczyły z sobą, co prawdopodobnie wynika z większej tolerancji środowiskowej tego gatunku. W efekcie, pełzacze ogrodowe zajmowały i broniły swoich terytoriów w warunkach stałego kontaktu z sąsiadami, który z jednej strony powodował częste „potyczki na śpiew” między sąsiadami, ale z drugiej strony prowadził do ich większego zrytualizowania. W przypadku pełzacza leśnego, naturalne kontakty między samcami były rzadsze, ale w razie symulowanej w eksperymentach inwazji, samce prowokowane były do silnej i agresywnej reakcji. Niniejsze badania wskazują na związek między terytorialnością pełzaczy wynikająca z ich preferencji środowiskowych i strategią obrony terytorium przy pomocy śpiewu.