

When an alien sings at a rival's post: a passerine excited by conspecific stimulus may show aggressive behaviour towards heterospecific individuals

Dedicated to Professor Karel Hudec in honour of his 80th birthday

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A b s t r a c t. We tested the hypothesis that males of meadow pipits (*Anthus pratensis*) respond differentially to simulated territorial intrusions (song playback + bird model) by conspecific, related (tree pipit, *Anthus trivialis*), and unrelated individuals (willow warbler, *Phylloscopus trochilus*), and evaluated the effect of playback order. All tested males responded aggressively to the conspecific playback; reactions to heterospecific stimuli occurred only after previous excitation by the conspecific song and dummy, and were usually weaker. Apparently, although males were able to discriminate between playbacks, excitation by intrusion of a conspecific rival elicited an aggressive reaction to otherwise neutral stimuli. Reactions to heterospecific playbacks closely following the conspecific one did not differ significantly between congeneric and unrelated species. The response to a subsequent heterospecific stimulus, however, was taxon-dependent: congeneric species elicited a significantly stronger reaction than an unrelated one. We presume that this was due to the morphological similarity between pipits, and that the more intensive reaction could have been caused by stronger visual stimulus from the respective model. We discuss the potential benefits as well as limitations of using models (dummies) in playback experiments, and suggest that overexcitation by previous stimuli should be considered during experimental setup and data analysis in studies focusing both on interspecific aggressiveness and on neighbour-stranger interactions.

Key words: meadow pipit, *Anthus pratensis*, interspecific territoriality, playback experiments, misdirected aggressiveness

Introduction

Correct species discrimination is crucial for bird species coexisting at the same localities. Identification of resident species is one of the mechanisms influencing habitat selection of migrants (Mönkkönen et al. 1996), and the ability to recognise conspecific and heterospecific competitors plays an important role in the competition for ecological resources (e.g., Catchpole 1978, Gil 1997, Matyjasiak 2005, Sedláček et al. 2006). Discrimination between conspecifics and individuals of similar species is also crucial for maintaining pre-copulation reproductive barriers in closely related co-occurring taxa (e.g., Baker 1991, Qvarnström et al. 2006). Accurate species recognition in hybridising species is advantageous not only for mate recognition: an aggressive response of territorial

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males to both conspecific and closely related heterospecific individuals may be adaptive, as both of these represent potential competitors for mates (Irwin & Price 1999). On the other hand, when there is no risk of hybridisation for congeneric sympatric species with different resource use, it pays to prevent unnecessary and potential costly responses to heterospecific individuals, which may be phenotypically similar but neither pose a threat nor compete (Lynch & Baker 1991, Elfström 1990).

In many bird species, especially passerines, song has important functions in territory establishment and defence (Kroodsmá & Miller 1996) and it is considered to serve primarily as an intraspecific signal, either for sexual partners or competitors of the singing individual (Kroodsmá & Byers 1991). Nevertheless, instances of interspecific territoriality, with an aggressive response to heterospecific song, have also been regularly documented (e.g., Orians & Willson 1964, Murray 1981, Martin et al. 1996). In cases when such interspecific aggression is non-adaptive, it can be minimised through increased vocal discrimination (Lynch & Baker 1991, Doutrelant & Lambrechts 2001).

In our study, we focused on mechanisms allowing the syntopic coexistence of two closely related, morphologically and ecologically similar congeneric passerine species, which differ in their vocal characteristics (Cramp 1988, Alström & Mild 2003) – the meadow pipit (*Anthus pratensis*) and the tree pipit (*Anthus trivialis*). Their breeding areas overlap in most of Europe except its southern part (Alström & Mild 2003), and both occur commonly in the Czech Republic in sympatry as well as in allopatry. Our previous study revealed that the core ranges of territorial males of the two species at a sympatric locality did not overlap (Kumstátová et al. 2004). It was not clear, however, whether the observed pattern was caused primarily by different habitat preferences of the two species, or whether interspecific territoriality influenced territory establishment.

To answer this question, we evaluated aggressive reactions of territorial pipit males by playback experiments simulating the intrusion of a singing male from the other species. In preliminary experiments, no reaction of tree pipit males to meadow pipit song playbacks was observed (Kumstátová 2001). However, if interspecific aggressiveness plays any role in the two species' coexistence, the direction of the territoriality would likely be opposite. Meadow pipits arrive in the Czech Republic about one month earlier than tree pipits during the spring migration (Štátný et al. 2006), and when males of the latter species select breeding grounds, meadow pipit males have already established territories to defend.

The first experiments testing the responses of meadow pipit males to the playback of tree pipit songs (T. Petrusková, unpublished) showed that interspecific reactions occurred only when the tree pipit (heterospecific) song was played after the meadow pipit (conspecific) playback; no reaction was observed if the stimuli were reversed. This suggested that the apparent interspecific territoriality may have been only an experimental artefact, a misdirected aggression resulting from the overexcitation of a territorial male. A similar observation of excited passerine males responding to apparently neutral stimuli was briefly noted by Ferry et al. (1969). In the present study, we focused on this phenomenon in more detail to 1) verify that meadow pipit males do not show interspecific aggressiveness towards tree pipits under normal conditions, 2) confirm that meadow pipits may exhibit an aggressive response to tree pipit playback after provocation by conspecific stimulus, and 3) test whether such a reaction is limited to similar species or can be elicited by the playback of an unrelated, and probably non-competitor, species. We hypothesised that aggressive reactions of males should be stronger in conspecific than in heterospecific playbacks, and

that the heterospecific playback of congeneric species should elicit stronger response than the playback of control (unrelated) species under the same conditions.

Methods

Experiments were carried out in the mountain range Krkonoše (English toponym: Giant Mountains) at the border between the Czech Republic and Poland during the breeding seasons in May and June 2005–2006. We studied a meadow pipit population nesting on the mountain plateau Úpské rašeliniště (50.44° N, 15.42° E, altitude ca. 1400–1450 m a.s.l.). The area is covered by alpine meadows and peat bogs, with sparse spruce and dwarf pine stands. Although tree pipits do not nest on the plateau, they occur in the close vicinity (the nearest tree pipit territories are located ca. 1 km away) and both populations may come into contact.

Altogether 24 paired meadow pipit males were tested, each of them once, by a playback session consisting of three stimuli (i.e., playbacks of three different species, see below). Males occupying adjacent territories were never tested on the same day. The experiments were conducted at a comparable breeding stage, when the territorial behaviour of males is strongest – after pair formation but before egg-laying (van Hecke 1979, Nowicki et al. 2002, Petrusková et al. 2007). We used focal sampling of individual males (Altman 1974) to determine the borders of their territories before experiments.

Each male was exposed to three different stimuli presented in the centre of its territory: conspecific playback (meadow pipit: MP), heterospecific playback of a closely related species (tree pipit: TP) and heterospecific playback of a non related species (willow warbler *Phylloscopus trochilus*: WW). The order of the three playbacks was chosen randomly for each bird. All different sequences of the stimuli were tested throughout the study; numbers of individuals exposed to particular sequences are indicated in Fig. 1. The playback of song was always accompanied by displaying a three-dimensional model (dummy) of the particular species, made of cotton and paper, stuffed, and coloured after real birds. Although the colouration of the dummies did not necessarily agree in all aspects (e.g., in the UV spectrum) with real birds, they elicited aggressive intraspecific responses from territorial males of all three species (T. Petrusková, unpublished data). The dummies were remotely operated, and could be either completely hidden from the view or exposed in a perching position.

As there is a significant individual variability in the song repertoire in both pipit species (Petrusková et al. 2008, and unpublished data), the playbacks of MP and TP songs used in the experiments were mixed from ten songs of different males of the corresponding species, recorded in the same region during the 2003 and 2004 breeding seasons. The song of the willow warbler, which was used as a control (unrelated species), has very constant composition; we therefore used a commercially available recording (Pelz 1993), which we found adequate after comparing its sonograms (using the software Avisoft SASLab Pro 4.23e) with the songs of three willow warbler males recorded at the studied areas. More details on song recording, their adjustment for playbacks, and on the equipment used for both recording and playbacks are given in Petrusková et al. (2007). The experimental design, using the same stimulus for multiple subjects, is problematic due to the potentially confounding effect of pseudoreplications (Kroodsma et al. 2001), and it would have been better to use different recordings for every tested male. We believe, however, that interpretations of our results may still be relevant: rather than comparing only the reaction to different types of stimuli, we were primarily interested in the response to the same stimulus under varying conditions (type of preceding playback), and evaluated the effect of these

conditions. Nevertheless, to test the general validity of the observed patterns, additional experiments with variable stimuli (and possibly on additional species) would be preferable.

The experimental design was identical for all sequences of stimuli: an 8-minute song playback (a one-minute test recording repeated continuously eight times) accompanied by the display of a relevant dummy, three minutes of silence (no dummy shown), followed by the next playback. The whole test sequence therefore lasted 30 minutes from the beginning of the first playback to the end of the last playback, and the tested bird was observed for a few minutes after the termination of the experiment to check for potential unusual behaviour. The short duration of pauses between playbacks was chosen in order to intensify the effect of potential excitation of the males by the preceding stimulus; the pauses were nevertheless sufficient to allow the bird to return to normal behavioural patterns. The experiment was initiated only after the tested bird became habituated to the experimental equipment placed in its territory, and no less than 30 minutes after its setup. The dummies were displayed at the same spot within the territory, in the immediate vicinity of the loudspeaker. The observer was hidden in a shelter built approximately 25 m from the test area and operated all the equipment from there, without any need to leave the shelter during the experiment itself.

During the experiment, the observer noted all behaviour of the tested pipit male and its timing. We differentiated the following categories of interest or aggressive behaviour (after Petrúšková et al. 2007, ordered by increasing aggressiveness): 1) expression of interest with no direct aggressive actions (approach to the dummy on the ground, attentive observation, walking in circles around the dummy); 2) flyover (male flying directly over the dummy higher than 1 m above it); 3) jump-flight (male approaching the model on the ground within 1 m, “jumping” into the air to a height less than 1 m, observing the model and usually chattering); 4) flight-attack (male diving in flight and approaching the model to a close distance, less than 1 m) and 5) physical contact (male physically attacking the “intruder”, usually by short contact in flight, in the most extreme form by sitting on the dummy and pecking it).

We evaluated two measures of interest and aggressive behaviour in the tested meadow pipit males: the maximal intensity of the reaction of each male (0 for no interest in the playback and dummy, other reactions ranking between 1 and 5 as above), and the proportion of time when the male showed some interest in the model (either by passive observation or by aggressive behaviour). The maximal intensity of the reaction corresponds well to the male overall aggressiveness (Petrúšková et al. 2007).

Using the Wilcoxon matched pairs test for the dependent samples, we compared the attained levels of these two variables (for the same males) between the two consecutive playback types: a preceding heterospecific playback with the following conspecific one (TP-MP or WW-MP), the conspecific with the immediately following heterospecific playback (MP-TP or MP-WW) and the two consecutive heterospecific playbacks after the conspecific one (TP-WW or WW-TP). The tested hypothesis was that the strength of male reaction should be ordered: MP (conspecific) > TP (congeneric) > WW (unrelated species). All males for which a particular playback sequence was available were pooled for the respective subsequent evaluation. (For conspecific-heterospecific sequences (TP-MP and TP-WW), we therefore pooled sequences in which the conspecific stimulus was either at the first or second position (Table 1); this could be done because the preceding heterospecific playback clearly did not affect the bird behaviour in any way; see Results and Fig. 1.) The number of males tested and calculated one-tailed exact probability values are provided in the Table 1. We did not adjust the table-wide *P*-values for multiple tests because the significance patterns were

consistent between the two evaluated variables, and the *P*-values of individual tests were below the 0.05 threshold for all but one test (see also Moran (2003) for the discussion of problems related to adjusting probability values for tables of multiple statistical tests in ecological studies, especially for small samples).

Additionally, we compared the intensity of reaction to the different heterospecific playbacks (TP and WW) at the same position in the test sequence relative to the conspecific playback: between those which immediately followed the conspecific playback, and between those played as the second heterospecific stimulus after the conspecific one (labelled as “second heterospecific playback” below). Finally, we tested whether the preceding heterospecific playback could have affected the reaction to the conspecific one. As each of these combinations was tested on a different group of males, we used the Mann-Whitney U-test (with exact calculation of the significance value of U statistics) for the comparisons. Statistical analyses were conducted in the software package StatXact 6.2 (Cytel Software Corporation, Cambridge, USA).

Results

All tested meadow pipit males responded to the conspecific playback with various aggressive reactions (maximal reactions: 25% flyovers, 21% jump-flights, 37.5% flight-attacks, 16.5% physical attacks). On the other hand, the reaction of males to heterospecific stimuli was context-dependent (Fig. 1). If not aroused by a conspecific playback, the males completely ignored the dummy accompanied by heterospecific songs (no male exhibited even a short-time interest in any of the 19 TP or WW heterospecific playbacks preceding the conspecific one). There was no significant difference in reactions to conspecific playbacks which would depend on the type of immediately preceding heterospecific stimulus (Mann-Whitney U-test, $n_1=6$ for WW-MP, $n_2=7$ for TP-MP, exact $P=0.45$ for intensity of reaction and 0.18 for time spent by expressions of interest).

After excitation by the conspecific playback, however, most males responded to heterospecific stimulus (for both TP and WW playbacks following MP, 8 out of 9 males exhibited some interest or aggressive reaction). The response to this “first heterospecific” stimulus did not differ significantly between TP and WW treatments, either in the maximal level of reaction attained or in the percentage of the time spent by expressing interest in the dummy (Mann-Whitney U-test, $n_1=9$, $n_2=9$, exact $P=0.30$ and 0.60, respectively). However, the reaction to such heterospecific stimuli was in most cases weaker than to the preceding conspecific playback, and not as long-lasting (Fig. 1); these differences were significant (Table 1). As a general rule, the male’s interest in the model and its aggressiveness decreased during the heterospecific playback, and the males often completely lost interest before the end of the 8-minute test recording playback.

The reaction to the “second heterospecific” stimulus (i.e., the last one in a sequence beginning with the conspecific playback followed by two heterospecific ones) was dependent on the sequence (MP-TP-WW vs. MP-WW-TP). The response to the willow warbler playback and dummy, which differed in both acoustic and visual cues from those of the meadow pipit, was significantly weaker (Fig. 1, Table 1) than the response to the preceding tree pipit playback, differing in the song but not in the dummy appearance (four out of six tested males did not react to the WW “second playback” at all). On the other hand, such an attenuation in the reaction did not occur during the MP-WW-TP sequence.

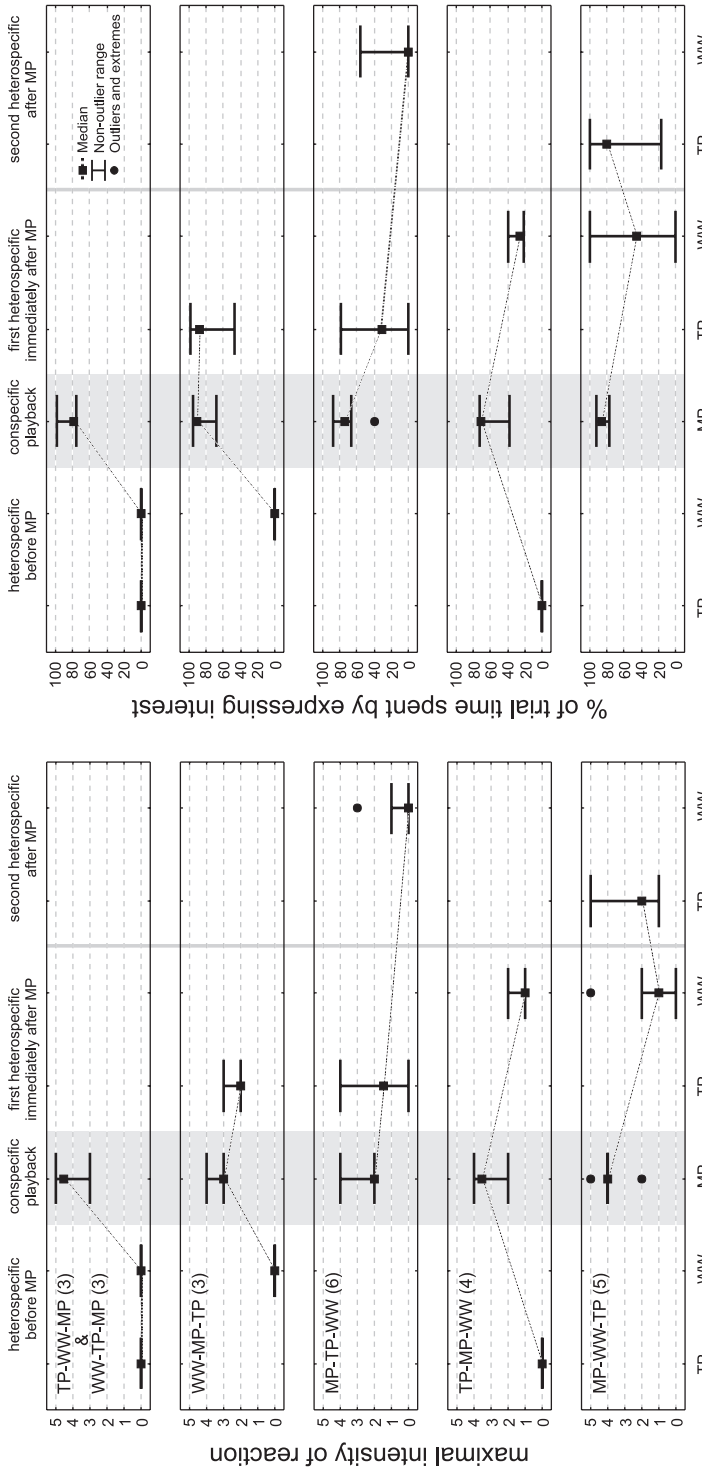


Fig. 1. Response of the tested males to conspecific (MP = meadow pipit) and heterospecific (TP = tree pipit, WW = willow warbler) playbacks in the different sequences of stimulus presentation (left: maximal level of reaction; right: percentage of trial time spent by expressions of interest in the dummy intruder or by aggressive behaviour). Conspecific playbacks are highlighted by a grey background. The sequences of playbacks together with the number of males tested (in parentheses) are indicated in the upper left of the respective graphs. As no male responded to the heterospecific stimuli preceding the conspecific one, the sequences ending with the conspecific playback (TP-WW-MP and WW-TP-MP) were pooled. Exact significance values for comparisons between two adjacent stimuli are given in Table 1.

Table 1. Results of the comparison of male responses to consecutive playbacks (exact probabilities of one-tailed Wilcoxon matched pairs test); the maximal intensity of the male reaction and proportion of the trial time spent by expressions of interest were compared.

order of stimuli	number of trials	stronger reaction	exact <i>P</i> -values	
			maximal reaction	interest time
TP-MP	7	MP	0.008	0.008
WW-MP	6	MP	0.016	0.016
MP-TP	9	MP	0.031	0.014
MP-WW	9	MP	0.004	0.027
(MP)-TP-WW	6	TP	0.031	0.031
(MP)-WW-TP	5	TP	0.125	0.031

All five males exposed to the TP “second playback” responded, four of them by flyovers or stronger aggressive reactions. The percentage of the trial time spent by expressing interest actually significantly increased over the preceding WW playback (Fig. 1, bottom right; Table 1). Differences between the reactions to TP and WW “second” heterospecific playbacks were significant both in the maximal level of reaction and in the time in which males were interested in the dummy (Mann-Whitney U-test, $n_1=6$, $n_2=5$, exact $P=0.030$ in both cases).

Discussion

Our experiments clearly show that meadow pipit males defending their breeding territories correctly discriminated among conspecific and heterospecific songs, as they never responded to playback of either tree pipit or willow warbler song if these were presented before the conspecific (meadow pipit) playback. The results suggest that under normal circumstances, interactions between meadow and tree pipits do not suffer from misdirected interspecific aggression (Murray 1971) and tree pipits arriving to already-established meadow pipit territories would not be attacked as competitors. This supports the conclusion discussed in Kumsátová et al. (2004) that different habitat preferences are primarily responsible for territory separation in areas where these two congeneric species come into contact. Our observations at the present study area also support the importance of habitat selection: meadow pipits occurred at open areas covered with peat bogs or wet meadows and sparse dwarf pines, while tree pipits bred in places with a higher density of trees or at the edges or clearings of spruce forests (T. Petrůvová, unpublished data). We may presume that the ability of good species discrimination is not limited to males – despite morphological similarity, songs of the two pipit species are distinct; it is therefore likely that females discriminate with at least the same accuracy as males, and the species are not prone to hybridisation.

The reaction to heterospecific stimuli in our experiments occurred only after excitation by the conspecific song and dummy. This is in agreement with the observations of Ferry et al. (1969), who pointed out that under such conditions, territorial males may react to otherwise neutral stimuli. The reaction of excited males nevertheless differed when exposed to playbacks and dummies of a closely related and unrelated species. The reaction to either of the heterospecific playbacks (TP or WW) following conspecific stimulus (MP) did not differ significantly (although there was some tendency for stronger reactions to tree pipit playbacks). The response to the last playback of the series beginning with the conspecific

stimulus, however, was substantially stronger in the case of the congeneric tree pipit song and dummy. This shows that excitation of territorial males remained strong enough to elicit an interspecific reaction at least 14 minutes after the presentation of conspecific stimuli.

Although the reaction of excited meadow pipit males to the stimulus of congeneric dummy and song was significantly stronger than to that of the unrelated species, it does not necessarily mean that the strength of reaction is directly dependent on the relatedness of the taxa in question. A more likely explanation of the observed pattern is that for meadow pipits, both auditory and visual cues are important for correct interspecific recognition. Although their song is different, meadow pipits closely resemble tree pipits in both morphology and colouration (Alström & Mild 2003), and the appearance of an appropriately-looking dummy could be a strong stimulus for overexcited males even if not accompanied by conspecific song.

Several studies have tested the reactions of territorial meadow pipit males to another congeneric species, the water pipit (*Anthus spinoletta*) (Ferry et al. 1969, Vitale & Brémont 1979, Elfström 1990). Songs of these two species are very similar to each other (Wallschläger 1984, Elfström 1990), they have similar habitat preferences at sympatric localities (Crampton 1988, Alström & Mild 2003), and phylogenetic analyses have revealed closer relatedness between meadow and water pipits than between meadow and tree pipits (Voelker 1999). In all of the above-mentioned studies on interspecific territoriality, reactions of meadow pipit males to heterospecific songs of water pipits were much rarer than to conspecific songs, but at least some of the tested males responded, although usually weakly, to the heterospecific playback (without any preceding conspecific stimulation): up to 44% at both syntopic and allopatric localities in France (Vitale & Brémont 1979) and 14–26% in Sweden (Elfström 1990).

These results may suggest that although the males usually recognise the conspecific song, heterospecific territoriality may occasionally occur between meadow pipits and other very similar congeneric species. As this behaviour is apparently much rarer than intraspecific territoriality, it could support the hypothesis on misdirected interspecific territorial aggression (Murray 1971, 1981). However, interpretation is complicated by the fact that none of the above-mentioned previous studies used a bird dummy to accompany the playback, and relied only on the distance of the male from the loudspeaker or its direction of flight. It is therefore impossible to directly compare the results of different studies. As Vitale & Brémont (1979) scored most of reactions as “weak or moderate”, and Elfström (1990) regarded an approach to within 5 m of the loudspeaker already as a tendency to attack, it is unclear whether such responses were unambiguous expressions of heterospecific aggressiveness.

The absence of a dummy in playback experiments is common in even recent studies on bird aggressive behaviour (e.g., Hyman 2002, Wiley 2005). In cases when the aim of a study is to test the reaction to acoustic stimuli only (e.g., Seondi et al. 2003, Osiejuk et al. 2007), the absence of a dummy is appropriate. However, when evaluating the aggressive behaviour to a simulated territorial intrusion, the physical absence of an “intruder” may be a methodological weakness. The importance of both visual and auditory signals has been recently discussed (e.g., Cucco & Malacarne 1999) and the long-term memory association between both types of species-specific cues was clearly shown (Matyjasiak 2005).

Apart from presenting a more realistic stimulus, there are also practical reasons for considering experimental designs involving both visual and acoustic cues in the playback experiments. Firstly, the absence of any visible intruder may influence the reactions of tested

birds, eliciting less natural behaviour. Secondly, use of a loudspeaker alone may complicate the evaluation of behaviour of the target individual, as exemplified above. Most studies on birds that use playback experiments (e.g., Martin & Martin 2001, Hyma n 2002, Nowicki et al. 2002) primarily evaluated the distance of tested birds from the sound source, the direction of their movement, or vocalisation. The model of “intruder” in the immediate vicinity of a loudspeaker, being a clear target for aggressive actions, allows the tested individual to express additional behavioural patterns, and subsequently the observer to analyse more precisely the strength of reaction.

On the other hand, using a dummy in an experiment adds to the complexity of the experimental design, and therefore introduces potential problems and confounding factors. The look of a particular dummy may certainly influence the target male’s behaviour. On one hand, the dummy may not be realistic enough and present unnatural visual cues. This may be overcome by using taxidermic mounts of real bird specimens, though handling such dummies is impractical, and they may be quickly destroyed by physically attacking birds. On the other hand, real bird skins (but also artificial models) may represent very low- or high-quality rivals, and affect the strength of the response accordingly. Preferably, different dummies should therefore be used in replicated experiments to avoid potential confounding effects and pseudoreplications; this would further complicate the preparation of experiments. We believe, however, that the importance of potential visual stimuli and both the risks and benefits of using a dummy should be considered when designing playback experiments.

Our results confirm that the excitation of territorial males plays, at least in meadow pipits, an important role in determining the reaction to otherwise apparently neutral stimuli. Although we intentionally kept the duration of pauses very short, and therefore we do not know for how long such an excitation lasts, this carryover effect should be considered when planning playback experiments. The excitation potentially affecting the behaviour of territorial birds is not limited to reactions to con- and heterospecific songs. A similar effect apparently exists also in neighbour-stranger interactions; excitation by songs of an unknown conspecific bird may subsequently alter reactions to the known neighbour’s song. For example, Lovell & Lein (2004) noted that a 30- to 60-minute pause after the playback of a stranger song was not sufficient for territorial alder flycatchers (*Empidonax alnorum*) to return to a prestimulus level of behaviour. Similarly, Hyma n (2002) observed an increase of aggression towards neighbours after a simulated intrusion of a stranger bird in Carolina wrens (*Thryothorus ludovicianus*), interpreting it as a complex tit-for-tat strategy. Pauses between different stimuli in the latter experiments usually lasted 25 minutes; it is therefore possible that the observed pattern was actually the non-adaptive result of overexcitation of the territorial bird by a strong “stranger” stimulus.

In general, if reactions to equivalent weaker stimuli before and after presentation of a strong stimulus differ, non-adaptive excitation must be considered as a possible interpretation of the observed pattern. When there is any doubt that an excitation persists until the next experimental stimulus, the most rigorous approach is to increase the length of pauses to an extent that the carryover effect can no longer be detected. In some cases, however, practical reasons such as the accessibility of an exotic site or weather instability may preclude the use of very long pauses (several hours to days) but behavioural experiments would still be valuable. In such situations, it might be more convenient to place the most stimulating signal (conspecific, stranger, etc.) at the end of the playback sequence rather than keeping the order of stimuli random, which is usually preferable in these types of experiments.

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