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Difference of Responsiveness of the Great Tit, Blue Tit, and Marsh Tit to Acoustic Stimuli

By

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Abstract. The main purpose of the experiments of acoustic play-back carried out under natural conditions was to compare the acoustic responsiveness of three species of tits: *Parus maior*, *P. caeruleus* and *P. palustris*. Each form of signals (attracting call, alarm call, anxiety call, aggressive call, territory song) exerted in a certain per cent of the observed cases an attracting effect. The repetition of the sound signals independently of their specific function, exerts an attracting effect (approaching in the perceiving birds), and that the specific structural, pitch, timbre etc. properties of sound signals express the concrete social drives and physiological condition (gregarious attraction, reproductive aggressivity, the gathering round the sitting predator, etc.) of the individuals.

The responsiveness of the great tit is higher than those of the blue and marsh tits. At times the great tit responded to the signals of the two related species more sensitively than the latter did to the conspecific signals. Building its nests in urban-industrial environment, and better adapting itself to the extreme human effects, the great tit is a progressive species as compared with the blue and marsh tits, and this ability is in part determined by its higher responsiveness to acoustic signals.

Acoustic experiments carried out under natural conditions spread in the last decades as specific research methods in ornithology. H. and M. Frings, J. Jumber, R. Busnel, J. Giban and P. Gramet (1958) opened the series of the known experimenters by comparing the responses of the *Corvus* and *Larus* species of America and France by acoustic play-backs. J. B. Falls (1963) carried out various modifications on the structural characteristics of the territory song, and examined in this way the effect of the signals eliciting responses. R. E. Lemon (1969) and M. A. Harris (1974) studied the similar geographic dialects of various North American species by means of acoustic play-backs, P. Marler and R. A. Stefanski (1972), as well as E. Curio (1971) and W. Fleuster (1973) examined the interspecific effect of alarm calls in a similar way. G. Thielcke (1970, 1971) studied the mutual responses of the tree and short-toed tree creepers as sympatric species to the songs of one another, and made, in his conclusions, statements about the evolutionary significance of learning. R. M. Evans (1970), J. R. Stevenson (1970) and S. T. Emlen (1971), 1972) studied by acoustic experi-

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ments the instances of individual recognition taking place upon vocal signals. M. SCHUBERT (1971) and H. W. HELB (1975) examined the conncection of and the reaction to the territory song with same method. As regards tits, G. THIELCKE (1969) carried out acoustic experiments with various *Parus ater* and *Parus maior* subspecies and K. L. *Dixon* and STEFANSKI (1970) with the North American *Parus atricapillus*. Unlike the investigations of the above researchers, the aim of my experiments was first of all to compare the responsiveness of the three tit species representing the same genus *(Parus maior, P. caeruleus* and *P. palustris)*.

Method

Between 1966 and 1975 I studied the social dinamics in a population of great, blue and marsh tits near Budapest. (On that work I reported in the Opuscula Zoologica under the title: "Social dinamics in populations of great tit, blue tit and marsh tit.") I determined the dispersion of the tits by playing back the most effective acoustic attracting signals: anxiety churrings; namely, when perceiving these signals, the individuals marked with coloured rings gathered round the loud-speaker placed in different points of the studied area. In the course of my investigations, however, I could register only the effect of the anxiety calls, so that I could survey responsiveness also experiments with other signals were necessary. Therefore I also carried out experiments with the attracting calls and territory songs of all three species, as well as with the alarm call of the great tit and with the aggressive call of the marsh tit.

In Figures 1 – 11 I illustrate the signals played back in the course of the experiments in a visual representation corresponding to the perceived sounds. *The sounds function as signals perceived as stimuli of various pitches*, consequently, I also study the nature of the sounds as *perceived* signs and also represent them accordingly. Complying with the physiological-anatomical analogy, the sound perception of the birds is vasically identical with the one of man, therefore I represent the signals played back in the course of the experiments with an objective recording and analysing method of perceiving human sound emission, with the one of musical notation which adequataly reflects the perceived pitch. Since the majority of the calls of the tits are gliding sounds passing through several pitches, and stabilitated pitches are few, for scoring the pitch not the representation by note heads but that by sound curves was to the purpose. For uniformity's sake I illustrate also the stabilitated pitches (e. g. the territory song of the great tit) by sound lines. The tremolos consisting of series of short sound elements, which are to be heard naturally trembling and rasping, I denoted with series of tiny dots. The signals sounding simultaneously in two parts I represent by sound lines drawn above and below one another. (Both of these forms of representation only occur with anxiety calls.) By means of the symbol system applied in the representation one may transform the visual picture into an audile one; however, for this also the key to the signs should be thoroughly studied. The Figures show sounds slowed down, extended in time since, in this way even naturally rapid changes in pitch, indistinctive for the human ear can be perceived in detail and so the sound structure can be analysed. The structural analysis and representation of the sounds were done by Mrs. ZSUZSA SASVÁRI. In the experiments I used UHER 4000 Report – L tape recorder and Orion Ritmus loud-speaker.

I carried out the experiments in the autumn and winter months, when the tits formed mixed flocks. However, in too cold weather (under Hungarian weather conditions below − 5°C) and in heavy fog I never did experiments, because then social cohesion became intense within the mixed groups, the drive of following one another was highly increased, and the reaction of approaching the loud-speaker of one or two individuals elicited responses also on the part of the others. Thus in such cases it was difficult to differentiate actual responsiveness to sound stimuli from responsiveness to the visual stimuli denoting the companions. Again, in other instances the flocks proceeding in close formation went past the source of sound without one of the individuals having responded, since the leading birds of the flock were indifferent to the sound signals and swept along with themselves all their companions. Still, such a situation, i. e. a too close social attachment and a mobility increased together with it was relatively infrequent. Generally, in the areas where I performed the experiments (on the outskirts of settlements, near farm buildings), although all three species formed mixed groups, their mobility was low on account of the abundance of food; neither did they show an intense following reaction towards in another. As a consequence, the number of individuals of the small groups showed hardly any change. I carried out the experiments in 10 different areas (all of them in the environs of Budapest) with 10 different groups of tits. In the groups the number of individuals of great tits varied between 17 – 25, that of the blue tits between 8 – 14 and that of marsh tits between 6 – 9.

During one experimental event I played back 11 different forms of signals, i. e. all three species could perceive their own specific sound signals and also those of the other two related species. The signals belonging to one species followed one another in one group, I did not alter their sequence in the course of the experiments. Thus the sound signals of the three species were divided into three separate groups, and I changed only the succession of these during the experiments (see Fig. 2). In this way the sound signals of each of the three species sounded at the beginning and in the middle and at the end of the experimental processes. This alteration was necessary so that responsiveness decreasing with the advance of the experiment should not at all times refer to the same sound forms. In one site (that is, with one group of tits) I experimented only on three occasions, i. e. I played back the three forms of sequences on one occasion each. After the autumn experiments I repeated all this in the same way in the same places also in winter.

I played back all signals with 3 seconds' intervals for 4 – 5 minutes. Between the play-backs of the different signals I made 10 – 20 minutes pauses, longer ones when some individuals of the group of tits moved too far away from the loud-speaker. During the play-backs of the voices the tits were 20 – 60 metres off the loud-speaker, and their approach to it I considered a positive reaction. I carried out the experiments at identical parts of the day, between 7 – 13°° a.m. In autumn the temperature was, generally, +10° – 0° C, in winter 0° – −5 °C; windy weather I made no experiments.

Since during the experiments the proportion of individuals of the three species was unequal, I expressed the measure of the responses at all times as the percentage of the individuals approaching the loud-speaker compared to the individuals of the same species who perceived all sound signals. Further, as I played back all three signal sequences in 10 different areas to 10 different groups of tits,

Visual representation of the acoustic signals played back in the course of the experiments

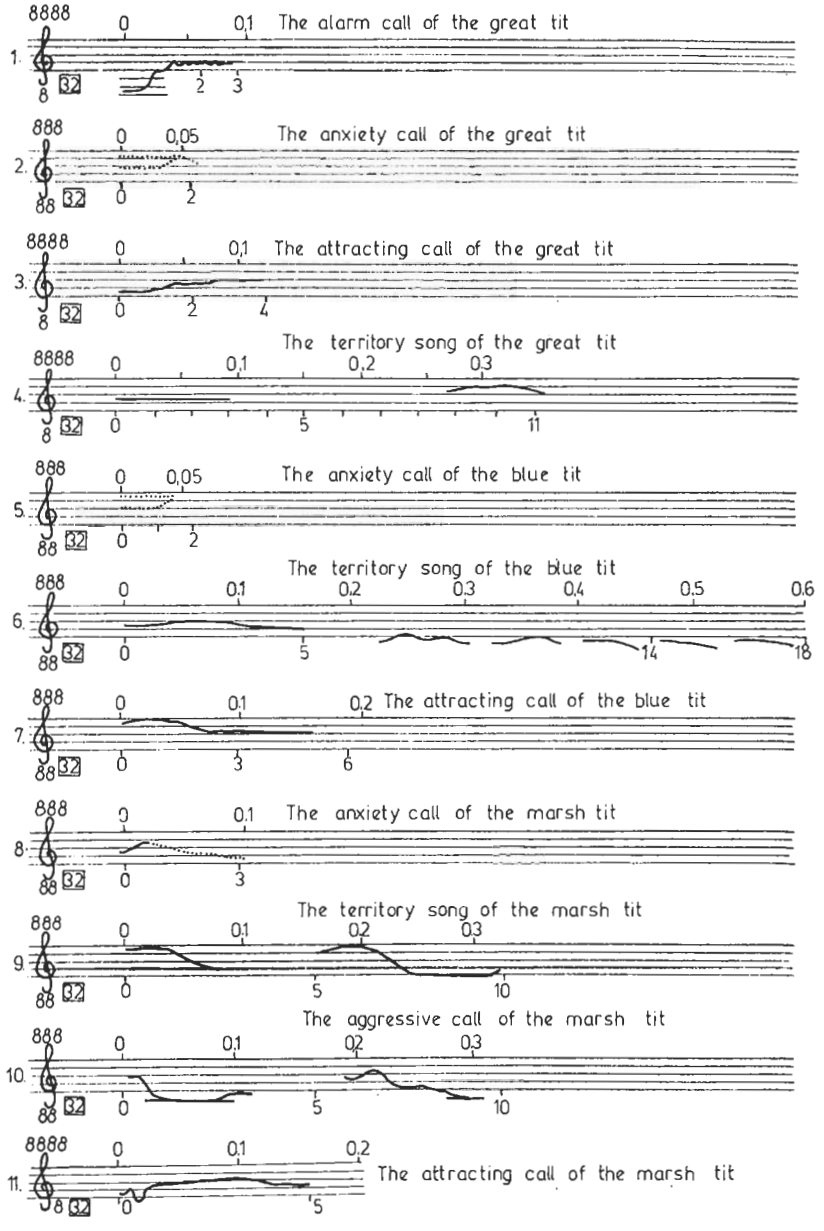

Fig. 1 – 11. Notes: 32 means that the natural duration is extended (i. e. the speed slowed down) 32 times. 8888 and 888, above the clef mean that the natural pitch is higher by 4 and 3 octaves, respectively, than notated. – 8 and 88 below the clef mean that the pitch of the slowed down play back, as a basis of graphic representation, is lower by 1 and 2 octaves, respectively, than notated. – The calibration in second above the five-line staff shows the natural duration of the sounds, while the one below the five-line staff their slowed down duration extended 32 times.

the data presented in Fig 12 and 13 reflect the average result of 10 experiments relying upon the above percentual evaluation. The lowermost part of the Figure shows – disregarding the succession of the sounds played back – a further averaging of the data, i. e. that, relying upon all experiments, which of the signals elicited a response and in what measure in autumn and winter.

Results

I. Generally, the value of the responses elicited by the signals decreased with the advance of the experiments; i. e. to the same sound stimuli less individuals responded towards the end of the play-back process than at its beginning; still, the difference was not significant. Evidently, the tits perceiving the repeated sound stimuli became in some measure accustomed to them, and it could be ascribed to the shorter or longer pauses, as well as to the different forms of the signals that they did not become indifferent to the voices. The decrease, extinction or revival of responsiveness I could have studied only if I had played identical sound signals to the same individuals, repeated at certain intervals; still, under the given circumstances I could not do this examination. (Individually marked tits were to be found only in the experimental areas, where I also studied the population dynamic processes.).

Comparing the experiments carried out in autumn and winter one can find that in the two seasons there is no significant difference in the responsiveness of the tits. This finds its explanation in the circumstance that I carried out experiments in an essentially identical social environment, in individuals of identical social drives.

In all three species the most intense response was elicited by anxiety churring. (In the course of the population dynamic investigations the tits showed response values of $90-100\%$ to that signal, as only that call was being sounded then, and the responsiveness of the individuals was not decreased previously by any other signal). Next to this the territory song elicited relatively frequent responses then, upon the attracting call the tits approached the loud-speaker less. The responses to aggressive calls of the marsh tit surpassed that to the attracting calls and, in some per cent of the experiments even the alarm call of the great tit exerted an approaching effect.

II. When comparing the reaction lines of the three species of tits it is conspicuous that, on an average, that of the great tit is much higher than those of the blue and marsh tits. Consequently, the great tit responded much more sensitively to the signals of its own species than did the other two species to similarly conspecific signals. Only the responses elicited by the attracting calls were exceptions in this respect; all three species responded, namely, in an approximately identical proportion to such calls of the identical species. The responsiveness to conspecific signals of the blue and marsh tit did not show significant differences.

It clearly appears from the lines of reaction represented in the Figures that the sensitivity of the great tit was high not only to conspecific signals, in certain instances even its responses to the signals of the blue and marsh tits came near to or even surpassed the ones of the related species to their conspecific signals. This is what can be stated on the values given for the attracting call and anxiety

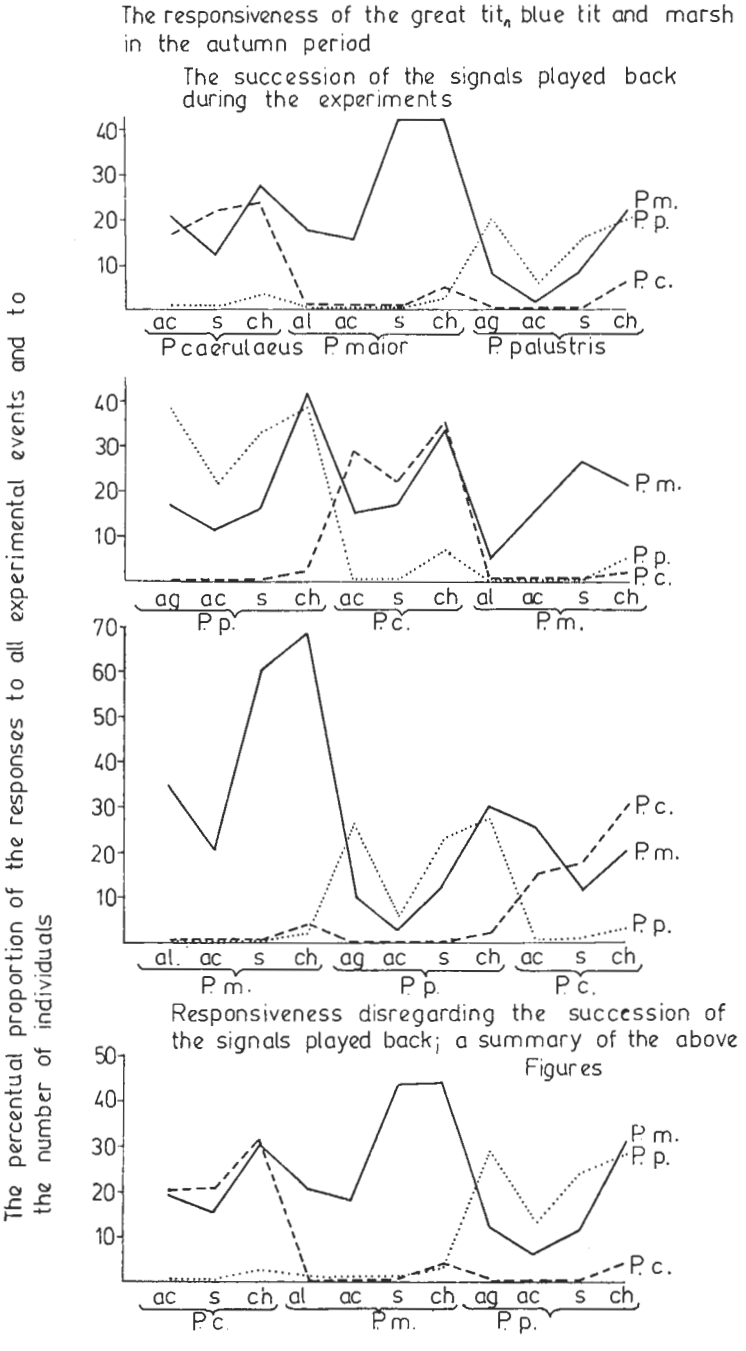
The responsiveness of the great tit, blue tit and marsh tit in the autumn period
The succession of the signals played back during the experiments
The percentual proportion of the responses to all experimental events and to the number of individuals
40
30
20
10
P m.
P p.
P c.
ac s ch al ac s ch ag ac s ch
P caerulaeus P maior P palustris
ag ac s ch ac s ch al ac s ch
P p. P c. P m.
70
60
50
40
30
20
10
al. ac s ch ag ac s ch ac s ch
P m. P p. P c.
Responsiveness disregarding the succession of the signals played back; a summary of the above Figures
50
ac s ch al ac s ch ag ac s ch
P c. P m. P p.

Fig. 12.

churring of the blue tit and for the anxiety call of the marsh tit. At the same time, the blue tit showed but very slight sensitivity of reaction to the signals of the great and marsh tits, even that only to thier anxiety calls and, in winter, to the attracting call as well as territory song of the great tit. The same can be found when evaluating the responsiveness of the marsh tit, i. e. that species responded in an insignificant measure to the anxiety churring of the great and blue tits, and in winter, to the territory song of the great tit.

The attracting calls of both the great and blue tit are simple gliding calls (Figures 3 and 4), the difference in them rather refers only to their timbres. The fundamental similarity of structure could give reasons why the great tit reacted with an approaching response to the attracting calls of the blue tit, however also the blue tit should respond in an approximately identical proportion to the attracting call of the great tit. There is a certain common feature also in the songs of the great tit and marsh tit insofar as both species build up their songs by frequently repeated a relatively simple sound construction, (the difference is that the great tit repeats musical intervals, and the repetitions of the marsh tit are constructions built up of gliding sounds, – see Figures 4 and 9), still, in this way both species should similarly show an approximately identical responsiveness to the sounds of one another. The same holds for the aggressive signal of marsh tit since in its construction this signal comes very close to the song of this bird (Figures 9 and 10). Among the acoustic signals of the three species difference is least in the anxiety churrings. The structure of these is almost fully identical, the only difference is that, in the course of the frequent repetition, the blue tit raises the last churring sounds to a somewhat higher pitch, and the marsh tit also inserts sharp cries between the tremolos (Figures 2, 5 and 8 – the sharp cry of the marsh tit is not presented). In the blue and marsh tits the anxiety churring elicited a response to the signals of the related species too, – even this reaction was by far inferior to the values of those shown by the great tit to the anxiety calls of the blue and marsh tits.

Discussion

I. In a certain per cent of the cases all types of acoustic stimuli elicited identical responses of locomotion during the experiments, i. e. the birds flew in the direction of the source of sound. The frequency, at which this response ensued to the single types of signals was determined by the specific structure of the signals in question. In fact, sounds perceived from the same direction and being repeated many times elicited, in certain instances, an attractive reaction even if they were alarm calls. Under natural conditions the alarm calls are being repeated once or two times, in infrequent instances three times, and thus elicit escape. An effect contrary to this ensued in consequence of frequent repetition.

That a repetition of signals brought about in a situation which differed from the natural ones elicited approach even in the case of call of repelling effect, is only possible if, *on account of the lasting repetition, the acoustic signals of this kind separate from their specific meaning, the differentiated information content based on their structure is pushed into the background and, as repeating impulses, they elicit a reaction of approaching in the perceiving individuals. Consequently, by this general function the voices ensure the maintenance of contact without concretely expressing*

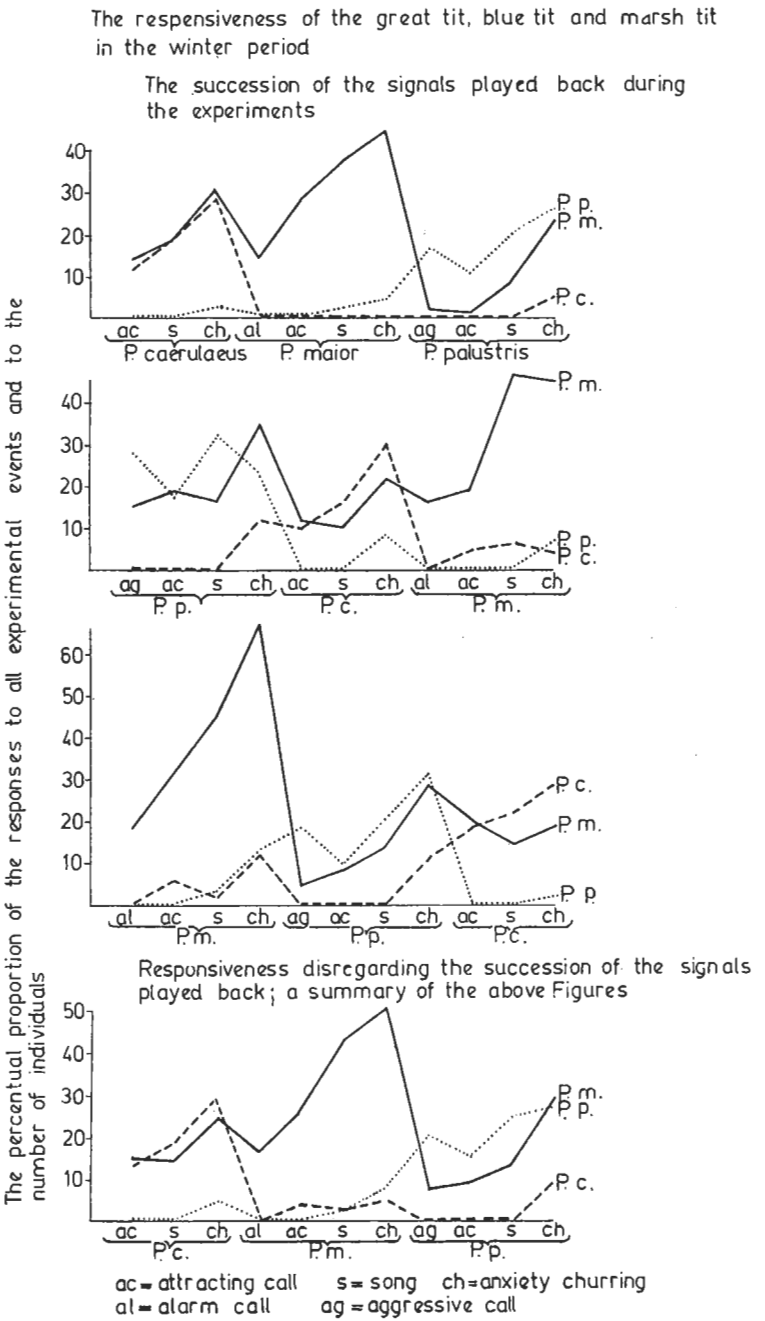
The respensiveness of the great tit, blue tit and marsh tit in the winter period
The succession of the signals played back during the experiments
The percentual proportion of the responses to all experimental events and to the number of individuals
P. p.
P. m.
P. c.
ac s ch al ac s ch ag ac s ch
P. caerulaeus P. maior P. palustris
ag ac s ch ac s ch al ac s ch
P. p. P. c. P. m.
al ac s ch ag ac s ch ac s ch
P. m. P. p. P. c.
Responsiveness disregarding the succession of the signals played back; a summary of the above Figures
ac = attracting call s = song ch = anxiety churring
al = alarm call ag = aggressive call

Fig. 13.

the individual relations in which exerted their attracting effect. The concrete relations are expressed by the specific sound structure. Only in this way can structurally separated and also functionally differentiated (in case of the alarm call: opposite) signals (songs, anxiety call, attracting call etc.) elicit an identical effect: that of approaching. Probably, when the alarm signals produced an attracting effect, the drive for social integration was operating with the highest intensity.

The tits staying within the range of audibility were attracted most by anxiety churring, since it was the reproduction of the anxiety churring that came nearest to the natural signalling processes. (Under natural circumstances, if the disturbing object – e. g. a sitting predator – does not change its place or moves but slowly, the sound signals of the perceiving bird, heard from the same direction and repeated for a long time gather the tits staying within the range of audibility.) What has been said in this paper about the alarm signals, is best supported by the structure of the anxiety call, as, in its specific construction this signal is essentially nothing else but a series of tiny sound elements repeated many times without vertically structure of pitch. As acoustic repetition this tremolo signal became connected with the necessity of the biologically most important situation: that of danger, in the evolution of acoustic communication. Thus it can be understood why out of the signals this one has the most intensive social function, and why, by sounding it, the individuals perceiving disturbing phenomena or objects, set in action a common social attitude.

The attracting effect of the territory songs can similarly be explained by multiple repetition, even if the process of singing does not consist of a series of identical pitches, but of identical repetition of structural units built up of various pitches. At breeding seasons it is upon the effect of the song that the male individuals get near one another and in the course of the ensuing aggressive behaviour they clear their relations of force and fix the borders of their territories. So the males use the attracting effect of the sound signals as a means of meeting each other and of dividing the nesting area among one another. The generally taken attracting effect of repetition was well supported by the experiments carried out with the song, since at the time of the experiments (autumn and winter) the reproductive behaviour, attached to the forms of signals was not present in the individuals, still, these signals often elicited a reaction of approaching.

The attracting effect of the attracting calls was lower than the one of the songs. The birds moving in pairs or in flocks repeat their attracting calls several times, but at the same time they permanently change their places, so that this sound never gives rise to a gathering of the birds. Yet, in part of the experiments, the sounds emitted from a fixed source elicited an attracting effect in the tits within the range of audition. Thus, by way of summing up what has been said above, it has to be stated, that the repetition of the sound signals, independently of their specific function, exerts an attracting effect, and that the specific structural, pitch, timbre etc. properties of the sound signals express the concrete social drives and physiological condition (gregarious attraction, reproductive aggressivity, the gathering round the sitting preadator, etc.) of the individuals.

II. The experiments have unambiguously proved that the responsiveness of the great tit is higher than that of the blue or marsh tits, since it has responded more sinsitively than the other two not only to the conspecific signals, but at times even to the signals of the two related species than they did themselves to

the conspecific signals. The increased sensitivity to acoustic signals expresses an increased social tendency, and helps in this way in the biologically advantageous joining in groups.

In the course of the social dynamic events taking place in the local populations part of the individuals of tits are driven out of the community, and forced to settle new areas. Settling in the new areas is facilitated by social attracting effects, since the pioneers increase the number of individuals round themselves by social attraction. In other cases, if more than one individual take possession of the that far untouched area at the same time, it is similarly the existing social connections that enable them to settle in the new area. At times the new area may also be a new ecological milieu, of which the actual occupation can ensue only by the formation of a stable nesting population. All this rests upon the social connections which efficiently act under the new living conditions. Still, social connections can come into existence only through well-functioning means of communication; and the more receptive is a species to the stimuli ensuring communication, the more sure and manisided is also its social life. The increased sensitivity to acoustic stimuli, which is thus the originator and also the safeguard of intensive social connection, is at the same time a means of the expansion and progression of species. Presumably, this relation also exists in the case of the great tit. In the course of its occupying to the urban environment, the great tit populates a new ecological milieu; the blue tit does this only in a moderate degree as it nests only in extensive parks, and the marsh tit does not nest in city or industrial environment at all. *The progressive effort, by which the great tit surpasses the blue and marsh tits is founded partly upon its faculties of behaviour. One of these faculties is its increased responsiveness to acoustic stimuli, which at the same time means an increased social sensitivity and is also of help in settlement new adaptive areas.* The minor social sensitivity of the blue tit and marsh tit is presumably related to the more restricted adaptation capability of these two species. Possibly behind the great tit's increased responsiveness to acoustic signals there is a comprehensive ability being manifested in general in an increased sensitivity to stimuli. This makes possible that the new constellations of stimuli should elicit approaching in the bird, and at the same time furthers a progressive moment, the settlement in the new ecological areas.

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Table 1. Significance relating to the difference of responsiveness

Acoustic signals played back in the experiments		The responsiveness of the blue tit is higher than that of the marsh tit	The responsiveness of the blue tit is higher than that of the great tit	The responsiveness of the marsh tit is higher than that of the blue tit	The responsiveness of the marsh tit is higher than that of the great tit	The responsiveness of the great tit is higher than that of the blue tit	The responsiveness of the great tit is higher than that of the marsh tit
Territory song	in autumn	–	–	–	–	$p<0.001$	$p<0.001$
of the great tit	in winter	–	–	–	–	$p<0.001$	$p<0.001$
Anxiety call	in autumn	–	–	–	–	$p<0.001$	$p<0.001$
of the great tit	in winter	–	–	$p<0.50$	–	$p<0.001$	$p<0.001$
Attrackting call	in autumn	–	–	–	–	$p<0.001$	$p<0.001$
of the great tit	in winter	$p<0.30$	–	–	–	$p<0.001$	$p<0.001$
Territory song	in autumn	$p<0.001$	$p<0.50$	–	–	–	$p<0.01$
of the blue tit	in winter	$p<0.001$	–	–	–	–	$p<0.001$
Anxiety call	in autumn	$p<0.001$	–	–	–	–	$p<0.001$
of the blue tit	in winter	$p<0.001$	$p<0.50$	–	–	–	$p<0.001$
Attrackting call	in autumn	$p<0.001$	–	–	–	–	$p<0.001$
of the blue tit	in winter	$p<0.001$	–	–	–	–	$p<0.001$
Territory song	in autumn	–	–	$p<0.001$	$p<0.05$	$p<0.001$	–
of the marsh tit	in winter	–	–	$p<0.001$	$p<0.05$	$p<0.001$	–
Anxiety call	in autumn	–	–	$p<0.001$	–	$p<0.001$	–
of the marsh tit	in winter	–	–	$p<0.01$	–	$p<0.001$	–
Attrackting call	in autumn	–	–	$p<0.001$	$p<0.10$	$p<0.10$	–
of the marsh tit	in winter	–	–	$p<0.001$	$p<0.20$	$p<0.05$	–