

The hearing of an avian predator and its avian prey

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Received September 4, 1984 / Accepted November 18, 1985

Summary. Auditory tuning curves of a small songbird, the great tit (*Parus major*), and of its principal avian predator, the European sparrowhawk (*Accipiter nisus*), were determined by an operant positive reinforcement conditioning procedure, using the method of constant stimuli. Thresholds were measured by the criterion of a 50% correct response and a d' of 1.5 for intra- and interspecific comparison, respectively. The best frequency of both species was 2 kHz, the hawk being 6.5 dB SPL more sensitive than the tit. Although the high-frequency cutoff was very similar in both species, at 8 kHz the great tit was about 30 dB more sensitive than the sparrowhawk. The hearing abilities of the prey and its predator are discussed with reference to the acoustic alarm communication of great tits confronted with sparrowhawks. Two alarm calls lie in the frequency range of the best hearing of both the hawk and the tits: the mobbing call and a call given in response to a nearby hawk when fleeing from it. In contrast, the "seet" call, an alarm call given mainly in response to distant flying sparrowhawks, can only be heard well by the tit. The implications of these results for hypotheses concerning the evolution of alarm calls in small songbirds are discussed.

Introduction

The evolution of communication systems and the adaptive value of certain characteristics of animal signals have received much recent interest. Besides the ultimate factors that determine the adaptive

use of a signal, there is a set of proximate factors that determine the adaptedness of its structure. The relevance of these proximate factors to the acoustic communication of birds in individual and species recognition, mate selection, territorial defence and song learning has recently been reviewed by Dooling (1982). He emphasized the role of the sensory capabilities for the outcome of the evolution of song and call structure.

Many years ago the question of the role of sensory capabilities of predators in the evolution of alarm calls was discussed by Marler (1955). In his classical paper he hypothesized that predators constitute a selective pressure that leads to convergent calls in the species upon which they prey. He argued that the call structure of avian calls in response to aerial predators is determined by their need to be non-localizable. However, as Klump and Shalter (1984) pointed out, locatability is only one factor influencing alarm call structure. Other factors, like the detectability of a call, may be of greater importance.

The sensory capabilities of the participants in communication enter into the cost-benefit ratio associated with their behaviour. The discussion of the function of alarm calling behaviour in birds and mammals gives many examples of this. An alarm call that attracts the attention of the hunting predator while the prey is rather vulnerable (e.g. not in cover) is associated with high cost. If the prey uses an alarm call that is not easily detectable by the predator (Marler 1977), or is non-localizable (Marler 1955), it reduces this cost. If the sensory processing of the alarm call by the prey and the predator differs, the prey might even evolve alarm calls that at the same time allow efficient communication with other prey, and are hardly perceptible by the predator. There are other hypotheses on the evolution of alarm calls that are based on the

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assumption that the predator is more sensitive to sound than the prey (e.g. Brown 1982).

An exemplary study of the processing of sound in a predator and one of its prey species will give better insight into the adaptedness of the structure of alarm signals. A predator-prey dyad that is especially suited for such a study is the European sparrowhawk (*Accipiter nisus*) and the great tit (*Parus major*). The aerial-predator calls of the great tit were one of the examples in the classical paper of Marler (1955), and the European sparrowhawk is the only relevant avian predator that could have selected for those calls. The sparrowhawk accounts for heavy losses in great tit populations (Geer 1978, 1982; Perrins and Geer 1980; Curio et al. 1983) and thus should be a strong selective agent on tit alarm calling behaviour and the structure of their alarm calls. The study of audibility curves of predator and prey provides a first step in understanding the adaptedness of acoustic alarm communication.

Methods

Threshold determination in the European sparrowhawk

Subjects. Two European sparrowhawks (*Accipiter nisus*), a male and a female, were successfully trained to react to auditory stimuli. Both birds had hatched in captivity. The male was hand-reared from the egg, the female from the age of 12 days onward. Experiments with the male and female were performed between the ages of 4–8 and 8–11 months, respectively. For the time of training and experimentation the birds were adapted to a daily feeding regimen that lowered their pre-session weights to 80%–90% of their free-feeding weights. They were mainly fed with small pieces of chicken, and obtained most of their food from their performance in the experimental sessions.

Apparatus. For the experimental sessions the hawks were transferred to an anechoic, soundproof room (Grünzweig and Hartmann, 5 m × 4 m × 3 m). The background noise in this room was below the minimum measurable noise level in octave-bands with center frequencies of 250 Hz and above (sound level meter: GenRad 1933 with 1/2" electret condenser microphone). To better estimate the suitability of the room for the determination of absolute thresholds, we measured the audibility thresholds (at 0.5, 1, 2, 4, 8 kHz) of a person known to be of very sensitive hearing in the soundproof room and compared them with unmasked thresholds obtained by using the standard procedure with closed earphones. There was no significant deviation of either threshold curve. Thus, the level of background noise was sufficiently low for the determination of absolute threshold curves.

During the experiments, an observer watched the experimental bird through a closed-circuit video system from outside the room. The hawk perched in one corner of this room. A loudspeaker (Isophon BPSL 65) was positioned at a distance of 3 m from the hawk. Pure tone stimuli with variable amplitude were generated by a Burchard sound generator (Akustischer Stimulator II, THD < 0.6%) with a built-in attenuator. During the experiment, frequency was monitored by an oscillo-

scope (Philips PM 3207). Tones had a duration of 300 ms and rise/fall times of 5 ms. For calibration we determined free-field sound pressure levels (SPLs) in the area where the bird's head would normally be located during a session (sound level meter, see above, fast and octave band settings).

Procedure. The hawks were first adapted to the anechoic room by seating them on a waiting perch in the room for 2–4 h per day, and were trained to eat from an automatic feeder. The feeder was mounted at a second perch at a distance of 1–3 m from the hawk's first perch, where it usually sat during the sessions. The hawks readily learned to leave the waiting-perch and fly to the feeder when it delivered a food item, eat it, and then fly back onto the waiting-perch. Food items were then delivered with an additional pure tone stimulus from the speaker for a number of sessions until the hawk flew to the feeder when only a tone was sounded. The hawk was given a reward every time it left its waiting-perch after a tone was switched on, but was "punished" by a toneless waiting period of 60–120 s if it left its perch without a tone having been sounded.

Each session, with a duration of 40–70 min, was composed of 20 or 30 groups of three trials: A first trial with a series of 30 tones (rate 1/s) of a frequency and sound pressure level that the bird could hear ("LT-trial"), followed by either a trial with a series of tones of the same frequency and a 10–20 dB lower sound pressure level (SPL, "test trial"), or a trial with a 30-s interval without tones ("catch trial"). The order of presentation of the latter two trials was randomized so that the bird could not predict whether a LT-trial would be followed first by a test trial and then by a catch trial, or vice versa. A trial started when the hawk sat on its waiting-perch. A response was scored if the hawk left its perch during the presentation of the tone-series and the number of tones necessary for this reaction was also recorded. "No reaction" was counted if the hawk did not leave its perch within the time of presentation of tones. Three to four sessions were conducted daily except at weekends.

Data analysis. We first tried to estimate the threshold for each frequency (0.25, 0.5, 1, 2, 4, 6, 8, 10 kHz: both hawks; 7, 9 kHz female only) performing a few trials at various sound pressure levels (all SPLs refer to 0.0002 Pa). The sound pressure levels in the various sessions were then chosen in such a way that the maximum difference in sound pressure level between a tone just below the estimated threshold and a tone just above threshold was not more than 10 dB for the male sparrowhawk or 8 dB (mostly 5 dB) for the female sparrowhawk. Thresholds were defined as the sound pressure level at which the hawk would show a correct response in 50% of the trials (or detected the signal with a d' of 1.5; this criterion was used for comparison of hawks and tits), and were calculated by linear interpolation between the reactions to tones with a sound pressure level just above and just below threshold. To make sure that the hawks were highly motivated, sessions in which the bird reacted in less than 90% of the LT-trials were excluded from the analysis (8% of the sessions). Catch trial rates were on average 18% in the male and 9% in the female. At least 30, but in most cases 60 trials were analysed at each sound pressure level.

Threshold determination in the great tit

Subjects. Three of four great tits (*Parus major*), two males and one female, were successfully trained to respond to auditory stimuli. All birds were handreared from the age of about 13 days onward. From the age of 30 days the birds were housed in individual cages (40 cm × 50 cm × 50 cm). Direct handling of

the birds was avoided, and they were routinely transported in their home cage. Prior to experimental sessions they were deprived of food for 3–4 h. During a session they received up to 16 quarter-mealworms (*Tenebrio molitor*) as rewards. Sessions were conducted hourly from 1 p.m. to 5 p.m., seven days a week. After the last afternoon session until the next morning they had free access to less preferred food (sunflower seeds and fly larvae). With this feeding regimen the pre-session weights were lowered to about 90% of their free-feeding weights. During the experiments the birds were 2–6 months old.

Apparatus. The experiments were conducted in the same anechoic room as the experiments with the hawks (see above). The tits were observed through a closed-circuit video system. Because the tits were much more agile subjects than the hawks, the training of the birds and the experimental sessions were fully controlled by a fast, suitably programmed microcomputer-system (TRS 80, Model I; for more details see Klump 1984). A custom-built interface presented tones of a duration of 300 ms, and with a rise/fall time of 5 ms. The output was passed through a Hewlett-Packard (model 350 D) variable attenuator and connected to a power-amplifier (Braun A 301) which drove the speaker (Isophon BPSL 65) mounted 1 m from the head of the bird. The total harmonic distortion of the system was at most 2.3% at 1 kHz and 1.3% at 6.3 kHz (most energy was found to be in the third harmonic), which was still low enough to allow the threshold determination for the basic frequency of the stimulus alone (see form of audibility curve below). The amplitude of the signal could be varied by the computer in fixed steps (adjustable up to 20 dB). The frequency of the tones was constantly monitored on an oscilloscope (Philips PM 3207). The system was calibrated at least once per day by the procedure described above for the hawk experiments.

Procedure. Because the great tits were more restless than the sparrowhawks, the procedure was different. Initially, the tits were trained by a series of programs (see Klump 1984) to sit on the perch in the doorway between their home cage and the experimental cage and wait up to 30 s for a tone. When a tone was presented the tit had to hop onto a second perch in front of a feeder to receive a reward. For the determination of threshold curves, tones were then presented singly (one tone per trial) after randomized waiting-periods of between 2 and 18 s (uniformly distributed). Reactions with a latency of more than 2 s were counted as no response. As in the case of the sparrowhawk, sessions were composed of groups of three trials, an LT-trial, followed by a test trial and a catch trial or vice versa (sequence randomized, see above). Each session was composed of 8–16 groups of three trials.

Data analysis. Thresholds were determined for 7 frequencies (0.25, 0.5, 1, 2, 4, 8, 10 kHz) with the same linear interpolation methods (50% criterion and d' of 1.5 for intra- and interspecific comparison, respectively) as were used with the sparrowhawks. The stimulus intensities near threshold differed not more than 5 dB allowing a very exact threshold determination. Sessions with more than 20% false alarms during the catch trials were excluded from the analysis (7% of all sessions). The average false-alarm rate in the sessions analysed was 7%.

Results

Audibility curve of the European sparrowhawk

The shaping of the response took about 2 weeks with 2–3 sessions daily. After this time the reaction

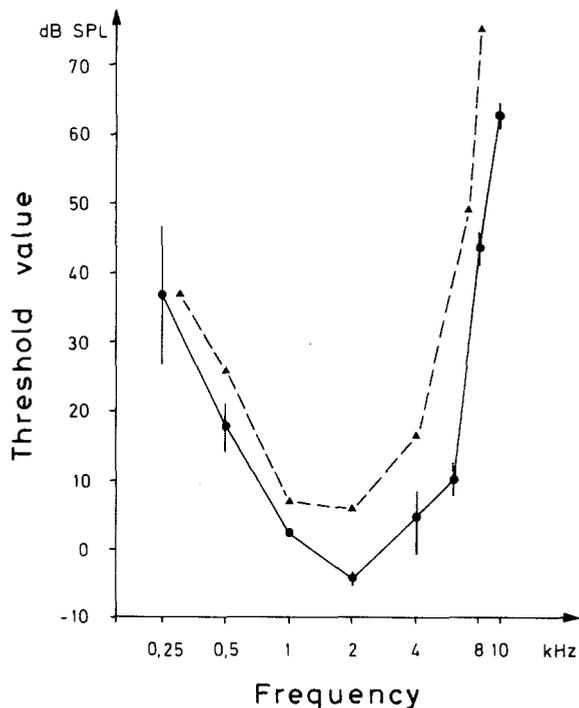


Fig. 1. Mean absolute threshold curve of two European sparrowhawks (*Accipiter nisus*: closed circles, bars indicate the range of obtained values), and the absolute threshold curve of the American kestrel (*Falco sparverius*: triangles, data from Trainer 1946)

to the test stimulus (2 kHz, 60 dB SPL) was more than 95% correct. The female was given some 10 additional training sessions to reduce a high false alarm rate. When the hawks were presented with the trial triplets (LT-trial, test trial, catch trial), and when both LT-trials and test trials were more than 5 dB above threshold (with a 10–20 dB difference in SPL between LT and test trials), there was no statistical difference between the performance in LT-trials and test trials (Fisher's exact probability test, $p_2 > 0.05$). The hawks' false-alarm rate was below 30% (see above), as was the percentage of correct reactions in test trials with a sound pressure level of more than 10 dB below threshold. This indicates that the psychophysical method employed was suitable for threshold determination.

The mean threshold values for both birds together with their ranges are shown for each test frequency in Fig. 1. The best frequency of the sparrowhawk was 2 kHz with a mean threshold of -4 dB. The low-frequency sensitivity (threshold at 0.5 kHz, see Dooling 1980) was 17.5 dB. At frequencies above the best frequency the threshold exceeded 60 dB above 9.6 kHz (high-frequency cutoff, Dooling 1980). Below the most sensitive point in the audibility function the threshold in-

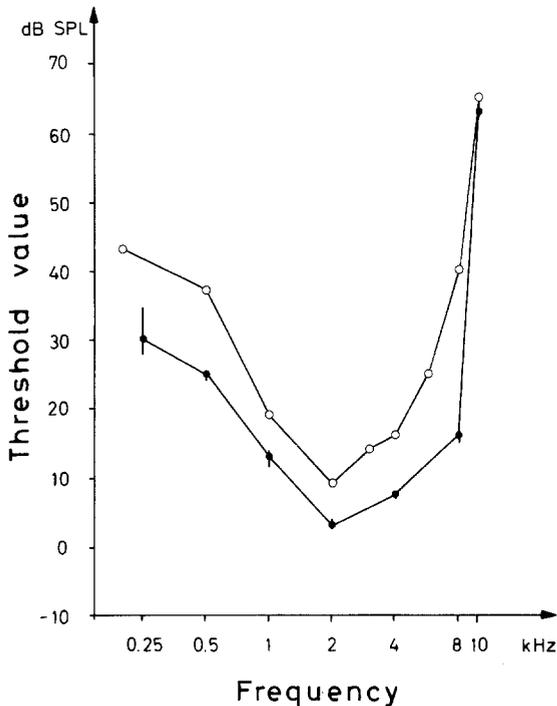


Fig. 2. Absolute threshold curve of the great tit (*Parus major*: closed circles, bars indicate the range of obtained values), and the average absolute threshold curve of nine songbird species (open circles, from Dooling 1980)

creased at a rate of 13.7 dB/octave. Above the most sensitive point it increased at a rate of 9.1 dB/octave up to 6 kHz, with a still steeper increase above 6 kHz, namely 71.9 dB/octave. The bandwidth 40 dB above the most sensitive point was 4.8 octaves (0.26–7.4 kHz).

In summary, the sparrowhawk is rather sensitive to sounds in the frequency region 1 kHz–4 kHz, but is very insensitive to frequencies of 8 kHz and above.

Audibility curve of the great tit

After an initial training of 4 weeks (3–4 sessions daily) the great tits responded reliably to a tone of 2 kHz with a sound pressure level of 60 dB. The conditioning paradigm used in this study worked well with the great tits: the probability of correct reaction was greater than 75% for tones with a sound pressure level of more than 5 dB above threshold and was low for tones with a sound pressure level of more than 5 dB below threshold, i.e. the psychophysical functions were relatively steep in the threshold region, resulting in an accurate threshold determination. For control purposes some thresholds were repeatedly determined on different days; however, these thresh-

old values never differed more than 3 dB for a given tit.

The mean threshold values of the three birds together with their ranges at each test frequency are shown in Fig. 2. The best frequency of the great tit was 2 kHz with a mean threshold of 3 dB. The low-frequency sensitivity was 25 dB. The high-frequency cutoff was found to be 9.7 kHz. Below the most sensitive point in the audibility function the threshold increased with a slope of 9 dB/octave. Above the most sensitive point, the threshold increased only at a rate of 6.5 dB/octave up to 8 kHz, but then increased steeply at a rate of 144.4 dB/octave. The bandwidth 40 dB above the most sensitive point was 6.5 octaves for the average great tit (0.1 kHz–9.1 kHz).

In summary, the great tit is relatively sensitive to sounds in the frequency region 1–8 kHz, but is relatively insensitive at 10 kHz.

Discussion

The relevance of absolute threshold curves

Dooling (1980) in his review on behaviour and the psychophysics of hearing remarked that “auditory mechanisms do not evolve in the near absolute quiet of a testing booth”. However, even in the natural environment some thresholds relevant for the evolution of communication are unmasked thresholds. In European temperate forests, the habitat of the great tit, wind-generated noise is the main source of background noise, but not the sounds of other animals (see also Brenowitz 1982). The level of this background noise is usually frequency-dependent. With moderate windspeeds (below Beaufort 6), for example, the spectrum level of background noise for frequencies of about 8 kHz becomes so low that usually the sum of the spectrum level plus the critical ratio of the great tit lies below the unmasked threshold (Klump and Curio 1983b; Klump 1984), thus no masking occurs. If masking were to occur in the sparrowhawk, its critical ratio would have to be about 30 dB higher than that of the great tit.

At the most sensitive region of the auditory tuning curves the spectrum level of background noise is likely to influence the hearing thresholds in the natural habitat. The spectrum levels measured in a deciduous forest with leaves were in the range of 3 dB–17 dB and –3 dB–12 dB for 2 kHz and 4 kHz, respectively. There was a substantial variation of spectrum levels with windspeeds. In the great tit, the sum of the spectrum level of background noise and the critical ratio for

the corresponding frequencies is often about 15–35 dB higher than absolute threshold (for critical ratios of the great tit see Klump and Curio 1983b), thus the great tits' hearing thresholds at 4 kHz and below are often raised through masking. We have no critical ratio data for the sparrowhawk. If critical ratios of hawk and tit were of the same magnitude, masking background noise would raise the auditory sensitivity of both sparrowhawk and the great tit to about the same level.

The hearing of the predator

The auditory threshold curves of the two sparrowhawks are very similar; the differences between the hawks are in the range of measurement error. The range of best hearing (1–4 kHz) matches the dominant frequencies in the sparrowhawks' species-specific vocalizations (Glutz et al. 1971). Evidence has been found that accipiters may use acoustic stimuli from their prey when hunting (Stoddard in Brown and Amadon 1968). If sparrowhawks use such acoustic stimuli, they should lie in the upper part of their range of best hearing (3–5 kHz), since at lower frequencies masking by background noise may play a greater role. At high frequencies (7 kHz and above) absolute thresholds and not masked thresholds are likely to determine the hearing ability of the sparrowhawk (see above).

Only one other diurnal raptor has been studied, the American kestrel (*Falco sparverius*), that can be compared with the European sparrowhawk. According to Trainer (1946), it has an auditory threshold curve similar to that of the European sparrowhawk (see Fig. 1). The best frequency is identical in both audiograms, and both diurnal raptors have bad high-frequency hearing.

The hearing of the prey

All three great tits have relatively similar audiograms as expressed by a threshold variation of smaller than 4 dB for frequencies of 0.5 kHz and above. The female great tit did not differ very much from the two males. Similarly no sex difference has been found in other species of songbirds (Dooling et al. 1978; Hienz et al. 1977). The dominant frequencies in many calls and also elements of the song of the great tit lie above the best frequency. However, this may be advantageous in the natural environment with background noise (Klump and Curio 1983b). One call of the great tit, the aerial-predator call described by Marler (1955), is a pure tone whistle with a dominant fre-

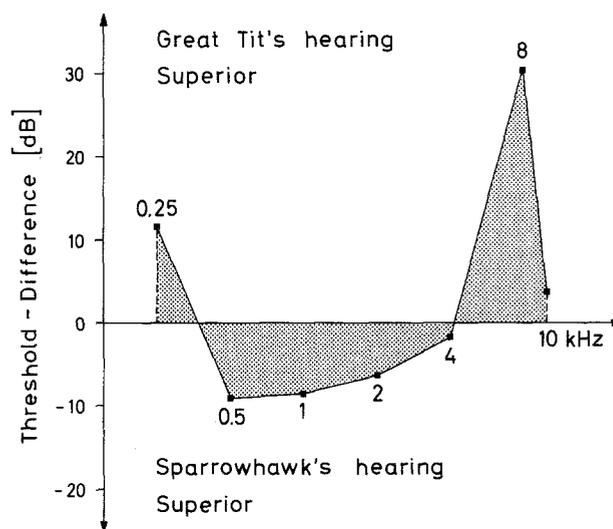


Fig. 3. The differences in the absolute thresholds between the great tit and the European sparrowhawk (thresholds in both species calculated using signal detection theory; $d' = 1.5$)

quency of about 7–8 kHz (“seeet” call). This call can be heard quite well by the great tit; even with a rather low unmasked threshold the effect of masking is insignificant, since the background noise in the natural environment has a very low spectrum level in this frequency range. Other alarm calls of the great tit, e.g. the call given on sight of a close aerial predator (see also Klump and Shalter 1984), and the mobbing call, lie only slightly above the best frequency in the auditory tuning curve. With a little background noise in the natural habitat these calls can be heard about as well by the great tit (Klump and Shalter 1984; Klump 1984) as the “seeet” call.

Compared with song birds on average, the great tit hears well, especially at frequencies of about 8 kHz (Fig. 2). Hearing as good in this frequency range has only been found in one other songbird species, the cowbird (Hienz et al. 1977). In both species this corresponds to the existence of very high-pitched sounds in their vocal repertoire.

Comparing the predator with its prey

The differences in the unmasked thresholds of the sparrowhawk and the great tit at various frequencies are shown in Fig. 3. For an easier comparison of the performance of sparrowhawk and great tit the thresholds used for this figure were calculated by means of the signal detection theory (thresholds refer to a d' of 1.5 for both hawks and tits, and were calculated using the tables in Swets 1964;

these threshold values were not very different from the thresholds obtained using the criterion of 50% correct response). In the midfrequency range (0.37–4.2 kHz) the hearing of the predator is superior to that of the prey. The difference, however, does not exceed 9 dB. Additionally, the dominant frequencies of the great tit's calls and song lie mostly above 3 kHz. This means that most of the low-frequency calls and song elements in the great tit's repertoire can be heard about equally well by the sparrowhawk and by other great tits. This does not hold for tit calls with dominant frequencies of 6–9 kHz. In this frequency range the hearing of the great tit is at least 15 dB more sensitive than that of the sparrowhawk, with the sensitivity difference peaking (30 dB) at 8 kHz. Thus, a tit call with a dominant frequency of about 8 kHz can still be heard quite well by other great tits, but is hardly heard by the predator.

Implications for the functions of alarm calls

When confronted with a European sparrowhawk, great tits use three different vocalizations. First, the mobbing call (dominant frequency 4.5 kHz, Latimer 1977) is mainly used by great tits when approaching a hawk or owl perched in their territory (for a description of the great tits' mobbing behaviour with a live sparrowhawk during the breeding season see Hinde 1952; Curio et al. 1983). In midwinter, when territoriality is low (Drent 1983), they rarely use this call when confronted with a live perched sparrowhawk (Klump, unpublished observation). They use instead a second call termed "scolding" (dominant frequency about 4 kHz, Klump 1984). This call is similarly found in other Paridae (e.g. in *Parus caeruleus*, Klump and Curio 1983a; and in the blackcapped chickadee, *Parus atricapillus*, Odum 1942). Unlike mobbing calls, which are used when approaching a raptor, these calls are associated with fleeing from the perched sparrowhawk. The great tits also use "scolding" when directly attacked by a sparrowhawk (Klump 1984). Third, the "seeet" call (dominant frequency 8 kHz) which is mainly used by the great tit when confronted with a sparrowhawk flying at some distance (Klump 1984). This call is the aerial-predator call described by Marler (1955). Other tit species (e.g. *Parus caeruleus*) also use this call in the same context (Klump and Curio 1983a).

The variation of the use of the calls with distance suggests that the different alarm calls are addressed to different receivers. When estimating the detection distances of alarm calls for the hawks

and the tits (see Klump and Shalter 1984), we must consider at least five factors: amplitude of the signal at the sound source, environmental attenuation, environmental background noise, the receiver's critical ratio, and its absolute threshold. The last three factors for the hawk-tit dyad were discussed along with the estimate of the birds' threshold with environmental background noise. Alarm call amplitudes have been measured for "seeet" calls ($60.1 \text{ dB} \pm 4.5 \text{ dB SD}$, 1 m distance) and mobbing calls (66–68 dB, Curio and Klump unpublished data). "Scolding", which has a sound spectrum similar to the mobbing calls, to the human observer sounds as loud as the mobbing calls. Environmental attenuation is different for the three alarm calls. Due to their high frequency "seeet" calls are attenuated very rapidly, whereas "scolding" and mobbing calls with a dominant frequency of about 4 kHz carry farther (Marten and Marler 1977). When calculating the distances at which different calls are audible for the hawk and the tit (see Dooling 1982; Klump and Shalter 1984), we find that the difference in audibility of the alarm calls depends mainly on the masked thresholds. With environmental masking noise, detection distances are probably very similar in the hawk and the tit for the "scolding" and the mobbing calls (about 40 m or more, see Klump and Shalter 1984), but they are very different for the "seeet" call (only up to about 10 m in the hawk and up to 40 m in the tits, see Klump and Shalter 1984). Hence, the tits can address "seeet" calls to flock members to the exclusion of the hawk, whereas "scolding" and mobbing calls can be heard about equally well by both tits and hawks.

The different audibility of the alarm calls must be taken into account when discussing their function. Both mobbing calls and "scolding" may be similarly directed both at other prey (as a warning signal, e.g. see Frankenberg 1981) and at the predator (as a pursuit deterrent signal or for "moving on" the predator, see Klump and Shalter 1984). We show that the "seeet" call is mainly directed at other prey, thus ruling out Brown's (1982) hypothesis of reciprocal treachery (callers draw the predator's attention to the flock of prey without making the flockmates aware of the danger; every bird who sees the predator first does it and thus "reciprocates") which was based on the assumption that the hearing of the predator is superior to the hearing of the prey. Furthermore, it can serve as a warning call by which the caller incurs only a minor cost. The evolution of such calls appears possible by individual selection if callers receive a future benefit, e.g. by decreasing the proba-

bility of future hunts of the predator in the area where they live (Trivers 1971; Klump and Shalter 1984).

Acknowledgements. We thank the family Dörschner for providing the sparrowhawks and Miss S. Düllmann for rearing the great tits. Mr. W. Windt helped to conduct the experiments with the hawks and tits. Miss A. Bassaris prepared the drawings and Dr. J. Scott polished our English. Furthermore, we thank Prof. Dr. J. Schwartzkopff and Dr. J. Rheinlaender for technical facilities, and the Deutsche Forschungsgemeinschaft for financial support (grant Cu 4/26-2 to E. Curio). We thank Prof. J.D. Delius, Prof. H.C. Brown, Prof. R.J. Dooling, and Prof. H.C. Gerhardt for comments on the manuscript.

References

- Brenowitz EA (1982) The active space of Red-winged Blackbird song. *J Comp Physiol* 147:511–522
- Brown CH (1982) Ventriloquial and locatable vocalizations in birds. *Z Tierpsychol* 59:338–350
- Brown L, Amadon D (1968) Eagles, hawks and falcons of the world. Country Life, London
- Curio E, Klump GM, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk? *Oecologia* 60:83–88
- Dooling RJ (1980) Behaviour and psychophysics of hearing in birds. In: Popper AN, Fay RR (eds) Comparative studies of hearing in vertebrates. Springer, Berlin Heidelberg New York, pp 261–288
- Dooling RJ (1982) Auditory perception in birds. In: Kroodsma DE, Miller HE (eds) Acoustic communication in birds, vol 1. Production, perception, and design features of sounds. Academic Press, New York London, pp 95–130
- Dooling RJ, Zoloth SR, Baylis JR (1978) Auditory sensitivity, equal loudness, temporal resolving power and vocalizations in the House finch (*Carpodacus mexicanus*). *J Comp Physiol Psych* 92:867–876
- Drent PJ (1983) The functional ethology of territoriality in the Great Tit (*Parus major* L.). PhD Dissertation, University Groningen
- Frankenberg E (1981) The adaptive significance of avian mobbing: IV. “Alerting others” and “perception advertisement” in blackbirds facing an owl. *Z Tierpsychol* 55:97–118
- Geer TA (1978) Effects of nesting sparrowhawks on nesting tits. *Condor* 80:419–422
- Geer TA (1982) The selection of tits *Parus* spp. by sparrowhawks *Accipiter nisus*. *Ibis* 124:159–167
- Glutz von Blotzheim UN, Bauer KM, Bezzel E (1971) *Accipiter nisus* – Sperber. In: Glutz von Blotzheim UN (ed) *Falconiformes. Handbuch der Vögel Mitteleuropas*, vol 4. Akademie, Wiesbaden, pp 415–442
- Hienz RD, Sinnott JM, Sachs MB (1977) Auditory sensitivity of the red-winged blackbird (*Agelaius phoeniceus*) and brown-headed cowbird (*Molothrus ater*). *J Comp Physiol Psych* 91:1365–1376
- Hinde RA (1952) The behaviour of the great tit (*Parus major*) and related species. *Behav [Suppl]* 2:1–201
- Klump GM (1984) Struktur und Funktion der Luftfeind-Alarmrufe der Kohlmeise (*Parus major*) außerhalb der Brutzeit. PhD Dissertation. Ruhr-Universität Bochum
- Klump GM, Curio E (1983a) Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. *Bird Behav* 4:78–81
- Klump GM, Curio F (1983b) Why don't spectra of songbirds' vocalizations correspond with the sensitivity maxima of their absolute threshold curves? *Verh Dtsch Zool Ges* 76:182
- Klump GM, Shalter MD (1984) Acoustic behaviour of birds and mammals in the predator context: I. Factors affecting the structure of alarm signals. II. The functional significance of alarm signals and their evolution. *Z Tierpsychol* 66:189–226
- Latimer W (1977) A comparative study of the songs and alarm calls of some *Parus* species. *Z Tierpsychol* 45:414–433
- Marler P (1955) Characteristics of some animal calls. *Nature* 176:6–8
- Marler P (1977) The structure of animal communication sounds. In: Bullock TH (ed) Workshop on recognition of complex acoustic signals. (Dahlem Konferenzen Berlin 1976) Abacon, Berlin, pp 17–35
- Marten K, Marler P (1977) Sound transmission and its significance for animal vocalizations. I. Temperate habitats. *Behav Ecol Sociobiol* 2:271–290
- Odum EP (1942) Annual cycle of the black-capped chickadee. Part 3. *Auk* 59:499–531
- Perrins CM, Geer TA (1980) The effect of sparrowhawks on tit populations. *Ardea* 68:133–142
- Swets JA (1964) Signal detection and recognition by human observers. Wiley, New York
- Trainer JE (1946) The auditory acuity of certain birds. PhD Dissertation, Cornell University, Ithaca
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57