DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

132

MOBBING BEHAVIOUR IN BIRDS: COSTS AND RECIPROCITY BASED COOPERATION

TATJANA KRAMA

Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Biology and Geography, University of Tartu, Estonia

Toetab Euroopa Liit

RAK
Eesti Riiklik Arengukava

CONTENTS

LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals. Original papers are reproduced with permission from the publishers.

I. Krama, T. & Krams, I. 2005. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16: 37–40.

II. Krama, T., Krams, I. & Igaune, K. Effects of cover on loud trill-call and soft seet-call use in the crested tit *Parus cristatus* (submitted manuscript).

III. Krams, I., Krama, T., Igaune, K. & Mänd, R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology*. DOI: 10.1093/beheco/arm079.

IV. Krams, I., Krama, T. & Igaune, K. 2006. Mobbing behaviour: reciprocity-based co-operation in breeding pied flycatchers *Ficedula hypoleuca*. *Ibis* 148: 50–54.

V. Krams, I., Krama T., Igaune, K. & Mänd, R. 2007. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*. DOI: 10.1007/s00265–007–0484–1.

VI. Krams, I. & Krama, T. 2002. Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *The Proceedings of the Royal Society of London, Series B* 269: 2345–2350.

VII. Krams, I., Krama, T. & Igaune, K. 2006. Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology* 37: 131–136.

The author's contribution to the papers:

The order of the authors' names reflects their involvement in the paper. In papers **I** and **II**, I participated in planning experiments and in data collection, performed all analyses and I was responsible for writing manuscripts. In papers **III, IV, V, VI** and **VII**, I was involved in planning experiments, data collection (since 1998 in the case of paper **VII**), analysis and participated in finishing the manuscripts.

1. INTRODUCTION

1.1. Antipredator decision-making, alarm calls and mobbing

Predation leads inevitably to the removal of prey individuals from ecological systems, which can have major impacts on prey population dynamics and on entire ecosystems. However, the obvious and dramatic lethal aspects of predation can obscure the nonlethal effects of the mere presence of predators in an ecological system (Krause & Ruxton 2002). In the presence of predators, prey may alter their behaviour so that they are more difficult to detect, encounter and capture. First of all, prey individuals can watch the predator from seclusion and thus escape its attention. Or, the prey can give just a few alarm calls warning its offspring and mate. Finally, because of the adaptive flexibility in prey behaviour in response of a changing risk of predation, prey individuals may cooperate to decrease the risk of being attacked. Cooperative behaviour within the group is an essential ingredient that turns an aggregation into society (Wilson 1975). Cooperative defence seems also to have been a principal element in the evolution to complex society. Sometimes the prey individuals move in complex patterns resembling military manoeuvres. This is particularly true of the defensive response called mobbing: the joint assault on a predator too formidable to be handled by a single individual in an attempt to disable it or at least drive it from the vicinity, even though the predator is not engaged in an attack on the group (Wilson 1975). Mobbing predators is a widespread phenomenon confirmed in a wide diversity of vertebrate groups (Dominey 1983), especially in birds, mammals and fish (Altmann 1956, Curio 1978, Pitcher et al. 1986). While mobbing, birds assemble around a stationary or moving predator, change locations frequently, perform stereotyped wing and/or tail movements and emit loud calls (Curio 1978, Curio et al. 1978, Shalter 1978, Dominey 1983, Shedd 1983, Arnold 2000). Hence mobbing behaviour is a combination of intense alarm calling and visual mobbing displays and both alarm calls and mobbing displays should be studied as parts of the same phenomenon. As a rule mobbing assembly builds quickly after the first individual has discovered the predator. Mobbing has a dual nature: the mere presence of a predator suffices to initiate it in the first individual, whereas as later members of the chorus are attracted by the mobbing behaviour of the initiator (Curio 1978).

1.2. The functions of alarm calls and mobbing behaviour

The main function of alarm calls is to alarm a mate, a groupmate or an offspring to any form of danger, while mobbing has more functional explanations. There is a little doubt that mobbing has a real survival value, but: 1. it is potentially dangerous for the mobber (e.g. Sherman 1977, Smith 1969); 2. like many other

anti-predator behaviours, it is time-consuming (Collias & Collias 1978); and 3. as already mentioned, it is extremely widespread, cutting right across many vertebrate taxa (e.g. Altmann 1956, Eibl-Eibesfeldt 1962, Curio 1963, Kruuk 1972). However, when considering the function of mobbing predators, no other type of behaviour has so many overlapping functional explanations at that of mobbing by birds (Curio 1978). Some proposed explanations are: 1. Silencing Offspring: mobbing calls have been observed to calm down vocalizations of nestlings and fledglings such that predators hunting by ear cannot find them (Perrins 1965, Curio 1975); 2. "Selfish Herd Effect": by assembling in a group, mobbers protect themselves simply by virtue of selfishly dividing the risk as a sheer function of numbers (Hamilton 1971, Owens & Goss-Custard 1976); 3. Confusion Effect: members of a mobbing party all behave similarly, i.e. they move unpredictably around the predator and most of them vocalize thus possibly confusing the predator (Hoogland & Shermann 1976, Owens & Goss-Custard 1976); 4. the "Move On" hypothesis: a predator should leave an area sooner the more intensely and/or longer it is molested (Curio 1963, Flasskamp 1994); 5. "Perception Advertisement": a number of fleet and elusive prey animals seem to indicate to a predator that they have seen it by their calling and/or conspicuous visual signals (Smythe 1970); 6. "Alerting Others": mobbing behaviour may well sensitise escape in signal receivers and thereby help them (Marler & Hamilton 1966, Frankenberg 1981); 7. "Attract the Mightier Predator": this hypothesis predicts that more powerful predators should be lured more often by a mobbing chorus (Nicolai 1973, Curio 1978); 8. "The Cultural Transmission Hypothesis": an individual learns to fear an object it witnesses other birds mob and thus avoids it later on and/or mobs it itself; another version of this hypothesis assumes that, by mobbing a quasi-stationary predator, a bird learns to avoid that place later on (Marler 1956, Marler & Hamilton 1966, Curio 1975, 1988); 9. "Aiding a Distressed Relative Hypothesis": distress callers are envisaged as the beneficiary of mobbing that may startle the predator to release its victim (Curio 1978) and the risk of mobbing could be compensated for if the mobbers are relatives of the seized victim.

1.3. The origin of alarm calls and mobbing behaviour

Any hypothesis designed to account for the survival value of mobbing behaviour, including alarm calling, needs to explain the benefits and costs both for the initiator of this conspicuous and risky behaviour and for a receiver of the call and the individuals joining the mobbing. However, none of the nine hypotheses provide a reasonable explanation for the benefits, costs and a trade-off between them. Therefore, the origin and evolution of mobbing behaviour is poorly understood.

Although it seems obvious in the case of mobbing that birds are assisting each other to drive a predator away, consideration of reciprocal altruism is usually excluded as a possible selective force. In the case of alarm calling, why should the focal individual warn others if it has already perceived the danger itself? Mobbing and giving the alarm calls puts the individual in jeopardy and, if it benefits others, it is altruistic per definition (Hoogland & Sherman 1976, Denson 1979, Curio & Regelmann 1985, Hauser et al. 2003). However, an altruistic act helping non-relatives only pays the altruist if it is directed at a particular individual that on later occasion reciprocates (Hamilton 1964, 1971, Clutton-Brock & Parker 1995). The current view is that mobbing bird aggregations are members of anonymous communities most of time (Wilson1975, Curio1978, Bradbury & Vehrencamp 1998). If the altruist would help the anonymous community, it could not prevent cheaters from exploiting its altruism. This contributed to a common view that acoustic signals such as alarm calls or mobbing behaviour cannot arise through reciprocal altruism among non-relatives since they are essentially undirected and can thus not be protected against cheating (Trivers 1971).

In multi-species communities of birds the beneficiaries are usually not kin of the first individual to mob. In this situation they could be exchanging altruistic favours in such a way that each does better from cooperating than it would from failing to cooperate. However, the Prisoner's Dilemma, a core theory of reciprocal altruism, shows that the rational pursuit of individual self-interest drives everyone away from cooperation, *i.e.* into an outcome that nobody prefers (Trivers 1971, 1985, Dawkins 1976, Axelrod & Hamilton 1981, Axelrod 1984). However, when the participants "play the game" repeatedly and each knows that the two of them are likely to meet an indefinite number of times, cooperation can evolve. The strategy Tit-for-Tat is based on the following idea: cooperate on the first move and afterwards copy what the other player did on the previous move (Axelrod 1984). Tit-for-Tat is never the first to defect; it retaliates against defection by defecting on the next move but subsequently lets bygones be bygones. It turns out that this highly cooperative strategy can evolve, even when initially pitted against exploitative, readily-defecting strategies. And Tit-for-Tat-like strategy can be stable against invasion by them (Axelrod 1984, Milinski 1987, Cronin 1991).

In many cases breeding birds know each other since in the previous non-breeding season they spent winter as members of small, coherent and often territorial flocks (Ekman 1989). Heterospecific individuals in migratory communities may also develop closer social ties during the course of breeding season to achieve a better protection of their nests. In both cases birds definitely reproduce as members of non-anonymous local communities. This makes reciprocity-based cooperation possible among mobbing individuals. An additional difficulty is that under natural conditions mobbing often occurs in heterospecific company (Wilson 1975, Hurd 1996, Desrochers et al. 2002). This

implies a possibility of reciprocity among individuals belonging to different species (Slagsvold 1980, Forsman et al. 1998a, b). Moreover, passerine birds can discriminate between conspecific and heterospecific individuals (e.g. Marler 1957, Sorjonen 1986, Hurd 1996) wich allows individual recognition of conspecific and heterospecific community members. However, reciprocal altruism between hetrospecific individuals has not been documented so far.

1.4. The aims of the study

While mobbing their natural enemies, birds emit loud calls usually having a broad frequency spectrum and transients. Since mobbing calls can eventually attract other prey, they probably can also attract other predators, especially acoustically oriented predators (Ryan et al. 1982, Krams 2001a, Haskell 2002). During the breeding season it is potentially dangerous for the mobber's brood. If repeated conspicuous mobbing calls may carry a significant cost for birds during breeding season, this should prevent the exaggeration of these signals and ensure mobbing honesty. The first aim of this study was to find out any brood costs associated with mobbing behaviour of adult birds (**I**). An experiment was carried out to examine whether mobbing calls of pied flycatchers *Ficedula hypoleuca* could lure predators such as the marten *Martes martes* to the nestboxes. Prey individuals warn other prey and mob their natural enemies also outside the breeding season. The long-range calls used as alarm calls are loud and frequency-modulated sounds which are designed to increase rather than decrease attenuation. Since the predation cost is mostly associated with the use of long-range contact calls, it was investigated whether wintering birds adjust the use of long- and short-range calls to the changes in habitat safety. An experiment was carried out to find out any relationship between utterance by the crested tit *Parus cristatus* of loud trilled calls which also can be used during predator mobbing and the presence of protective cover (**II**).

The real value of mobbing as a type of adaptive behaviour could be dependent on its duration. However, the costs of mobbing may also increase with time. The next aim of the study was to investigate whether the short- and long-lasting vocalizations of the mobbing bird cause different rates of nest predation (**III**). It was predicted that long call nests could be depredated by acoustically oriented predators more often than short call nests, which may suggest some trade-offs between benefits of long duration mobbing and costs in terms of attracting other predators from the vicinity.

The breeding season of most migratory birds seems to be too short for them to establish a real cooperation with their territorial neighbours while defending nests against attacking predators (Curio 1978). However, the birds living in breeding communities are not anonymous and their social behaviour such as collective mobbing is evidently based on temporal stability of the breeding

communities (Naguib *et al.* 1999, Krams & Krama 2002) and the positive relationships with conspecific and heterospecific neighbours (Mönkkönen *et al.* 1997, Forsman *et al.* 1998*a,b*). The third aim of this study was to test experimentally whether neighbouring passerine birds can engage in cooperative reciprocity-based relationships with their conspecifics by playing a Tit-for-Tat-like game where the players copy each of their opponents' moves (**IV, V**).

Since mobbing can be often observed as a community level event with more than one prey species involved (Arnold & Zuberbühler 2006), it may be admitted that prey individuals belonging to different species may be involved in the reciprocity-based cooperation when defending their offspring. The fourth aim of this study was to test whether the mobbing behaviour of the chaffinch *Fringilla coelebs* may be explained in terms of interspecific reciprocity (**VI**). It was expected that chaffinches would not initiate the harassment of a predator when a member of an anonymous community, such as at the moment of formation of communities composed only of migratory passerines. Then, in the contrary case, chaffinches were expected to initiate a mob when a member of non-anonymous communities with a stable composition, such as those composed by sedentary birds or communities composed of migratory birds towards to the middle of breeding season.

The studies carried out on bird nestbox defence allow testing of the basis of antipredator decisions outside the breeding season. Since alarm calling could attract acoustically oriented predators, the cost of predator attraction must be outweighed by factors beneficial to the caller. The fifth aim of this study was to find out whether alarm calls of wintering birds can be explained in terms of mate warning, reciprocal altruism rather than notifying the predator of detection (**VII**). A long-term experiment was carried out on the social context of alarm calling by wintering great tits *Parus major*.

2. MATERIAL AND METHODS

2.1. Study species

The pied flycatcher is a small (10–15 g) insectivorous songbird (Lundberg & Alatalo 1992). It is a summer visitor to northern Europe and winters in western Africa. This species can be attracted to any type of forest by providing nest-boxes. Because of their propensity to use nestboxes and a semi-colonial breeding behaviour, they are an ideal bird species for experimental studies of cooperation (**I, III, IV, V**). In winter quarters, the pied flycatcher is apparently solitary and not uncommonly sedentary (Smith 1966). In immediate post-breeding dispersal, this species is fairly gregarious with cospecifics and with parids (Haartman & Löhrl 1950).

The crested tit is a small (10–13 g) year-round resident of coniferous forests of Europe which spends the non-breeding season in dominance structured flocks (Ekman et al. 1981, Krams 1996, 2001, Krams et al. 2001). During the non-breeding season they are easily attracted to feeders. However, crested tits do not rely on feeders for winter survival (**II**).

The chaffinch is a small (18–28 g) migratory passerine bird, which occasionally winters in northern Europe. This bird tends to be social in all seasons. This is one of the commonest birds in Europe, and breeds in all types of woodland and in parks and gardens. Mobbing reactions of the chaffinch are widely studied (Hinde 1954, Marler 1956, Korbut 1989) (**VI**).

The great tit (18–20 g) is the most widely distributed member of the *Parus* genus, ranging throughout the Palearctic to Singapore and from Marocco to northern Norway. It is one of the few non-hoarding species in the genus and during the winter months great tits show a loose social organization. In northern Europe they are closely associated with man from whom they obtain winter food, and this probably allows the species to persist in areas otherwise unsuitable (Jansson et al. 1981, Orell 1989). The great tit is one of the most intensively studied species of birds (**VII**).

2.2. Study area

The data were collected near the town of Krāslava, in south-eastern Latvia (55° 53′N, 27°11′E). The study area covers about 25 km^2. More than 80% of the total area is covered by a mosaic of forests, bogs, rivers and lakes. The forests are dominated by common spruce *Picea abies* and Scots pine *Pinus sylvestris*. Forest clear-cuts, pine plantations and the secondary succession of abandoned fields further increase the mosaic pattern of the landscape. During the breeding season for birds, the ambient temperature ranges from 6°C to 32°C. In winter snow cover lasts typically from November to March-April. Day length is 6.7 h

at winter solstice. The winter climate during the study years was cold with average daytime temperatures around –7°C with regular cold spells ranging from –34°C to –12°C.

2.3. Capturing, marking and processing of birds

Crested tits were trapped by mist nets near feeders during autumn (**II**) while chaffinches were mist-netted in the beginning of spring (**VI**). Great tits were trapped by baited traps in autumn and winter (**VII**). All crested tits, chaffinches and great tits were individually colour-ringed (**II, VI, VII**).

Adult individuals of the pied flycatcher were marked with light colours of water resistant ink several days before experimental trials (**IV, V**). The birds marked themselves by touching a piece of ink saturated foam-rubber while entering/leaving the entrance of their nestboxes. A portion of the pied flycatchers was captured in nestboxes. A strip of transparent plastic was attached to the entrance inside of the nestbox, so that the birds could enter the nestbox but could not leave it.

2.4. Determining costs of mobbing in the breeding season

In this experimental study I examined the risks associated with mobbing calling (**I**). To test this possibility we compared the frequency of nest predation in nestboxes with playbacks of pied flycatcher mobbing calls to other nestboxes for which blank tapes were used as controls.

Wooden board nestboxes were used in all the experimental trials. The nestboxes were arranged in pairs. Before the beginning of the playbacks we put a *Coturnix coturnix* quail egg into each of the nestboxes. Predation was considered to have occurred if the top of a nestbox was opened and the egg was missing or broken. In the study area pine martens easily enter nestboxes by removing the top. Within each of 56 areas, from the top of one of the nestboxes of a pair we played back mobbing sounds of pied flycatchers while no calls (blank tapes) were played back from the top of the other nestbox. According to the design of this experiment, playbacks of both mobbing calls and blank tapes were carried out simultaneously in each area. The duration of the playbacks was 20 min in each area. The trials with mobbing calls were carried out 1–2 hours before sunset. The nestboxes were checked the next morning some hours after sunrise.

2.5. The risk of predation and
the use of long-range calls in winter

The general method for this study was direct observation of individuals in social groups under natural conditions while they visited either safe or risky feeders (**II**). Two feeding sites that differed with respect to predicted safety were arranged. The sites were at sharp edges between an open and a closed habitat. The "safe" site was placed within a canopy of trees closest to the forest edge since parids prefer places offering cover (Koivula et al. 1994). The "exposed" site was placed near the edge but out in the open. For all flocks the open habitat sites were in small clear-cuts (400–900 m^2 in size) within a mature coniferous forest. The feeders were attached to poles of 1.2–1.4 m height. The birds had been trained to come and take food when hearing a specific call. Therefore the sites could be arranged at almost any point around the edge of a clear-cut without using permanent feeders. The order of arranging feeders first in a safe or in a risky site was selected by tossing a coin. As soon as observations at one site were done, the observers moved the feeder to another site within the same flock territory. As soon as observations were finished, the temporary feeders were removed. Focal-bird sampling (Altmann 1974) was used in sessions lasting 15 min when recording the utterance of long-range trills and 5 min when recording the utterance of the high-pitched calls given by the focal individual. The order of counting the two call types was selected by tossing a coin. Signalling by dominant males only was observed because use of long-range calls in the crested tit can be biased among individuals of different social ranks (Krams 2000). Crested tits often use trilled calls to mob predators.

2.6. Determining a relationship between duration
of calling and predator attraction

To examine the risks associated with mob calling, the frequency of nest predation in nest-boxes with playbacks of long-lasting mobbing calls was compared to those in nestboxes with short-lasting mobbing calls (**III**). The study was done at 78 areas, which were on average 3.0 km apart from each other (range 0.5 – 38 km). The duration of long-lasting playbacks was 15 min and the duration of the short-lasting playbacks was 2 min. Duration of mobbing up to 10–15 min can be often observed in the pied flycatcher during the breeding season.

   At each study site the nestboxes were arranged in pairs and they were placed 70–85 m apart. Supposedly pine martens use a nestbox as a search image while hunting for nestlings and adult birds. To avoid the possible attraction of the predators, we placed empty nestboxes at each experimental area some days before the trials. Just before the beginning of the playbacks we put pieces of

recently abandoned nests of pied flycatchers and a quail egg into each of the nestboxes. This was done to equalize the olfactory attractiveness of the experimental nestboxes. We considered predation to have occurred if the top of nestbox was opened and the egg was missing or broken. The study was carried out in young (25–50 years old) dry pine plantations with a sparse understorey. The nestboxes were placed in pine plantations about 25–35 m away from 85–150 year old mixed forests. Martens usually live in older forests and rarely come into less productive pine plantations. The results of a census indicated that the study area was inhabited by at least 40 adult martens. Within each of the study areas, from the top of one of the paired nestboxes we played back long-lasting mobbing sounds of pied flycatchers while the short-lasting mobbing sounds were played back from the top of the other nestbox. The nestboxes for the long-lasting playbacks were selected by tossing a coin. According to the design of this experiment, playbacks of both long- and short-lasting mobbing calls were carried out simultaneously. The trials with mobbing calls were carried out 1–2 hours before the sunset in calm, warm and dry weather. We usually did playbacks at 3–4 areas during one evening. The nestboxes were checked the next morning 2–4 hours after sunrise. Within 18 areas out of 78 areas, the experimental trials were repeated one more time when no nestboxes were depredated during the first trial. In this case we relocated the nestboxes about 500–800 m away and repeated the experimental procedure after 6–10 days. The experimental design suggests that each trial was carried out at the territory of a different predator.

2.7. Reciprocity in breeding pied flycatchers: two nestbox system

During the nestling phase we presented a predator at nestboxes occupied by pied flycatchers (**IV**). A stuffed tawny owl *Strix aluco* served as predator stimulus in all trials (Bautista & Lane 2000). The nestboxes were arranged in pairs and they were placed within 34–47 m distance apart. The distance between neighbouring pairs of nestboxes was at least 350 m. Seventeen pairs of nestboxes were assigned to the experimental group and another 17 pairs served as control group.

Just before the owl was presented at one of the experimental nestboxes, we captured both parents breeding in the second nestbox of the pair. These birds were kept in captivity for 15 min while the owl was presented at the first nestbox. Since the captured birds were not allowed to assist their neighbours, they automatically behaved like deceivers in the eyes of their neighbours. Since captured birds were out of their neighbours' sight, the defecting was not obvious to the neighbours. To ensure that defecting was recognized, we played back the alarm calls of the captured nest owners. One hour later we presented

the owl for another 15 min at the nest of the 'deceivers' to see the response of those birds which had not received assistance. In the control group consisting of 17 pairs of nestboxes, no birds were captured in their nests and they could freely choose whether cooperate or not.

We divided the mobbing response of pied flycatchers, according to their displays and voice, into four categories: (i) no response to the dummy predator (0 points) when birds investigated the predator from a distance usually without any alarm calls while continuing activities such as foraging or singing; (ii) weak response (1 point) when there was frequent approaching and retreating to/from the predator; (iii) average response (2 points) characterized by the birds tending to be close to the predator, and they restlessly moved around it by bowing, pivoting, tail-flicking or hovering in the air in front of it; and (iv) strong response (3 points) with intense movements and display which included frequent dive-attacks to the predator. During weak, average and strong responses pied flycatchers used "pik" calls (Bergmann & Helb 1982).

We observed and evaluated the behaviour of pied flycatchers from a blind or hide. The owl was installed when no pied flycatchers were nearby. The predator was positioned 1.0–1.5 m from the nestbox. After a 15-min period of presenting the stuffed owl, this dummy was moved in the hide. At the time when the experiments were performed pied flycatchers were feeding nestlings which were at least 5 days old. The maximum difference in age of nestlings in two neighbouring nestboxes was five days.

2.8. Reciprocity in the breeding pied flycatchers:
three nestbox system

In this study the nestboxes for pied flycatchers were arranged in triplets and the three nestboxes in each of the triplets (n = 32) were placed in triangles within 48–54 m apart (**V**). The distance between neighbouring triplet sets of nestboxes was at least 470 m. By tossing a coin for each triplet, one breeding pair was randomly assigned to be the experimental pair, one breeding pair was chosen to be deceivers and one breeding pair was chosen to be cooperators. The pair that would become "deceivers" was trapped just before the owl was presented at the experimental nest-box. The deciever birds were kept in captivity for 15 min while the life-like stuffed tawny owl was presented at the experimental nestbox. Since the captured birds were not allowed to assist their neighbours, they behaved like deceivers in the eyes of their neighbours. As soon as the harassment of the predator was over, we released the deceivers. The birds breeding in the third or "cooperator" nestbox of each triplet were free to join in mobbing initiated by the first pair of birds. In every case these flycatchers joined the first pair and they were therefore cooperators in the eyes of the experimental pair. One hour after the first experiment, we carried out a second 15 min experiment

in which we presented simultaneously one owl at the nestbox of the deceivers, and a second owl at the nestbox of the cooperators. Again we recorded the birds' responses. During the second experiment no birds were caught and all three pairs were free. We scored the degree of mobbing response of these pied flycatchers in the same way as in the two nestbox experiment.

In order to test if the strength of mobbing response of "deceiver" individuals was affected by having been captured and conditions of captivity, we performed a control experiment in additional locations using 16 more nestbox triplets. In this case, we performed the first trial in the same way as it was done in the previous experiment. During the second trial we demonstrated just one owl at the nestbox of only the "deceivers" in order to see the response of the cooperators and experimental birds. We predicted that neither cooperators nor experimental flycatchers would attend mobbing initiated by "deceivers" if their mobbing behaviour had somehow affected by the fact of their capture 1 hr previously.

2.9. Stability of heterospecific community and probability of mobbing

To find out the effect of community stability at each of 24 study areas we carried out two experimental trials, which were done on separate sites (**VI**). At one site in each area we presented a predator to a community composed by a pair of chaffinches and some pairs of sedentary passerine birds. At the other site within the same area we presented the same predator to a pair of chaffinches and some pairs of other migratory birds. All the above sedentary and migratory bird species are known as mobbers (Snow & Perrins 1997). We selected the sites so that a only small fraction of migratory birds (no more than one pair) was present in communities composed of sedentary birds, and so that sedentary birds never occurred at the sites of migratory birds.

To avoid the dilution effect we selected communities so that the number of passerine birds was nearly the same, within the ranges of 8–12 individuals including the resident chaffinches. So each study site was inhabited by a pair of chaffinches and some pairs of passerines, either migratory or sedentary. Therefore, each test, even made in the same area, can be treated as an independent data point.

We used a stuffed tawny owl which we mounted near the chaffinch nest and kept under cover. It was uncovered and presented so that a male chaffinch was the first individual to find it. The response of each chaffinch was observed and evaluated within 5 min after the predator was detected. We also investigated whether the mobbing calls of chaffinches could lure other neighbouring passerine birds. In order to test the ability of birds to cooperate in mobbing, we repeated the experimental trials a week later at each site. We divided the

mobbing response of male chaffinches according to their displays and voice into four categories: no response, weak response, average response and strong response.

2.10. Identifying the reasons to give the alarm in winter

The alarm calling of wintering dominant male great tits was studied within and outside their home ranges (**VII**). The great tits permanently live in the forest. During cold spells great tits from the forest temporarily moved to the town 5 km away, where we also made observations at a single location. To induce alarm calls, adult males were caught manually in a baited trap covered by light-coloured fabric. After alarming, the captured birds either stopped feeding for 15–20 min or, in the town, immediately left the feeder area. We took care that surrounding individuals were not able to see the capture and hence did not give alarm calls that might have influenced the behaviour of the captured bird. Each adult male was kept in the trap for 3–4 s and then released by opening the trap from a distance. Capturing and releasing was done from a hide and therefore birds were not aware of the presence of the observers. We observed the beha-viour of each male for at least 1 min from the moment of release. We recorded whether it gave any alarm calls and also the duration of calling since this can increase the risk of predation (Krams 2001a).

We tested dominant male alarm calling in five different situations. To test the pursuit-deterrent hypothesis, male great tits were alarmed within home ranges when they were attending the feeders alone. This was done at dawn when dominant great tits often are the earliest visitors at feeders (de Laet 1985, Krams 2000). Other flock members usually appeared 10–20 min later than these adult males. Since nestboxes around the feeder were occupied by resting tree sparrows *Passer montanus*, great tits usually spent the night in the forest, outside hearing distance of the male at dawn. In order to test the reciprocal altruism hypothesis we alarmed males within their home ranges in the presence of their juvenile flock-mates when their females were absent. Males were also alarmed at the town feeders during their short visits there while travelling alone. These birds were surrounded by unfamiliar great tits. In order to test the warning of mate hypothesis, males were alarmed within their home ranges in the presence of their mates when no other great tits were present. Some males visited the town together with their females and we alarmed them in the presence of their mates and other unfamiliar great tits. We included in the analysis only those males which were observed in all the first four experimental situations at the two study areas and in winter were paired with the same female as in the previous breeding season. Each winter only 1–3 males met these requirements. In total, the data set comprised observations on 24 adult males. Fourteen out of 24 males were also tested in the fifth experimental situation

when they arrived at the town together with their females. Methodology was the same in all study years (1989–2003).

2.11. Preparation of experimental tapes for playback trials

To make the experimental tapes and to avoid pseudo-replication, we recorded mobbing calls of several pairs of pied flycatchers (**I, III**). While mobbing predators, pied flycatchers use "pik" calls (Bergmann & Helb 1982, Krama & Krams 2005). The calls were recorded with a Sony W6DC cassette recorder connected to a parabolic microphone. A sonogram of calls was produced using Avisoft-SASLab Light software (Raimund Specht, Berlin). Experimental tapes consisted of continuous calling without pauses of silence in order to simulate the natural situation. Each 20 s calling period consisted of records taken from one pair of birds and the next calling period contained the records taken from another pair of birds. The order of the birds on the tape was random and the calls played back were never repeated (McGregor et al. 1992). Playback amplitude was standardized to natural sound level (**I, III**).

3. RESULTS

3.1. Cost of mobbing in breeding pied flycatchers (I, III)

Both studies (**I, III**) clearly showed that artificial nests with playbacks of pied flycatcher mobbing calls attracted pine martens. Nestboxes with mobbing calls were depredated significantly more than nestboxes with blank tapes. In 13 cases predators depredated nestboxes having playbacks of mobbing calls while nestboxs with blank tapes were attacked only once (**I**).

3.2. Adjustment of use of risky calls to the habitat safety (II)

Calling rates of the long-range calls, often used also as mobbing calls, were highest when male crested tits foraged at the safe site. The long-range trills were given significantly less often while visiting risky feeders placed just a few meters away from the safe sites. This study revealed that long-range communication in crested tits is strongly affected by the perceived level of predation risk.

3.3. Association between mobbing duration and mobbing costs (III)

It was found that artificial nests with playbacks of long-lasting mobbing calls of pied flycatchers were depredated significantly more by martens than the nests with short-lasting calls (**III**). Out of 23 depredated nests only one was associated with short-lasting mobbing.

3.4. Reciprocity-based interactions among breeding pied flycatchers (IV, V)

In paper **IV**, for the control group it was found that all neighbouring pairs of pied flycatchers responded during the first trial to mob the owl placed at the nests of their neighbours. One hour later, when the owl appeared at these cooperators' nestbox, all of the previously supported pairs of pied flycatchers reciprocated and attended mobs initiated by the cooperators. During the first trial with the experimental group, assistance by "deceiver" neighbours was prevented. Then, during the second trial, only four "deceiver" pied flycatchers were assisted by their neighbours whom they had not helped 1 hr earlier. The

behaviour of birds given a chance to assist their neighbours in control and experimental groups differed significantly during the second trial.

In paper **V**, it was found that when given a choice, pied flycatchers assisted in mobbing initiated by cooperating neighbours and did not join in mobbing when initiated by the neighbours which had defected from necessary assistance one hour before. The control supported this result.

3.5. Initiation of harassment by chaffinches and community stability (VI)

Community stability clearly affected antipredator behaviour of migratory chaffinches (**VI**). In the stable company of sedentary birds, chaffinches actively initiated harassment of the predator in the beginning of the breeding season. In contrast, chaffinches showed either no response or their response to the owl was weak in unstable communities composed by migratory passerines only. During trials repeated later, the chaffinches surrounded by sedentary birds remained as active mobbers as they were a week before. Chaffinches in the community of migratory birds significantly increased the intensity of alarm giving as their communities become more stable. The intensity of alarm did not differ between the two types of communities towards mid season. The number of community members joining the mobbing chaffinches was not dependent on the season. In all cases the mobbing chaffinches were joined by more than half of the local passerines.

3.6. Alarm call giving outside the breeding season (VII)

Within their home ranges all male great tits gave alarm calls when accompanied by mates, while only four individuals within home ranges gave alarm calls when alone. Outside home ranges all dominants (n=14) gave alarm calls when accompanied by mates while only a few of them gave the calls when surrounded only by unfamiliar conspecific individuals. The callers often gave more than one call both when accompanied by their females and other flock-mates. The males spent significantly less time calling outside home ranges when they were surrounded by unfamiliar great tits than when they were accompanied by their females. Within their home ranges all the male great tits gave alarm calls when accompanied by flock members other than mates. The number of individuals giving calls when within home range while surrounded by flock members other than mates was significantly different than when outside home range surrounded by unfamiliar conspecifics. The number of calling individuals when surrounded by permanent flock members other than mates was significantly greater than the number of male great tits calling when alone within home ranges.

4. DISCUSSION

4.1.1. Eavesdropping of long-range calls by predators

Undoubtedly, mobbing in birds may be considered as one of the best examples of adaptive behaviour. Cooperating individuals have a greater opportunity to drive the predator from the neighbourhood than those that are not cooperating (Lorenz 1931, Hoogland & Sherman 1976, Bildstein 1982, Buitron 1983, Pettifor 1990, Flasskamp 1994, Pavey & Smyth 1998, Zuberbühler et al. 1999). Cooperation by means of mobbing should be of special value for species with a high rate of nest predation such as small passerine birds (Hansky & Laurila 1993). However this study revealed a new type of mobbing cost (**I**). Mobbing individuals giving long-duration easily locatable calls can increase the risk of nest predation (Mougeot & Bretagnolle 2000, Krams 2001a, Haskell 2002). This was supported by significantly higher levels of depredated artificial nests when mobbing calls were played back nearby. Alarm calling is an effective way to notify the predator that it is noticed by the prey (Klump & Shalter, 1984, Klump et al. 1986, Hailman, 1989, Ficken 1990, Kroodsma & Miller 1996, Krause & Ruxton 2002). Since predators rely on surprise, the predator should move to another area to become successful. Still alarm calling is a straightway form to inform other prey individuals including mates and offspring about the approaching enemy. Therefore prey individuals may benefit of using alarm calls. However, these calls belong to the so called type of long-range calls, which can be easily eavesdropped by acoustically oriented predators (Smith 1977). This is supported also by the results of our experiment with foraging crested tits in winter (**II**), revealing that the long-range part of contact communication in crested tits is strongly affected by the level of perceived predation risk. In accordance with the data on the hearing ability of predators, dominant males of crested tits decreased their exposure to predation in risky habitats by giving loud calls less often and choosing less a risky type of communication with high-pitched sounds (**II**). These findings indirectly indicate that mobbing under natural condition is a trade-off between the costs and benefits.

4.1.2. Trade-off between benefits and costs of alarm calling in mobbing predators

The results of this field experiment also show that mobbing behaviour incurs more costs than traditionally thought (**III**). They support the previous results (**I**) (Krama & Krams 2005) showing a substantial increase of predation to artificial nests in the case for long-duration calling at nestboxes. It could mean that a mobbing individual should reach two goals simultaneously: to move the

predator away and do it so that the mobbing activities would not attract another predator from the vicinity. However, we found that longer-duration mobbing helps predators to locate the nests significantly better. This indicates that there is a real trade-off in mobbing predators between benefits of getting predators out of the territory and the costs of attracting other predators to the vicinity. The results of this study show that long-lasting conspicuous mobbing calls carry a significant cost for the breeding birds. The costs associated with mobbing behaviour can prevent the exaggeration of these signals and ensure mobbing honesty. Because mobbing incurs cost, this fact may improve our understanding of the origin and evolution of this type of antipredator behaviour (Zahavi & Zahavi 1997).

In the case of short-lasting mobbing, predators could perceive these calls as detection-notification signals (**III**) (Bradbury & Vehrencamp 1998). Predators that stalk their prey rely heavily on surprise (Caro 1995). If prey detect a stalking predator and signal this fact to it through short-duration mobbing, the predator may give up its current hunt since it is now likely to be unccuccessful. Besides the indication to a stalking predator that it has been spotted, prey individuals giving just a few calls have an opportunity to alarm their mates, offspring and neighbours and they can recruit the neighbouring prey individuals into the mobbing aggregation (Curio 1978). In this way mobbing goals can be achieved without attracting the attention of another predator.

4.2. Reciprocity in behaviour of mobbing neighbours

During the breeding season predator inspection and mobbing behaviour is a part of nest/offspring defence (Taborsky, 1987, Newton 1998, Olendorf et al. 2004). The level of nest defence generally increases with advanced time in the breeding season, as well as with the age of young being defended. Therefore, mobbing is expected to be longer and more intense closer to offspring maturation. One would suggest short and effective harassment of cooperating neighbours as a way to drive the predator away without increasing the nest predation. This goal can be reached by means of joint efforts of mobbing by conspecific and/or heterospecific prey individuals breeding in the same area.

The first experimental work on possible cooperative mobbing in pied flycatchers (**IV**) shows a clear result: pied flycatchers attended mobs initiated by their cooperating neighbours while non-cooperators (defectors) were not assisted in the tests an hour later. Bird behaviour during the primary experiment and the secondary experiment of the second experimental work supported these results (**V**). However, males of many monogamous species of birds do not only guard their own female and help her to raise a brood but also attempt to obtain sneaky copulations with other females, especially those of neighbouring males (Birkhead & Møller 1992). If some chicks in neighbouring nests are sired by

these extra-pair matings, males may have a genetic interest in protecting neighbouring nests. As there was no information about occurrence of extra-pair matings, one cannot exclude a possibility that the payoffs associated with the mobbing were influenced by kinship. However, none of the males joined in mobbing of neighbours without their mates as would be expected if this were the case. If this is not an extra-pair paternity, what factors then are responsible for the striking differences in behaviour of control and experimental pied flycatchers? The observed behaviour resembles the first move in the tit-for-tat strategy where only cooperating individuals are supposed to be supported accordingly by their partners on the next move. Mobbing by pied flycatchers has some essential features of a prisoner's dilemma problem with a scale of pay-offs: T (temptation to defect), R (reward for mutual cooperation), P (punishment for mutual defection), and S (sucker's payoff). T is the best and S is the worst outcome. Mobbing harassment has been shown to entail a risk of injury or even death to the prey individual engaged in mobbing owing to their proximity to the predator (Curio & Regelmann 1985, 1986, Denson 1979, Hoogland & Sherman 1976, Sordahl 1990). Therefore the *temptation to defect* may pay better than cooperation. Although it is risky to harass a predator, the prey animals may profit from a joint defence against predators since mobbing decreases the risk of being attacked (Pavey & Smyth 1998). Also, the strength of a mobbing response increases with group size and more mobbers increase the chances of successfully driving away a predator (Becker 1984, Robinson 1985, Verbeek 1985). As a predator vacates its immediate foraging area, it gives an opportunity for prey individuals to continue their interrupted daily activities (Pettifor 1990), and this benefit can be shared by individuals within a given area. Hence, the increased inclusive fitness of breeding neighbours is the *reward for mutual cooperation*. If no neighbours squeal and mobbing is not initiated, then the predator may remain in the vicinity for longer times. In this case no individual increases its risk of predation. However, feeding of offspring is usually not possible while a predator is present, and this is costly. This is the *punishment for mutual defection*. Finally, the initiator of mobbing and its offspring may be under increased risk of predation by attracting the predator's attention, especially if not joined by other neighbouring prey individuals (Krama & Krams 2005). This case could be treated as the *sucker's payoff*. It may seem that this is a three-person game, which in nature appears to be an n-person game. Luce and Raiffa (1957) suggest that multi-player games are much more unstable. However, under our study design the birds were not able to make coalitions and it indicates that the birds were involved in a stable two-person-like game, which is assumed by the Prisoner's Dilemma (Dugatkin et al. 1992, Stephens et al. 2002). A very important condition for reciprocity to evolve is that there must be repeated interactions between the participants (de Waal 2000), so failing to cooperate on one occasion has a penalty in the future through not having the cooperative act reciprocated next time. For this reason,

such behaviours as mobbing are expected to be characteristic of animals that stay together over long periods of time, enough for the roles of donor and recipient to be exchanged many times. A second condition is that cheats can be recognized and penalized. It only seems so that the breeding season of most migratory birds is too short for them to establish a real cooperation with their territorial neighbours (Curio 1978). The birds living in breeding communities are not anonymous and their social behaviour such as collective mobbing is evidently based on temporal stability of the breeding communities (Naguib et al. 1999, Krams & Krama 2002) and the positive relationships with conspecific and heterospecific neighbours (Mönkkönen et al. 1997, Forsman et al. 1998a,b). In the field experiments it appeared that the pied flycatchers could individually identify their neighbours. The nestbox A pied flycatchers assisted in mobbing initiated by their previously cooperating neighbours and did not assist non-cooperators who had defected in tests one hour previously. The observed behaviour may be a part of the Tit-for-Tat strategy where only cooperating individuals are supposed to be supported accordingly by their partners on the next move. In this experimental study cooperating flycatcher families won the reward for mutual cooperation on every encounter (**IV, V**). Non-cooperators were immediately punished. The results show that the origin and evolution of mobbing behaviour of breeding pied flycatchers can be explained in terms of reciprocal altruism.

Many strategies have been proposed to explain reciprocal altruism. Most theoretical models of reciprocal altruism assume that individuals base their behavior on knowledge about a partner's previous behavior, either towards themselves (direct reciprocity) (Axelrod & Hamilton 1981) or towards others (indirect reciprocity) (Nowak & Sigmund 1998, Leimar & Hammerstein 2001, Wedekind & Braithwaite 2002, Dugatkin & Druen 2004, Hamilton & Taborsky 2005, Nowak & Sigmund 2005, Lehmann & Keller 2006). According to direct reciprocity, A helps B because B has helped A before; individuals remember who did what in past interactions with them and base their decision whether to cooperate or defect on this knowledge (Axelrod & Hamilton 1981, de Waal & Berger 2000). According to indirect reciprocity, A helps B because B has helped C before; indirect reciprocity involves reputation, which increases through helping and is assessed to decide whether to help a partner or not (Nowak & Sigmund 1998, Leimar & Hammerstein 2001, Nowak & Sigmund 2005, Pfeiffer et al. 2005, Rutte et al. 2006). Both direct and indirect reciprocity require that animals possess specific cognitive abilities (Stevens & Hauser 2004, Stevens et al. 2005, Bartlett & DeSteno 2006, Nowak & Roch 2007) which may impede the evolution of cooperation through these mechanisms (Stephens et al. 2002.). Strong reciprocity assumes that individuals punish noncooperators altruistically (Fehr & Gächter 2002, Boyd et al. 2003, Brandt et al. 2006). Although some of experimental evidence for strategies predicted by direct reciprocity models remains controversial (Milinski et al. 1990), in this

study cooperation among unrelated individuals may be achieved by reciprocal altruism in which two or more individuals help each other in turn (Trivers 1971, Alexander 1987). The decision to cooperate is based on expected future help, which may be judged from past interactions, and the observed mobbing behaviour in the pied flycatcher resembles the Tit-for-Tat strategy. However, it is not completely clear whether it is a real Tit-for-Tat. Axelrod (1984) identified several properties – in particular, being "nice" (never the first to defect), "provokable" (retaliating against defection) and "forgiving" (letting bygones be bygones and resuming cooperation). Niceness generates the rewards of cooperation; provokability discourages persistent defection; and forgiveness heads off long, reverberating bouts of recrimination and counter-recrimination. I only can suppose that the neighbouring flycatchers were nice to each other during the first encounters since I did not test this property of Tit-for-Tat. The "forgiving" property also should be tested in the further studies. Still, it is important to understand how sexual selection may influence the cooperation within a single pair and between neighbouring pairs of breeding pied flycatchers (Kokko & Mappes 2005, Kokko et al. 2006) since extra-pair copulations, fertilization and offspring are possible (Björklund & Westman 1983, Rätti et al. 1995).

4.3. Mobbing as reciprocal altruism under conditions of heterospecific community

Under natural conditions the duration of mobbing may be placed between the two studied extremes. There is a group size effect in mobbing (Becker 1984, Robinson 1985) and in case of few prey individuals, mobbing may become time-consuming. Supposedly many birds stay in patches not only because they are restricted by availability of suitable microhabitats and food resources but because they are influenced by potential predation risks as well (Mönkkönen et al. 1997, Forsman et al. 1998a,b). In such cases cooperation among neighbouring individuals is of crucial importance for mobbing to be successful (Kruuk 1964, Slagsvold 1980).

Mobbing behaviour is defined as a joint assault on a predator too formidable to be handed by a single individual (Wilson 1975). The risk of mobbing predators decreases with increasing group size due to the affect of dilution (Hamilton 1971). Thus the response of neighbouring birds have a major influence on survival prospects of the initiator. Taking a higher risk would take sense only if the benefit aimed at was to increase accordingly (Alatalo & Helle 1990). If no neighbours join the first individual to mob, there is no dilution effect and the lone harasser takes a deadly risk (Curio & Regelmann 1986). So the initiator has to be confident about the response of its closest neighbours before the harassment. It seems that when surrounded by sedentary heterospecifics

chaffinches were quite confident about their prospects of receiving external help (**VI**). Indeed, in all of the observed cases the initiator chaffinches attracted the majority of their sedentary neighbours (**VI**). The origin and the success of mobbing assembly thus critically depended on the number of attendants and social context. In the non-experimental field study chaffinches breeding in the communities composed of heterospecific migratory individuals behaved in two distinct ways during successive trials (**VI**). At the beginning of the breeding season most male chaffinches gave no alarm calls at all. Although during the spring migration many birds often sing on their stop-over sites, only a few of them remain in these areas as residents. Therefore, the initiator individual should assess whether it can get its neighbours involved into a mobbing party. Mobbing is costly and non-residents may not benefit from driving the predator away. This could explain why resident chaffinches did not rely on their migrant neighbours during the first trials (**VI**). Supposedly they considered their neighbouring heterospecifics as birds of passage. Passerine birds can discriminate between conspecific and heterospecific individuals (e.g. Marler 1957, Sorjonen 1986, Hurd 1996). It suggests that a week later chaffinches had developed the ability to recognize their heterospecific neighbours individually (**VI**). This assumption is supported by the result that chaffinches initiated harassment of the owl during the repeated trials (**VI**). Korbut (1989) has shown that any substantial increase in the mobbing activity of chaffinches usually takes more than a week. Therefore, it is doubtful that the difference in the bird activity between two trials can be explained by other possible factors such as mating status, reproductive value of a mobber, prospects of another breeding episode in the same season, etc.

However, the Prisoner's Dilemma indicates that if it pays each of the two players to defect whatever the other one does, yet if both defect, each does less well than if both had cooperated; what is best for each player individually leads to mutual defection, whereas everyone would have been better off with mutual cooperation (Axelrod 1984). According to the traditional view on breeding bird communities, which is they are anonymous (Wilson 1975, Curio 1978, Bradbury and Vehrencamp 1998), the mobbing behaviour cannot be explained by means of reciprocity (Trivers 1971, Curio 1978). However, we suppose that the birds stay at their breeding grounds for a quit a long time. So participants may play the game repeatedly and two or more neighbours can recognize each other and they know that they are likely to meet an indefinite number of times. It is the right time to recall Axelrod's potent metaphor that the future can cast a long shadow backwards onto the present (Axelrod 1984). Under such conditions cooperation can evolve. I would like to suggest that it is just what accounted for the difference between initially anonymous community of newly arrived migratory birds and communities composed by permanent members of the winter flocks (**VI**). At the beginning of the breeding season most male chaffinches did not cooperate with their migratory neighbours. On contrary, sedentary birds

survived the winter season because of their mutual cooperation. The breeding season is the crucial point either for the fitness lost or for the fitness increase (**I, III**). Therefore we suggest that cooperation by means of mobbing behaviour can be important to increase personal fitness of members of breeding communities.

So far it was suggested that birds, especially migratory passerines, don't spent enough time together and their relationships are not so tight to explain mobbing behaviour in terms of reciprocity (Curio 1978). However, recent studies have revealed that mixed-species foraging flocks exist also during the breeding season (Mönkkönen et al 1996). Our results indicate that birds in such associations can engage in mutual cooperation (**VI**). In non-anonymous community, any altruistic act helping non-relatives thus can be directed at particular individuals (Clutton-Brock & Parker 1995). If this is correct, reciprocal altruism can be used to explain the evolution of alarm calls in general and mobbing calls in particular. The results, thus suggest a link between the benefits of gregariousness and clumped distribution of forest passerines during the breeding season (**VI**) (Mönkkönen et al 1996, 1997, Forsman et al. 1998a,b). Finally, mobbing was observed to occur in heterospecific company. It gives us an opportunity to suggest that cooperation among individuals belonging to different species in driving the predator away may be explained as interspecific reciprocity based on interspecific recognition and temporal stability of the breeding communities (**VI**). This possibility could be admitted since many live in multispecies groups and they may benefit from antipredator behaviour of other species (Slagsvold 1980, Ekman 1989, Forsman et. al. 1998a,b). Heterospecifics in such mixed groups are generally considered to substitute for conspecifics in predator protection at low competition cost (Ekman 1989). Moreover, flocking with heterospecifics may be profitable in the breeding season because there is no risk of being cuckolded while driving the predator away.

4.4. Reasons to initiate alarm calling in wintering birds

In the winter study on male great tits all of the alarmed males gave more low-risk alarm calls when accompanied by their mates both within and outside their home ranges (**VII**). The results support several previous studies showing that animals give alarm calls when related kin or a mate is nearby (Sherman 1980, 1985, Hoogland 1983, Sullivan 1985, Beletsky 1996). This is likely when long-term cooperative efforts favour stable pair bonds (Sherman 1980, 1985, Hogstad 1995). Existing evidence suggests that among parids adult and juvenile individuals may be paired in mid-winter or already before formation of winter flocks (Hogstad 1987, Haftorn 1997). Warning its mate therefore may be a major function of altruistic alarm calling of great tits outside breeding season (Morton & Shalter 1977, Witkin & Ficken 1979, Hogstad 1995, Haftorn 2000).

All the male great tits within home ranges also warned flock mates other than their sexual partners (**VII**). Winter groups of great tits are dominance-structured (Saitou 1979, de Laet 1985, Krams 1998a, 2000). Dominants enjoy more benefits (e.g. Alatalo et al. 1986, 1987, Suhonen et al. 1993, Krams 1998b) and survive better than subordinate flock members (Lambrechts & Dhondt 1986). Aggressive behaviour of adults may make flocking less attractive to subordinate individuals and flocks of wintering parids often split up into subflocks (Hogstad 1988a,b). Detection of an approaching predator may be reduced in smaller groups (Ekman 1987, Ekman & Hake 1988) and this suggests a link between aggressive behaviour of dominant individuals and the risk of being attacked by predators. Warning their subordinate flock mates may be a way in which dominant individuals compensate for their despotic behaviour. Adult males were familiar with their permanent flock mates for weeks and months. An altruistic act helping a non-relative only pays the altruist if it is directed at a particular individual that on a later occasion reciprocates (Trivers 1971, Alatalo & Helle 1990). If the altruist would help an anonymous community, as it may be considered to be with the town resident great tits, it could not prevent cheaters from exploiting its altruism. Thus, reciprocal altruism may be responsible for alarm signalling of top-ranked males when they forage together with permanent members of their winter flocks.

The results failed to support the pursuit-deterrent hypothesis (Cresswell 1994a,b) since males signalled towards a threatening object strictly according to the social situation (**VII**). Evidently the birds can discriminate between a predator and just a threatening situation.

The results of the study (**VII**) show that there can be different social reasons to give alarm calls. This finding may indicate that there are also different reasons to initiate the mobbing behaviour. Therefore nest defence behaviour, alarm calling and mobbing outside the breeding season appears to be dependent on a set of ecological and social strategies to alter behaviour of a predator in order to increase individual and inclusive fitness.

SUMMARY

In this thesis some questions were answered but new questions were raised. Human behaviour abounds with reciprocal altruism consistent with theory, but animal behaviour seemed to be almost devoid of it. The main finding of this thesis is that mobbing behaviour of the breeding animals can be explained in terms of reciprocal altruism at least in the case of some passerine birds (**IV, V, VI, VII**). This results show that reciprocal altruists in the animal kingdom have some means of recognizing one another, a means of discriminating in favour of those who do good turns and against those who do not.

Cooperation among familiar animals may bring social benefits such as increased personal fitness. Therefore the results regarding cooperation of breeding passerine birds on conspecific (**IV, V, VII**) and heterospecific (**VI**) levels, while actively moving predators away, is new but not surprising. It is in line with some previous studies stressing the role of positive interspecific interactions in structuring northern breeding bird communities. This suggests that bird behaviour can be much more linked to their spatial distribution than previously thought. However, the idea of reciprocity-based cooperation among birds belonging to different species needs to be proven experimentally.

In some respect, the results were surprising as acoustically similar alarm calls may be given because of socially different reasons (**VII**). It was found that territorial male great tits can give the same alarm calls under different social contexts: to warn their sexual partners, and other flock members. Supposedly they may notify also the approaching predator that it is seen by the prey. It may mean that there might be more than one reason to start alarm calling or initiate other mobbing activities. Thus, mate protection and reciprocal altruism may be responsible for alarm signalling of territorial male great tits when they forage together with their mates and other permanent members of winter flocks (**VII**).

This study also revealed a new type of mobbing cost. This cost is due to abilities of acoustically oriented predators to eavesdrop the long-range calls of their prey (**I**). It was also found that birds generally avoid giving of loud, easily-locatable calls in risky situations (**II**). More detailed study revealed that long-duration, easily locatable calls can increase the risk of nest predation, suggesting that mobbing under natural conditions is a trade-off between the costs and benefits (**III**). The costs associated with mobbing may prevent the exaggeration of these signals and ensure mobbing honesty.

To sum up, the results presented in this thesis add some new data about mobbing predators as an adaptive type of behaviour. At the same time, this study revealed that mobbing behaviour may be more complex than it was previously thought. Finally, this thesis shows that mobbing behaviour may be a good model for empirical studies and theoretical modelling in the field of evolutionary ecology.

REFERENCES

Alatalo, R. V., Erikson, D., Gustafson, L. & Larsson, K. 1987. Exploitation competition influences the use of foraging sites by tits: experimental evidence. *Ecology,* 68, 284–290.

Alatalo, R. V., Gustafson, L. & Lundberg, A. 1986. Interspecific competition and niche shifts in tits *Parus*: evaluation of non-experimental data. *American Naturalist*, 127, 819–834.

Alatalo, R.V. & Helle, P. 1990. Alarm calling by individual willow tits, *Parus montanus*. *Animal Behaviour*, 40, 437–442.

Alexander, R.D. 1987. *The Biology of Moral Systems*. Hawthorne (New York): Aldine de Gruyter

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour***,** 49, 227–267.

Altmann, S.A. 1956. Avian mobbing behavior and predator recognition. *Condor*, 58, 241–253.

Arnold, K. E. 2000. Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird. *Ethology*, 106, 385–393.

Arnold, K. & Zuberbühler, K. 2006. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour*, 72, 643–653.

Axelrod, R. 1984. *The Evolution of Cooperation.* New York: Basic Books.

Axelrod, R. & Hamilton, W.D. 1981. The evolution of cooperation. *Science*, 211, 1390–1396.

Bartlett, M.Y. & DeSteno, D. 2006. Gratitude and prosocial behavior. *Psychological Science*, 17, 319–325.

Bautista, L.M. & Lane, S.J. 2000. Coal tits increase evening body mass in response to tawny owl calls. *Acta Ethologica*, 2, 105–110.

Becker, P. 1984. Tageszeitliche Steigerung der Feindabwehr der Fluseeschwalbe (*Sterna hirundo*). *Zeitschrift für Tierpsychologie,* 66, 265–280.

Beletsky, L. 1996. *The Red-winged Blackbird. The Biology of a Strongly Polygynous Songbird*. London: Academic Press.

Bergmann, H. H. & Helb, H. W. 1982. *Stimmen der Vögel Europas*. München: BLV Verlagsgesellschaft.

Bildstein, K.L. 1982. Responses of northern harriers to mobbing passerines. *Journal of Field Ornithology*, 53, 7–14.

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.

Björklund, M. & Westman, B. 1983. Extra-pair copulations in the pied flycatcher (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology*, 13, 271–275.

Boyd, R., Gintis, H., Bowles, S. & Richerson, P.J. 2003. The evolution of altruistic punishment. *Proceeding of National Academy of Sciences of USA,* 100, 3531–3535.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of animal communication.* Sunderland: Sinauer Associates.

Brandt, H., Hauert, C. & Sigmund, K. 2006. Punishing and abstaining for public goods. *Proceeding of National Academy of Sciences of USA*, 103, 495–497.

Buitron, D. 1983. Variability in the responses of black-billed magpies (*Pica pica*) to natural predators. *Behaviour,* 87, 209–236.

Caro, T. M. 1995. Pursuit-deterrence revisited. *Trends Ecology and Evolution,* 10, 500–503.

Clutton-Brock, T.H. & Parker, G.A. 1995. Punishment in animal societies. *Nature*, 373, 209–216.

Collias, N. E. & Collias, E. C. 1978. Group territory, dominance, co-operative breeding in birds, and a new factor. *Animal Behaviour,* 26, 308–309.

Cresswell, W. 1994a. Song as a pursuit-deterrence signal and its occurrence relative to other antipredator behaviors of the skylark on attack by merlins. *Behavioral Ecology and Sociobiology,* 34, 217–223.

Cresswell, W. 1994b. The function of alarm calls in redshanks *Tringa totanus. Animal Behaviour,* 47, 736–738.

Cronin, H. 1991. *The Ant and the Peacock.* Cambridge, Cambridge University Press.

Curio, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie.,* 48, 175–183.

Curio, E. 1988. Cultural transmission of enemy recognition by birds. In: Social Learning: Psychological and Biological Perspectives (Zental T. & Galef BG eds). Hillsdale, New Jersey: Lawrence Erlbaum Associates, 75–97.

Curio, E. & Regelmann, K. 1985. The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Zeitschrift für Tierpsychologie*, 69, 3–18.

Curio, E. & Regelmann, K. 1986. Predator harassment implies a real deadly risk: a reply to Hennessy. *Ethology*, 72, 75–78.

Curio, E., Ernst, U., & Vieth, W. 1978. The adaptive significance of avian mobbing II. Cultural transmission of enemy recognition in Blackbirds: effectiveness and some constraints. *Zeitschrift für Tierpsychologie*, 48, 184–202.

de Laet, J. F. 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. *Ibis*, 127, 372–377.

Denson, R.D. 1979. Owl predation on a mobbing crow. *Wilson Bulletin*, 91, 133.

Desrochers, A., Bélisle, M. & Bourque, J. 2002. Do mobbing calls affect the perception of predation risk by forest birds? *Anim Behaviour*, 64, 709–14.

Dominey, W.J. 1983. Mobbing behaviour in colonially nesting fishes, especially the bluegill, *Lepomis macrochirus*. *Copeia*, 4, 1086–1088.

Dugatkin, L. A., Mesterton-Gibbons, M. & Houston, A. I. 1992. Beyond the prisoner's dilemma: towards models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology and Evolution*, 7, 202–205.

Dugatkin, L.A. & Druen, M. 2004. The social implications of winner and loser effects. *Proceedings of Biological Sciences* 271(Suppl 6), S488–S489.

Ekman, J. 1987. Exposure and time use in willow tit flocks: the costs of subordination. *Animal Behaviour,* 35, 445–452.

Ekman, J. 1989. Ecology of non-breeding social systems of *Parus*. *Wilson Bulletin,* 101, 263–288.

Ekman, J., Cederholm, G. & Askenmo, C. 1981. Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P.cristatus* – a removal study. *Journal of Animal Ecology*, 50, 1–9.

Ekman, J. & Hake, M. 1988. Avian flocking reduces starvation risk: an experimental demonstration. *Behavioral Ecology and Sociobiology,* 22, 91–94.

Fehr, E. & Gächter, S. 2002. Altruistic punishment in humans. *Nature*, 415, 137–140.

Ficken, S. M. 1990. Acoustic characteristics of alarm calls associated with predation risk in chickadees. *Animal Behaviour*, 39, 400–401.

Flasskamp, A. 1994. The adaptive significance of avian mobbing. V. An experimental test of the 'move on' hypothesis. *Ethology*, 96, 322–333.

Forsman, J.T., Mönkkönen, M., Inkeröinen, J. & Reunanen, P. 1998a. Aggregate dispersion of birds after encountering a predator: experimental evidence. *Journal of Avian Biology* 29, 44–48.

Forsman, J.T., Mönkkönen, M., Helle, P. & Inkeröinen, J. 1998b. Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. *Oecologia* 115, 278–286.

Frankenberg, E. 1981. The adaptive significance of avian mobbing: IV. "Alerting others" and "perception advertisement" in blackbirds facing an owl. *Zeitschrift für Tierpsychologie* 55, 97–118.

Haartman, L. & Löhrl, H. 1950. Die Lautääusserungen des Trauer- und Halsbandfliegenschnäppers, *Muscicapa h.hypoleuca* (Pall.) un *M.a albicollis* Temminck. *Ornis Fennica*, 27, 85–97.

Haftorn, S. 1997. Natal dispersal and winter flock formation in the willow tit *Parus montanus*. *Fauna norvegica,* Series C Cinclus, 20, 17–35.

Haftorn, S. 2000. Contexts and possible functions of alarm calling in the willow tit, *Parus montanus*; the principle of "better safe than sorry". *Behaviour,* 137, 437–449.

Hailman, J. P. 1989. The organization of major vocalizations in the *Paridae*. *Wilson Bulletin*, 101, 305–343.

Hamilton, I.M. & Taborsky, M. 2005. Contingent movement and cooperation evolve under generalized reciprocity. *Proceedings of the Royal Society of London, Series B,* 272: 2259–2267.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology,* 7, 1–52.

Hamilton, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology,* 31, 295–311.

Hanski, I.K. & Laurila, A. 1993. High nest predation rate in the chaffinch. *Ornis Fennica* 70, 65–70.

Haskell, D. G. 2002. Begging behaviour and nest predation. In: The Evolution of begging: competition, cooperation and communication (Wright J, Leonard M. L., eds), Dordrecht: Kluwer Academic, 163–72.

Hauser, M. D., Chen, M. K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated Cotton-top Tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society of London, Series B,* 270, 2363–2370.

Hinde, R.A. 1954. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*): I. The nature of the response, and an examination of its course. *Proceedings of the Royal Society of London, Series B,* 142, 306–331.

Hogstad, O. 1987. Social rank in winter flocks of willow tits *Parus montanus*. *Ibis,* 129, 1–9.

Hogstad, O. 1988a. Advantages of social foraging of willow tits *Parus montanus*. *Ibis*, 130, 275–283.

Hogstad, O. 1988b. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flock. *Ibis*, 130, 45–56.

Hogstad, O. 1995. Alarm calling by willow tits, *Parus montanus*, as mate investment. *Animal Behaviour,* 49, 221–225.

Hoogland, J.L. & Sherman, P.W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecological Monographs*, 46, 33–58.

Hurd, C.R. 1996. Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology* 38, 287–292.

Klump, G. M. & Shalter, M. D. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie*, 66, 189–226.

Klump, G. M., Kretzschmar, E. & Curio, E. 1986. The hearing of an avian predator and its avian prey. *Behavioral Ecology and Sociobiology,* 18, 317–323.

Koivula, K., Lahti, K., Rytkönen, S & Orell, M. 1994. Do subordinates expose themselves to predation? Field experiments on feeding site selection by willow tits. *Journal of Avian Biology*, 25, 178–183.

Kokko, H. & Mappes, J. 2005. Sexual selection when fertilization is not guaranteed. *Evolution*, 59, 1876–1885.

Kokko, H., Jennions, M.D. & Brooks, R. 2006. Unifying and testing models of sexual selection. *Annual Reviews of Ecology Evolution and Systematics*, 37, 43–66.

Korbut, V.V. 1989. Variability and stability of acoustical signalization of chaffinch in defence reactions. *Russian Zoological Journal*, 68, 125–134.

Krama, T. & Krams, I. 2005. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology*, 16, 37–40.

Krams, I. A. 1996. Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. *Journal of Avian Biology*, 27, 153–156.

Krams, I. 1998a. Dominance-specific vigilance in the great tit. *Journal of Avian Biology,* 29*,* 55–60.

Krams, I. 1998b. Individuals adjust their body reserves to dominance position within mixed flocks of the willow (*Parus montanus*) and the crested tit (*P. cristatus*): a field experiment. *Polish Journal of Ecology,* 46*,* 207–216.

Krams, I. 2000: Long-range call use in dominance-structured crested tit *Parus cristatus* winter groups. *Journal of Avian Biolgy*, 31, 15–19.

Krams, I. 2001. Communication in crested tits and the risk of predation. *Animal Behaviour*, 61, 1065–1068.

Krams, I.A., Krams, T. & Černihovičs, J. 2001. Selection of foraging sites in mixed willow and crested tit flocks: rank-dependent survival strategies. *Ornis Fennica*, 78, 1–11.

Krams, I. & Krama, T. 2002. Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *Proceedings of the Royal Society of London, Series B,* 269, 2345–2350.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford University Press.

Kroodsma, D. E. & Miller, E. H. 1996. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca, NY: Cornell Univ. Press.

Kruuk, H. 1964. Predators and anti-predator behaviour of the black-headed gull (*Larus ridibundus* (L.)). *Behaviour Supplement*, 11, 1–129.

Lambrechts, M. & Dhondt, A. A. 1986. Male quality, reproduction and survival in the great tit (*Parus montanus*). *Behavioral Ecology and Sociobiology,* 19*,* 57–63.

Leimar, O. & Hammerstein, P. 2001. Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society of London, Series B,* 268, 745–753.

Lehmann, L. & Keller, L. 2006. The evolution of cooperation and altruism – a general framework and a classification of models. *Journal of Evolutionary Biology*, 19, 1365–1376.

Lorenz, K. 1931. Beiträge zur Ethologie sozialer Corviden. *Journal für Ornithology*, 79, 67–127.

Lundberg, A. & Alatalo, R. V. 1992. *The Pied Flycatcher*. Poyser: London.

Marler, P. 1956. The voice of the chaffinch and its function as a language. *Ibis*, 98, 231–261.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. *Behaviour* 11, 13–39.

McGregor, P.K., Catchpole, C.K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, H C., Gilbert, F., Horn, A. G., Klump, G. M., Kroodsma, D. E., Lambrechts, M. M., McComb, K. E., Nelson, D. A., Pepperberg, I. M., Ratcliffe, L., Searcy, W. A., Weary, D. M., 1992. Design of playback experiments: the Thornbridge Hall NATO ARW Consensus. In: Playback and Studies of Animal Communication (McGregor PK, ed). New York: Plenum Press, 1–9.

Milinski, M. 1987. Tit for tat and the evolution of cooperation in sticklebacks. *Nature*, 325, 433–437.

Milinski, M., Pfluger, D., Külling, D. & Kettler, R. 1990. Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behavioral Ecology and Sociobiology*, 27, 17–21.

Mönkkönen, M., Forsman, J. & Helle, P. 1996. Mixed-species foraging aggregations and heterospecific attraction in boreal bird communities. *Oikos*, 77, 127–136.

Mönkkönen, M., Helle, p., Niemi, G. & Montgomery K. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology* 75, 2077–2083.

Morton, E. S. & Shalter, M. D. 1977. Vocal response to predators in pair-bonded Carolina wren. *Condor*, 79, 222–227.

Mougeot, F. & Bretagnolle, V. 2000. Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology,* 31*,* 376–386.

Newton, I. 1998. *Population Limitation in Birds*. San Diego: Academic Press.

Nowak, M. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature*, 393, 573–577

Nowak, M.A. & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature* 437, 1291–1298.

Nowak, M.A. & Roch, S. 2007. Upstream reciprocity and the evolution of gratitude. *Proceedings of the Royal Society of London, Series B,* 274, 605–610.

Olendorf, R., Getty, R. & Scribner, K. 2004. Cooperative nest defence in red-winged blackbirds: reciprocal altruism, kinship or by-product mutualism? *Proceedings of the Royal Society of London, Series B,* 271, 177–182.

Pavey, R. C. & Smyth, A. K. 1998. Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Animal Behaviour*, 55, 313–18.

Pettifor, R.A. 1990. The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Animal Behaviour*, 39, 821–827.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005. Evolution of cooperation through generalized reciprocity. *Proceedings of the Royal Society of London, Series B*, 272, 1115–1120.

Pitcher, T.J, Green, D.A. & Magurran, A.E. 1986. Dicing with death: predator inspection behaviour in minnow shoals. *Journal of Fish Biology,* 28, 439–448.

Ratti, O., Hovi, M., Lundberg, A., Tegelström, H. & Alatalo, R.V. 1995. Extra-pair paternity and male characteristics in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 37, 419–425.

Robinson, S. K. 1985. Coloniality in the yellow-rumped cacique (*Cacicus cela*) as a defense against nest predators. *Auk*, 102, 506–519.

Rutte, C., Taborsky, M. & Brinkhof, M. 2006. What sets the odds in winning and losing? *Trends in Ecology and Evolution*, 21, 16–21.

Ryan, M. J., Tuttle, M.D. & Rand, A.S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *American Naturalist*, 119, 136–139.

Shalter MD, 1978. Effect of spatial context on the mobbing behaviour of pied fly-catchers to a predator model. *Animal Behaviour*, 26:1219–21.

Slagsvold T, 1980. Habitat selection in birds: on the presence of other bird species with special regard to *Turdus pilaris*. *Journal of Animal Ecology*, 49:523–536.

Shedd, D.H. 1982. Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). *Auk*, 99, 342–346.

Sherman, P.W. 1977. Nepotism and the evolution of alarm calls. *Science*, 197, 1246–1253.

Smith, S. T. 1977. Communication and other social behavior in *Parus carolinensis*. *Publications of Nuttall Ornithological Club,* 11, 1–125.

Smith, V. W. 1966. Autumn and spring weights of some Palearctic migrants in central Nigeria. *Ibis*, 108, 492–512.

Snow, D. & Perrins, C. 1997. *The Birds of the Western Palearctic*. Oxford: Oxford University Press.

Sordahl, T. A. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bulletin*, 102, 349–52.

Stephens, D. W., McLinn, C. M. & Stevens, J. R. 2002. Discounting and reciprocity in an iterated prisoner's dilemma. *Science*, 298, 2216–2218.

Stevens, J.R. & Hauser, M.D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences,* 8, 60–65.

Stevens, J.R., Cushman, F.A. & Hauser, M.D. 2005. Evolving the psychological mechanisms for cooperation. Annual Review of Ecology, Evolution, and Systematics, 36: 499–518.

Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. *Ecology*, 74, 1197–1203.

Taborsky, M. 1987. Cooperative behaviour in fish: coalitions, kin groups and reciprocity. In: Ito Y, Brown JL, Kikkawa J (eds) Animal societies: theories and facts. Japan Scientific Societies Press, Tokyo, pp 229–239.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology,* 46, 35–57.

Verbeek, N. A. 1985. Behavioural interactions between avian predators and their avian prey: play behaviour or mobbing? *Zeitschrift für Tierpsychologie*, 67, 204–214.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, 60, 253–261.

de Waal, F.B.M. & Berger, M.L. 2000. Payment for labour in monkeys. *Nature*, 404, 563.

Wedekind, C. & Braithwaite, V.A. 2002. The long-term benefits of human generosity in indirect reciprocity. *Current Biology*, 1012–1015.

Wilson, E.O. 1975. *Sociobiology*. Cambridge: Belknap Press.

Zahavi, A. & Zahavi, A. 1997. *The Handicap Principle*. Oxford: Oxford Univ. Press.

Zuberbühler, K., Jenny, D. & Bshary, R. 1999. The predator deterrence function of primate alarm calls. *Ethology*, 105, 477–490.

SUMMARY IN ESTONIAN

Grupiviisiline ründekäitumine (*mobbing*) lindudel: selle hind ja retsiprooksusel põhinev koostöö

Inimestele on iseloomulik retsiprookse altruismi teooriale vastava käitumise rohke esinemine, kuid loomade analoogsest käitumisest tõendid praktiliselt puuduvad. Käesoleva väitekirja peamiseks tulemuseks on tõdemus, et pesitsevatel loomadel sageli täheldatav nn grupiviisiline ründekäitumine ehk *mobbing* võib olla seletatav retsiprookse altruismiga, vähemalt mõnedel värvuseliikidel (**IV, V, VI, VII**). Siinsed tulemused näitavad, et loomariigi retsiprooksed altruistid suudavad üksteist ära tunda ja et neil on olemas võimalused tasuda neile, kes on teinud koostööd, ning karistada selliseid, kes on koostööd vältinud.

Üksteist tundvate loomade omavaheline koostöö võib kaasa tuua sotsiaalseid hüvesid, mis väljenduvad suurenenud individuaalses kohasuses. Seepärast on tulemused, mis viitavad pesitsevate värvuliste liigisisesele (**IV, V, VII**) ja liikidevahelisele (**VI**) koostööle röövlindude tõrjumisel, küll uudsed, kuid mitte üllatavad. Need tulemused langevad kokku mõnede varasemate uuringute tulemustega, mis on rõhutanud liikidevaheliste positiivsete interaktsioonide rolli põhjapoolsete linnukoosluste struktureerumisel. See osutab võimalusele, et lindude käitumine on nende ruumilise levikuga seotud märksa suuremal määral, kui varem arvatud. Siiski, idee eri liikidesse kuuluvate lindude vahelisest retsiprooksusel põhinevast koostööst vajab veel eksperimentaalset kinnitust.

Mõnevõrra üllatuseks olid tulemused, mis näitasid, et sotsiaalses mõttes erinevatel põhjustel võidakse kasutada akustiliselt sarnaseid häirehüüdeid (**VII**). Leiti, et territoriaalne isane rasvatihane võib esile tuua sarnaseid häirehüüdeid erinevais sotsiaalseis kontekstides – nimelt nii seksuaalpartnerite kui ka teiste salgaliikmete hoiatamiseks ohu eest. Võimalik, et need annavad ka lähenevale kiskjale märku, et teda on saakobjekti poolt märgatud. See võib tähendada, et üheaegselt võib esineda mitmeid erinevaid põhjusi, miks tasub esile tuua häirehüüdu või ilmutada mõnda muud grupiviisilist ründekäitumist initsieerivat aktiivsust. Niisiis võib talvel üheskoos oma partnerite ja teiste alaliste salgaliikmetega toituvate territoriaalsete isaste rasvatihaste häirehüüdude põhjuseks olla nii paarilise kaitsmine kui ka retsiprookne altruism (**VII**).

Käesolevas uurimuses tehti kindlaks ka grupiviisilise ründekäitumise hinna üks senikirjeldamata vorm. See seisneb kuulmismeelele orienteerunud kiskjate võimaluses salaja pealt kuulata ja ära kasutada oma saakobjektide poolt esile toodavaid kaugelekostuvaid häirehüüdeid (**I**). Samal ajal leiti, et riskantseisse situatsioonidesse sattunud linnud üldiselt väldivad valjude, kergesti lokaliseeritavate häirehüüete esiletoomist (**II**). Detailsem uuring selgitas, et valjud ja kergesti lokaliseeritavad hüüded võivad suurendada pesade rüüstamise riski, mis näitab seda, et looduslikes oludes peaks grupiviisiline ründekäitumine olema kompromiss sellest käitumisest tuleneva kasu ja hinna vahel (**III**). Grupiviisilise

ründekäitumisega seotud hind võib aidata vältida nende signaalidega liialdamist ja tagada nende usaldusväärsust.

Kokkuvõttes lisavad käesolevas väitekirjas esitatavad tulemused uusi teadmisi kiskjate grupiviisilise ründekäitumise kui adaptiivse käitumisvormi kohta. Samal ajal demonstreerib käesolev uurimus seda, et grupiviisiline ründe-käitumine võib olla seniarvatust märksa komplitseeritum nähtus. Lõpuks tõendab see väitekiri, et grupiviisiline ründekäitumine võib endast kujutada sobivat mudelit nii empiirilisteks uuringuteks kui ka teoreetiliseks modellee-rimiseks evolutsioonilises ökoloogias.

ACKNOWLEDGEMENTS

First of all, I would like to thank my principal supervisor Raivo Mänd for giving me the opportunity to undertake my master and PhD projects at Tartu University. Thank you for organizing my study process, taking care of me so much, always having time to answer questions and regulating all necessary formalities. Your support and encouragement, your help and advice since my master studies helped me to become a biologist despite my doubts and psychologist's background.

My most sincere thanks belongs to my husband and supervisor Indrikis Krams for making me work, for teaching me how to handle with birds, for showing me the whole world of the forest and birds living there. You have been my mentor, friend and companion for all these years. I would have never achieved this without you. The days we spent together carrying nestboxes, whistling at the feeders and watching birds have been one of the best days of my life.

I thank all the people at the Chair of Animal Ecology for creating such a constructive and stimulating environment. I owe my gratitude for all the friendly people there, who made by they work and ideas such a good place and accepted my presence among them. Two persons made my way of thinking more organized and precise. Toomas Tammaru whose questions let me feel competent enough to understand how much I don't understand. Peeter Hõrak which philosophical way of critics made me feel not competent at all, but that was not for a long time.

My time being a PhD student in Tartu would not have been the same without all the other PhD students, researchers and people coming for doctoral schools at Arbavere and Lepanina. This was indeed priceless chance to acquire some talk experience and simply good contacts with people doing similar things as me.

I thank Astrid and Staffan Ulfstrand for their encouragement and high evaluation of our ideas, for warm and sincere attitude to all my family.

Gary Ramey deserves a lot of thanks for reading and improving the texts I wrote. Your native speaker's proofs, wise comments and suggestions helped me to bring my papers in to editors and reviewer's asked condition.

Seppo Rytkönen, Jukka Suhonen, Ilva Everte and Derek Parsons have also sacrificed plenty of their time improving written English of my papers. Thanks a lot.

I owe my thanks to Kristīne Igaune who joined our pied flycatcher team in 2005. Doing fieldwork you were always ready to talk, always ready to help and always ready to laugh.

I thank Margret Sisask for the help with administrative tasks, regular sending numerous messages and reminding me about all the obligate formalities during my study process.

Last, but not least, I would like to thank my parents and parents in law, for all the support and help I received from them. Thank you for everything.

ORIGINAL PAPERS

Krama, T. & Krams, I. 2005.
Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*.
Behavioral Ecology 16: 37–40.

II

Krama, T., Krams, I. & Igaune, K.
Effects of cover on loud trill-call and soft seet-call use in the crested tit *Parus cristatus*
(submitted manuscript).

Effects of cover on loud trill-call and soft seet-call use in the crested tit *Parus cristatus*

Tatjana Krama*, Indrikis Krams† & Kristīne Igaune†

*Institute of Zoology and Hydrobiology, Tartu University, Tartu, Estonia
†Institute of Systematic Biology, Daugavpils University, Daugavpils, Latvia

The contact vocalization of crested tits (*Parus cristatus*) can be easily divided into two categories: long- and short-range communication calls. The long-range trills of the crested tit are loud, frequency-modulated calls which provide the optimal arrangement for acoustic communication over long distances. Their soft high-pitched tonal calls are designed to increase rather than decrease attenuation. Since the predation cost is mostly associated with the use of loud calls, we investigated whether crested tits adjust the use of loud trill-calls and of soft seet-calls to changes in habitat safety. We arranged two feeding sites that differed with respect to predicted safety and observed the utterance of loud trill-calls and soft seet-calls. Calling rates of the loud trill-calls were highest when male crested tits foraged at the safe site. The loud trill-calls were given significantly less often while visiting risky feeders placed just a few meters away from the safe sites. The soft seet-calls were uttered at risky and safe feeders at similar rates. This study revealed that the long-range part of contact communication in crested tits is strongly affected by the level of perceived predation risk. In accordance with the data on the hearing ability of predators, dominant male crested tits decreased their exposure to predation in risky habitats by choosing a less risky type of communication with high-pitched sounds.

Introduction

Natural selection can be effective in the shaping of behaviour. However it often results not in the absolute best for a particular function but in the compromise of some other functions involved because one single aspect of behaviour can rarely evolve in isolation. Displays and loud vocal activities which male individuals use to attract their mates are also likely to attract unintended receivers. Thus, the acoustically oriented predators use signals emitted by their potential prey as cues to eavesdrop the signals to obtain information about the signaller (Yasukawa 1989; Zuk & Kolluru 1998; Grafe 2005; Bernal et al. 2006). Contact communication used by many social animals is relatively specialized to indicate an individual's localization to other flock members and maintain spatial integrity of the flock. Although a large number of studies show that unintended

receivers exploit sexual signals (Zuk & Kolluru 1998; McGregor & Peake 2000) and the possibility of coding of information concerning some aspects of the nature of the predator and/or the degree of predation risk in alarm calls (Seyfarth et al. 1980; Ficken 1990; Zuberbühler et al. 1997, 1999), less is known whether contact calls also increase conspicuousness of the signaller to predators (Krams 2001a).

The contact vocalization of animals may be divided into two categories: long- and short-range communication calls (Wiley & Richards 1982). Calls that belong to the long-range communication signal category include complex modulated vocal units composed of two or more different note types put together in either a fixed sequence or a variable order (Marler 1967). Long-range calling consisting of frequency-modulated sounds provides the optimal arrangement for acoustic communication over long distances (Wiley & Richards 1982). For effective use of amplitude in long-range signals, the amplitude patterns incorporate enough redundancy, usually simple repetition. The trilled calls show this sort of repetitive amplitude modulation. Short-range communication in animals occurs over distances of a few meters at most (Smith 1977; Shalter 1978; Klump et al. 1986). Calls are not only low in intensity, but the characteristics of many such calls seemed to be designed to increase rather than decrease attenuation (Wiley & Richards 1982). The physical differences between these two types of signals may reflect the differences in their function. Marler (1955) reasoned that there are signals adapted for easy location of their sources and sounds suitable for confusing location by predators (Ficken 1990). Experimental evidence of this theory is still insufficient relating to contact communication.

Purring tremolo or trills of crested tits (*Parus cristatus*) are known as their commonest long-range calls, while high-pitched tonal (*seet* calls) signals represent most important short-range calls (Bergmann & Helb 1982, Krams 2000). The crested tit is a small year-round resident of coniferous forests of Europe which spend the non-breeding season in dominance structured flocks (Ekman et al. 1981; Krams 1996, 2001a; Krams et al. 2001). Since the predation cost is mostly associated with the use of loud trill-calls (Krams 2001b), we investigated whether crested tit dominant males adjust the use of loud trill-calls and soft seet-calls to the changes in habitat safety.

Methods

Study area
The data were collected between October and February during the four successive winter seasons of 2001–2004, near the town of Krāslava, in south-eastern Latvia. We studied loud trill-call and soft seet-call use in an individually colour-marked population of free-living crested tits. The study area covers about

10 km^2 of mainly Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) forests of different ages, from open clear-cuttings and bogs to closed forests.

Experimental Set-up and Procedure
The data covers information of 24 dominant males of the crested tit belonging to 24 winter flocks. All of the adults were known from the previous breeding season. The rank of the bird was additionally tested at feeders during autumn. Ranking was based on pairwise aggressive and submissive interactions (Koivula & Orell 1988). All members of a flock of crested tits were captured during the same day. We trapped crested tits by mist nets. It usually took 15–45 min to capture all flock members of a single flock. We marked birds using standard metal rings and a combination of two plastic rings (111 individuals in total). Trapping took place under calm and dry weather from 1000 to 1400. Since 69 observed birds resumed foraging within 4–20 min [$\bar{x}$ (SE): 10.68 min (0.48)], we concluded that the trapping procedure had not any serious adverse effect.

We investigated signalling by only dominant males because use of loud trill-calls in the crested tit can be biased among individuals of different social ranks (Krams 2000). Loud trill-calls are often used not only as contact calls but also as mobbing calls at the presence of a predator (Krams and Krama 2002) and territorial advertisement calls. Long-range trills as territorial calls are emitted by dominant males in quick series during flights along territorial borders (Krams 2000). Signals emitted by a prey individual in the presence of a predator typically represent an alarm intended to warn others or may be designed to deter the predator from attack (Klump and Shalter 1984). Thus, territorial and mobbing behaviour can be be easily separated from within-group communication.

Two feeding sites that differed with respect to predicted safety were arranged. The sites were at sharp edges between an open and a closed habitat. The "safe" site was placed within a canopy of trees closest to the forest edge and parids preffer places offering cover (Koivula et al. 1994). The "exposed" site was placed 5 m from the edge out in the open. The distances between the two sites was 7–9 m. For all 24 flocks the open habitat was a small clear-cut (400–900 m^2 in size). The feeders were attached to poles of 1.2–1.4 m height. The birds had been trained to come and take food when hearing a specific call. Therefore the sites could be arranged in any part of the territory without using permanent feeders. The order of arranging feeders in a safe or in a risky site was selected by tossing a coin. As soon as observations at one site were done, we moved the feeder to another site within the same flock territory. We usually spent about 40–50 min at each site. We made the observations during calm weather and between 10.00–13.00 hours. As soon as observations were finished, the temporary feeders were removed. The presence of observers supposedly did not influence the behaviour of parids since wintering crested tits are generally

tame while such predators as sparrowhawks may attack tit flocks independetly of the presence of humans in the vicinity.

The general methodology for this study was direct observation of individuals in social groups under natural conditions while they visited either safe or risky feeders. We used focal-bird sampling (Altmann 1974) in sessions lasting 15 min when recording the utterance of loud trill-calls (Fig. 1) and 5 min when recording the utterance of soft seet-calls (Fig. 2) given by the focal individual. The order of counting the two call types was selected by tossing a coin. The soft seet-calls were counted only for 5 min since it was not often possible to follow the focal individual for a longer time. When the birds were hidden by twigs and branches in the canopy or when they foraged more than 30 m away from the observers it was rather problematic to assess whether the calls were given by the focal individual. It was much easier to count call number given by the focal individual in case of loud trill-calls since it was possible to identify the calling individual even if it was foraging more than 30 m away from the observers. During the same day we recorded the utterance of both loud trill-calls and soft seet-calls given by the same individual. On average the data set includes 17.6 ± 0.96 ($\bar{x} \pm$SE) observation sessions per individual and only the mean number of calls per individual was used in the analysis. We also recorded the frequency of visits of male crested tits to feeders of both types during the first 5 min of each observation period. The foraging site use and vocal activity was recorded with a delay of 5 min after the arranging of a feeder.

Statistical analysis
Data were analysed using SPSS 11.0 statistical package for Windows. The level of significance was set at 0.05 and all tests were two tailed.

Results

The male crested tits visited more exposed feeders [$\bar{x}$ (SE): 0.41 visits/min (0.01)] as often as safe feeders [$\bar{x}$ (SE): 0.42 visits/min (0.01] (paired t-test: t = 1.635, .df = 23, p = 0.116). Calling rates of the loud trill-calls were highest when foraging at the safe site [$\bar{x}$ (SE): 0.87 calls/min (0.05); Fig. 3]. The loud trill-calls were given significantly less often while visiting risky feeders in small clear-cuts [$\bar{x}$ (SE): 0.62 calls/min (0.04)] (Wilcoxon's matched-pairs signed-ranks test: z =–3.41, n = 24, p = 0.01). The loud trill-calls were never given while flying to exposed feeders and during the return flights. Since just a few of the loud trill-calls were uttered from the feeders while collecting sunflower seeds, the loud trill-calls were always given by crested tits foraging under the protective cover. High-pitched soft seet-calls were uttered at risky [$\bar{x}$ (SE): 9.47 calls/min (0.48)] and safe feeders [$\bar{x}$ (SE): 9.98 calls/min (0.35)] at similar rates (Wilcoxon's matched-pairs signed-ranks test: z =–0.30, n = 24, p = 0.76; Fig. 3).

4

Discussion

This study revealed that the long-range part of contact communication in crested tits is strongly affected by the level of perceived predation risk. The quality of habitats is partly determined by the presence of cover for effective protection from attacking predators (Schneider 1984; Ekman 1986; Hogstad 1988; Krams 1996, 2001a). Forest birds usually perceive the foraging outside the protective cover as a risky adventure (Caraco et al. 1980; Grubb & Greewald 1982; Ekman 1987). Several studies have revealed that inner sites in the tree canopy are safer from attacks by avian predators (Ekman & Askenmo 1984; Suhonen 1993; Krams 2001a, c) indicating that crested tits were more vulnerable while visiting "exposed" feeders.

When crested tits changed foraging from safe feeders to exposed feeders, they had to move for the average distance of 8 m. This means that the individual visiting the exposed feeder increased its distance from other flock members. Under such conditions, one would expect the increase in rate of loud trill-calls. However, it was not the case and crested tits used fewer trilled calls while foraging at more distant exposed feeders. Moreover, after collecting seeds from exposed feeders, crested tits always returned back under the shelter of tree canopies where they could visually track each other equally well while foraging in either feeders. In this case one would expect an equal rate of loud trill-calls while visiting either feeders. However, the rate of trill-calls significantly decreased from safe to exposed feeders.

Most predation on wintering adult crested tits is done by avian predators (Snow & Perrins 1997). Among them, the European sparrowhawk (*Accipiter nisus*) (Geer 1978; Perrins & Geer 1980) and the pygmy owl (*Glaucidium passerinum*) (Ekman 1986; 1989, Suhonen 1993) are probably the most frequent parid predators. The sensory capabilities of predators and their potential prey should be taken into account when considering the cost-benefit ratio associated with their behaviour (Klump et al. 1986). The hearing abilities of the prey and its predator have been studied with reference to the acoustic communication of great tits *P.major* confronted with sparrowhawks (Klump et al. 1986). Only one nocturnal raptor has been studied, the barn owl (*Tyto alba*) (Konishi 1973) that can be compared with the pygmy owl. The hearing abilities of crested tits could be comparable with these of great tits since both species often occur in mixed-species flocks and their call structure and evolution are similar (Hailman 1989).

Loud contact calling of parids lie within 3.8–8 kHz (dominant frequency 4.7 kHz) (Klump et al. 1986, Hailman 1989, Ficken 1990, Krams 2001b) while their best hearing range may lie between 4–8 kHz (Klump et al. 1986). However, there is some evidence that accipiters may use acoustic stimuli from their prey when hunting (Krams 2001b). The range of best hearing of sparrowhawks matches the dominant frequencies of their species-specific

vocalizations which lie within 1–4 kHz. It is also expected that sparrowhawks could use for hunting also higher frequencies of 5–6 kHz since at higher frequencies masking by background noise may play a less important role than at lower frequencies (Klump et al. 1986). The owls locate wide-banded noises containing frequencies optimal for location more accurately than narrow-band and pure tone signals, and the best location abilities of noises by barn owls lie between 2–6 kHz (Konishi 1973). These comparisons show that the loud trill-calls of crested tits can be easy to locate and eavesdropped by sparrowhawks and owls.

At high frequencies of 7 kHz and above absolute thresholds are likely to determine the hearing ability of the sparrowhawk, while the frequency of tones best suited for location in the barn owl is 7–8 kHz. However, the pygmy owl does not rely on sound location so much as the barn owl. Pygmy owls are active mainly during the light hours, and usually act as "sit-and-wait predators" during summer and follow bird flocks from higher in the tree canopy during winter (Mikkola 1970; Kellomäki 1977; Ekman 1986; Suhonen 1993; Kullberg 1995). Thus, pygmy owls mainly rely on their vision while hunting which may mean that their hearing ability within the range of high frequencies could be less excellent as that of the barn owl. Since 8 kHz is the dominant frequency of soft seet-calls of crested tits, these sounds do not match the range of superior hearing of sparrowhawks and pygmy owls. Still, the soft seet-calls lie within the best hearing range of parids.

In accordance with the data on the hearing ability of predators, dominant males of crested tits decreased their exposure to predation in risky habitats by choosing less risky type of communication of high-pitched sounds. Besides the hearing ability of predators, the locatability of sounds can be influenced by frequency-dependent attenuation (Wiley & Richards 1982). Since scattering of sounds is a function of the frequency, attenuation of low-frequency sound increases less steeply as foliage density increases compared to attenuation of high-pitched sounds which makes localization of high-pitched sounds less possible. With environmental masking noise, detection distances at which sounds become audible for the hawk and parids can be very different for high-pitched calls. Klump et al. (1986) calculated that the detection distances are about 10 m in the hawk and up to 40 m in the tits. Hence, parids can address high-pitched calls to their mates or other group members to the exclusion of the predators. The decreased risk of predation associated with the use of soft seet-calls may make these calls preferable for communication over an extended period of time and maintaining the spatial integrity of bird pairs and flocks foraging in dense vegetation of the forest. Perhaps the use of "predation free" communication calls make winter groups of parids coherent and compact.

Acknowledgements

Literature cited

Altmann, S. A. 1956: Avian mobbing behavior and predator recognition. Condor **58**, 241–253.

Arnold, K. & Zuberbühler, K. 2006: The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. Anim. Behav. **72**, 643–653.

Bernal, X. E., Rand, A. S. & Ryan, M. J. 2006: Acoustic preferences and localization performance of blood-sucking flies (*Corethrella* Coquillet) to túngara frog calls. Behav. Ecol. **17**, 709–715.

Bradbury, J. W. & Vehrencamp, S. L. 1998: The Principles of Animal Communication. Sinauer, Cambridge, Massachusetts.

Bergmann, H. H. & Helb, H. W. 1982: Stimmen der Vögel Europas. BLV Verlags-gesellschaft, München.

Caraco, T., Martindale, S. & Pulliam, H. R. 1980: Avian flocking in presence of a predator. Nature **285**, 400–401.

Ekman, J. 1986: Tree use and predator vulnerability of wintering passerines. Ornis Scand. **17**, 261–267.

Ekman, J. 1987: Exposure and time use in willow tit flocks: the cost of subordination. Anim. Behav. **35**, 445–452.

Ekman, J. 1989: Ecology of non-breeding social systems of *Parus*. Wilson Bull. **101**, 263–288.

Ekman, J. & Askenmo, C. E. H. 1984: Social rank and habitat use in willow tit groups Anim. Behav. **32**, 508–514.

Ekman, J., Cederholm, G. & Askenmo, C. 1981: Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P.cristatus* – a removal study. J.Anim. Ecol. **50**, 1–9.

Ficken, S. M. 1990: Acoustic Characteristics of alarm calls associated with predation risk in Chickadees. Anim. Behav. **39**, 400–401.

Geer, T. A. 1978: Effects of nesting sparrowhawks on nesting tits. Condor **80**, 419–422.

Grafe, T.U. 2005: Anuran choruses as communication networks. In: Animal Communication Networks (McGregor, P. K., ed). Cambridge University Press, Cambridge UK, pp. 277–299.

Grubb, T. C. & Greenwald, L. 1982: Sparrows and a brushpile: foraging response to different combinations of predation risk and energy cost. Anim. Behav. **30**, 637–640.

Hailman, J. P. 1989: The organization of major vocalizations in the *Paridae*. Wilson Bull. **101**, 305–343.

Hogstad, O. 1988: Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis *131*, 128–134.

Kellomäki, E. 1977: Food of the pygmy owl *Glaucidium passerinum* in the breeding season. Ornis Fennica **54**, 1–29.

Klump, G. M. and Shalter, M. D. 1984: Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. Z. Tierpsychol. **66**, 189–226.

Klump, G. M., Kretzschmar, E & Curio, E. 1986: The hearing of an avian predator and its avian prey. Behav. Ecol. Sociobiol. **18**, 317–323.

Koivula, K. & Orell, M. 1988: Social rank and winter survival in the willow tit *Parus montanus*. Ornis Fennica **65**, 114–120.

Koivula, K., Lahti, K., Rytkönen, S & Orell, M. 1994: Do subordinates expose themselves to predation? Field experiments on feeding site selection by willow tits. J. Avian Biol. **25**, 178–183.

Konishi, M. 1973: Locatable and nonlocatable acoustic signals for Barn owls. Am. Nat. **107**, 775–785.

Krams, I. A. 1996: Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. J. Avian Biol. **27**, 153–156.

Krams, I. 2000: Long-range call use in dominance-structured crested tit *Parus cristatus* winter groups. J. Avian Biol. **31**, 15–19.

Krams, I. 2001a: Seeing without beeing seen: a removal experiment with mixed flocks of willow and crested tits *Parus montanus* and *cristatus*. Ibis **143**, 476–481.

Krams, I. 2001b: Communication in crested tits and the risk of predation. Anim. Behav. **61**, 1065–1068.

Krams, I. 2001c: Perch selection by singing chaffinches: a better view of surroundings and the risk of predation. Behav. Ecol. **12**, 295–300.

Krams, I. & Krama, T. 2002: Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. Proc. R. Soc. Lond. B. **269**, 2345–2350.

Krams, I.A., Krams, T. & Černihovičs, J. 2001: Selection of foraging sites in mixed willow and crested tit flocks: rank-dependent survival strategies. Ornis Fennica **78**, 1–11.

Kullberg, C. 1995: Strategy of the pygmy owl while hunting avian and mammalian prey. Ornis Fennica **72**, 72–78.

Macedonia, J.M., & Evans, C.S. 1993: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology **93**, 177–197.

Marler, P. 1955: Characteristics of some animal calls. Nature **76**, 6–8.

Marler, P. 1977: The structure of animal communication sounds. In: Workshop on recognition of complex acoustic signals (Bullock, T. H., ed). 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.

Maynard Smith, J & Harper, D. 2003: Animal Signals. Oxford University Press, Oxford.

McGregor, P. K. & Peake, T. M. 2000: Communication networks: social environments for receiving and signalling behaviour. Acta Ethol. **2**, 71–81.

Mikkola, H. 1970: On the activity and food of the pygmy owl *Glaucidium passerinum* during breeding. Ornis Fennica **47**, 10–14.

Perrins, C. M. & Geer, T. A. 1980: The effect of sparrowhawks on tit populations. Ardea **68**, 133–142.

Schneider, K. J. 1984: Dominance, predation, and optimal foraging in white-throated sparrow flocks. Ecology **65**, 1820–1827.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980: Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science **210**, 801–803.

Shalter, M. D. 1978: Effect of spatial context on the mobbing behaviour of pied flycatchers to a predator model. Anim. Behav. **26**, 1219–1221.

Sherman, P. W. 1985: Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self- preservation? Behav. Ecol Sociobiol. **17**, 313–324.

Smith, S. T. 1977: Communication and other social behavior in *Parus carolinensis*. Publ. Nuttall Ornithol. Club **11**, 1–125.

Snow, D. W. & Perrins, C. M. 1998: The Birds of the Western Palearctic; Concise Edition, Vol. 2. Oxford University Press, Oxford.

Suhonen, J. 1993: Predation risk influences the use of foraging sites by tits. *Ecolog*y **74**, 1197–1203.

Wiley, R. H. & Richards, D. G. 1982: Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Acoustic Communication in Birds, vol. 1 (Kroodsma, D. E., Miller, E. H. & Quellet, H., eds). Academic Press, New York, pp. 131–181.

Yasukawa, K. 1989: Costs and benefits of a vocal signal: the nest-associated 'chit' of the female red-winged blackbird, *Agelaius phoeniceus*. Anim. Behav. **38**, 866–874.

Zuberbühler, K., Nöe, R. & Seyfarth, R. M. 1997: Diana monkey long-distance calls: message for conspecifics and predators. Anim. Behav. **53**, 589–604.

Zuberbühler, K., Jenny, D. & Bshary, R. 1999: The predator deterrence function of primate alarm calls. Ethology **105**, 477–490.

Zuk, M. & Kolluru, G. R. 1998: Exploitation of sexual signals by predators and parasitoids. Q. Rev. Biol. **73**, 415–438.
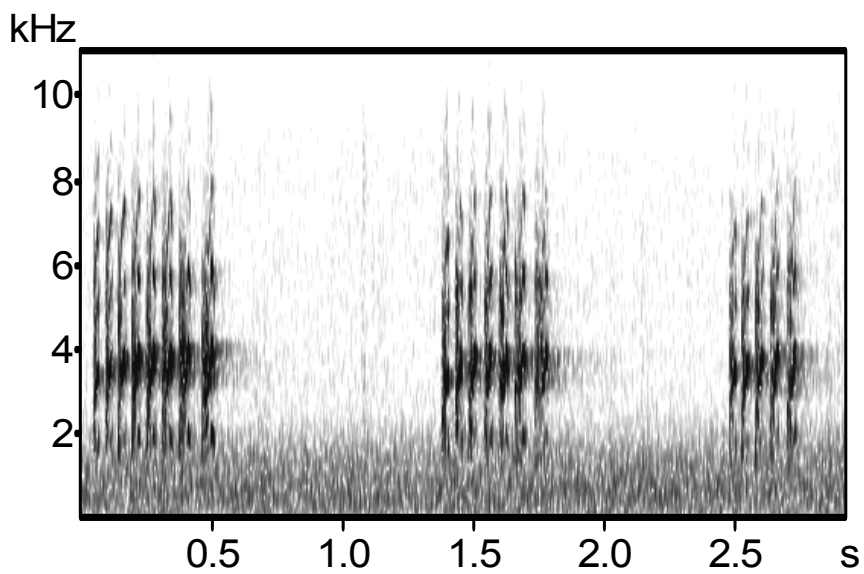
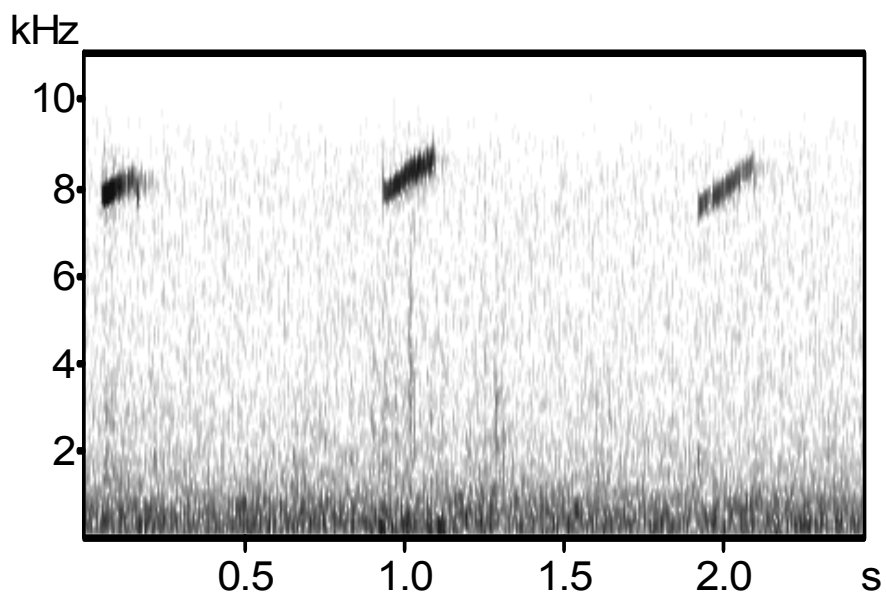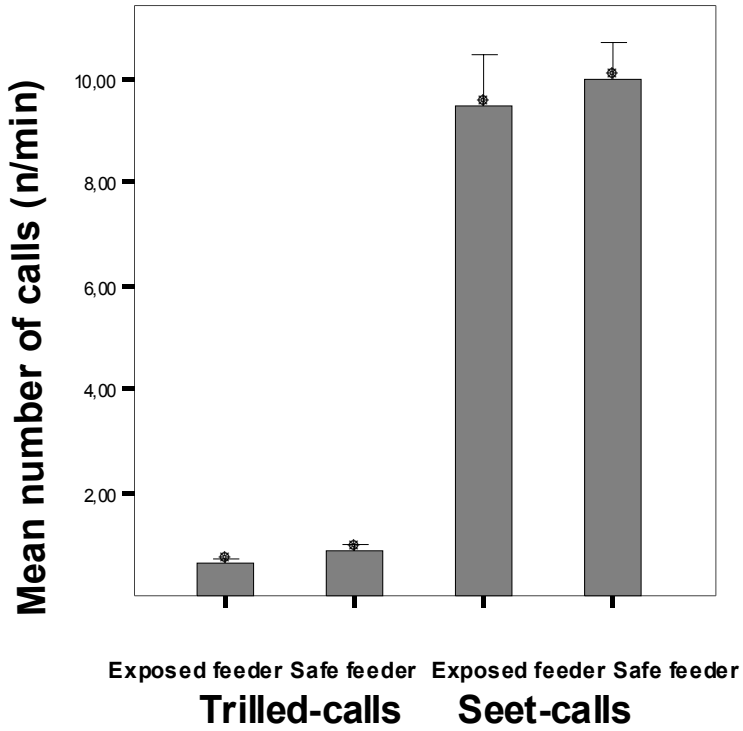**Fig. 1.** Sonogram of loud trill-calls of crested tits

Fig. 2. Sonogram of soft seet-calls of crested tits

Fig. 3. Number of loud trill-calls and soft seet-calls given by dominant males differs between risky and safe feeders

III

IV

Krams, I., Krama T., Igaune, K. & Mänd, R. 2007.
Experimental evidence of reciprocal altruism in the pied flycatcher.
Behavioral Ecology and Sociobiology. DOI: 10.1007/s00265–007–0484–1.

VI

Krams, I. & Krama, T. 2002.
Interspecific reciprocity explains mobbing behaviour
of the breeding chaffinches, *Fringilla coelebs*.
The Proceedings of the Royal Society of London, Series B 269: 2345–2350.

VII

Krams, I., Krama, T. & Igaune, K. 2006.
Alarm calls of wintering great tits *Parus major*: warning of mate,
reciprocal altruism or a message to the predator?
Journal of Avian Biology 37: 131–136.

CURRICULUM VITAE

I. General

1.	Name	Tatjana Krama
2.	Date and place of birth	20.01.1975, Krāslava, Latvia
3.	Citizenship	Latvian
4.	Marital status	Married, 2 children
5.	Address, phone, e-mail	Bauskas Street 6–12, LV–5400 Daugavpils, Latvia
6.	Current position	PhD student, University of Tartu
7.	Educational history	
		1990, BS, Psychology, Daugavpils Pedagogical University;
		2003, MSc, Master thesis "Mobbing behaviour in Birds", Institute of Zoology and Hydrobiology, Tartu University
8.	Languages spoken	Latvian, English, Russian
9.	Working experience	Teaching of behavioural ecology at Daugavpils University

II. Research history

1. Research interests

    (Avian) behavioural ecology, mobbing behaviour, reciprocal altruism

2. List of publications

Krams, I. & Krama, T. 2002. Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *The Proceedings of the Royal Society of London, Series B* 269: 2345–2350.

Krama, T. & Krams, I. 2005. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16: 37–40.

Krams, I., Krama, T. & Igaune, K. 2006. Mobbing behaviour: reciprocity-based co-operation in breeding Pied Flycatcher *Ficedula hypoleuca*. *Ibis* 148: 50–54.

Krams, I., Krama, T. & Igaune, K. 2006. Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology* 37: 131–136.

Krams, I., Krama, T., Igaune, K. & Mänd, R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology*. DOI: 10.1093/beheco/arm079.

Krams, I., Krama T., Igaune, K. & Mänd, R. 2007. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*. DOI: 10.1007/s00265–007–0484–1.

CURRICULUM VITAE

I. Üldandmed

1. Ees- ja perekonnanimi   Tatjana Krama
2. Sünniaeg ja koht   20.01.1975, Krāslava, Läti
3. Kodakondsus   Läti Vabariik
4. Perekonnaseis   Abielus, 2 last
5. Aadress, telefon, *e-mail*
     Bauskas Street 6–12, LV-5400 Daugavpils, Latvia.
     E-mail: tkrama@ut.ee
6. Current position   Doktorant, Tartu Ülikool
7. Educational history
     1990, BSc, Psühholoogia, Daugavpilsi
     Pedagoogikaülikool, Läti;
     2003, MSc, magistritöö "Mobbing behaviour in
     Birds", Zooloogia ja Hüdrobioloogia Instituut,
     Tartu Ülikool
8. Languages spoken   Läti, inglise, vene
9. Working experience   Käitumisökoloogia õpetamine Daugavpilsi
     ülikoolis

II. Teaduslik ja arendustegevus

3. Peamised uurimisvaldkonnad

     (Lindude) käitumisökoloogia,
     grupiviisiline rändekäitumine
     loomadel, retsiprookne altruism

4. Publikatsioonide loetelu

Krams, I. & Krama, T. 2002. Interspecific reciprocity explains mobbing beha-viour of the breeding chaffinches, *Fringilla coelebs*. *The Proceedings of the Royal Society of London, Series B* 269: 2345–2350.

Krama, T. & Krams, I. 2005. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16: 37–40.

Krams, I., Krama, T. & Igaune, K. 2006. Mobbing behaviour: reciprocity-based co-operation in breeding Pied Flycatcher *Ficedula hypoleuca*. *Ibis* 148: 50–54.

Krams, I., Krama, T. & Igaune, K. 2006. Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology* 37: 131–136.

Krams, I., Krama, T., Igaune, K. & Mänd, R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology*. DOI: 10.1093/beheco/arm079.

Krams, I., Krama T., Igaune, K. & Mänd, R. 2007. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Socio-biology*. DOI: 10.1007/s00265–007–0484–1.

DISSERTATIONES BIOLOGICAE
UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel**. Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe**. Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
5. **Maia Kivisaar**. Studies on phenol degradation genes of *Pseudomonas* sp. strain EST 1001. Tartu, 1992, 61 p.
6. **Allan Nurk**. Nucleotide sequences of phenol degradative genes from *Pseudomonas sp.* strain EST 1001 and their transcriptional activation in *Pseudomonas putida.* Tartu, 1992, 72 p.
7. **Ülo Tamm**. The genus *Populus* L. in Estonia: variation of the species biology and introduction. Tartu, 1993, 91 p.
8. **Jaanus Remme**. Studies on the peptidyltransferase centre of the *E.coli* ribosome. Tartu, 1993, 68 p.
9. **Ülo Langel**. Galanin and galanin antagonists. Tartu, 1993, 97 p.
10. **Arvo Käärd**. The development of an automatic online dynamic fluorescense-based pH-dependent fiber optic penicillin flowthrought biosensor for the control of the benzylpenicillin hydrolysis. Tartu, 1993, 117 p.
11. **Lilian Järvekülg**. Antigenic analysis and development of sensitive immunoassay for potato viruses. Tartu, 1993, 147 p.
12. **Jaak Palumets**. Analysis of phytomass partition in Norway spruce. Tartu, 1993, 47 p.
13. **Arne Sellin**. Variation in hydraulic architecture of *Picea abies* (L.) Karst. trees grown under different enviromental conditions. Tartu, 1994, 119 p.
13. **Mati Reeben**. Regulation of light neurofilament gene expression. Tartu, 1994, 108 p.
14. **Urmas Tartes**. Respiration rhytms in insects. Tartu, 1995, 109 p.
15. **Ülo Puurand**. The complete nucleotide sequence and infections *in vitro* transcripts from cloned cDNA of a potato A potyvirus. Tartu, 1995, 96 p.
16. **Peeter Hõrak**. Pathways of selection in avian reproduction: a functional framework and its application in the population study of the great tit (*Parus major*). Tartu, 1995, 118 p.
17. **Erkki Truve**. Studies on specific and broad spectrum virus resistance in transgenic plants. Tartu, 1996, 158 p.
18. **Illar Pata**. Cloning and characterization of human and mouse ribosomal protein S6-encoding genes. Tartu, 1996, 60 p.
19. **Ülo Niinemets**. Importance of structural features of leaves and canopy in determining species shade-tolerance in temperature deciduous woody taxa. Tartu, 1996, 150 p.

20. **Ants Kurg**. Bovine leukemia virus: molecular studies on the packaging region and DNA diagnostics in cattle. Tartu, 1996, 104 p.
21. **Ene Ustav**. E2 as the modulator of the BPV1 DNA replication. Tartu, 1996, 100 p.
22. **Aksel Soosaar**. Role of helix-loop-helix and nuclear hormone receptor transcription factors in neurogenesis. Tartu, 1996, 109 p.
23. **Maido Remm**. Human papillomavirus type 18: replication, transformation and gene expression. Tartu, 1997, 117 p.
24. **Tiiu Kull**. Population dynamics in *Cypripedium calceolus* L. Tartu, 1997, 124 p.
25. **Kalle Olli**. Evolutionary life-strategies of autotrophic planktonic microorganisms in the Baltic Sea. Tartu, 1997, 180 p.
26. **Meelis Pärtel**. Species diversity and community dynamics in calcareous grassland communities in Western Estonia. Tartu, 1997, 124 p.
27. **Malle Leht**. The Genus *Potentilla* L. in Estonia, Latvia and Lithuania: distribution, morphology and taxonomy. Tartu, 1997, 186 p.
28. **Tanel Tenson**. Ribosomes, peptides and antibiotic resistance. Tartu, 1997, 80 p.
29. **Arvo Tuvikene**. Assessment of inland water pollution using biomarker responses in fish *in vivo* and *in vitro*. Tartu, 1997, 160 p.
30. **Urmas Saarma**. Tuning ribosomal elongation cycle by mutagenesis of 23S rRNA. Tartu, 1997, 134 p.
31. **Henn Ojaveer**. Composition and dynamics of fish stocks in the gulf of Riga ecosystem. Tartu, 1997, 138 p.
32. **Lembi Lõugas**. Post-glacial development of vertebrate fauna in Estonian water bodies. Tartu, 1997, 138 p.
33. **Margus Pooga**. Cell penetrating peptide, transportan, and its predecessors, galanin-based chimeric peptides. Tartu, 1998, 110 p.
34. **Andres Saag**. Evolutionary relationships in some cetrarioid genera (Lichenized Ascomycota). Tartu, 1998, 196 p.
35. **Aivar Liiv**. Ribosomal large subunit assembly *in vivo*. Tartu, 1998, 158 p.
36. **Tatjana Oja**. Isoenzyme diversity and phylogenetic affinities among the eurasian annual bromes (*Bromus* L., Poaceae). Tartu, 1998, 92 p.
37. **Mari Moora**. The influence of arbuscular mycorrhizal (AM) symbiosis on the competition and coexistence of calcareous crassland plant species. Tartu, 1998, 78 p.
38. **Olavi Kurina**. Fungus gnats in Estonia (*Diptera: Bolitophilidae, Keroplatidae, Macroceridae, Ditomyiidae, Diadocidiidae, Mycetophilidae*). Tartu, 1998, 200 p.
39. **Andrus Tasa**. Biological leaching of shales: black shale and oil shale. Tartu, 1998, 98 p.
40. **Arnold Kristjuhan.** Studies on transcriptional activator properties of tumor suppressor protein p53. Tartu, 1998, 86 p.

41. **Sulev Ingerpuu.** Characterization of some human myeloid cell surface and nuclear differentiation antigens. Tartu, 1998, 163 p.
42. **Veljo Kisand.** Responses of planktonic bacteria to the abiotic and biotic factors in the shallow lake Võrtsjärv. Tartu, 1998, 118 p.
43. **Kadri Põldmaa.** Studies in the systematics of hypomyces and allied genera (Hypocreales, Ascomycota). Tartu, 1998, 178 p.
44. **Markus Vetemaa.** Reproduction parameters of fish as indicators in environmental monitoring. Tartu, 1998, 117 p.
45. **Heli Talvik.** Prepatent periods and species composition of different *Oesophagostomum* spp. populations in Estonia and Denmark. Tartu, 1998, 104 p.
46. **Katrin Heinsoo.** Cuticular and stomatal antechamber conductance to water vapour diffusion in *Picea abies* (L.) karst. Tartu, 1999, 133 p.
47. **Tarmo Annilo.** Studies on mammalian ribosomal protein S7. Tartu, 1998, 77 p.
48. **Indrek Ots.** Health state indicies of reproducing great tits (*Parus major*): sources of variation and connections with life-history traits. Tartu, 1999, 117 p.
49. **Juan Jose Cantero.** Plant community diversity and habitat relationships in central Argentina grasslands. Tartu, 1999, 161 p.
50. **Rein Kalamees.** Seed bank, seed rain and community regeneration in Estonian calcareous grasslands. Tartu, 1999, 107 p.
51. **Sulev Kõks.** Cholecystokinin (CCK) — induced anxiety in rats: influence of environmental stimuli and involvement of endopioid mechanisms and erotonin. Tartu, 1999, 123 p.
52. **Ebe Sild.** Impact of increasing concentrations of O_3 and CO_2 on wheat, clover and pasture. Tartu, 1999, 123 p.
53. **Ljudmilla Timofejeva.** Electron microscopical analysis of the synaptonemal complex formation in cereals. Tartu, 1999, 99 p.
54. **Andres Valkna.** Interactions of galanin receptor with ligands and G-proteins: studies with synthetic peptides. Tartu, 1999, 103 p.
55. **Taavi Virro.** Life cycles of planktonic rotifers in lake Peipsi. Tartu, 1999, 101 p.
56. **Ana Rebane.** Mammalian ribosomal protein S3a genes and intron-encoded small nucleolar RNAs U73 and U82. Tartu, 1999, 85 p.
57. **Tiina Tamm.** Cocksfoot mottle virus: the genome organisation and translational strategies. Tartu, 2000, 101 p.
58. **Reet Kurg.** Structure-function relationship of the bovine papilloma virus E2 protein. Tartu, 2000, 89 p.
59. **Toomas Kivisild.** The origins of Southern and Western Eurasian populations: an mtDNA study. Tartu, 2000, 121 p.
60. **Niilo Kaldalu.** Studies of the TOL plasmid transcription factor XylS. Tartu 2000. 88 p.

61. **Dina Lepik.** Modulation of viral DNA replication by tumor suppressor protein p53. Tartu 2000. 106 p.
62. **Kai Vellak.** Influence of different factors on the diversity of the bryophyte vegetation in forest and wooded meadow communities. Tartu 2000. 122 p.
63. **Jonne Kotta.** Impact of eutrophication and biological invasionas on the structure and functions of benthic macrofauna. Tartu 2000. 160 p.
64. **Georg Martin.** Phytobenthic communities of the Gulf of Riga and the inner sea the West-Estonian archipelago. Tartu, 2000. 139 p.
65. **Silvia Sepp.** Morphological and genetical variation of *Alchemilla L.* in Estonia. Tartu, 2000. 124 p.
66. **Jaan Liira.** On the determinants of structure and diversity in herbaceous plant communities. Tartu, 2000. 96 p.
67. **Priit Zingel.** The role of planktonic ciliates in lake ecosystems. Tartu 2001. 111 p.
68. **Tiit Teder.** Direct and indirect effects in Host-parasitoid interactions: ecological and evolutionary consequences. Tartu 2001. 122 p.
69. **Hannes Kollist.** Leaf apoplastic ascorbate as ozone scavenger and its transport across the plasma membrane. Tartu 2001. 80 p.
70. **Reet Marits.** Role of two-component regulator system PehR-PehS and extracellular protease PrtW in virulence of *Erwinia Carotovora* subsp. *Carotovora*. Tartu 2001. 112 p.
71. **Vallo Tilgar.** Effect of calcium supplementation on reproductive performance of the pied flycatcher *Ficedula hypoleuca* and the great tit *Parus major,* breeding in Nothern temperate forests. Tartu, 2002. 126 p.
72. **Rita Hõrak.** Regulation of transposition of transposon Tn*4652* in *Pseudomonas putida*. Tartu, 2002. 108 p.
73. **Liina Eek-Piirsoo.** The effect of fertilization, mowing and additional illumination on the structure of a species-rich grassland community. Tartu, 2002. 74 p.
74. **Krõõt Aasamaa.** Shoot hydraulic conductance and stomatal conductance of six temperate deciduous tree species. Tartu, 2002. 110 p.
75. **Nele Ingerpuu.** Bryophyte diversity and vascular plants. Tartu, 2002. 112 p.
76. **Neeme Tõnisson.** Mutation detection by primer extension on oligonucleotide microarrays. Tartu, 2002. 124 p.
77. **Margus Pensa.** Variation in needle retention of Scots pine in relation to leaf morphology, nitrogen conservation and tree age. Tartu, 2003. 110 p.
78. **Asko Lõhmus.** Habitat preferences and quality for birds of prey: from principles to applications. Tartu, 2003. 168 p.
79. **Viljar Jaks.** p53 — a switch in cellular circuit. Tartu, 2003. 160 p.
80. **Jaana Männik.** Characterization and genetic studies of four ATP-binding cassette (ABC) transporters. Tartu, 2003. 140 p.
81. **Marek Sammul.** Competition and coexistence of clonal plants in relation to productivity. Tartu, 2003. 159 p

82. **Ivar Ilves.** Virus-cell interactions in the replication cycle of bovine papillomavirus type 1. Tartu, 2003. 89 p.
83. **Andres Männik.** Design and characterization of a novel vector system based on the stable replicator of bovine papillomavirus type 1. Tartu, 2003. 109 p.
84. **Ivika Ostonen.** Fine root structure, dynamics and proportion in net primary production of Norway spruce forest ecosystem in relation to site conditions. Tartu, 2003. 158 p.
85. **Gudrun Veldre.** Somatic status of 12–15-year-old Tartu schoolchildren. Tartu, 2003. 199 p.
86. **Ülo Väli.** The greater spotted eagle *Aquila clanga* and the lesser spotted eagle *A. pomarina*: taxonomy, phylogeography and ecology. Tartu, 2004. 159 p.
87. **Aare Abroi.** The determinants for the native activities of the bovine papillomavirus type 1 E2 protein are separable. Tartu, 2004. 135 p.
88. **Tiina Kahre.** Cystic fibrosis in Estonia. Tartu, 2004. 116 p.
89. **Helen Orav-Kotta.** Habitat choice and feeding activity of benthic suspension feeders and mesograzers in the northern Baltic Sea. Tartu, 2004. 117 p.
90. **Maarja Öpik.** Diversity of arbuscular mycorrhizal fungi in the roots of perennial plants and their effect on plant performance. Tartu, 2004. 175 p.
91. **Kadri Tali.** Species structure of *Neotinea ustulata*. Tartu, 2004. 109 p.
92. **Kristiina Tambets.** Towards the understanding of post-glacial spread of human mitochondrial DNA haplogroups in Europe and beyond: a phylogeographic approach. Tartu, 2004. 163 p.
93. **Arvi Jõers.** Regulation of p53-dependent transcription. Tartu, 2004. 103 p.
94. **Lilian Kadaja.** Studies on modulation of the activity of tumor suppressor protein p53. Tartu, 2004. 103 p.
95. **Jaak Truu.** Oil shale industry wastewater: impact on river microbial community and possibilities for bioremediation. Tartu, 2004. 128 p.
96. **Maire Peters.** Natural horizontal transfer of the *pheBA* operon. Tartu, 2004. 105 p.
97. **Ülo Maiväli.** Studies on the structure-function relationship of the bacterial ribosome. Tartu, 2004. 130 p.
98. **Merit Otsus.** Plant community regeneration and species diversity in dry calcareous grasslands. Tartu, 2004. 103 p.
99. **Mikk Heidemaa.** Systematic studies on sawflies of the genera *Dolerus, Empria,* and *Caliroa* (Hymenoptera: Tenthredinidae). Tartu, 2004. 167 p.
100. **Ilmar Tõnno.** The impact of nitrogen and phosphorus concentration and N/P ratio on cyanobacterial dominance and N_2 fixation in some Estonian lakes. Tartu, 2004. 111 p.
101. **Lauri Saks.** Immune function, parasites, and carotenoid-based ornaments in greenfinches. Tartu, 2004. 144 p.

102. **Siiri Rootsi.** Human Y-chromosomal variation in European populations. Tartu, 2004. 142 p.
103. **Eve Vedler.** Structure of the 2,4-dichloro-phenoxyacetic acid-degradative plasmid pEST4011. Tartu, 2005. 106 p.
104. **Andres Tover.** Regulation of transcription of the phenol degradation *pheBA* operon in *Pseudomonas putida*. Tartu, 2005. 126 p.
105. **Helen Udras.** Hexose kinases and glucose transport in the yeast *Hansenula polymorpha*. Tartu, 2005. 100 p.
106. **Ave Suija.** Lichens and lichenicolous fungi in Estonia: diversity, distribution patterns, taxonomy. Tartu, 2005. 162 p.
107. **Piret Lõhmus.** Forest lichens and their substrata in Estonia. Tartu, 2005. 162 p.
108. **Inga Lips.** Abiotic factors controlling the cyanobacterial bloom occurrence in the Gulf of Finland. Tartu, 2005. 156 p.
109. **Kaasik, Krista.** Circadian clock genes in mammalian clockwork, metabolism and behaviour. Tartu, 2005. 121 p.
110. **Juhan Javoiš.** The effects of experience on host acceptance in ovipositing moths. Tartu, 2005. 112 p.
111. **Tiina Sedman.** Characterization of the yeast *Saccharomyces cerevisiae* mitochondrial DNA helicase Hmi1. Tartu, 2005. 103 p.
112. **Ruth Aguraiuja.** Hawaiian endemic fern lineage *Diellia* (Aspleniaceae): distribution, population structure and ecology. Tartu, 2005. 112 p.
113. **Riho Teras.** Regulation of transcription from the fusion promoters generated by transposition of Tn*4652* into the upstream region of *pheBA* operon in *Pseudomonas putida*. Tartu, 2005. 106 p.
114. **Mait Metspalu.** Through the course of prehistory in india: tracing the mtDNA trail. Tartu, 2005. 138 p.
115. **Elin Lõhmussaar.** The comparative patterns of linkage disequilibrium in European populations and its implication for genetic association studies. Tartu, 2006. 124 p.
116. **Priit Kupper.** Hydraulic and environmental limitations to leaf water relations in trees with respect to canopy position. Tartu, 2006. 126 p.
117. **Heili Ilves.** Stress-induced transposition of Tn*4652* in *Pseudomonas Putida*. Tartu, 2006. 120 p.
118. **Silja Kuusk.** Biochemical properties of Hmi1p, a DNA helicase from *Saccharomyces cerevisiae* mitochondria. Tartu, 2006. 126 p.
119. **Kersti Püssa.** Forest edges on medium resolution landsat thematic mapper satellite images. Tartu, 2006. 90 p.
120. **Lea Tummeleht.** Physiological condition and immune function in great tits (*Parus major* l.): Sources of variation and trade-offs in relation to growth. Tartu, 2006. 94 p.
121. **Toomas Esperk.** Larval instar as a key element of insect growth schedules. Tartu, 2006. 186 p.

122. **Harri Valdmann.** Lynx (*Lynx lynx*) and wolf (*Canis lupus*) in the Baltic region: Diets, helminth parasites and genetic variation. Tartu, 2006. 102 p.
123. **Priit Jõers.** Studies of the mitochondrial helicase Hmi1p in *Candida albicans* and *Saccharomyces cerevisia*. Tartu, 2006. 113 p.
124. **Kersti Lilleväli.** Gata3 and Gata2 in inner ear development. Tartu, 2007. 123 p.
125. **Kai Rünk.** Comparative ecology of three fern species: *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *D. expansa* (C. Presl) Fraser-Jenkins & Jermy and *D. dilatata* (Hoffm.) A. Gray (Dryopteridaceae). Tartu, 2007. 143 p.
126. **Aveliina Helm.** Formation and persistence of dry grassland diversity: role of human history and landscape structure. Tartu, 2007. 89 p.
127. **Leho Tedersoo.** Ectomycorrhizal fungi: diversity and community structure in Estonia, Seychelles and Australia. Tartu, 2007. 233 p.
128. **Marko Mägi.** The habitat-related variation of reproductive performance of great tits in a deciduous-coniferous forest mosaic: looking for causes and consequences. Tartu, 2007. 135 p.
129. **Valeria Lulla.** Replication strategies and applications of Semliki Forest virus. Tartu, 2007. 109 p.
130. **Ülle Reier**. Estonian threatened vascular plant species: causes of rarity and conservation. Tartu, 2007. 79 p.
131. **Inga Jüriado**. Diversity of lichen species in Estonia: influence of regional and local factors. Tartu, 2007. 171 p.