

Pro Gradu –tutkielma

Alarm calls in action – does it pay off to help?

Santtu Kareksela



Jyväskylän yliopisto

Bio- ja ympäristötieteiden laitos

Ekologia ja ympäristöhoito

2.7.2008

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos
Ekologia ja ympäristönhoito

KAREKSELA, S. : Hömötiaisen, *Parus montanus*, varoitusäänen vaikutus varpuspöllön, *Glaucidium passerinum*, saaliinvalintaan

Pro Gradu –tutkielma: 21 s.
Työn ohjaajat: FT Jukka Suhonen, FT Heli Siitari
Tarkastajat: FT Tapio Mappes, FT Heli Siitari
Heinäkuu 2008

Hakusanat: alarm call, localize, prey preference, pygmy owl, willow tit

TIIVISTELMÄ

Perinteisesti varoitusäänen antamisesta on katsottu aiheutuvan kustannuksia varoittajalle, koska varoituksen on ajateltu kiinnittävän pedon huomion varoittajaan. Tämän vuoksi varoittamiseen mahdollisesti liittyvät kustannukset ovat herättäneet keskustelua varottamiskäyttäytymisen altruistisuudesta eli siitä kuka tai ketkä varoituksesta hyötyvät ja miten? Tutkimukset ovatkin paljastaneet monia eri mekanismeja, jotka ylläpitävät varoitusääniin liittyvää käyttäytymistä. Sukulaisvalintaan liittyvät teoriat selittävät varoitusäänten hyödyllisyyttä jälkeläisten paremman selviytymisen kautta, mutta eivät pysty selittämään varoittamista lisääntymiskauden ulkopuolella. Sen sijaan, ilman sukulaisten läheisyyttä tapahtuvaa varoittamista on selitetty äänten paikallistettavuuden avulla. Klassisen lähestymistavan mukaan varoitusääni on fyysisesti rakentunut siten, että pedon on vaikea paikallistaa sitä, jolloin varoittamisesta aiheutuvat kustannukset pienenevät saaliin säilyttäessä piilopaikkansa. Vaihtoehtoisesti on esitetty, että varoitus voisi olla myös suoraan pedolle tarkoitettu viesti, joka kertoisi, että peto on nähty, jolloin peto on menettänyt yllätyshyökkäyksen tuoman edun saaliin tietäessä sen sijainnin. Runsaasta teoreettisesta taustasta huolimatta vain harvassa tutkimuksessa on suoraan testattu tätä pedon kykyä paikallistaa varoitusääniä sekä niiden vaikutuksia pedon saalistustilanteessa tekemiin ratkaisuihin. Näiden tutkimiseksi suoritettiin kaksi käyttäytymiskoetta, jotka käsittelivät varoitusäänten paikallistettavuutta ja hyökkäyksestä saaliille aiheutuvia mahdollisia kustannuksia pedon näkökulmasta. Aluksi selvitettiin pystyykö varpuspöllö, *Glaucidium passerinum*, paikallistamaan varoitusäänen, jota hömötiaiset, *Parus montanus*, käyttävät pedon (esim. väijyvä varpuspöllö) yllättäen ilmestyessä lähietäisyydelle. Seuraavaksi verrattiin varoittajan ja hiljaa pysyvien saaliiden välistä todennäköisyyttä joutua varpuspöllön saaliiksi varoitustilanteessa. Kokeet osoittivat, että pedot pystyivät selvästi paikallistamaan hömötiaisten antaman varoitusäänen. Varoittamisesta ei tässä yhteydessä kuitenkaan ollut kustannuksia varoittajalle, koska pöllöt valitsivat aina ei-varoittavan hiljaisen saaliin. Tämä tutkimus osoittaa, että tilanteessa jossa tutkittua varoitusääntä käytetään, varoitus viestittää pedolle, että varoittaja on nähnyt sen, jolloin se on vaikeampi saalis. Pedon suosiessa helpompia saaliita varoittaja jopa hyötyy varoituksen antamisesta, koska sen riski joutua saaliiksi vähenee varoittamisen myötä.

UNIVERSITY OF JYVÄSKYLÄ, Faculty of Science

Department of Ecological and Environmental Science

KAREKSELA, S.: Alarm calls in action: does it pay off to help?

Master of Science Thesis: 21 p.

Supervisors: PhD Jukka Suhonen, PhD Heli Siitari

Inspectors: PhD Tapio Mappes, PhD Heli Siitari

July 2008

Key Words: alarm call, localize, prey preference, pygmy owl, willow tit

ABSTRACT

Traditionally alarm call behavior has been considered costly for the caller because launching an alarm has been thought to attract a predator's attention. This has induced discussion considering alarm calls as an altruistic action, raising a question who actually benefits from an alarm and how? Many theories and studies have revealed different mechanisms that could maintain alarm call behavior. According to kin selection theories alarming pays off because it increases survival of the caller's offspring. However, kin selection theory fails to explain the alarming behavior outside the breeding season. Alarm calling in the absence of relatives has led to controversial theories about the inconspicuousness of alarm calls. Classically it has been suggested that the structure of the call makes it hard to be located by a predator, decreasing the costs of alarming. Alternatively it has been suggested that one function of an alarm call is to deliver a message also to the predator saying that it has been seen and there is no reason to continue the attack now that the advantage of surprise is lost. Despite this versatile theoretical background there has been only few studies dealing predators' ability to locate alarm calls and there is no experimental data considering the effect of alarm calls on predator's prey preferences. Thus, to test these assumptions about the conspicuousness of the calls, two experiments were conducted dealing the conspicuousness and the costs of alarming from the predators perspective. First pygmy owls, *Glaucidium passerinum*, were tested, to determine if they could localize an alarm call used by willow tits, *Parus montanus*, at a sudden appearance of a close predator (i.e. a stalking pygmy owl). Next, it was investigated how the alarm affects the probability of being attacked by a stalking predator (pygmy owl) between an individual giving the alarm and its silent flock mates. The experiments show that the alarm call used by willow tits in this context is clearly locatable for the predator. However, alarming did not involve any costs as the owls only attacked the non-alarming individuals. The results indicate that the alarm call in this context includes a message for the predator that it has been seen by the caller, making the catching of this specific individual more difficult for the predator. Moreover, it seems that in this situation the caller actually benefits from alarm calling as it reduces the risk of predation.

Contents

| | |
|--------------------------------------|-----------|
| 1. INTRODUCTION..... | 5 |
| 2. MATERIALS AND METODS | 8 |
| 2.1 Study species..... | 8 |
| 2.2 Call types | 9 |
| 2.3 Experimental design..... | 10 |
| 2.3.1 Localization accuracy | 10 |
| 2.3.2 Prey preference | 11 |
| 2.4 Statistical analyses | 12 |
| 3. RESULTS..... | 13 |
| 3.1 Localization accuracy | 13 |
| 3.2 Prey preference | 16 |
| 4. DISCUSSION | 16 |
| Acknowledgments | 19 |
| Literature cited..... | 19 |

1. INTRODUCTION

In order to survive, prey species have evolved numerous ways to avoid attacks. Consequently, predators are evolving to minimize the energy expenditure of obtaining prey. In other words, the arms race between predator and prey produces more and more efficient predators and more and more effectively defending prey species trying to minimize the risk of being hunted. In many mammal and bird species predation has led to evolution of accurate vocalizations that are effectively used to inform the other nearby individuals about the presence of a predator (e.g. Marler 1955, Klump & Shalter 1984). These calls can be either purely informative or include a request to action. Informative calls can include various information from the type of a predator to its distance (e.g. Seyfarth et al. 1980, Ficken 1989, Zuberbühler 2001, Fichtel & Kappeler 2002, Templeton et al. 2005). Calls requesting an action are usually mobbing calls which are used to frighten the predator and to break its prey image (i.e. to confuse a predator by behaving unexpectedly) together with other members of the flock or herd (Sherman 1977, Klump & Shalter 1984). Many different types of calls can be described and classified in more detail according to their functions (e.g. alarming, harassing or confusing) and physical properties (e.g. duration, pitch and changes in frequency) enabling these functions (Marler 1955, Klump & Shalter 1984,).

Research on alarm calls was initiated by Marler (1955). In that article Marler introduced a dilemma in alarming. He suggested that by giving an alarm an individual draws the predator's attention to itself. Thus by alarming its companions the caller would increase its own risk to be attacked. How could this kind of behaviour evolve? Marler's solution was that when giving an alarm about a predator, animals use high, monotonic and fading "seeet" calls which are hard to locate and therefore do not reveal the alarming individual. Marler's conclusions were later criticized for leaning too much on human physiology and our constraints in locating sound sources. However, his hypotheses have inspired many researchers to produce studies on animal communication abilities to altruism (Maynard Smith 1965, Trivers 1971, Charnov & Krebs 1975, Sherman 1977, Klump et al. 1986).

Physically relatively similar, conspecific alarm calls that are hard to locate, e.g. the "seeet" alarm (Marler 1955, Klump & Shalter 1984, Klump et al. 1986), give indirect evidence that using locatable vocalizations include a possible cost of increased predation risk. There have been several studies dealing with the cost of alarming. For instance, Sherman (1977) showed that ground squirrels, *Spermophilus beldingi*, giving an alarm suffered a greater risk of being preyed upon by ground predators but not by flying predators (see also Sherman 1985). In addition, Alatalo & Helle (1990) found out in their experiment that willow tits, *Parus montanus*, gave alarms more frequently when a hawk shaped model was flown further from an individual than at shorter distances. They concluded that this was a result of a greater risk of the source of the alarm (the individual itself) being located by the predators when it was nearer. Moreover, Krams (2001) compared short and long distance communication calls of crested tits, *Parus cristatus*, and found out that long distance calls attracted more hawks to attack at the stuffed crested tit dummies at their study sites.

The results from these empirical studies clearly state that a vocalization includes a risk of attracting predator's attention. However, the question is whether the risk is reduced when using high pitched "seeet" calls as Marler (1955) suggested? Some experiments have been performed dealing with predator's ability to detect sounds. Konishi (1973), Klump et al. (1986) and Brown (1982) found out that "seeet" typed calls and sounds were harder to

locate for the predator than lower pitched sounds, such as mobbing calls. However, in Shalter's experiments (1978) goshawks, *Accipiter gentilis*, and two species of pygmy owl, *Glaucidium perlatum* and *G. brasilianum*, could reliably locate high pitched alarm calls. This indicates that the conspicuousness of the sound cannot alone explain the alarm call behaviour in all situations and/or with all species as there is variation between predator species in their ability to locate sound sources. At least the distance of the predator (Alatalo & Helle 1990) is an essential factor of the usefulness or cost of the alarm. The further away the predator is the less accurately it can locate the sound source and the more time the possible preys have to react, decreasing the possible costs of alarming. In other words the costs of alarming action seem to be highly context dependent (Caro 2005).

Despite the costs presented, alarm calling seems to be a beneficial trait as it is maintained in populations. One explanation is that the benefits are gained through kin selection (Maynard Smith 1965, Sherman 1977, 1980). According to Hamilton's rule (1964) an individual benefits from helping (e.g. alarming) if the increase in receivers fitness multiplied by receivers relatedness to the helper is bigger than the fitness cost of the alarming individual. Sherman (1977) found support for Hamilton's rule as ground squirrels he observed gave alarm calls more frequently when they had their own offspring near them. Sherman concluded that the increased predation risk caused by giving an alarm was paid off by the increased survival of the offspring or other relatives of the alarming individual. However Sherman's hypothesis about kin selection making alarming beneficial does not apply in all cases of alarm call behaviour. For instance, wintering tit flocks often contain birds from many species and usually even the individuals from the same species are not relatives (e.g. Ekman 1979). Naturally in these flocks the alarming behaviour cannot be explained by kin selection (Maynard Smith, 1965, Klump & Shalter, 1984). Alatalo and Helle (1990) found out that old males of willow tit, *Parus montanus*, captured from stable winter flocks, gave alarm calls more frequently than subordinate males or females. They suggested that the alarm could thus be an investment to a future mating partner's survival (see also Hogstad 1995, Krams et al. 2006). However, they found out that also the subordinates gave alarms implying that individuals with different status might gain different benefits from alarming.

Also inspired by the fact that alarm calls are used outside the breeding season, Trivers (1971) discussed alarm calling without any relatives near, for example after dispersal, as a case of reciprocal altruism. Although an alarming individual may suffer from greater predation risk (at least occasionally) and thus behaves seemingly altruistic, helping is mutually beneficial as previously alarmed individual is alarming reciprocally in the future. However reciprocal alarming is open to cheating when some individuals might even benefit from the death of another flock member (Ekman 1986, Alatalo & Helle 1990) and the chance to reciprocate could be lost for example as a result of migration. This means that truly reciprocal behaviour can only occur in relatively stable groups (Alatalo & Helle 1990), which can be found among some mammals but are rare among bird aggregations (Caro 2005). Trivers (1971) realized that cheating and the requirement for stability set constraints for reciprocal actions and introduced an alternative hypothesis for alarming behaviour. According to Trivers (1971) the benefits of otherwise costly alarming comes from reduced functional responses of a sedentary predator. That is, the predator's ability to specialize on a prey group is reduced as groups with alarming individuals are harder to prey upon and the predator thus catches them less frequently. This would increase the relative fitness of the caller as it is always in a group with at least one caller whereas the non-alarming individuals occasionally end up in groups without any callers in an area where a predator has been able to specialize on the prey group.

Charnov and Krebs (1975) criticized Trivers' (1971) idea about the reduced learning

of the predator making the alarming beneficial. Using a theoretical model they stated that alarming would not be favourable once the frequency of the groups containing alarming individuals reaches a certain level (i.e. there are not enough groups without a caller so predators have to prey upon the groups with callers as well). Instead they suggested that alarming in a flock of birds is a form of manipulation. It has been shown that even the alarm calls of passerine birds include a lot of information about the predator and the degree of danger (Templeton et. al. 2005). Nevertheless, there has been no evidence that the exact location of the predator could be included in any alarm calls. According to Charnov & Krebs's theory, the alarmed individuals of the flock unaware of the predator's location flee in panic and will be easy targets for the predator. Thus, the giver of the alarm gains safety by manipulating the other flock members to attract the predator's attention. However, the usual reaction to an alarm call in a flock of passerine birds is freezing in order to avoid predator's attention (Ficken & Witkin 1977, Rajala et al. 2003). Suggested by Witkin and Ficken (1979), this kind of manipulation could be possible only in an open landscape where freezing without any cover offers little protection.

Even though there have been both theoretical and experimental studies on alarm calls, none of them tested whether predators could actually benefit from the alarm calls of their prey species, either by locating prey or by concentrating on the individuals unaware of the predators location. In addition, most of the previous experiments handling the predator in alarm call context cover only the birds of preys' ability to locate passerine bird's high "seeet" alarm calls. The results of these experiments have been controversial and, even though giving important knowledge about the audible thresholds of predatory birds and their prey (e.g. Klump et al. 1986), we still lack the knowledge of predators reaction to alarming when they are actually stalking prey. To investigate how predators react to alarm calls, this study contains two behavioural experiments in controlled conditions in an aviary. A predator's, pygmy owl (*Glaucidium passerinum*), ability to locate an alarm call given in a sudden appearance of the predator (pygmy owl) at close distance (Haftorn 1993), and how this alarm call affects the predator's (pygmy owl) prey preference were both tested in this study. Alarm calls tested were given by willow tit, *Parus montanus*, which is one of the most abundant tits in Finnish forests. The pygmy owl was used as a predator because it is the main predator of tits in winter flocks in boreal forests (Suhonen 1993a, Kullberg & Ekman 2000). Bullfinch's, *Pyrrhula pyrrhula*, contact call was chosen as the control call because of its physical properties which were quite parallel to the alarm call (Table 1). Willow tits, and also bullfinches, are common birds in coniferous forests in same regions in central Finland.

In the first experiment the conspicuousness of two types of calls differing in their structure was studied (Table 1) namely, a) an alarm call given when a predator is already near the flock and ready to hit a suitable target and b) bullfinch's contact call. The alarm call (a) chosen is physically quite different from the classical "seeet" alarm which is usually given when a flying predator is further away (e.g. Marler 1955, Klump & Shalter 1984, Alatalo & Helle 1990) (Table 1). The willow tit's alarm call given for a pygmy owl at close distance seems relatively easy to be located. It consists of a sequence of high pitched short notes with alternating frequencies. It starts and ends clearly and, at least compared to the bullfinch call, has a relatively long duration (Table 1). These are all features of locatable vocalizations (Marler 1955, Klump & Shalter 1984). The control call (b) is a contact call given in a situation where predator is not known to be present and therefore the bullfinch call should be relatively conspicuous i.e. not too hard to be detected or localize, at least in relatively close distance. However, the bullfinch call, despite being a contact call, has many physical properties usually associated with unlocatable calls (i.e. the "seeet" call), thus being quite the opposite of the alarm call in question. The contact call

fades in and out and has a monotonic frequency, which both make the binaural comparison (i.e. the direction of the sound source is determined by comparing the differences in information received by each ear) difficult (e.g. Marler 1955, Klump & Shalter 1984). In addition the duration of the call is quite short (at least compared to the alarm call), which naturally makes the localization even more difficult, giving less time to spot the sound source. However, the frequency of the bullfinch call is distinctly low (e.g. compared to the alarm call), which makes locating the vocalization easier by phase difference in binaural comparison, i.e. vocalizations in mid range frequencies are easier to locate than higher vocalizations (Marler 1955, Klump et al. 1986). If the alarm call (a) is locatable by predators as suggested by its physical attributes, it should not be significantly harder to be located than the contact call (b). By comparing predator's reactions to these two different types of calls information about the conspicuousness of this alarm call could be achieved.

In the second experiment the ability of the predator to actually use these alarm calls as cues when choosing the prey was examined in more detail. A prey preference experiment was conducted, where alarming and non-alarming preys were presented simultaneously to a predator, and the predator's attack preferences (the attacked prey item) on different dummy preys (stuffed willow tits) were measured. Two alternative hypotheses were generated. Giving the alarm could either increase the risk of being attacked or it could decrease it (or there could naturally be no effect). If the individual detecting the predator gives the alarm, and all the others will either freeze or take cover, then the alarming individual is the only one who definitely knows where the predator is. This information makes the caller the hardest one to catch, because it can see the attack and is able to escape from the attacking (diving) owl. Thus trying to minimize the energy required to the catching of the prey, the owl should avoid the caller and instead concentrate its hunting effort to the other members of the flock. In this way, the alarm could also be a message to the predator: "you have been seen, do not try to catch me" (Shalter and Schleidt 1977). In contrast to the classical view about alarming behaviour, giving the alarm would then be an instant benefit to the individual by reduced predation risk.

2. MATERIALS AND METHODS

2.1 Study species

Pygmy owls, *Glaucidium passerinum*, are diurnal (day active) sit-and-wait predators (Mikkola 1983, Kullberg 1995) meaning that they stalk their prey at a relatively close distance, for example, sitting in a tree. The summer diet of the pygmy owls includes small mammals, mainly voles, but during winter, the amount of birds in diet increases (Kullberg 1995). Pygmy owls are being reported to locate tit flocks, for example, by following their contact calls (Kullberg 1995). After locating a flock, they sneak close to it, by flying around the flock in the surrounding trees looking for a good place to wait for the right moment to hit (Kullberg 1995). When a member of a tit flock sees a stalking owl it usually immediately gives an alarm (Rajala et al. 2003). As a reaction the members of the flock usually freeze or try to flee (Ficken & Witkin 1977, Rajala et al. 2003). Willow tits, *Parus montanus*, are a relative large tit species of the parus guild and form small, stable conspecific groups outside breeding season (Ekman 1986). The individuals in these groups are not closely related (e.g. Ekman 1986) and these flocks show a hierarchy in respective to the social rank of the individuals (e.g. Hogstad 1988). Willow tits also appear in mixed species tit flocks where they are at the top division in hierarchy between species, second only to crested tits, *Parus cristatus*. For example Coal tits, *P. ater*, and goldcrests, *Regulus regulus*, are subdominants to willow tits. Both inter- and conspecific hierarchy shows in

individuals' foraging sites in respect to food abundance and cover against predation e.g. by pygmy owls (e.g. Ekman 1986, Hogstad 1988, Suhonen et al. 1992, Suhonen 1993a & b, Suhonen et al. 1993). Despite of their high rank in the mixed species flock hierarchy, willow tits can form a relatively large proportion of a pygmy owls food supply (Suhonen 1993a).

The owls for the experiments were captured using passive traps installed at storage boxes at central Finland (62°N) at Jyväskylä and Konnevesi areas at autumn and early winter in 2003 and 2004. The traps were installed on boxes that the owls had started to use as larders, i.e. they contained dead prey (mainly tits, voles and shrews). The traps activated when an owl flew in, trapping the owl inside a 13 x 13 x 33 cm nesting box with a 45 mm flying hole. When trapped, the owls had their own prey items in the box to feed on. The owls used these boxes also as resting places at nights. The traps were checked within 24 hours at the latest (usually sooner).

The experiments were conducted at Konnevesi research station of University of Jyväskylä. Both experiments were performed in an aviary of 7 x 8 m and 3.5 m in height. The behaviour of owls was observed through one-way-window during the experiment. The experiments were always conducted during the daytime mimicking the natural activity rhythm of the pygmy owls during the winter (e.g. Mikkola 1983). The localization experiment (exp. 1) was conducted in both years (four owls in 2003 and 7 owls in 2004) and the prey preference experiment (exp. 2) in 2004. Before the actual experiments owls were familiarized with the aviary by letting them fly inside it. Before the prey preference experiments they were also accustomed to catch prey items in the test arena (the aviary) by offering them dead voles (voles were pulled across the floor with a string attached to them). After the experiment, the birds were released at their capture sites (near their storage boxes) with additional food added to their larders. Maximum time in captivity for an owl was one month. All owls generally remained in good health throughout their captivity. Their weights were measured frequently, e.g. before every experiment, and they had gained weight when released. Two owls died (1 in year 2003 and 1 in year 2004) and one was excluded from the experiments and released (with abundant larder) as it refused to feed in captivity. The Central Finland Regional Environmental Center gave us permission to capture and keep the pygmy owls. All experiments (41/8.9.2003, 53/21.10.2003, 54/21.10.2003) were conducted under a license from the Experimental Animal Committee of the University of Jyväskylä.

2.2 Call types

The alarm calls of willow tits (Table 1) used in both experiments were recorded in the wild by using a stuffed pygmy owl placed near a feeder for passerine birds. The owl was first covered and revealed when a flock was present. The given alarms were then recorded (see Rajala et al. (2003) for more detailed methods). The calls used in first experiment were all recorded from different individuals. In the prey preference experiment, only one of the alarm calls was used. Both types of the calls were recorded in forests near the Jyväskylä area. Background noises were cleared from the calls.

Table 1. Properties of the experimental calls (alarm call and contact call) and their differences to "seeet" alarm call described in literature (e.g. Klump & Shalter 1984).

| Call type | Species | Predatory context | Mean duration | Pitch (frequency) | Frequency | start/end |
|--------------|---------------|-------------------|---------------|-------------------|-------------|-----------|
| alarm | willow tit | near | 1.1 | high | alternating | clear |
| contact | bulfinch | not present | 0.3 | low | monotonic | fading |
| seeet -alarm | interspecific | far | | high | monotonic | fading |

2.3 Experimental design

2.3.1 Localization accuracy

In the first experiment the localization accuracy of the pygmy owls between two call types, willow tit alarm call and bullfinch contact call (Table 1) was compared. The number of cues the owls needed to localize the correct sound source and the accuracy of the localization were measured. One small loudspeaker was placed in each corner of the square aviary, on one meter stands. Small (c. 1.5 m) spruces were placed right in front of the loudspeakers so that the sounds seemed to come from the trees. Heavy, dark green cloth, was placed behind the speakers, from the ceiling down to the floor, to prevent echoing in the room. In the middle of the room there was a two meter high perching pole which was four meters away from each loudspeaker. Directly above the perch was attached a digital video camera from the ceiling (1.5 meters above the perch) (see Figure 1 for experimental design).

An owl was released to the room via the door to the observation room. It usually perched on the pole after a short flight around the room or straight after release. The owls were let to perch at least five minutes (or until the individual seemed calm enough) before playbacks were started. If an owl flew from the perch during playbacks, it was paused until it came back and then continued. For each owl eight bullfinch, contact call playbacks and eight willow tit alarm call playbacks were played. The playbacks were played once a minute. Each playback consisted of three replays of the same call with two second silent intervals between the repetitions (for mean durations of single calls for both call types see Table 1). Equal amounts of both types of calls were played from each corner (both call types twice from each corner) (Table 2). The playing order for the corner and for the call type was randomised and it was ensured that the same sound type never came repeatedly from the same corner (thus trying to minimize the cases where the owl would stare at the right corner already before a call started). The sound pressure levels of the playbacks were adjusted in respect to the ambient noise level (mainly air conditioning). Altogether 11 owls were tested for localization accuracy.

The localizations of the calls were determined from the video recordings afterwards. The degrees of the angles at which the owls turned their heads were compared to the exact directions of the loudspeakers. The directions of all head turns during each playback and until five seconds after the last sound of each playback were measured. The localization was interpreted as being correct when the owls looked towards the spruce in front of the right loudspeaker (spruces being the only major visual attractions of the room). The width of one tree was approximately 22° so the "correct" direction was the exact degree of the loudspeaker $\pm 11^\circ$. To minimize measuring error the angles of the head turns were measured twice and the means of the values were used in the tests.

Since every call had three immediate replays points were given according to how many replays an owl needed to locate the correct sound source (corner). If they looked at the right corner after the first replay they got three points, after two replays two points, after three replays one point and zero points if they could not locate the right corner at all. These points were then compared between the two call types (i.e. the more points owls got the less cues they needed to localize the calls). It was also measured how much the first hit to the sector (a spruce in a corner) and the best result (not necessarily the first hit to the sector, since the owls turned their heads usually several times during the playbacks, see Table 2) differed from the exact direction of the sound source. The accuracies of the localizations were then compared between the two call types.

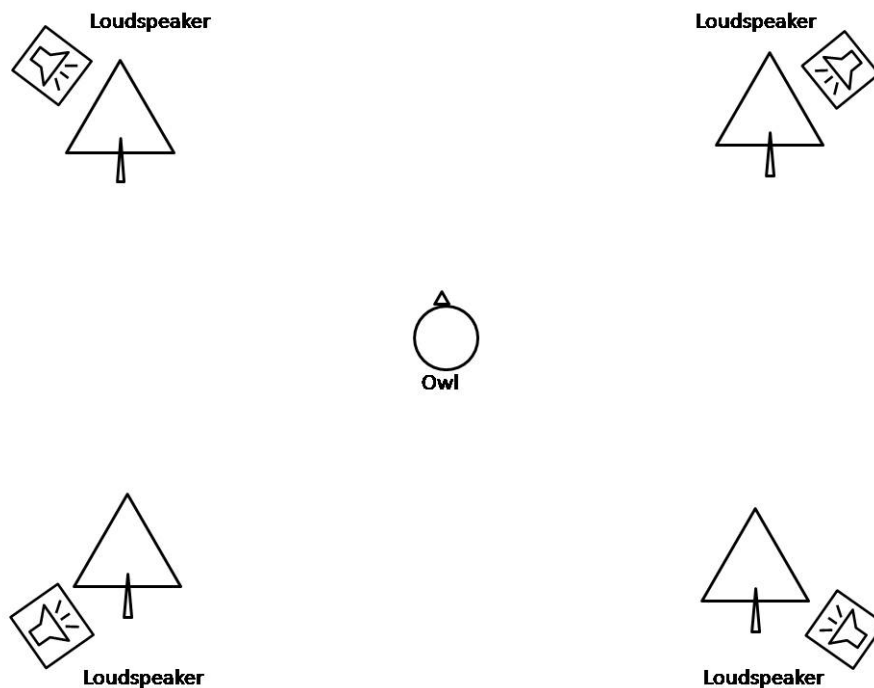


Figure 1. Design of the localization experiment. A video camera was attached to the ceiling at 1.5 meters above the owl (the dimensions are directional).

2.3.2 Prey preference

The attractiveness of alarming and non-alarming preys was compared. In preliminary experiments of the prey preference five prey items were used (stuffed willow tits) in small spruces at one meter height (three attacks were performed by three owls when the preys were at the spruces). As the owls seemed reluctant to attack the prey items at the spruces, the spruces were changed to one meter stands, to increase the attractiveness of the prey items. In the actual experiments the prey items were on one meter poles (14 attacks) in a row forming an arc 3 meters away from the two meter perching pole (see Figure 2 for experimental design). As the owls were behaving similarly in the preliminary and the actual experiment (with the exception of the longer hesitation times in the preliminary experiment) and the experimental designs were identical (except for the change from spruces to poles), their results were pooled into the same data set. Altogether there were 7 owls measured for their prey preference (see Table 2).

At each end and in the middle of the row a small loudspeaker was put right behind the stuffed preys. When an owl was released to the aviary, an alarm call (same as in experiment one but only one replay) was played once every minute (in the first three trials with the spruces the playbacks were stopped during short flights of the owls) from one previously determined loudspeaker at one of the ends of the row. It was then observed which of the four non-alarming and one alarming prey items the owl would choose to attack. Attacks that were launched from the pole were the only ones that were counted. The experiments were stopped as soon as an owl attacked or after 20 minutes without any attacks. The owls usually flow straight to the pole when released and attacked a prey item within few minutes (on average 4 min 30 s for the preys on poles and 13 min 20 s for the preys on spruces). The fastest attacks were made even before perching or before the first alarm was played, in which cases experiments were disqualified. At slowest the attack was performed after 17 minutes with the preys in the spruces and after 13 minutes with the preys on the stands. The experiment was conducted successfully 1-4 times with each owl (only once a day per owl), some of them being more willing to attack than the others (probably due to individual differences in characters). The order of the prey items and the direction of the alarm (i.e. left or right end of the row) were changed between the experiments.

The owls' intentions towards the prey were obvious since after catching the stuffed prey they usually tried to kill them by ripping them to pieces and were reluctant to let go even when an experiment was ended and the owl captured. The owls hit approximately the same amount at the prey items on each poles and they did not specialize on attacking only one pole. In addition, there were no rewards for the owls for attacking so there was no risk of learning during the prey preference experiment.

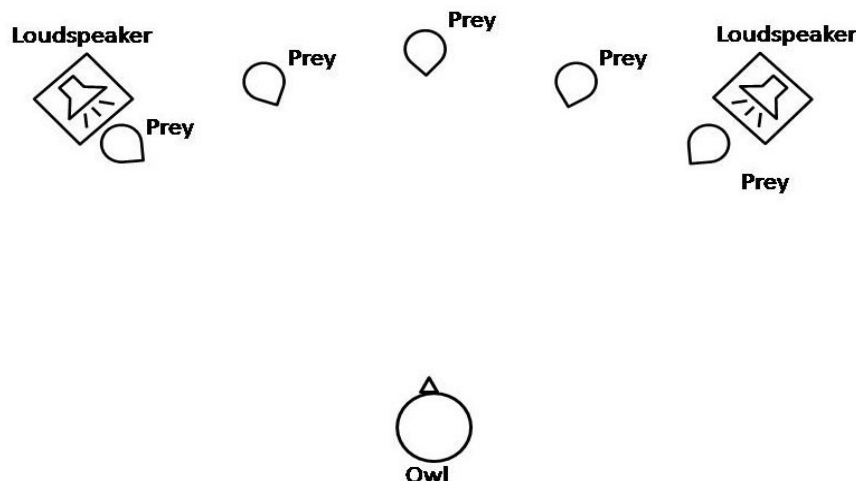


Figure 2. Design of the prey preference experiment. Call came from either end of the arc of the prey items (the dimensions are directional).

2.5 Statistical analyses

A mixed model ANOVA was used to test whether the call type (willow tit's alarm call or bullfinch's contact call) affected the accuracy rate of the localization of sound source (i.e. direction of the caller). The amount of cues (three repetitions of a call within a playback) an owl needed to localize a sound source and the accuracy of the first localization of the

sound source was used as a dependent variable in the model. Because there was generally more than one correct localization action, the accuracy of the most correct localization of the sound source was also examined. Call type was used as a fixed factor and the possible effect of the variation among the owl individuals was included into the model as a random factor.

The prey preference data was analysed by counting the probability for the observed distribution of the attacks between one alarming and four non-alarming prey to be random. The probability was calculated using the equation for binomial distribution (Kankainen 2000):

$$P(X=k) = \binom{n}{k} p^k (1-p)^{n-k}$$

Table 2. Owls in the experiments.

| Owl | Year | Alarm calls played | Contact calls played | Prey preference trials |
|-------|------|--------------------|----------------------|------------------------|
| 1 | 2003 | 8 | 8 | |
| 2 | 2003 | 6 | 6 | |
| 3 | 2003 | 8 | 8 | |
| 4 | 2003 | 8 | 8 | |
| 5 | 2004 | 8 | 8 | 3 |
| 6 | 2004 | 8 | 8 | 1 |
| 7 | 2004 | 8 | 8 | 4 |
| 8 | 2004 | 8 | 8 | 4 |
| 9 | 2004 | 8 | 8 | 1 |
| 10 | 2004 | 8 | 8 | 2 |
| 11 | 2004 | 8 | 8 | 2 |
| Total | | 86 | 86 | 17 |

3. RESULTS

3.1. Localization accuracy

The owls needed less cues to localize the alarm calls than the contact calls (Table 4). There was no significant difference between the accuracy of the first localizations between the alarm and the contact call (Table 4, Figure 3). However, when the most accurate localization actions were measured during the three call repetitions, the owls could localize the alarm calls significantly better than the contact calls (Table 4, Fig 4). This suggests that the accuracy of the localization of the alarming individual increases as a function of the amount of cues given (Figure 3). There were no interactions between the owl individual and the treatments (Table 4).

Table 3. Statistics for the measured values.

| Call type | 3-call play-backs | head-turns (n) | Mean headturns /playback | Mean activity (headturns /s) /playback) | Points (n) | Mean, points | First hit (n) | Mean accuracy, degrees (first hit) | Best hit (n) | Mean accuracy, degrees (best hit) |
|-----------|-------------------|----------------|--------------------------|---|------------|--------------|---------------|------------------------------------|--------------|-----------------------------------|
| alarm | 86 | 502 | 5.7 | 0.47 | 86 | 2.4 | 69 | 4.4 | 69 | 3.6 |
| contact | 86 | 345 | 4.0 | 0.43 | 86 | 2.2 | 60 | 5.3 | 60 | 5.1 |

Table 4. Results of the analyses of variances (mixed model) of the localization experiment.

| Source of variation | df | MS | <i>F</i> | <i>p</i> |
|--|-----------|--------|----------|----------|
| <i>Mean points</i> | | | | |
| Call type | 1, 10.836 | 7.414 | 8.360 | 0.016 |
| Owl | 10, 10 | 2.334 | 2.643 | 0.071 |
| Mean points X Owl | 10, 150 | 0.883 | 0.600 | 0.812 |
| <i>Accuracy of first localization</i> | | | | |
| Call type | 1, 10.986 | 20.270 | 4.154 | 0.066 |
| Owl | 10, 10 | 11.486 | 2.394 | 0.092 |
| Accuracy of first localization X Owl | 10, 107 | 4.797 | 0.636 | 0.780 |
| <i>Accuracy of the best localization</i> | | | | |
| Call type | 1, 10.836 | 64.456 | 13.162 | 0.004 |
| Owl | 10, 10 | 6.282 | 1.296 | 0.345 |
| Accuracy of the best localization X Owl | 10, 107 | 4.848 | 0.747 | 0.679 |
| <i>Mean activity (headturns/s)</i> | | | | |
| Call type | 1, 10.086 | 0.078 | 1.595 | 0.235 |
| Owl | 10, 10 | 0.249 | 5.051 | 0.009 |
| Mean activity X Owl | 10, 148 | 0.049 | 1.474 | 0.154 |

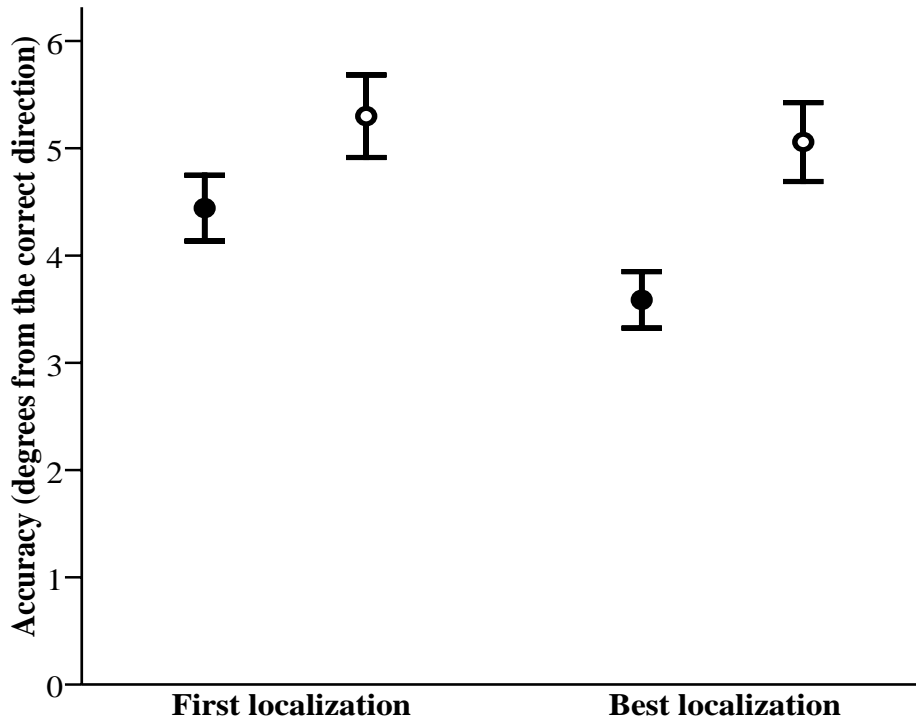


Figure 3. The accuracies of the first and the best localizations of both call types with standard errors (± 1). Filled circles are for the alarm call and the hollow circles for contact call. The higher the value the more the localization differed from the exact direction of the sound source.

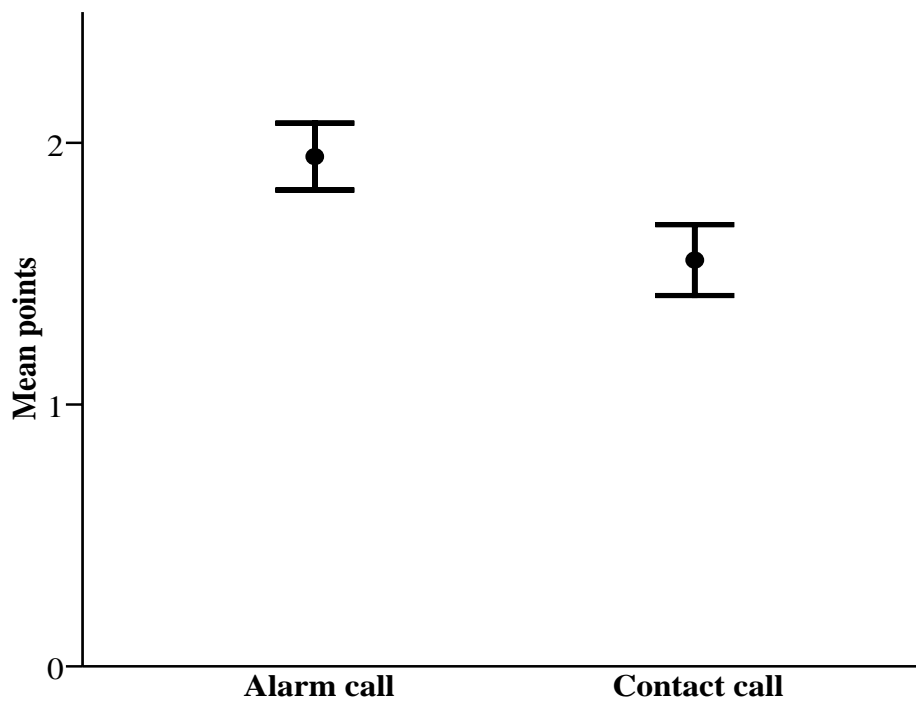


Figure 4. Points between the alarm and the contact call with standard errors (± 1). Higher scores mean less cues needed.

3.2 Prey preference

In all trials of the prey preference experiment all the owls chose a non-alarming prey. Thus the total amount of attacks towards non-alarming prey was 17, whereas there were zero attacks towards the alarming prey. Since the total number of trials (n) is equal to the number of non-alarming individuals taken (k) the equation will be reduced to the probability (p) powered by the number of trials. The probability (p_{trial}) of picking a non-alarming prey item in a single trial is 0.8 (four out of five prey items) and the non-alarming prey items were chosen 17 times and the alarming prey zero times. Thus $P(X=17)$, when $X \sim \text{Bin}(1, 0.8)$, $= p_{\text{trial}}^{17} = 0.8^{17} = 0.023$. This suggests that the alarm does not persuade the owl to attack the caller. Moreover, it seems that the owls prefer to choose non-alarming preys over the alarming ones.

4. DISCUSSION

Traditionally, the behavioural response of staying motionless or fleeing to cover is associated with unlocatable alarm calls. Conspicuous, possibly harassing, mobbing behaviour is thought to result from easily located, loud alarms (e.g. Marler 1955, Ficken & Witkin 1977; Klump & Shalter 1984). In contrast to these assumptions, the results from this study show that an alarm call inducing inconspicuous response of freezing or taking cover (Rajala et al. 2003) is clearly more localizable for a predator in comparison to physically different contact call. That is, the owls needed less cues (Table 4) to localize willow tits' alarm call than bullfinches' contact call and the localization of the alarm call was more accurate (Table 4). In addition, despite the conspicuousness of the alarm call to the predator, it decreased the predation risk of the alarming individual, as predators in the prey preference experiment never attacked the alarming prey individuals. Together these results suggest that the alarm offers information for predators as well and it can be used when they are choosing a prey to attack. Another question is, whether or not this information is deliberately delivered. In other words, the alarm could be a message for a predator that it has been seen and there is no point in launching an attack. In addition, the message might be even more precise saying "I have seen you do not try to catch me", since the first caller is the only one who has seen the predator for sure and is thus the hardest one to catch.

Altruism in the context of alarm calls, as defined by Charnov and Krebs (1975), means that the act of alarm increases the chance of survival of the receivers while placing the caller in a greater danger than remaining silent. Alarm calls are often discussed as a classic case of altruistic behaviour (Maynard Smith 1965, Trivers 1971, Charnov & Krebs 1975). However, as mentioned earlier, and being something of a paradigm in evolutionary science, evolution tends to eliminate this kind of unselfish costly behaviour (Ridley 2004). Supporting this paradigm, the results of the prey preference experiment show that giving the alarm did not increase the risk to be attacked by a predator. Moreover, the fact that the non-alarming preys were preferred over the alarming one naturally mean that a) an individual actually benefits from giving an easily located alarm by reduced predation risk and b) the alarm calling in this context is thus maintained through individual selection and is not a case of altruism, even a reciprocal one.

In comparison to "seet" alarm call for distant predators, alarm for sudden appearance of a close predator used in these experiments is seemingly more intense (consisting of several rapid, short notes with high, varying pitch), perhaps indicating that danger of predation is immediate, not forthcoming. Moreover, as mentioned above, the conspicuous nature of the call indicates that the alarm also offers information for the

predator. However, an alternative explanation for the conspicuousness of the alarm call may simply be the close distance of the predator, since distance could be a critical factor determining whether or not a sound can be made unlocatable. That is, the properties making a sound unlocatable begin to work after a certain distance (e.g. due to attenuation by the surrounding vegetation, Klump et al. 1986, Alatalo & Helle 1990). If this is the case, it may be better to put all the effort to the intensity of the alarm in order to signal about the urgency of the situation, instead of trying to make the alarm unlocatable just in case. However, this is not in contrast to the conclusion that alarm calls include a message also for a predator, since the message could be an unintended side effect. Thus, both of these functions could maintain this behavioural trait simultaneously.

Some details in these experimental designs may arouse criticism. First, in the localization experiment, even though the owls were familiarised with the testing premises the abnormality of the situation might have influenced the owls' interests (i.e. their eagerness to react) towards the vocalizations. However, the situation presumably affected owl's motivation similarly towards both call types, so it should not have affected the results. Since the two call types tested are given in quite different situations in the wild (the alarm tightly concerning a predator's presence), there is probably some natural variation in the owls' motivation to respond them. However even the contact call, given in non-predatory context should raise pygmy owls' interests since they are reported to find flocks of passerine birds by their contact calls (Kullberg 1995), and bullfinches do belong to pygmy owls diet (personal observation). In addition the difference in activity (head turns per second) between the call types was not significant (Table 4). The durations of the three call playback series differed profoundly between the two call types. This can for some part explain the difference in the owls' measured ability to locate these calls. The longer the duration, the longer the time for the owls to locate the sound source. However, this difference in the duration results from the different durations of the single calls that form the three call repetitions. Clearly the duration of a sound is one factor affecting the ease of location, since it determines how much time there is to locate the source of the sound. Since the call types compared in the localization experiment are from different species, there remains some uncertainty in whether the effect is due to the differences in the conspicuousness of the call types or to the species of the caller. In other words, if the owl's reactions toward the calling prey differ depending on the species of the caller, the comparison between these two call types could be invalid. In the prey preference experiment all the prey items, the alarming and the non-alarming ones, were in a same position regarding location and cover. This is usually not the case in the wild, where many things besides alarm calls may affect predators' prey preference. It has been stated that uncovered individuals seldom give an alarm (East 1981, Klump & Shalter 1984) indicating that there should be even more tempting prey present for a predator, making alarming less risky for the caller. Indeed it has been shown that different foraging sites offer different degrees of cover (Suhonen 1993a & b, Kullberg 1998). Furthermore, there are many results showing hierarchy between individuals and species exploiting the foraging sites (e.g. Suhonen et al. 1993). However, with this simple experimental design it was possible to control the situation and reveal the way the alarm calls affected pygmy owls hunting strategy. Finally, since we compared alarming and silent individuals in the prey preference experiment, there is a possibility that the owls are responding to the sound irrespective of its nature as an alarm call. That is, they might for some reason find the call unnatural and thus avoid it. However, the owls did actively catch prey, indicating that the situation was not altogether unnatural. Using of a control sound could have given a greater certainty that the owls are specifically avoiding an alarming prey individual and not only the voice in this artificial situation.

In the prey preference experiment only one prey in a trial gave the alarm. However, normally more than one bird can give an alarm (this was usually the case when the calls were recorded) although in general majority of birds remain silent after the first alarm is given (observation by Jukka Suhonen). The giving of an additional alarm could simply be a confirmation of the danger since false alarms exist (Haftorn 2000), especially with juveniles (Seyfarth et al. 1980). However it is tempting to speculate that this could be a strategy to avoid attack i.e. telling the predator that it has also been seen by another prey individual. This naturally brings us to honesty of signalling if members of a flock give additional alarms also when they have not personally seen the predator. In other words the message to the predator loses its effect if it is commonly used as a lie. However, since only a minority of the flock give additional alarms there should be enough non-alarming prey individuals for the predator to keep alarming beneficial.

When recorded in the wild, the alarm calls used here were usually given several times (with a median of three repetitions), which was imitated by the three call repetitions in the experiment. Since the accuracy to locate the calls got higher when more repetitions were provided (3 repetitions in a playback series) the variance in the amount of repetitions could result from trying to avoid a predator's attention. In other words, birds in better cover should give a longer sequence of calls. However this indication of a costly alarm is in contrast to the prey preference results in this study. An alternative explanation could be that the amount of repetitions indicates a degree of danger as experienced by an individual giving an alarm (Ficken 1989, Fichtel & Kappeler 2002, Platzen & Magrath 2005).

As the pygmy owls in the localization experiment turned their heads more or less accurately towards the source of alarm calls, it suggests that the alarm can draw the owl's attention to the caller. Furthermore, this argument could be supported by the observation that the owls in some cases flew to the spruce in front of the loudspeaker, seemingly making more profound inquiries about the source of the alarm. Even though the results of the prey preference experiment show that the alarming in this situation did not increase the risk of being attacked by a predator, this may not be the case in other situations where an alarm call could catch a predator's attention as well. The aspect of altruism has emerged especially in the case of the "seeet" alarm, which has been a classical example of a call type that is inconspicuous in order to avoid predators' attention (e.g. Marler 1955). The call has been reported to be unlocatable, given only when in cover and with distance to the predator, thus trying to reduce the costs of this altruistic helping. As Maynard Smith (1965) said "It may be that, although it is better to give an unlocatable than a locatable alarm, it is better to give a locatable alarm than no alarm." As an example he used a situation where a hawk spots a flock of prey but instead of selecting a target immediately it approaches the flock for further inquiry. In this situation alarming would be favourable if it caused the other flock members to remain still allowing the hawk to pass by without getting any more visual stimuli (Maynard Smith, 1965). Furthermore, if the hawk had not yet spotted the flock and the alarm was unlocatable the hawk might not spot the flock at all. However, if the alarm call was locatable it might draw the predator's attention to the flock but a visual stimulus would presumably do it with a greater certainty. Moreover, if the hawk had to approach the flock for further inquiry before picking an individual to attack, the cost of the alarm would not be for the alarming individual alone but divided for the whole flock. The increased risk of alarming for the individual would then be defined by the seeing and hearing abilities and the distance of the predator as well as the density of the flock (i.e. the distance between the individuals in the flock) and the position of the caller compared to the rest of the flock. In conclusion, the seeet alarm should rather reduce than increase the risk of being spotted by a predator by reducing visual stimulus performed by the flock members and being unlocatable for a distant predator. Indeed Klump et al. (1986) proved that the

seeet alarm attenuates with distance and Alatalo & Helle (1990) showed that willow tits give alarms more frequently when a predator (a hawk figure) is further away. In this way also the “seeet” alarm could have evolved through individual selection and thus be out of the context of altruism. However, the benefits of alarming could be even greater, possibly involving the increased survival of future mate (Alatalo & Helle 1990, Hogstad 1995, Krams et al. 2006) and through kin selection, in case any relatives were near (Sherman 1977).

To conclude, who benefits from the alarm in this pygmy owl versus passerine flock situation? As these experiments showed, the caller seems to benefit from telling the predator not to catch it. The other members of the flock benefit from the information about the presence of a predator and having a possibility to choose their strategy according to it. On the other hand, the predator benefits from not trying to catch the caller, thus saving energy for more potential and easier prey items, yet the optimal situation from the predator's point of view was lost when the alarm was given in the first place (thus the sum of the effects for a predator's point of view would be negative). In future, more data and carefully controlled experiments of the hunting success of predators are needed to compare the relative benefits of alarm calling in both predators' and preys' point of view. However, in the light of these results and former studies, it seems that evolutionary forces maintaining alarm call behaviour are most likely to work through both kin- and individual selection by various mechanisms together in various situations.

ACKNOWLEDGEMENTS

I want to thank both my supervisors Jukka Suhonen and Heli Siitari for being very supportive and trusting in this project. I thank Tapio Mappes for inspecting this masters thesis and for giving valuable comments. Oskari Härmä deserves great thanks for invaluable help and collaboration. I also want to thank Osmo Rätti and Timo Marjomäki for their work in constructing the voice tapes. I wish to thank the Finnish Biological Society of Vanamo and The Finnish Academy for funding and the Konnevesi Research Station for great working facilities and atmosphere. Warm thanks to Kevin Deegan for great comments. Very special thanks to Carita Lindstedt for priceless academic and mental support!

LITERATURE CITED

- Alatalo R. V. & Helle P. 1990: Alarm calling by individual willow tits, *Parus montanus*. *Anim. Behav.* 40: 437-442.
- Brown C. H. 1982: Ventroloquial and Locatable Vocalizations in Birds. *Z. Tierpsychol* 59: 338-350.
- Caro T. 2005: *Antipredator defences in birds and mammals*. -585 p. University of Chicago Press
- Charnov E. L. & Krebs J. R. 1975: The evolution of alarm calls: altruism or manipulation? *Am. Nat.* 109:107-112.
- East M. 1981: Alarm calling and parental investment in the robin *Erithacus rubecula*. *Ibis* 123: 223-230.
- Ekman J. 1979: Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis. Scand.* 10: 56-68.
- Ekman J. 1986: Tree Use and Predator Vulnerability of Wintering Passerines. *Ornis Scand.* 17: 261-267.
- Fichtel C & Kappeler P. M. 2002: Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behav. Ecol. Sociobiol.* 51: 262-275.
- Ficken M. S. 1989: Acoustic characteristics of alarm calls associated with predation risk in chickdees. *Anim. Behav.* 39: 400-401.
- Ficken M. S. & Witkin S. R. 1977: Responses of blackcapped chickadee flocks to predators. *Auk* 94: 156-157.

- Haftorn S. 1993: Ontogeny of the vocal repertoire in the willow tit *Parus montanus*. *Ornis. Scand.* 24: 267-289.
- 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.
- Hamilton W. D. 1964: The genetical evolution of social behavior. *J. Theoret. Biol.* 31: 1-52.
- Hogstad O. 1988: Rank-related resource access in winter flocks of willow tits. *Ornis Scand.* 19: 169-174.
- Hogstad O. 1995: Alarm calling by willow tits, *Parus montanus*, as mate investment. *Anim. Behav.* 49: 221-225.
- Kankainen A. 2000: *Tilastotieteen peruskurssi 2 (TILA02)*. Jyväskylän Yliopisto, Tilastotieteen laitos 60 p.
- Klump G. M. & Shalter M. D. 1984: Acoustic behavior 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 predator and its avian prey. *Behav. Ecol. Sociobiol.* 18: 317-323.
- Konishi M. 1973: Locatable and nonlocatable acoustic signals for barn owls. *Am. Nat.* 107: 775-785.
- Krams I. 2001: Communication in crested tits and the risk of predation. *Anim. Behav.* 61: 1065-1068.
- Krams I., Krama T. & Igaua K. 2006: Alarm call of wintering great tits *Parus major*: Warning of a mate, reciprocal altruism or a message to the predator. *Journal of Avian Biology* 37: 131-136.
- Kullberg C. 1995: Strategy of the Pygmy owl while hunting avian and mammalian prey. *Ornis Fennica* 72: 72-78.
- Kullberg C. 1998: Spatial Niche Dynamics under Predation Risk in the Willow Tit *Parus montanus*. *Journal of Avian Biology* 29: 235-240.
- Kullberg C. & Ekman J. 2000: Does predation maintain tit community diversity? *Oikos* 89: 41-45.
- Marler P. 1955: Characteristics of some animal calls. *Nature* 176: 6-8.
- Maynard Smith J. 1965: The evolution of alarm calls. *Am. Nat.* 94: 59-63.
- Mikkola H. 1983: *Owls of Europe*. T & A D Poyser. 397 p.
- Platzen D. & Magrath R. D. 2005: Adaptive differences in response in to two types of parental alarm call in altricial nestlings. *Proc. R. Soc. B* 272: 1101-1106.
- Rajala M., Rätti O. & Suhonen J. 2003: Age differens in the response of willow tits (*Parus montanus*) to conspecific alarm calls. *Ethology* 109: 501-509.
- Ridley M. 2004: *Evolution*, 3. edition. Blackwell Publishing. 751 p.
- 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: Localization of Passerine Seet and Mobbing Calls by Goshawks and Pygmy Owls. *Z. Tierpsychol.* 46: 260-267.
- Shalter M. D. & Schleidt W. M. 1977: The ability of the barn owls, *Tyto alba*, to discriminate and localize avian alarm calls. *Ibis* 119: 22-27.
- Sherman P. W. 1977: Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.
- Sherman P. W. 1980: The meaning of nepotism. *Am. Nat.* 116: 604-606.
- Sherman P. W. 1985: Alarm calls of belding's ground squirrels to aerial predators: nepotism or self-preservation. *Behav. Ecol. Sociobiol.* 17: 313-323.
- Suhonen J. 1993a: Predation risk influences the use of foraging sites by tits. *Ecology* 74: 1197-1203.
- Suhonen J. 1993b: Risk of predation and foraging sites of individuals in mixed species tit flocks. *Anim. Behav.* 45: 1193-1198.
- Suhonen J., Halonen M. & Mappes T. 1993: Predation risk and the organization of the parus guild. *Oikos* 66: 94-100.
- Suhonen J., Alatalo R. V., Carlson A. & Hoeglund J. 1992: Food resource distribution and the Organization of the Parus Guild in a Spruce Forest. *Ornis Scand.* 23: 467-474.
- Templeton C. N., Greene E. & Davis K. 2005: Allometry of alarm calls: Black-Capped chickadees encode information about predator size. *Science* 308: 1934-1937.

- Trivers R. L. 1971: The evolution of reciprocal altruism. *Quart. Rev. Biol.* 46: 35-57.
- Witkin S. R. & Ficken M. S. 1979: Chickadee alarm calls: does mate investment pay dividends? *Anim. Behav.* 27: 1275-1276.
- Zuberbühler K 2001: Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behav. Ecol. Sociobiol.* 50: 414-422.