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Information, predation risk and foraging decisions during mobbing in Great Tits *Parus major*

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To maximise survival during foraging animals must decide when and for how long foraging should be interrupted in order to avoid predators. Previous experiments have shown that birds that hear other individuals' alarm calls resume feeding later than those that see a flying predator. However, the responses of prey animals to enemies are highly context-dependent. We therefore investigated how birds respond to a threat less serious than a flying hawk depending on different amount of information about the predator. We used Great Tits dyads where one individual saw a perched model predator (sender), whereas the other individual could only hear the conspecific's mobbing calls (receiver). The sender responded appropriately as shown by comparing their responses to how they responded to a control. We also found that while senders were exposed to the predator, receivers became more wary and reduced their activity level. However, despite the receivers having less information about predation risk they still did not prolong the time they took to resume foraging. Hence, once the mobbing ceased (and consequently the transmission of information about the predator stopped) there was no effect of only having second-hand information. This also shows that receiver's rely upon the sender's mobbing calls suggesting that mobbing calls may act as honest signals of the prevailing predation risk. In conclusion, our results support the view that responses of prey to predators are highly context-dependent and that birds' anti-predator responses are a result of an interaction between the amount of information and the level of the threat.

1. Introduction

One central trade-off during foraging is whether the risk of being preyed upon is greater than the benefits of foraging (Cuthill & Houston 1997). To optimise this trade-off on a small temporal scale individuals need information about the predation risk and to estimate prevailing predation risk time and energy should be allocated to assess the environment (Abrams 1994). Because individuals not always have first-hand information about potential threats, they must at times rely upon information given by other individuals in the surroundings. A recent experiment showed that when animals only receive second-hand information about an imminent threat they become more risk averse than the individuals having first-hand information about the same threat. Yellowhammers (*Emberiza citrinella*) that only heard warning calls took longer to resume feeding than individuals that saw the actual threat, a stuffed flying hawk model (van der Veen 2002). This result is suggested to be caused by the inverse relationship between information and predation risk; animals with less complete information overestimate predation risk and behave accordingly. For example, if an animal detects a predator more appropriate cautionary measures can be taken because they can collect more information about the nature of the predator and they will also know when the threat disappears. On the other hand, if animals only receive second-hand information via alarm calls, it becomes more difficult for the prey animal to assess where the predator is heading and when the threat is gone. Threat assessment is complicated by the fact that the sender may benefit from being quiet after the initial alarm calls were emitted, because emitting alarm calls is costly (Sherman 1977). Hence, the receiver can not be certain about the prevailing risk. Alarm calls are not directed towards the predator, which makes it difficult for the receiver to know whether the predator is still hunting in the vicinity or not.

Because the responses of prey animals to enemies are highly context-dependent (e.g. Curio 1975, Cresswell 1993), it is possible that the antipredator response in Yellowhammers is not generally applicable to other contexts, such as mobbing. Mobbing is when prey animals, instead of moving away from a predator, approach the predator while emitting loud, easily localizable calls repeatedly which also attracts additional prey animals around the predator (Curio 1978). Mobbing calls are directed both to the predator and conspecifics, as opposed to alarm calls. Further, a perched predator which is being mobbed is less dangerous than a hunting predator and a perched raptor usually attracts other prey birds which soon take part in the mobbing of the predator (Hurd 1996, Krams & Krama 2002), thereby diluting predation risk (Hamilton 1971). Here, we want to investigate how birds respond to a less serious threat than a flying hawk when only receiving second-hand information from a conspecific. We hypothesise that there is an interaction between the amount of information an animal has about a potential threat and the level of the risk coupled with that particular threat which will affect the trade-off between the risks and benefits connected to foraging. Since a flying raptor is a much greater threat than an already detected perched predator, we investigate how a less serious threat affects the interaction between information and foraging decisions. We use a similar set-up as van der Veen (2002), but instead of subjecting birds to a flying predator we used a perched predator, which should represent a less serious threat.

2. Methods

2.1. Study site and species

We conducted the experiment at Tovetorp Zoological Research Station in south-east Sweden (58°56’ N 17°08’ E) during December 2003. Great Tits (*Parus major*) were caught during early winter, outside the breeding season, with mist-nets and the birds were housed individually in cages (40 cm × 60 cm × 80 cm) with a light regime simulating the outside conditions (15.5 h darkness, 8.5 h light). Because the experiment was conducted outside the breeding season we used both sexes which were randomised with respect to treatment. The birds had ad libitum access to sunflower seeds, suet and water. We also gave the birds mealworms (*Tenebrio molitor*) twice daily.

2.2. Housing

In a neighbouring room (3m × 3m × 2m) we constructed the experimental set-up where two cages (61 cm × 95 cm × 90 cm) were placed on opposite sides of the room with almost 2 m between the two (Fig. 1). We put branches from artificial spruce-trees in the cages to provide the birds with protective cover during the experiment. We also gave them free access to fresh water, and two bowls containing mealworms, one with a closed lid, were

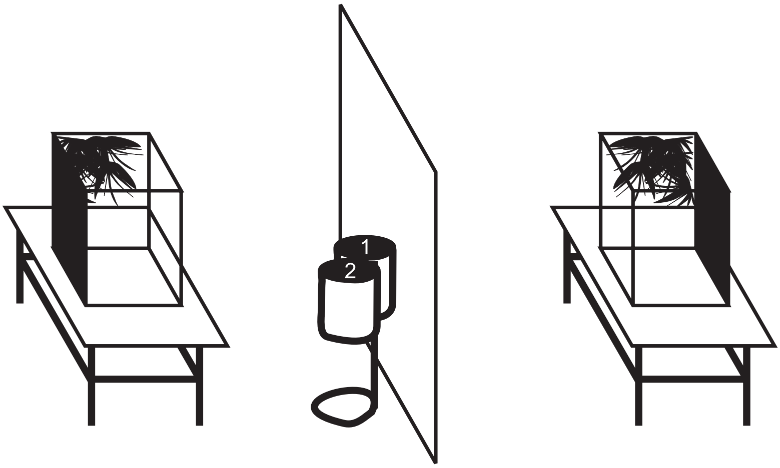

Fig. 1. A schematic image of the experimental room showing two cages with protective cover on each side of the tarpaulin. We controlled the Pygmy Owl in cylinder one and the Robin in cylinder two by remote from the observation room.

put at one of the short sides of both cages. The lid could be operated from outside the room where we made the observations through a window in the door; hence the mealworms in the closed bowl could be exposed without disturbing the bird in the cage. To obstruct the view from one cage to the other we hung a tarpaulin from the ceiling between the two cages. Close to the tarpaulin in front of one of the cages we put two cylinders, one contained a stuffed Pygmy Owl (*Glaucidium passerinum*), an important predator of Great Tits (Ekman 1986), and the other contained a stuffed Robin (*Erithacus rubecula*). These species were chosen because we had access to them in a perched position, they are rather similar in size and they coexist with the Great Tits around the research station. Importantly, Pygmy Owls have also been shown to be perceived as a less important threat to Great Tits than are Sparrowhawks *Accipiter nisus* (Curio et al. 1983). When not in use, the stuffed birds were positioned approximately 10 cm below the upper edge of the cylinder so they could not be seen from the cage until they were pulled up from the cylinder. These stuffed birds were also operated from outside the experimental room.

2.3. Experimental set-up and procedure

We had four treatments in the experiment. The treatments were as following. 1) Birds that saw the Pygmy Owl (sender), 2) birds that could only get acoustic information about the Pygmy Owl through the individual that saw the owl in treatment 1 (receiver), 3) birds that saw the Robin, and lastly 4) birds that could only get acoustic information about the Robin through the individual that saw the Robin in treatment 3. The logic behind the last treatment was to control for the number of birds in the room so all that differed between treatment one and three was the stimulus. As a result, we collected no data from birds in treatment four. All birds were subjected to all four treatments and to avoid any order effects we gave each bird a unique order of treatments and no two birds took part in the same experiment more than once.

In order to control the feeding motivation of the birds, we kept individuals in a holding bag made of cloth for 45 min before the experiment. In the experimental room we put them in the cages, each bird on a different side of the tarpaulin with only one of the birds able to see the cylinders containing the stuffed birds. The birds were then given fifteen minutes in the experimental cage to let them adjust to this new cage before we started an experiment. During these fifteen minutes the bowl with the lid was kept close so they had only access to two mealworms in the open bowl. These mealworms helped motivating the birds to start foraging in the cage. After the fifteen minutes of acclimatisation we pulled the string and thereby exposed the other bowl full of mealworms. Three minutes later we pulled up either the Robin or the Pygmy Owl (depending on treatment) and the stuffed bird was then kept still and clearly visible for the bird on the same side of the tarpaulin for one minute. When the exposure of the stuffed bird ended and the birds resumed foraging we then observed the birds again for three minutes.

During the three minutes of observation before and after the exposure we recorded the number of mealworms consumed and the number and type of vocalisations (scolding or seet calls, Hinde 1952). We also recorded the time it took for the birds to resume foraging. We also quantified their behaviour and categorised it as active (meaning that they flew around in the cage) or still (meaning that they either froze or only moved very little, still birds did for example not move between perches). We ended the experiment either when both birds had resumed foraging within ten minutes or if the birds had not started eating ten minutes after the stuffed bird was hidden. As soon as a bird had gone through all four treatments they were released at the catching site.

2.4. Statistical Analysis

To compare the responses of the birds within the focal pairs we used Wilcoxon matched pairs test and when testing whether the birds responded differently to the owl treatments we used Fischer's exact test. To test if the foraging decisions depended on the number of calls emitted by the receiver we used Mann-Whitney U-test as a post-hoc test. Because of skewness, all descriptive statistics are presented as medians (m) instead of means, and the lower and upper bounds of 95% confidence intervals (CI). All analyses were performed using SPSS 11 (SPSS Inc.).

3. Results

All Great Tits but two elicited scolding calls, a hard churring call, when they saw the Pygmy Owl. The individuals which did not receive any information about the present predator or control were consequently excluded from the analysis, because their responses were irrelevant since they did not receive any information. Only one bird elicited a scolding call as a response to the Robin. We intended to note the type of call elicited by the Great Tits; however no other warning calls (seet call, Hinde 1952) were heard during this study than the scolding calls (henceforth referred to as mobbing calls). In addition, all receivers were silent during the owl-treatment.

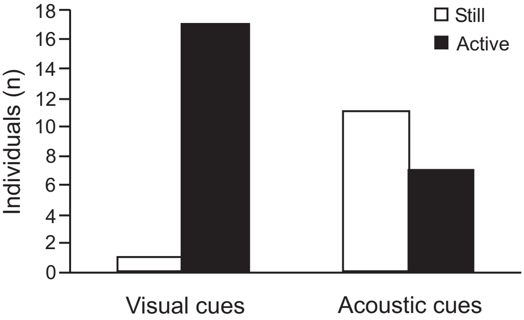

Fig. 2. Behaviour of the birds in the experiment. Shown are the frequencies of behaviour dependent on what kind of cues they had access to.

First we wanted to make sure that our stuffed owl worked as a relevant stimulus for the Great Tits in this experiment. The difference in the number of mobbing calls elicited as response to the owl (m = 9.5, lower/upper bounds of confidence interval, CI = 4.6/12.9 calls) and Robin (m = 0, CI = –0.1/0.3 calls) respectively shows clearly that the birds perceived the owl as a serious threat (Wilcoxon's matched pairs test, Z = 3.7, P < 0.001, n = 20). In addition to mobbing calls, the Great Tits waited longer to resume feeding after they saw the owl (m = 271 s, CI = 119.1/353.3 s) than when they saw the Robin (m = 102.5 s, CI = 17.9/295.7 s, Wilcoxon's matched pairs test, Z = 2.5, P = 0.01, n = 20).

We were then interested in how the difference in information affected the birds' behaviour in the two Pygmy Owl treatments. Frequencies of behaviour during the two treatments show that birds which saw the predator were very active during the presentation of the owl whereas birds who only heard the other bird mobbing and lacked visual cues of predation risk remained still (Fischer exact test, P < 0.001, n = 18, Fig. 2). However, when examining the time the birds took to resume foraging after they were exposed to either the Robin or owl, the treatments had no effect (visual cues: m = 271 s, CI = 119.1/353.3 s, acoustic cues: m = 230 s, CI= 130.9/491.3 s, n = 18, Wilcoxon's matched pairs test, Z = 0.6, P = 0.5, n = 18). Birds showed great variation and time to resume feeding varied between 0 and 600 s in both treatments. We hypoth-

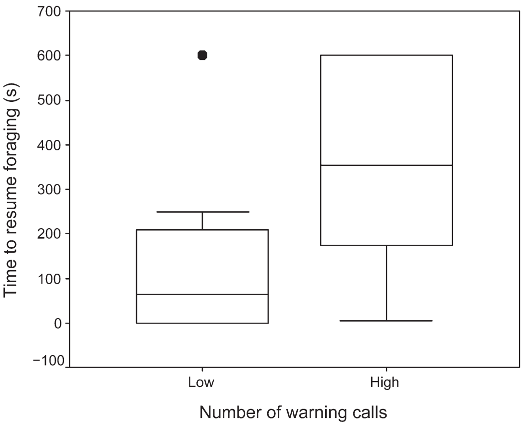

Fig. 3. Graph is showing how long the birds receiving information about the owl waited until they resumed feeding. Receivers were grouped according to if they were exposed to a low (<8.5, the median number of calls emitted by senders in the experiment) or a high (>8.5) number of calls during the time the sender was exposed to the owl. The inter-quartile range is represented by the box, the lines show the median and the range is represented by the whiskers. Extreme values are depicted as filled circles.

esised that, because the treatment had no effect and since there was great variation in the number of elicited warning calls, possibly the number of calls the birds with visual cues (sender) elicited could help explain the variation in time to resume feeding for birds with only acoustic cues (receiver). Therefore, we grouped all times to resume feeding after how many calls the birds had heard when they were receivers. Birds were put in two groups, birds that had heard less than the median number of calls (< 8.5 calls) and birds that had heard more than the median number of calls (> 8.5 calls). This showed that birds which heard a high number of calls waited longer before starting to feed on the mealworms again (Mann-Whitney U-test, U = 22.5, P = 0.036, n = 20, Fig. 3). Finally, to see if the difference in information affected the foraging itself, we also quantified food intake rate (and subtracted the number of mealworms eaten during the three minute period before the owl came up with the period after the owl disappeared). When comparing the intake rate before and after the exposure we found no significant difference between the two treatments (visual cues: m = 2, CI = –0.4/4.0, acoustic cues: m = 0.5, CI = –0.3/2.5, Wilcoxon's matched pairs test, Z = 1.8, P = 0.08, n = 18).

4. Discussion

4.1. Threat and foraging

We found that the amount of information an individual has about predation risk greatly affects its behavioural response. Earlier studies have shown that birds are generally attracted to mobbing calls, and they often start mobbing themselves when the threat is identified (e.g. Hurd 1996, Forsman & Mönkkönen 2001). However, in our study, birds without full information about the threat kept very still and remained silent. This makes sense, because if they can not find the source of danger, they will only increase their own vulnerability by emitting calls (Mougeot & Bretagnolle 2000, Krams 2001) and without information precautionary measures, apart from remaining still and silent, are probably very risky. Birds can remain completely still even more than half an hour if the perceived risk of predation is high enough (Lind 2002).

It is well established that birds are able to discriminate between harmless and harmful stimuli (e.g. Curio 1975), and that Great Tits at this age discriminate between friend and foe (Kullberg & Lind 2002). However, we still wanted to validate our experimental setup and were able to show that birds responded appropriately to our predation risk treatment by discriminating between the owl and the Robin. The Great Tits waited longer before resuming feeding after they saw the owl. In addition, that Great Tits perceived the owl as a predator was evident because eighteen of the 20 twenty birds elicited warning calls when they saw the owl whereas only one bird reacted to the Robin in a similar manner. This one bird probably just reacted to the situation itself when things started to move during the appearance of the Robin because when the Robin had appeared completely from the cylinder the Great Tit stopped alarm calling immediately.

In contrast to the similar study carried out on Yellowhammers by van der Veen (2002), we could not find an effect of less visual information about predation risk on foraging decisions. We cannot be certain that receivers did not change their food intake rate, simply because of the risk of committing a type II-error. Still, in comparison with van der Veen's (2002) study, we think it is possible that the Great Tits in our experiment did not prolong the time to resume feeding after the sender was exposed to the predator. This is supported by the fact that the receivers actually had a lower median in time to resume feeding than the senders. We believe that the discrepancy between these two studies can be caused by the context in how the predator was presented to the senders and in turn how this difference is manifested in different types of alarm calls which most likely transmit dissimilar information.

The Great Tits in our study emitted mobbing calls (scolding calls) indicating to the receiver that the threat is located and most likely mobbed by the calling individual, whereas the Yellowhammers in van der Veen's study responded to a flying predator. The receivers in our study showed reduced activity levels during the time the sender was emitting mobbing calls, but they still did not wait longer to resume feeding than the senders did. This result implies that when mobbing calls were no longer emitted, a receiver would behave as if the threat is no longer present and therefore not considered a serious threat anymore. A perched avian predator, which has been detected, is not as big a threat as a flying predator, because Sparrowhawks and Pygmy Owls rely heavily on surprise attacks for successful hunting (Cramp & Perrins 1994, Cresswell 1996).

Although Great Tits should perceive a perched Sparrowhawk as more dangerous than a perched Pygmy Owl once it has been detected (Curio et al. 1983), this difference in perceived risk is probably much smaller than that between a perched, and detected, predator and a flying predator that disappears to potentially come back and launch a new surprise attack. Because mobbing calls are not only directed towards conspecifics but also towards the predator the receiver can assume that the threat has disappeared when mobbing calls are no longer emitted. Since the receiver did not wait longer than the sender to resume foraging, our results suggest that the sender's mobbing calls acts as an honest signal to the receiver and carries information about the absence of the predator. In conclusion, lack of visual information will affect individual foraging decisions more when the threat is more severe than when a predator has been detected and subsequently is being mobbed.

4.2. Information and foraging

Although receivers did not behave differently than senders with respect to time to resume feeding and feeding rate, it is interesting to note that the receivers' time to resume feeding was dependent on the number of mobbing calls that senders emitted. Possibly, the receiver uses the number or intensity of calls as a source of information about the prevailing predation risk, and that the scolding call of Great Tits thereby may serve as one form of tonic communication (Schleidt 1973). If so, then each repetition, or the calling rate, of the mobbing call could add to the previously sent information and longer calling bouts will then accrue a greater effect on the receivers' anti-predator behaviour (Loughry & McDonough 1988).

To manage foraging decisions when encountering a predator, it is important for prey animals to recognise, assess and respond to the enemy (McLean & Rhodes 1991). Interestingly, even when the recognition phase is excluded, it appears that responses by birds are context-dependent as shown by the combination of the present study and van der Veen's (2002) study. This implies that birds can use second-hand information and, at least to some extent, assess the level of threat purely from vocalisations.

In conclusion, we found that birds are greatly affected by the amount of information they have while the predator was present, however, once the mobbing calls transmitting information about the predator ceased, the effect of only having second-hand information appeared to be lost.

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Information, predationsrisk och födosök under mobbing hos talgoxe *Parus major*

En viktig avvägning nästan alla djur står inför under födosök är om risken att bli tagen av ett rovdjur är större än fördelarna som födosökandet innebär. För att djur skall kunna optimera sina beteenden med avseende på denna avvägning behöver de information om den rådande predationsrisken.

Eftersom djur inte alltid kan få förstahandsinformation om potentiella faror måste de ibland använda sig av information från andra individer i miljön, till exempel om ett djur hör ett annat djurs varningsläten.

Ett tidigare experiment har visat att gulsparvar som bara får information om en flygande predator genom andra gulsparvars varningsläten väntar längre med att återgå till födosökandet än de gulsparvar som såg predatorn flyga förbi. Detta kan tolkas som att de individer som har relativt sämre information om ett hot är mindre riskbenägna då de inte riktigt vet vad predatorn har tagit vägen eller vad predatorn gjorde då andra individer såg den. Men eftersom bytesdjur reaktioner på predatorer är mycket situationsberoende och uppvisar stor variation testade vi om detta mönster kunde upprepas i en mindre riskfylld situation.

Vi använde oss av talgoxar (*Parus major*) som satt i varsin bur i ett rum med ett ogenomskinligt skynke emellan. Den ena individen (sändaren) fick se en sittande uppstoppad sparvuggla (*Glaucidium passerinum*) medan den andra individen (mottagaren) kunde bara få information om den sittande sparvugglan genom den andres varnings- och mobbingläten.

Sändarna betedde sig enligt förväntningarna då genast började mobba sparvugglan (de utstötte varningsläten och var mycket aktiva) då den blev synlig medan mottagarna däremot tystnade och blev stillasittande. Däremot var det ingen skillnad mellan dessa två grupper i hur lång tid de väntade med att återta sitt födosökande trots att de två grupperna hade olika mycket information om predationsrisken. Det tyder på att det i detta fall inte var någon effekt av att bara ha andrahandsinformation om en predator som blir mobbad för mottagarens beslut om när den skall börja äta igen. Detta skiljer sig tydligt ifrån situationen då en fågel bara har andrahandsinformation om en potentiellt jagande predator.

En annan slutsats är att då en fågel hör en annan fågel mobba en predator så tolkar mottagaren mobbinglätena som en ärlig signal om den rådande predationsrisken. Som slutsats så föreslår våra resultat att bytesdjurs reaktioner på predator är mycket situationsberoende och att deras anti-predatorbeteenden är ett resultat av en kombination mellan hur mycket information ett byte har om den rådande risken och hur stor faran är.

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