

Brief reports · Tiedonantoja

Changes in predator surveillance in a foraging Great Tit *Parus major* in response to presence and group size of Yellowhammers *Emberiza citrinella*

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In recent years, there has been a growing tendency to consider the foraging behaviour of animals as a compromise between different and often conflicting demands (e.g. McCleery 1978, Krebs 1980, Sih 1980, Cerri & Fraser 1983, Curio 1983). For example, birds that are clearly visible when feeding run the risk of being attacked by predators. In such a situation a bird cannot devote all its time to efficient feeding, but must also spend some time on surveillance, in order to minimize the risk of being taken by a predator. A compromise is thus needed in the allocation of time to different activities while feeding. In particular, much theoretical and empirical work has been devoted to the time budgeting of birds feeding in groups and its relation to feeding group size (e.g. Caraco 1979a, b, Elgar & Catterall 1981, Barnard et al. 1982, Studd et al. 1983, Sullivan 1984). A general result of these studies is that when feeding in groups individual birds can reduce the time spent scanning for predators (the time spent scanning per individual being negatively correlated with feeding group size) and thus increase their feeding efficiency. Almost all this modelling and testing deals with single species groups, and little attention has been paid to possible alteration of foraging behaviour and predator surveillance in response to the presence of individuals of other bird species (see, however, Barnard et al. 1982, Sullivan 1984). In this paper I present data from a short period of field observations, which will show how a Great Tit *Parus major* male changed its predator scanning while feeding, in response to the presence and number of foraging Yellowhammers *Emberiza citrinella*.

Observations were made in SE Finland (61°35'N, 29°42'E) from 4 to 8 March 1984. A feeding site was established in the afternoon on 3 March, in an open garden (ca. 1.5 acre with eight apple-trees and one maple situated in the immediate vicinity of a house. A bird-table was covered with sunflower seeds and a sheaf of oats was hung on the branch of an apple-tree at a distance of about 4 metres from the bird-table. On 4 March in the fore-moon a Great Tit male was seen for the first time handling a sunflower seed in the garden. The Great Tit fed almost exclusively on sunflower seeds. Yellowhammers arrived in the garden on 4 March in the afternoon and were seen for the last time on 6 March in the afternoon. They foraged exclusively at the oatsheaf or on the snow and were never seen at the bird-table. Data were gathered mainly between 11.00 and 16.00. The air temperature was between -1° and +2°C and the wind conditions were fairly constant (although not measured) during the whole study period. Observations were made from inside the nearby house, and the distance to the foraging Great Tit male was at most 6 to 7 metres. Gathering of data for this study was not started until about one and a half hours after the Great Tit male was first seen dealing with a sunflower seed. The conclusions thus seems warranted that the Great Tit male was sufficiently trained in husking sunflower seeds when the measurements for this study were made. Handling time is defined here as the time the bird spends on a branch husking one sunflower seed and then eating the kernel of the seed. During the handling process the bird frequently scans its environment. I assume that

this scanning behaviour has primarily an antipredator function in the Great Tit (for evidence for this interpretation in other bird species, see Barnard 1980, Caraco et al. 1980a, b). The number of scanning bouts during the handling of one sunflower seed was counted and the duration of the handling of one seed was measured with a stop-watch to the nearest half second. The presence and number of Yellowhammers in the garden was noted immediately after each measured handling period. No other birds, not even other Great Tits, were present in the garden when these data were collected. The certainty is great that all the data for this study are from the same Great Tit male, since the male sang territorial song many times in the garden and repeatedly chased other Great Tit males from the garden, but allowed a female to forage in its vicinity without any disturbance.

In principle there are two different strategies (not necessarily mutually exclusive) by which an individual bird can alter its vigilance level in response to changes in predation risk while handling a food item. First, keeping the mean length of scanning bouts constant, the bird can alter the rate of scanning (i.e. number of scanning bouts per unit of handling time). Second, keeping the scanning rate constant, the bird can adjust the mean length of the scanning bouts (see also Studd et al. 1983). In addition to these strategies while handling a food item, the bird can also change its vigilance level by altering the length of the time it spends on a branch between handling one food item and fetching a further food item, i.e., the 'inspection time' of Lendrem (1983). Unfortunately I have no measurements of this.

With my data it was possible to plot the scanning rate of the Great Tit male against the number of Yellowhammers present, which ranged from 0 to 7. Although the scanning rate of the Great Tit male varied, it showed no relation with the number of Yellowhammers present (Fig. 1A: $r = -0.052$, $N = 33$, not significant). Thus the bird did not seem to adopt the first of the strategies mentioned above.

Unfortunately, data on the total amount of time spent scanning or the mean length of the scanning bouts during the handling of one seed are not available for plotting against the group size of the Yellowhammers. I can, however, study the second strategy mentioned above indirectly, using data on the length of the handling time and its relationship to the number of Yellowhammers and data on the relationship between the number of long scanning bouts and the handling time. On 7 and 8 March I measured the length of 65 scanning bouts, the mean length and standard deviation of which were 1.3 ± 1.4 seconds. I grouped this material into two groups, short bouts (≤ 2 seconds) and long bouts (>2 seconds), and found that the means and standard deviations of these two groups were 0.8 ± 0.4 ($N=53$) and 3.6 ± 4.8 ($N=12$). Furthermore, 47 of the 65 scanning bouts lasted one second or less, 6 exceeded one but not two seconds and 12 exceeded two seconds, i.e. the frequency distribution of the scanning bout lengths seems to be bimodal in this material. So, it seems that there is a reasonable difference between long and short scanning bouts, although the distinction and grouping used here are highly subjective. On 8 March I measured the duration of

21 handling events (range 18–226 seconds) and recorded simultaneously the number of long scanning bouts for each of these handling events (range 1–12 long scanning bouts per handling event). In this material there is, not unexpectedly, a strong positive correlation between the handling time and the number of long scanning bouts per handling event: $r = 0.951$, $P < 0.001$.

Now, let us return to the second strategy open to the Great Tit male if it was willing to reduce the time devoted to predator surveillance in response to the number of Yellowhammers present and thus gain more time for active feeding. There was a significant negative correlation between the handling time and the number of Yellowhammers (Fig. 1B; $r = -0.465$, $N = 33$, $P < 0.01$). Since the scanning rate was not dependent on the number of Yellowhammers and the data base used in the two comparisons (Fig. 1A and B) was the same, this result suggests that the Great Tit male reduced the time spent scanning when handling the seed by shortening the mean length of the scanning bouts. Similarly, Studd et al. (1983) found that in the House Sparrow *Passer domesticus* the scanning bouts of individual birds shortened in response to the foraging group size, while the scanning rate did not vary significantly with the group size. It is tempting to suggest that as the number of Yellowhammers present increased, the Great Tit male was able to reduce the number of long scanning bouts. By doing this, it would gain more time for active feeding, i.e. husking the seed and eating the kernel.

Foraging in groups may reduce the risk of predation for an individual in many different ways (for reviews see e.g. Morse 1977, Krebs & Davies 1981). In the case of the Great Tit male foraging near Yellowhammers, the bird could derive benefit from the vigilance of the Yellowhammers, and in addition the risk of its being the victim if the whole group were attacked by a predator was statistically reduced. The larger the size of the Yellowhammer group, the greater would be the advantage to the Great Tit male and the greater the decrease that it could afford in its predator surveillance. It was not possible with the data available to study whether there would be any further decline in the predator surveillance of the Great Tit male with a still greater number (i.e. > 7 individuals) of Yellowhammers. In the House Sparrow Elgar & Catterall (1981) found that birds which joined flocks greater than five did not reduce the time spent scanning much further, and Studd et al. (1983) found that the scanning bout length began to level off at the group size of four birds. This aspect of predator surveillance could be examined in further studies of Great Tits feeding at birdtables and also the total time budget, including the inspection time (see above) and the time spent on intraspecific aggression (see e.g. Caraco 1979a, b).

Selostus: Pedon havainnoinnin muuttuminen eräällä talitiaisyksilöllä suhteessa keltasirkkujen läsnäoloon ja ryhmäkoko

Linnuilla, kuten monilla muillakin eläinryhmillä yksilön ruokailukäyttäytyminen määräytyy useiden valintatekijöiden alaisena. Esimerkiksi avoimella paikalla ruokailevat linnut ovat ruokaileessaan usein petoriskin alaisia ja eivät sen vuoksi voi käyttää aikaansa pelkästään aktiiviseen ruokailuun, vaan niiden tulee käyttää osa ajastaan pedon havainnointiin. Ryhmässä ruokailevien lintujen on havaittu monessa tapauksessa ratkaisevan tämän aktiivisen ruokailuan ja pedon havainnointiin käytetyn ajan välillä vallitsevan ristiriitatilanteen muuttamalla pedon havainnointiin käyttämäänsä aikaa suhteessa ryhmän kokoon; ryhmäkoon kasvaessa yksittäiset linnut käyttävät yhä vähemmän aikaa pedon havainnointiin.

Tässä työssä tarkastellaan erään talitiaisyksilön pedon havainnointia suhteessa keltasirkkujen läsnäoloon ja ryhmäkoko. Talitiainen käytti ravintonaan auringonkukan

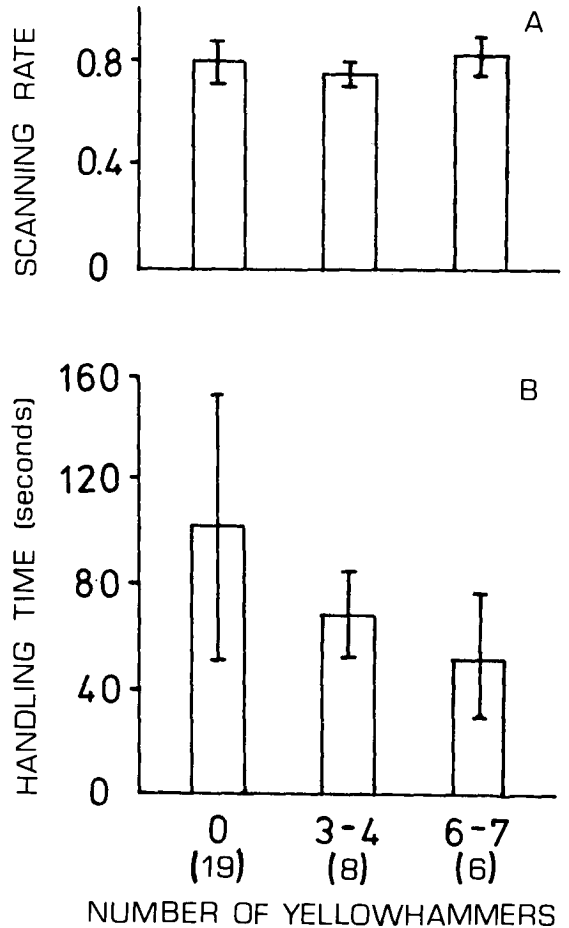


Fig. 1. A) Mean (\pm SD) scanning rate (number of scanning bouts per second of the total handling time) and B) mean handling time for a Great Tit foraging alone, with three or four, and with six or seven Yellowhammers. The number of observations for each situation are in parentheses.

siemeniä, joita se haki lintulaudalta ja käsitteli puun oksalla. Yksittäisten siementen käsittelyyn kulunut aika mitattiin ja samalla laskettiin vilkkuilujen (tulkitaan pedon havainnoinniksi) lukumäärä sekä kunkin käsittelyjakson loputtua tarkastettiin paikalla olevien keltasirkkujen lukumäärä. Keltasirkut ruokailevat läheisellä kauralyhteellä. Tätä aineistoa kerättyä muita lintuja ei ollut paikalla. Vilkuilujen lukumäärä/sekunti siemenen käsittelyaikaa ei korreloinut merkittävästi paikalla olevien keltasirkkujen lukumäärän kanssa ($r = -0.052$, $N = 33$; kuva 1A), mutta yksittäisen siemenen käsittelyyn kulunut kokonaisaika korreloi merkittävästi negatiivisesti keltasirkkujen lukumäärän kanssa ($r = -0.465$, $N = 33$, $P < 0.01$; kuva 1B). Koska pitkäkestoisien (> 2 sekuntia) vilkuilujen lukumäärä korreloi merkittävästi positiivisesti siemenen käsittelyajan kanssa ($r = 0.951$, $N = 21$, $P < 0.001$), edelle saatu tulos viittaa siihen, että talitiaisyksilö käytti keltasirkkujen läsnäollessa ja niiden ryhmäkoon kasvaessa yhä vähemmän pitkäkestoisia vilkuiluja. Näin talitiaisyksilö hyötyi keltasirkkujen läsnäolosta kyeten käyttämään siemenen käsittelyyn kuluneesta kokonaisajasta suhteessa yhä enemmän aktiiviseen ruokailuun ja vähemmän pedon havainnointiin.

References

- Barnard, C. J. 1980: Flock feeding and time budgets in the House Sparrows (*Passer domesticus* L.). — *Anim. Behav.* 28:295—309.
- Barnard, C. J., Thompson, D. B. A. & Stephens, H. 1982: Time budgets, feeding efficiency and flock dynamics in mixed species flocks of Lapwings, Golden Plovers and Gulls. — *Behaviour* 80:44—69.
- Bertram, B. C. R. 1980: Vigilance and group size in ostriches. — *Anim. Behav.* 28:278—286.
- Caraco, T. 1979a: Time budgeting and group size: a theory. — *Ecology* 60:611—617.
- Caraco, T. 1979b: Time budgeting and group size: a test of theory. — *Ecology* 60:618—627.
- Caraco, T., Martindale, S. & Pulliam, R. H. 1980a: Avian time budgets and distance to cover. — *Auk* 97:872—875.
- Caraco, T., Martindale, S. & Pulliam, R. H. 1980b: Avian flocking in the presence of a predator. — *Nature* 285:400—401.
- Cerri, R. D. & Fraser, D. F. 1983: Predation and risk in foraging minnows: balancing conflicting demands. — *Am. Nat.* 121:552—561.
- Curio, E. 1983: Time-energy budgets and optimization. — *Experientia* 39:25—34.
- Elgar, M. A. & Catterall, C. P. 1981: Flocking and predator surveillance in House Sparrows: test of an hypothesis. — *Anim. Behav.* 29:868—872.
- Krebs, J. R. 1980: Optimal foraging, predation risk and territory defence. — *Ardea* 68:83—90.
- Krebs, J. R. & Davies, N. B. 1981: An introduction to behavioural ecology. — Blackwell Scientific Publications, Oxford.
- Lendrem, D. W. 1983: Predation risk and vigilance in the Blue Tit (*Parus caeruleus*). — *Behav. Ecol. Sociobiol.* 14:9—13.
- McCleery, R. H. 1978: Optimal behaviour sequences and decision making. — *In* Krebs, J. R. & Davies, N. B. (eds.): Behavioural ecology: an evolutionary approach: 377—410. Blackwell Scientific Publications, Oxford.
- Morse, D. H. 1977: Feeding behavior and predator avoidance in heterospecific groups. — *BioSci.* 27:332—339.
- Sih, A. 1980: Optimal behavior: can foragers balance two conflicting demands? — *Science* 210:1041—1042.
- Studd, M., Montgomerie, R. D. & Robertson, R. J. 1983: Group size and predator surveillance in foraging House Sparrows (*Passer domesticus*). — *Can. J. Zool.* 61:226—231.
- Sullivan, K. A. 1984: The advantages of social foraging in downy woodpeckers. — *Anim. Behav.* 32:16—22.

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Significance of the behaviour of incubating tetraonid hens for population dynamics: case reports on the Black Grouse

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The populations of the Black Grouse *Tetrao tetrix* are known to fluctuate considerably from year to year in the northern part of its range (e.g. Siivonen 1957, Helminen 1963, Rajala & Lindén 1984). A number of hypotheses and theories have been presented to explain this phenomenon. Naturally, both varying natality and mortality rates may be involved. Small variation in the natality (Angelstam 1983) and great variation in the mortality (Angelstam 1985, Storaas & Wegge 1985) have been demonstrated. In principle, mortality begins at the moment when the first egg of a clutch has been laid and is exposed to the risk of a predator finding the nest. The incubating hen tends to protect her eggs against predators (Pulliainen 1971), but the flushing distance of incubating hens seems to vary. We intend to show here that when the Black Grouse population reached a peak in 1980 (Rajala & Lindén 1984), the flushing distance of the hens was remarkably short.

Case reports:

- (1) Oulu, Sanginjoki, 22 May 1980 (observers Kauko Huhtala & A. Marjakangas)
- A nest with 10 eggs; flushing distance (FD) of hen 1 m.
 - A nest with 7 eggs; FD 2 m.
 - A nest with 7 eggs; when the hen was flushed only when the observer walked over her.
- All three nests in a forest.

- (2) Sievi, Kukonkylä, 5 June 1980 (observers Jorma and Jari Peltokorpi, and Kauko Huhtala)
- A nest with 10 eggs on a abandoned field; the hen was flushed only when a nearby birch sapling was cut down. The flushing distance was exceptionally short later as well. All 10 eggs hatched.
 - A nest with 10 eggs on a abandoned field; a very short flushing distance.
- (3) Kalajoki, in the beginning of June 1980 (observer M. Marttala)
- An incubating hen flew up below a falling tree whose top tore out some of her tail feathers. The same hen (without her tail feathers) was incubating in the same nest some days later.
- (4) Merijärvi, in the beginning of June 1980 (observer M. Marttala)
- A hen flew up at the last moment in front of a digging machine. The nest remained untouched, but its surroundings were completely altered. In spite of this, the hen was seen incubating in the nest on the following day.
- (5) Juva, Kilpola, in the beginning of June 1980 (observer Kalevi Huhtala)
- A nest with 10 eggs, FD 1 m.
 - A nest with 8 eggs, FD 2 m.
 - A nest with 7 eggs, FD 1 m.
 - A nest with 7 eggs, FD 2 m.
 - A nest with 5 eggs, FD 2 m.