Oecologia (1989) 78:490–495

Oecologia

Mixed species flocking of tits (Parus spp.): a field experiment

T. Székely [1,*], T. Szép [2], and T. Juhász [3]

[1] Edward Grey Institute of Field Ornithology, University of Oxford, UK
[2] Hungarian Ornithological Society, Budapest, Költö u. 21., H-1121, Hungary
[3] Department of Ecology, Kossuth University, Debrecen, H-4010, Hungary

Summary. We tested two general models of flocking behaviour, namely the antipredation model and foraging efficiency model on mixed-species tit flocks (Parus spp.). After food addition the size of mixed-species flocks was significantly less than in the control samples. In the presence of extra food significantly more birds were observed either in monospecific flocks or solitary, than during the control observations. In the presence of a living predator the birds foraged in larger mixed-specifies flocks than during the control observations. In addition, the social behaviour of Great Spotted Woodpecker, Middle Spotted Woodpecker and Nuthatch shifted to mixed-specific flocking. The size of monospecific flocks was independent of both treatments. The density of birds increased significantly after food addition, while in the predator presence the birds tended to leave the forest. These results support the view that both the antipredation model and foraging efficiency model seem to be valid for mixed-species flocking. However, in the case of monospecific flocks, the territory maintenance could be the most important factor.

Key words: Tits – Density – Mixed-species flocking – Foraging efficiency – Anti-predator behaviour

Two general models have been developed to explain flocking behaviour during the nonreproductive season: the foraging efficiency model and the antipredation model (see reviews Bertram 1978; Morse 1980; Barnard and Thompson 1985; Pulliam and Caraco 1984). Being in a flock may be advantegous due to social learning (Krebs et al. 1972), the beating effect (Heatwole 1965), the skill pool effect (Giraldeau 1984), the benefits of the information centre hypothesis (Ward and Zahavi 1973), the increased probability of finding food patches and reduced variation in food intake rate (Krebs 1974; Pulliam and Millikan 1982). On the other hand, the birds are less vulnerable to predators while in flocks since they can detect a predator earlier (Kenward 1978), they can deter it (Kruuk 1964) or they can confuse it (Milinski 1984).

In monospecific flocks the validity of both models has been demonstrated (Caraco et al. 1980; Ekman 1987). Recently Berner and Grubb (1985) and Grubb (1987) tested the foraging efficiency models in mixed-species flocks. They manipulated the food availability as in this study. However, they did not manipulate both the predation and the food availability. So the adequacy of both models in the case of mixed-species flocks has not yet been proven.

To clarify both the role of foraging efficiency and antipredation in mixed-species flocks we performed a field experiment on birds wintering in Central-European oak forests. In one forest plot superabundant food was provided in feeders, while in another one a natural predator was presented. Our predictions were that after food addition (1) the density of birds would increase and, if foraging efficiency is important for flocks, then (2) the size of flocks would decrease and (3) the proportion of flocking birds would decrease. On the other hand, one could expect that in the presence of a predator (4) density of birds would decrease and, if antipredation is a benefit of flocking then (5) the size of flocks would increase and (6) the proportion of flocking birds would increase.

Methods

Two 90 year old oak forests referred to as Hadhaz and Teglas were sampled in East Hungary, near Debrecen. The distance between the two sites is 11.2 km. The forests consist of oak (*Quercus robur*) with less than 1% Locust-Tree (*Robinia pseudoacacia*). In both forests an elliptical route was marked out. Ten sampling points along the route were selected for measuring the vegetation. At each point the height of the trees was estimated and the number of trees (>10 cm) in a 10 m circle was counted. The estimated height of trees was 21.00 m (±1.05) in both Hadhaz and Teglas, while the density of trees was 152.64/ha (±36.10) in Hadhaz, and 193.98/ha (±58.92) in Teglas. The density of trees was not different in the two sites (unpaired t-test).

Birds within 25 m of both sides of the route were included in the calculations of density. The length of the routes were 1154 and 1025 m, respectively. Since the shrubs and the underlayer vegetation were sparse, we assume that coefficient of detectability was 100% within 25 m of the transect line (Emlen 1971). The density was affected by the time taken to complete the route in both study sites (t-test, $P < 0.001$), so we removed this effect by standardizing the time taken.

Flocks were identified either as a cluster of birds which called to each other, or when a bird clearly followed another one (Berner and Grubb 1985). Both the size and composi-

* *Present address and address for offprint requests:* T. Székely, Hungarian Ornithological Society, Budapest, Költö u. 21, H-1121, Hungary

Table 1. Weather parameters (mean ± S.D.). Asterisks indicate significant difference between control and treatment

	Hadhaz		Teglas	
	Control	Extra Food	Control	Extra Predator
Wind (m/s)	0.11 (±0.24)	0.02 (±0.05)	0.04 (±0.12)	0.03 (±0.06)
Light (1000 lux)	11.84 (±13.11)	15.23 (±19.03)	13.76 (±10.87)	10.63 (±13.07)
Temperature (°C)	−6.53 (±4.32)	−0.96 (±2.45)*	−8.71 (±6.01)	−1.64 (±2.49)*

tion of flocks, and the number of solitary individuals were counted along the route. Each bird encountered was categorised as participating in mixed-species flock, in a monospecific flock or being solitary. Usually 5–10 min were spent observing each flock or individual to ensure the correct flocksize and social behaviour. One observation was made on each flock sighted. Care was taken to avoid repeated counts of the same flock. During the density estimations social behaviour was not observed. Between 26 January 1987 and 2 February 1987 control observations were made for 8 days in both Hadhaz and Teglas. From 4 February 1987 to 9 February 1987 extra food was set up for 6 days in Hadhaz, while during the same period an extra predator was presented in Teglas. In Hadhaz sunflower seeds in a feeder and two suet balls in wire netting containers were provided in each of four places along the elliptical route. Feeders were filled regularly to ensure a superabundant food supply. Social behaviour was not recorded within 30 m of feeders. The closest bird-tables to the study areas were further than 1 km away. In Teglas a falconer walked along the route with a female Goshawk (*Accipiter gentilis*) on his hand. This species is a natural predator of both tits and woodpeckers.

The field observations were made between 8 am and 1 pm. One of us (T. Székely) made the observations on the social behaviour and flocksize in Hadhaz, while T. Juhász recorded the same parameters in Teglas. The two observers regularly practised to identify the same social behaviour and flocksize. T. Szép alternated between the two plots making two density estimations every other day in each plot.

Three weather parameters were measured, the wind speed, light intensity and temperature (Table 1). All measurements were made at 1 m height every hour. Only the temperature was significantly different between control and experimental period, so we tested the effect of temperature on density and flocksize by GLIM (Payne 1987). The correlation was not significant in any case.

Results

Density

The same species wintered in the two study sites: Great Tit (*Parus major*), Blue Tit (*Parus caeruleus*), Marsh Tit (*Parus palustris*), Long-tailed Tit (*Aegithalos caudatus*), Great Spotted Woodpecker (*Dendrocopos major*), Middle Spotted Woodpecker (*Dendrocopos medius*), Lesser Spotted Woodpecker (*Dendrocopos minor*), Grey-headed Woodpecker (*Picus canus*), Nuthatch (*Sitta europaea*), Mistle Thrush (*Turdus viscivorus*) and Fieldfare (*Turdus pilaris*). Since the two Treecreepers (*Certhia familiaris* and *C. brachydactyla*) living in this area are difficult to identify in winter, we recorded them as *Certhia sp.* On the day following the setting up of the feeders the birds found them and regularly fed there. The feeders attracted birds to the area, so the density was significantly higher during the extra food presentation, than before (Fig. 1). The tits, especially the Great Tit, reacted strongly to the addition of food, while the frugivorous thrushes neither visited the feeders nor became more abundant (Table 2).

The tits gave alarm calls after spotting the predator, or they flew away. We found fewer birds in Teglas after the presence of the Goshawk (Fig. 1). In this case all birds including the Mistle Thrush was a potential victim, so they left the forest plot, but the differences were not significant (Table 2).

Flock-size

In both study sites the flocks consisted of all species studied, except the thrushes. In Hadhaz the mean size of mixed-species flocks was 5.87 (±3.13) before the provision of extra food, and afterwards it decreased to 3.96 (±2.28) (Fig. 2) (unpaired t-test, $P<0.001$). While in Teglas the flocksize

Table 2. Mean densities of birds and the standard deviations in the two studied forests (individuals/10 ha, ±SD). The N means the number of routes

	Hadhaz			Teglas		
	Control $N=6$	Extra Food $N=6$		Control $N=8$	Extra Predator $N=6$	
Great Tit	2.83±4.12	29.47±5.95	$P<0.001$	13.77±7.51	7.92±7.25	NS
Blue Tit	4.82±2.50	11.9 ±4.02	$P<0.01$	9.5 ±9.31	7.6 ±4.33	NS
Marsh Tit	3.4 ±3.04	9.92±4.08	$P<0.01$	3.09±1.41	2.22±2.22	NS
Great Spotted Woodpecker	1.42±1.28	3.97±1.76	$P<0.001$	2.37±2.43	1.27±1.55	NS
Nuthatch	5.95±1.42	7.37±2.56	NS	5.94±2.95	5.7 ±2.40	NS
Mistle Thrush	21.53±4.12	20.4 ±1.86	NS	17.81±5.27	13.62±2.22	NS
Fieldfare	22.95±9.11	18.7 ±5.16	NS	–	–	

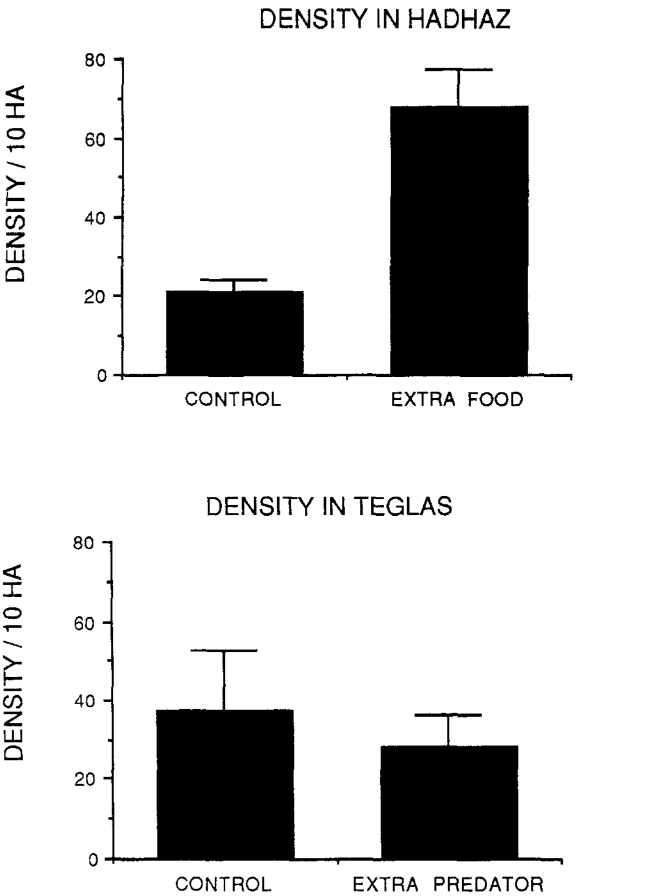

Fig. 1. The mean total density of birds in the two localities (+S.D.) before the treatments (control), and after treatment (extra food: Hadhaz, extra predator: Teglas). Both treatments were significant (paired t-test, $P<0.001$ and $P<0.1$)

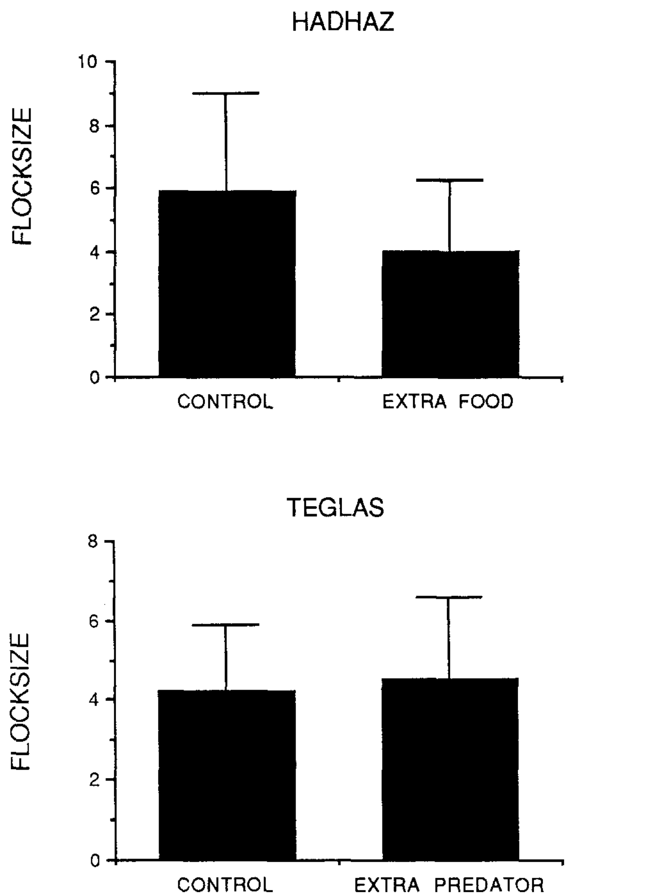

Fig. 2. Size of mixed-species flocks measured by number of individuals per flock. The number of flocks was 46 (control) and 28 (extra food) in Hadhaz (unpaired t-test, $P<0.001$), while in Teglas it was 58 (control) and 40 (extra predator) (unpaired t-test, NS)

increased from 4.24 ($\pm$1.64) to 4.52 ($\pm$2.05) (Fig. 2) (unpaired t-test, NS) after addition of the predator.

The most common monospecific flocks were formed by the Great Tits and Blue Tits. The mean size of monospecific flocks in Hadhaz was 2.06 ($\pm$0.25) before the food addition (sample size, $N=16$), and 2.22 ($\pm$0.51) after ($N=50$) (paired t-test, NS). In Teglas during the control observations the mean size of homospecific flocks was 2.37 ($\pm$0.65) ($N=24$), while after it was 2.29 ($\pm$0.59) ($N=30$) (paired t-test, NS).

Social behaviour

Observations of social behaviour have shown that the birds usually foraged in mixed-specifies flocks in both forests during the control observations (Fig. 3). In Hadhaz 75.84% of all birds were found in mixed-species flocks before food addition (Fig. 4). After the food addition the birds left the mixed-species flocks and foraged either in monospecific flocks or solitarily (χ^2-test, $P<0.001$). The most marked shifts were observed in the Marsh Tit, Great Tit and Blue Tit (Fig. 5).

In Teglas the Great Spotted Woodpecker, the Nuthatch and the Middle Spotted Woodpecker were found more often in mixed-species flock when the extra predator was present than before (Fig. 5).

Discussion

The food limits the density of tits in winter (Lack 1954; Jansson and Ekman 1981). The addition of food attracted tits to the area. The Great Tit immigration was the most pronounced. In Hungary one part of the Great Tit population overwinters near villages and human settlements, but they regularly inspect the forests. As soon as the conditions are appropriate, they establish territories. The frugivorous Mistle Thrush and Fieldfare were insensitive to food addition. We have never seen these species on feeders. In Teglas after showing the Goshawk, the birds including the Mistle Thrush tended to leave the forest, and probably foraged elsewhere. Therefore, the density of birds increased in Hadhaz, while in Teglas it decreased. In both forests the density modification was the same as predicted.

The food provision modified the birds' social behaviour too. The size of mixed-species flocks decreased after food addition, while solitary individuals and monospecific flocks became more common. In flock the birds could locate food earlier (Krebs et al. 1972; Benkman in press), inform each other of its wherabouts (Elgar 1986) and for flockmembers the food intake rate is high (Barnard 1980). When food supply increases, the benefit from foraging efficiency decreases. Therefore, the birds could leave the flocks and forage either in smaller flocks, or alone. We have not measured

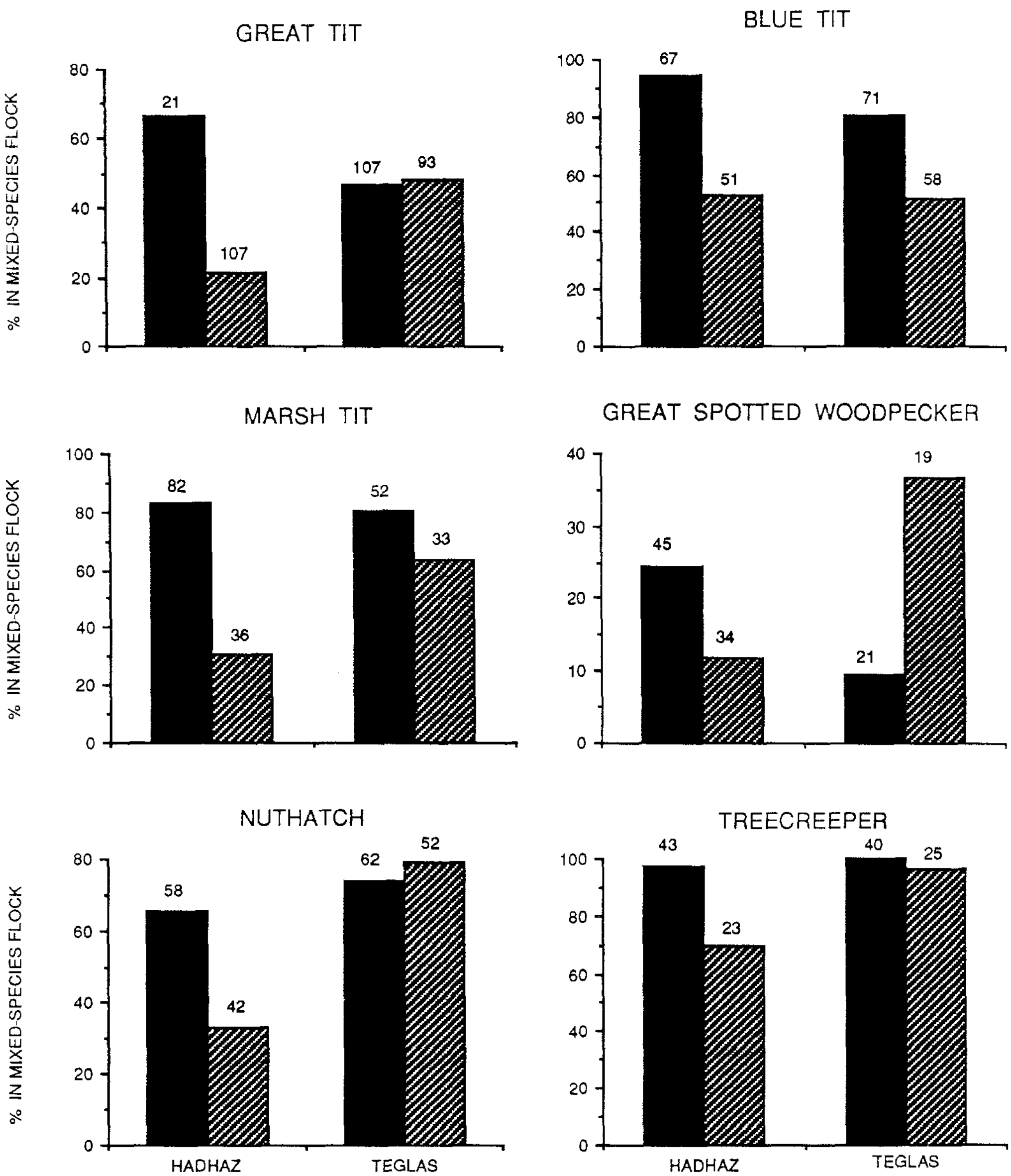

Fig. 3. Social behaviour of birds in both study plots. On the y axis the % occurence in mixed-species flocks are depicted (100% = total occurence both in flocks and solitary) before treatments (■), and after treatments (▨). The treatment was extra food in Hadhaz, while in Teglas a predator was presented. The number of observations of each species are given above the bars

the actual benefits of foraging efficiency, but evidences suggest, that the foraging efficiency is higher in flock (Glück 1986 and studies cited above). Our results indicate, that the flocksize do decrease after food addition. Our findings support the results of Berner and Grubb (1985), and Grubb (1987) that foraging efficiency has a definite role in the facilitation of mixed-species flocking in winter. Since both social learning and information on food patches could work among conspecifics (Krebs 1973), we assume that these two mechanisms facilitated mixed-species flocking. The tits and woodpeckers forage on hidden insects and acorns in winter, so the beating effect could not play a role in their flocking behaviour.

After food addition the birds left the mixed-species flocks, which implicates that being in flock could be costy. What can the cost be? Most workers have assumed, that the main cost of flocking is competition (Barnard and Thompson 1985; Alatalo et al. 1986). However, by adding food you would expect decreased competition. So that hypotheses does not really explain, why flocksize decreases with food addition. Another, hidden cost of flocking could be the 'lost opportunity cost', or another words the lost opportunity to begin territory establisment (J.R. Krebs, pers. comm.). When we put food in the area, not only the benefit of foraging efficiency decreased, but the territories became more available for breeding. Flocking and territory defence may be two endpoints of a continuum (Davies and Houston 1981; Krebs and Davies 1987), so in future more efforts would be needed to test the costs and benefits of switch between flocking and territory establishment.

On the other hand, in the presence of the Goshawk the size of mixed-species flocks increased, but not significantly. Since tits can not deter an active hawk, the most probable benefit of flocking could be the early detection and dilution of an attack. Moynihan (1962) suggested, that the predator detection range of various birds are different, so the detection range of mixed-species flocks are larger, than that of a mixed-species one. An additional benefit could be the increased time spent feeding (Caraco et al. 1980). The alarm calls of tits are similar, so they can re-

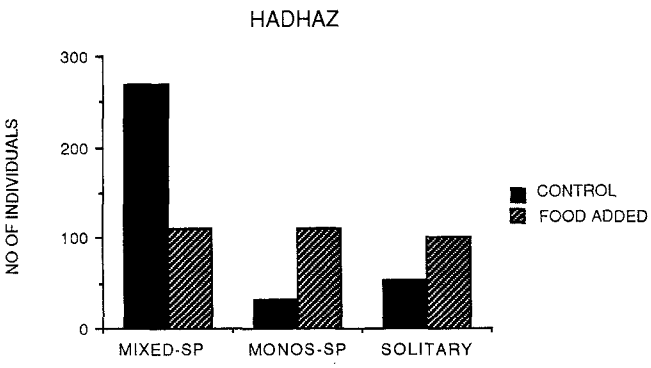

Fig. 4. Social behaviour of all birds studied in Hadhaz. The shift to monospecific flocking and to solitary behaviour after food addition is significant (χ^2-test, $P<0.001$)

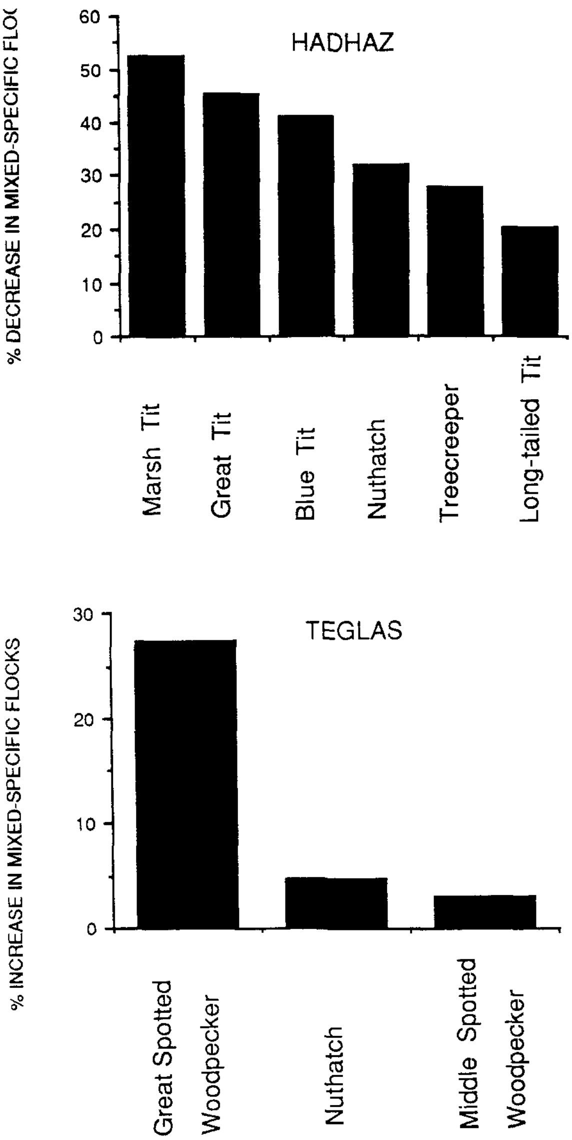

Fig. 5. Percent reduction in mixed-species flocks in Hadhaz (% in control minus % in food added), and percent increase in mixed-species flocks in Teglas (% in predator presence minus % in control)

spond to the calls of each other. Not only the tits react to alarm calls, but other species as well, e.g. woodpeckers (Sullivan 1984). Due to their foraging methods, the trunk-forager's view is restricted, so they are less vulnerable, if they join to flocks. In our study the Great Spotted Woodpecker, Nuthatch and Middle Spotted Woodpecker joined flocks in the presence of Goshawk, while Treecreeper was observed very rarely outside the flocks.

The role of woodpeckers is controversial in mixed-species flocks. The foraging behaviour of woodpeckers is very different from tits (Székely and Moskat 1987), so their foraging efficiency is probably not affected by flocking. Sullivan (1984) suggested that they exploit the tits, since they use the tits as a sentinels against predators. Our results support this view. On the other hand the woodpecker's foraging method is loud, not only could we easily locate a flock on the basis of the woodpecker's hammering, but the predators may also have been able to do so. In this case the woodpeckers can attract predators to flocks. So both from the sentinel hypothesis and predator attraction hypothesis the tits are parasitised by woodpeckers. However, the size and plumage of woodpeckers is different from the tits. There is a strong selection against oddity in fish flocks (Landeau and Terborgh 1986). This might be the case for the woodpeckers too. So the benefit of flocking for the woodpeckers could be reduced by the cost of oddity.

In both study areas the size of monospecific flocks was about two birds, and our treatments had no effect on the size of monospecific flocks. Since monospecific flocks often consist of bonded pairs (Ekman 1987), so these birds were probably pairs. The monospecific flocks of various tit species are stable from year to year, e.g. Black-capped Chickadee (Glase 1973), Carolina Chickadee (Dixon 1963), Crested Tit (Ekman 1979), and the flocks have definite hierarchy order (Dixon 1963; Smith 1976). The breeding pairs are formed within a particular flock. Therefore we suggest, that the main reason for being in a monospecific flock is neither foraging efficiency nor predator avoidance, but pair formation and territory protection (Berner and Grubb 1985).

The size and composition of mixed-species flocks is not stable (Hinde 1952; Morse 1970). We observed, that the mixed-specific flocks were regularly split up or joined together. The formation of flocks are usually interpreted by the nuclear species hypothesis (Rand 1954; Moynihan 1962), so the flocks are formed around one species, preferably around the most numerous one. Due to their loud foraging method, Cieslak (1983) suggested the woodpeckers as nuclear species. The foraging speed of birds in mixed-species flocks is different (Székely unpubl). The flocks, especially the large ones (>10) are usually led by the Long-tailed Tit, and they are followed by other tits (Great Tit, Blue Tit, Marsh Tit), while the woodpeckers, nuthatch and treecreepers usually follow at the rest. It seems to us that the different foraging speeds separated the species along the axis of flock. So we propose, that which species follows which is basically determined by foraging speed, rather than dominance or the loudness of a particular bird.

To summarize, both the antipredator model and foraging efficiency model seem to operate in mixed-specific flocks. On the other hand for the monospecific flocks the pair formation and territory maintenance seem to be more important than either foraging efficiency or antipredator behaviour.

Acknowledgements. We are very grateful to Dr. J.R. Krebs, Dr. C.M. Perrins and A. Vliet for their critism and valuable comments on the manuscript. The project could not have been carried out without the gracious help of Dr. Cs. Aradi and Dr. J. Aradi. J. Csuhaj presented the Goshawk in Teglas. The meterological instruments were supplied by the Kossuth University and by J. Kozma. One author was supported by a Soros-MTA grant.

References

Alatalo RA, Gustafsson L, Lundberg A (1986) Interspecific competiton and niche changes in tits (Parus spp.): evaluation of nonexperimental data. Am Nat 127:819–834

Barnard CJ (1980) Flock feeding and time budgets in the House Sparrow (Passer domesticus L.). Anim Behav 28:295–309

Barnard CJ, Thompson DBA (1985) Gulls and Plovers. The Ecology and Behaviour of Mixed-Species Feeding Groups. Croom Helm, London

Benkman CW (1988) Flock size, food dispersion, and the feeding behaviour of crossbills. Behav Ecol Sociobiol (in press)

Berner TO, Grubb TC (1985) An experimental analysis of mixed-species flocking in birds of deciduous woodland. Ecology 66:1229–1236

Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford, pp 64–96

Caraco T, Martindale S, Pulliam HR (1980) Avian flocking in the presence of a predator. Nature 285:400–401

Cieslak M (1983) Heterospecific winter flocks of birds in a pine forest. Ekologia Polska 31:219–234

Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, Motacilla alba. J Anim Ecol 50:157–180

Dixon KL (1963) Some aspects of social organization in the Carolina Chickadee. Proceedings XIII. International Ornithological Congress, vol 1. Allen Press, Kansas, pp 240–258

Ekman J (1979) Coherence, composition and territories of winter social groups of the Willow Tit Parus montanus and the Crested Tit P. cristatus. Ornis Scandinavica 10:56–68

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

Elgar MA (1986) House sparrows establish flocks by giving chirrup calls if the resources are divisible. Anim Behav 34:169–174

Emlen JT (1971) Populations of birds derived from transect counts. Auk 88:323–342

Giraldeau L (1984) Group foraging: the skill pool effect and frequency-dependent learning. Am Nat 124:72–79

Glase JC (1973) Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235–267

Glück E (1986) Flock size and habitat-dependent food and energy intake of foraging Goldfinches. Oecologia 71:149–155

Grubb TC (1987) Changes in the flocking behaviour of wintering English titmice with time, weather and supplementary food. Anim Behav 35:794–806

Heatwole H (1965) Some aspects of the association of cattle egrets with cattle. Anim Behav 13:79–83

Hinde RA (1952) The behaviour of the Great Tit (Parus major) and some other related species. Behaviour [Suppl] 2:1–201

Jansson C, Ekman J, Bromssen A von (1981) Winter mortality and food supply in tits Parus spp. Oikos 37:313–322

Kenward RE (1978) Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. J Anim Ecol 47:449–460

Krebs JR (1973) Social learning and the significance of mixed-species flocks of chickadees (Parus spp). Can J Zool 51:1275–1288

Krebs JR (1974) Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (Ardea herodias). Behaviour 51:99–134

Krebs JR, Davies NB (1987) An Introduction to Behavioural Ecology. Blackwell, Oxford

Krebs JR, MacRoberts MH, Cullen JM (1972) Flocking and feeding in the great tit (Parus major): an experimental study. Ibis 114:507–530

Kruuk H (1964) Predators and anti-predator behaviour of the black headed gull, Larus ridibundus. Behaviour [Suppl] 11:1–129

Lack D (1954) The natural regulation of animal numbers. Clarendon, Oxford

Landeau L, Terborgh J (1986) Oddity and the 'confusion effect' in predation. Anim Behav 34:1372–1380

Milinski M (1984) A predator's costs of overcoming the confusion-effect of swarming prey. Anim Behav 32:233–242

Morse DH (1970) Ecological aspects of some mixed-species foraging flocks of birds. Ecol Monogr 40:119–168

Morse DH (1980) Behavioural mechanisms in ecology. Harvard University Press, Cambridge, MA

Moynihan M (1962) The organization and probable evolution of some mixed-species flocks of neotropical birds. Smiths Miscell Collect 143:1–140

Payne CD (ed) (1987) The GLIM system. Release 3.77. Royal Statistical Society, London

Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davies NB (eds) Behavioural Ecology: An Evolutionary Approach. 2nd ed Blackwell Oxford, pp 122–147

Pulliam HR, Millikan GC (1982) Social organization in the nonreproductive season. In: Farner DS, King JR, Parkers KC (eds) Avian Biology vol VI. Academic Press, New York, pp 169–197

Rand AL (1954) Social feeding behaviour of birds. Fieldiana Zoology 36:1–71

Smith SM (1976) Ecological aspects of dominance hierarchies in black-capped chickadees. Auk 93:95–107

Sullivan KA (1984) Information exploitation by downy woodpeckers in mixed-species flocks. Behaviour 91:294–311

Székely T, Moskát Cs (1987) Guild-structure of a bird-society in an oakwood. Aquila 93–94:273–277

Ward P, Zahavi A (1973) The importance of certain assemblages of birds as 'information centres' for food finding. Ibis 115:517–534

Received April 11, 1988