

Flexible foraging behaviour in the Danish *Parus* guild: a privilege of the Coal Tit?

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(Med et dansk resumé: *Fleksibel fourageringsadfærd hos småfugle i mejsegildet: Sortmejsens privilegium?*)

Introduction

Ever since Darwin (1859) introduced his charismatic ideas and views, competition has had a leading role in the scientific discipline of ecology. However, interest first became intensified when studies of niches were undertaken (Grinnell 1917, Lack 1944). Niche shifts, where species expand their resource utilisation in the absence of ecological similar species, have most often been interpreted as indirect proofs of the existence and significance of interspecific competition (see also Herrera (1978), Sørensen (1997) and Sørensen (1998)). Numerous studies have investigated niches and demonstrated niche shifts in a wide range of organisms, such as bees (Inouye 1978), birds (Alerstam et al. 1974, Alatalo 1981, Grant & Grant 1982, Madsen 1985), fishes (Werner & Hall 1976), lizards (Pacala & Roughgarden 1982) and primates (Ganzhorn 1989).

A number of tit species belonging to the genus *Parus* are prominent members of bird communities in most temperate woodlands. Together with additional species they form distinct assemblages (*Parus guilds*) of foliage-gleaning species, which are often seen foraging together. Comparative studies of tits have shown niche shifts consistent with the interpretation of interspecific competition (Alerstam et al. 1974, Herrera 1978, Hogstad 1978, Alatalo 1980, 1981). Such shifts have been demonstrated on both regional and local scales,

between areas of allopatry and sympatry (e.g., Gotland vs Swedish mainland (Alatalo 1981)). In addition, field experiments have confirmed that competition occurs among species in the *Parus* guild (Alatalo et al. 1985, 1987).

In a previous study (Sørensen 1997), I reported consistent niche shifts in Coal Tit *Parus ater* populations on two Danish islands, compared to two mainland sites and, in addition, local niche shifts in relation to flock composition. But what about the other species in the Danish *Parus* guild? A study from Finland demonstrated niche shifts in response to different flock compositions by Goldcrests *Regulus regulus* and Willow Tits *P. montanus* (Alatalo 1981) (see also Hogstad (1978) for Norwegian data). On the other hand, Alerstam et al. (1974) found that only Coal Tits performed niche shifts when Swedish mainland and insular populations were compared. Moreover, Herrera (1978) demonstrated niche shifts by Blue Tits *P. caeruleus* in Spanish oak woodlands. Hence, the picture is blurred.

The aim of the present study was to investigate whether species in the Danish *Parus* guild (apart from Coal Tits) respond to changes in flock composition by modifying their foraging behaviour, locally, as well as geographically. The local shifts were examined by observing mixed flocks, which generally provide an excellent opportunity to study niche shifts in ecological time, since dif-

ferent species can be observed with or without putative competing species. Niche shifts between sites (geographical niche shifts) were assessed by observing tit populations at two mainland sites and two islands. As far as I know, previous studies have not involved multiple islands and mainland sites. The present study was performed in autumn, whereas most earlier studies on foraging behaviour have been performed during winter.

Populations, study areas and methods

Five species of tits commonly breed in Denmark. Four species are widely distributed, whereas Crested Tits *P. cristatus* are restricted to Jutland and Funen. In addition, Crested Tits, and to some extent Marsh Tits *P. palustris*, are largely absent from isolated islands in the Danish archipelago (Wiggins & Møller 1997). The data were gathered in autumn 1995 at four sites: Mols (56°14'N, 10°34'E) and Stensbæk (55°16'N, 8°57'E) (mainland); and Anholt (56°42'N, 11°34'E) and Læsø (57°16'N, 11°00'E) (islands). Observations were

made from mid-September to early November at Mols; in mid-October at Stensbæk; from late September to early November on Anholt; and in late October on Læsø. The data were collected alongside with the Coal Tit data previously presented (Sørensen 1997).

The islands Anholt and Læsø in the Kattegat covers 23 km² and 100 km², respectively. The shortest distance from Anholt to the mainland is 48 km, from Læsø 29 km. The distance between the two islands is 72 km. Pines *Pinus sylvestris* and *P. mugo* dominated the woods on Anholt; on Læsø, pine, spruce *Picea abies* and *P. sitchensis*, and deciduous trees were all common. The Mols site was dominated by pine and spruce with some larch *Larix decidua* and deciduous trees, especially birch *Betula* spp. The Stensbæk site was dominated by spruce with some pine.

Anholt and Læsø sustain the same *Parus* species, namely Great *P. major*, Blue and Coal Tits. The mainland sites also hold these species, but here Crested and Marsh Tits are present as well. The study sites thus represent pairwise geographi-

Tab. 1. Tests of potential study site differences in median foraging site scores (Mann-Whitney U-tests). Mols and Stensbæk are mainland sites, Anholt and Læsø islands. GT: Great Tit, BT: Blue Tit, GCr: Goldcrest. SE: Standard error of the mean.

Mann-Whitney U-tests af potentielle forskelle mellem valg af fourageringssted på studielokaliteterne. Mols og Stensbæk er fastlandslokaliteter, Anholt og Læsø er øer. GT: Musvit, BT: Blåmejse, GCr: Fuglekonge. Tests er lavet for 3 forskellige trætyper; Pine: Fyrretræer, Deciduous: Løvtræer, Spruce: Grantræer. SE: Middelfejl på middelværdi.

Species Art	Study sites Lokalitet	Tree Trætype	Score ^a	SE	N	Z ^b	P
GT	Mols vs Anholt	Pine	2.29/2.37	0.10/0.09	40/43	-1.8	0.86
	Mols vs Læsø	Pine	2.29/2.25	0.10/0.15	40/36	-1.2	0.24
	Mols vs Anholt	Deciduous	2.41/2.49	0.07/0.13	60/20	-0.6	0.54
	Mols vs Læsø	Deciduous	2.41/2.43	0.07/0.08	60/44	-0.1	0.96
	Anholt vs Læsø	Pine	2.37/2.25	0.09/0.15	43/36	-1.5	0.15
BT	Mols vs Anholt	Pine	2.46/2.85	0.21/0.22	12/9	-1.6	0.10
	Mols vs Anholt	Deciduous	2.74/2.14	0.09/0.38	23/6	-1.7	0.09
GCr	Mols vs Anholt	Pine	3.42/3.58	0.16/0.04	19/153	-0.7	0.50
	Mols vs Læsø	Pine	3.42/3.61	0.16/0.07	19/51	-0.9	0.36
	Mols vs Anholt	Spruce	3.66/3.58	0.08/0.12	29/15	-0.4	0.67
	Mols vs Læsø	Spruce	3.66/3.68	0.08/0.09	29/24	-0.1	0.89
	Stensbæk vs Anholt	Spruce	3.82/3.58	0.06/0.12	28/15	-1.5	0.13
	Stensbæk vs Læsø	Spruce	3.82/3.68	0.06/0.09	28/24	-1.2	0.22
	Anholt vs Læsø	Pine	3.58/3.61	0.04/0.07	153/51	-0.5	0.60
	Anholt vs Læsø	Spruce	3.58/3.68	0.12/0.09	15/24	-0.5	0.59
	Mols vs Stensbæk	Spruce	3.66/3.82	0.08/0.06	29/28	-1.5	0.12

^a Mean values *middelværdier*

^b Corrected for ties *korrigeret teststørrelse*

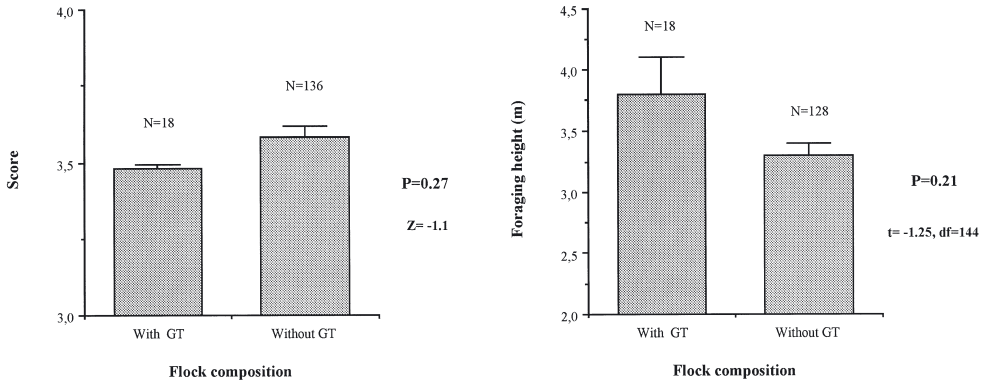


Fig. 1. Foraging site scores (left) and foraging heights (right) for Goldcrests on Anholt during foraging-bouts in spruce stands with or without Great Tits (GT) present. Bars indicate one SE.

Fourageringsscorer (til venstre) og fourageringshøjder (til højre) for Fuglekonger på Anholt under fouragering i grantræer med eller uden tilstedeværelsen af Musvit (GT). SE er angivet over søjlerne.

cal replicas (Anholt/Læsø and Mols/Stensbæk) in terms of *Parus* guild composition, thus diminishing the problem of potential differences in local environments of the study sites. Additional species, such as Goldcrest, Treecreeper *Certhia familiaris*, and Chiffchaff *Phylloscopus collybita* were sometimes part of the guilds. Thus, besides Coal Tits, Goldcrests, Great and Blue Tits are found at all four sites; these were all included in the investigation for geographical niche shifts. Potential niche shifts in relation to flock composition (local shifts) were investigated at Mols, and for Goldcrests also on Anholt, using the presence/absence procedure previously applied (Alatalo 1981, Sørensen 1997).

After localising flocks or single birds, foraging sites were recorded every 15 s. Due to the activity of the birds and the dense canopy, the number of observations usually ranged between one and three; more than five observations per individual were never made. In order to minimise observer bias, the first record was not taken until 15 s after the focal bird was sighted. Tree category (pine, spruce, larch or deciduous), foraging site, estimated foraging height (to the nearest m), and flock size and composition were recorded. The following foraging sites were distinguished: trunk, branch, twig and needle (Ulfstrand & Nilsson 1976). Foraging site scores were defined on an ordinal scale signifying a spatial gradient: trunk=1, branch=2, twig=3 and needle=4.

To assess the degree of intraspecific competition between Coal Tits, observations were divided

into two categories: Coal Tits foraging alone and Coal Tits foraging with conspecifics only.

In order to minimise the detrimental effect of pseudoreplication (Hurlbert 1984), which has plagued most earlier investigations, mean values of foraging site scores and foraging heights for each individual were used in all statistical treatments. Possible niche shifts were investigated by Mann-Whitney U-tests (foraging site medians) and unpaired t-tests (foraging height means).

Results

No significant differences could be found in any mainland/island comparisons of foraging site scores of Goldcrests, Great and Blue Tits. Furthermore, there were no inter-island, nor any inter-mainland differences with respect to foraging site scores of the three species (Tab. 1).

Potential local niche shifts (flock composition shifts) at Mols were investigated, but could not be demonstrated for any species. This applied to foraging site scores (Tab. 2) as well as foraging heights (Tab. 3). The same picture emerged in the Goldcrest population on Anholt, during foraging bouts in spruce stands with or without Great Tits present (Fig. 1). Unfortunately, I was unable to gather enough data on the Goldcrest with and without Coal Tits present from any of my study sites.

Finally, I found no differences in foraging site scores when Coal Tits were observed alone or with conspecifics only (Tab. 4). Hence, the degree of

Tab. 2. Foraging site scores of birds in the *Parus* guild in relation to flock composition at Mols. CrT: Crested Tit, MT: Marsh Tit, CC: Chiffchaff (other abbreviations as in Tab. 1).

Fourageringsscorer for arter tilhørende mejsegildet sat i relation til floksammensætning, Mols. CrT: Topmejsje, MT: Sumpmejsje, CC: Gransanger (øvrige forkortelser som i Tab. 1).

Species Art	Flock composition Floksammensætning	Tree Trætype	Score ^a	N	Z ^b	P
GT	Without CrT and BT	Pine	2.33 ± 0.11	35	-1.1	0.27
	With CrT		2.14 ± 0.14	7		
GT	Without BT and CrT	Deciduous	2.46 ± 0.09	33	-0.4	0.66
	With BT		2.36 ± 0.13	25		
MT	Without GT and BT	Deciduous	2.72 ± 0.10	15	-0.8	0.43
	With GT		2.79 ± 0.11	16		
CrT	Without GT	Pine	2.14 ± 0.11	32	-0.7	0.46
	With GT		2.01 ± 0.12	16		
BT	Without GT and MT	Deciduous	2.73 ± 0.14	11	-0.1	0.89
	With GT		2.79 ± 0.10	14		
BT	Without GT and MT	Pine	2.51 ± 0.35	7	-0.3	0.74
	With GT		2.40 ± 0.19	5		
CC	Without GT	Pine	3.35 ± 0.15	10	-1.1	0.26
	With GT		3.14 ± 0.11	14		

^a Mean ± SE

^b Corrected for ties *korrigeret teststørrelse*

Tab. 3. Foraging heights (m) of birds in the *Parus* guild in relation to flock composition at Mols (see Tab. 1 and Tab. 2 for abbreviations).

Gennemsnitlige fourageringshøjder (m) for arter tilhørende mejsegildet sat i relation til floksammensætning, Mols (forkortelser som i Tab. 1 og Tab. 2).

Species Art	Flock composition Floksammensætning	Tree Trætype	Height ^a	N	t	P
GT	Without CrT and BT	Pine	4.9 ± 0.4	35	-1.53	0.13
	With CrT		6.3 ± 1.0	7		
GT	Without BT and CrT	Deciduous	3.5 ± 0.2	33	1.53	0.13
	With BT		2.9 ± 0.3	25		
MT	Without GT and BT	Deciduous	2.6 ± 0.3	14	1.80	0.083
	With GT		1.9 ± 0.2	16		
CrT	Without GT	Pine	6.8 ± 0.6	32	-0.17	0.87
	With GT		7.0 ± 0.7	16		
BT	Without GT and MT	Deciduous	3.6 ± 0.4	11	1.51	0.14
	With GT		2.8 ± 0.4	14		
BT	Without GT and MT	Pine	5.1 ± 0.37	5	-1.56	0.15
	With GT		6.0 ± 0.5			
CC	Without GT	Pine	6.3 ± 1.4	10	0.77	0.45
	With GT		5.2 ± 0.4	10		

^a Mean ± SE

Tab. 4. Foraging site scores for Coal Tits foraging alone or together with other Coal Tits. *Fourageringsscorer for Sortmejsler fouragerende alene eller sammen med artsfæller.*

	Score ^a				
	Coal Tits alone <i>Sortmejsler alene</i>	Coal Tits with conspecifics <i>Sortmejsler med artsfæller</i>	Z ^b	P	N
Mols, pine	3.75 ± 0.20	3.44 ± 0.19	-1.5	0.13	10/13
Mols, spruce	3.57 ± 0.11	3.50 ± 0.08	-0.9	0.36	39/57
Anholt, pine	3.20 ± 0.13	3.15 ± 0.10	-0.6	0.55	45/53
Stensbæk, spruce	3.69 ± 0.13	3.61 ± 0.11	-0.2	0.88	12/31

^a Mean ± SE

^b Corrected for ties *korrigeret teststørrelse*

intraspecific competition on foraging site choice among Coal Tits appears to be negligible.

Discussion

Niche shifts in species belonging to the *Parus* guild have previously been demonstrated in Sweden (Alerstam et al. 1974), Spain (Herrera 1978) and Finland (Alatalo 1981), so local niche shifts by subdominant species, such as Goldcrest, Chiffchaff and Marsh Tit were to be expected in Denmark. Due to the missing Marsh and Crested Tits on both islands, geographical niche shifts were anticipated by at least the Goldcrest. However, none of these expectations were met. The results might have turned out differently if the study had been performed in winter, when resources are scarce, thus creating a greater incentive to optimise foraging efficiency (Alatalo 1980). Still, it is likely that no niche shifts have occurred over evolutionary time or are occurring (ecological time). The former is in accordance with Wiggins & Møller (1997), who conclude that the present breeding distributions of the *Parus* guild species in the Danish archipelago are largely a result of biogeographic factors (island size and isolation) and dispersal propensity, but not interspecific competition. Consequently, interspecific competition might not have been a strong selective agent in the three species (Goldcrest, Great and Blue Tit) on the two islands, unlike insular Coal Tits (Sørensen 1997).

Previous studies have not considered intraspecific competition. The present study suggests that the degree of intraspecific competition among Coal Tits of foraging site selection is negligible. A possible explanation of this lack of competition

might be kinship among Coal Tits in the same flock. Coal Tits might by this *non-competitive approach* promote the survival of relatives.

The studied species showed little flexibility in their foraging behaviour, indicating a rather rigid foraging organisation, at least in the non-winter period. My study does not exclude the possibility of small-scale flexibilities (e.g. foraging flexibility as a response to differential microhabitat prey density (Smith & Sweatman 1974)). Other factors that could have influenced searching efficiency are morphological constraints (e.g. large size of Great Tits (Wiggins et al. 1998)), predation risk, prey abundance, palatability and conspicuousness (see Royama (1970) for details). However, these considerations are beyond the scope of this paper.

The evidence from the present study, combined with my earlier findings, indicates that the Coal Tit is the only species in the Danish autumn *Parus* guild that alters its foraging behaviour in response to differential flock composition, geographically as well as locally. This flexibility is probably necessitated by the small size of the Coal Tit, as a method of coping with the competitive pressures exerted by the other species in the guild, whereby foraging optimisation might be achieved. Another way for Coal Tits to optimise their foraging efforts, in spite of fierce interspecific competition, seems to be an overall refrainment from intraspecific competition.

The other species in the autumn *Parus* guild occupy, by virtue of their dominance status, profitable foraging sites (e.g. Great Tits and Crested Tits), or are forced to occupy low-quality foraging sites (e.g. Goldcrests and Coal Tits), in return for the many benefits of flocking (Krebs et al. 1972, Krebs 1973).

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Resumé

Fleksibel fourageringsadfærd hos småfugle i mejsegildet: Sortmejsens privilegium?

Fourageringsadfærd hos en lang række småfugle blev i efteråret 1995 studeret på fire lokaliteter i Danmark. Undersøgelsen blev udført på to øer, Anholt og Læsø, samt på to jyske lokaliteter, Mols Bjerge og Stensbæk. Jeg var interesseret i at undersøge potentielle nicheforskydninger for derigennem at kunne sige noget om graden af interspecifik konkurrence i disse fuglesamfund, hvori de fleste arter er mejser.

Denne artikel, der er en opfølgning på Sørensen (1997), undersøger to slags nicheforskydninger: (1) geografiske adfærdsforskelle mellem øer og fastlandslokaliteter og (2) lokale og midlertidige forskelle i fravær/tilstedeværelse af dominante arter, såsom Musvit *Parus major* og Topmejsen *P. cristatus*. På Anholt og Læsø er Topmejsen og Sumpmejsen *P. palustris* fraværende.

De to nicheparametre fourageringsscore og -højde blev undersøgt; fourageringsscoren er en talmæssig angivelse af fourageringsstedet på træet: stamme=1, gren=2, kvist=3, nåle=4. Jeg fandt hverken geografiske nicheforskydninger med hensyn til fourageringsscore (Tab. 1) eller lokale forskydninger i fourageringsscore og -højde (Tab. 2, Tab. 3).

Den nærværende undersøgelse indikerer, at interspecifik konkurrence er (og har været) en svag evolutionær drivkraft for de undersøgte arters udvikling og udbredelse. Disse indikationer er i overensstemmelse med konklusionerne fra et nyligt studium af mejsers udbredelse på 53 danske øer (Wiggins & Møller 1997).

Undersøgelsen understreger Sortmejsens *P. ater* unikke status i "mejsегildet" med hensyn til dens fleksible fourageringsadfærd (Sørensen 1997). Hermed antydes en temmelig veletableret fourageringsorganisation i resten af gildet – i hvert fald om efteråret.

Sortmejsen er med sine 9,5 gram den næstmindste art i gildet, og er derfor en af de laveste i hierarkiet. En Sortmejs, der konfronteres med en stor Musvit eller en hidsig Blåmejs *P. caeruleus*, må ofte nøjes med mindre optimale fødekilder. Sortmejsens fleksibilitet bevirker imidlertid, at den hurtigt kan skifte til mere profitabile fødeområder, når chancen byder sig. Min undersøgelse indikerer også en anden måde, hvorpå fødekongurrence mindskes – Sortmejsen undgår nemlig i vid udstrækning konkurrence med artsfæller (Tab. 4).



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