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Foraging niche differences between species are correlated with body-size differences in mixed-species flocks near Seoul, Korea

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In December 1996/January 1997, we studied the distribution of foraging sites of a guild of 5 species of birds (from larger to smaller: *Sitta europaea, Parus varius, P. major, P. palustris, P. ater, Aegithalos caudatus*) wintering in Korea. Correlations between body size and the use of foraging sites in trees are well described for European tits. Our results indicate that similar correlations exist in this Korean guild. There were significant differences among species in frequency of use of five foraging site categories in trees: trunks, branches, twigs, leaves, needles. The larger the species, the more often it used trunks and branches for foraging. There was a positive correlation between body-size difference and the difference in the foraging sites between species, indicating that species of similar body sizes foraged in similar sites in trees. For four species not specialized in using conifers (*Parus varius, P. major, P. palustris, Aegithalos caudatus*), there was a negative correlation between body size difference between species and the difference in the frequency of foraging in conifers, suggesting that birds of similar body sizes foraged in different tree species. We suggest a possible role of dominance in creating this relationship. This is one of the few reports of foraging niche differences among tits in temperate forests in Asia. This report is important in that it shows, for the first time, foraging niche differences in a previously unstudied guild of tits, and that the differences are correlated with size differences, just as in the well studied guild of tits in Europe.

1. Introduction

Body size is one of the factors contributing to the separation of ecological niches among birds (Lack 1954, Krebs 1994, Schoener 1983) including tits, *Paridae* (e.g., Norberg 1979, Alatalo 1982, Alatalo et al. 1986, Alatalo and Moreno 1987, Carascal et al. 1990, Suhonen et al. 1994, Carlson 1992). Separation of ecological niches among tits in mixed species flocks in winter has been studied extensively in boreal (Ekman et al. 1981, Alatalo 1981, 1982, Alatalo et al. 1986, Alatalo & Moreno 1987, Alatalo et al. 1987, Dhondt 1989, Ekman 1989, Hogstad 1989, Suhonen et al. 1992, Suho-

nen 1993, Suhonen et al. 1993, 1994) and temperate zones of Europe (e.g., Herrera 1978, Rolando 1983, Szekely et al. 1989, Sasvari 1992, Carascal & Moreno 1992), and in North America (e.g., Hamerstrom 1942, Hartzler 1970, Dixon 1965, Smith 1967, Cimprich & Grubb 1994, Yaukey 1995). The tit species usually forage in trees, and occasionally on the ground. The foraging sites in trees are distributed narrowly: bark crevices of tree trunks, branches, or twigs, tips of twigs, basal parts of needles (in conifers), dry leaves on twigs (in some deciduous trees like oaks). Foragers in the inner tree parts (trunk, branches) are better protected against predation than foragers in the outer tree parts (Suhonen 1993a, Suhonen 1993b, Suhonen et al. 1993). Hence, the size-related dominance results in competition for food and for safer foraging sites (predation) and shapes selection of the foraging niche of species in the flocks (Alatalo 1982, Alatalo et al. 1985, 1986, Alatalo and Moreno 1987, Carlson 1992).

It has been well documented in a series of studies during the last 40 years that heavier species dominate smaller ones in aggressive interactions (e.g., Hinde 1952, Gibb 1954, Morse 1978, Hogstad 1978), and that heavier species forage in inner tree parts, on trunks and branches, while smaller species forage in outer foliage, on smaller twigs (e.g., Snow 1949, Gibb 1954, Ulfstrand 1962, Alatalo 1982, Alatalo et al. 1986, Carrascal et al. 1990, Suhonen et al. 1994). Accordingly, Alatalo and Moreno (1987) and Carlson (1992) provided experimental evidence that interference competition and avoidance of larger species by smaller ones largely contribute to the size-dependent distribution of foraging sites of birds in the guilds. Additionally, the size dependent separation of niches may be enhanced by exploitation competition: avoidance by dominant birds of outer parts of trees in the presence of smaller, subordinate species has been experimentally documented in northern Europe (Alatalo et al. 1987). Partridge (1976), Norberg (1979) and Carascal et al (1990) suggested that body size and other morphological variables may also directly influence foraging niches through their impact on profitability of foraging behavior at certain locations in trees or in certain tree species. As a result of all these processes, the greater is the difference in body size and morphology between species, the more the species differ in their foraging niche. Also, the smaller the morphological, difference the stronger the competition between the species, as indicated by divergent shifts in foraging site distribution in response to the presence of a competitor species (review in Alatalo et al. 1986).

Most of this knowledge about guilds of *Paridae* and associated species comes from Europe. Therefore, it would be important to see whether the relationships known for European tits also hold in tit flocks of different species composition. The flocks in Korea contain the large-bodied Varied Tit (*P. varius)*, absent in Europe, and a subspecies of the Great Tit — *P. major minor,* which is smaller than the European subspecies. The aim of this paper is to describe foraging sites in trees and to look for a relationship (well documented for European tits) between body size and foraging niche in trees of a guild of six bird species in Korea. We asked whether in this guild species differ from each other in their use of foraging sites in trees and whether there is a correlation between similarity in body size and similarity of feeding site distributions. We also asked whether there is a correlation between body-size difference between species and the difference in the frequency of foraging in conifers.

2. Methods

In December 1996 and January 1997 we watched tits in forests on mountain slopes near Seoul (within 50 km from the city, 0–488 m above sea level). The forests consisted of pines (*Pinus rigida, P. densiflora,* and *P. koraiensis),* firs (*Abies holophylla*) or oaks (*Quercus accutissima, Q. aliena, Q. mongolica, Q. serrata, Q. variabilis, Q. dentata*) intermixed variously. *Alnus japonica, Robinia pseudo-acacia, Castanea crenata, Rhododendron* spp., *Prunus* spp., *Betula* spp., and *Zelkova serrata* were also present. We recorded foraging site positions of birds with regard to five categories of the substrate on which they fed: trunk, branches (more than 3 cm in diameter), twigs (approximately 3 cm or less in diameter), dry leaves (in deciduous trees) or needles (in coniferous trees). After recording the foraging site of a bird we changed the direction of the search for the next bird to avoid consecutive repeated observations of the same indi-

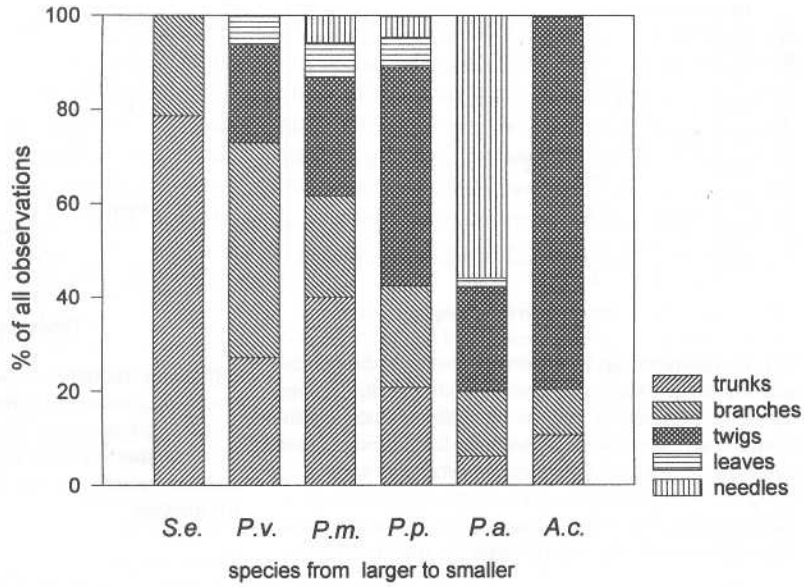

Fig. 1. Foraging site distributions of five species, *Sitta europaea* (*S.e.*, n = 14), *P. varius* (*P.v.*, n = 48), *P. major* (*P.m.*, n = 190), *P. palustris* (*P.p.*, n = 230), *P. ater* (*P.a.*, n = 161), and *A. caudatus* (*A.c.*, n = 83), in trees in forests near Seoul, in winter 1996/97.

vidual. As birds moved fast, the same individuals might have been recorded more than once, in different trees. The birds were not individually marked. We recorded 14 foraging sites of *Sitta europaea,* 48 of *P. varius,* 190 of *P. major*, 230 of *P. palustris*, 161 of *P. ater*, and 83 of *A. caudatus.* These observations were used in the analysis of the use of foraging sites in trees. We also recorded interactions between individuals.

To study whether there is a relationship between a species' size and its foraging site characteristics, we calculated correlations between the species' body size and the percentage of observations of a given species on trunks and branches. We used the weights in the middle of the body size range for each species reported for Korea (Won 1981): *Sitta europaea amurensis*,19 g (range: 18–20); *Parus varius varius,* 17 g (14–20); *Parus major minor*, 12.75 g (12–13.5); *Parus palustris brevirostris*, 11.5 g (11–12); *Parus ater ater*, 10.25 g (9.6–10.9); *Aegithalos caudatus magnus*, 7 g (6–8).

To study the relationship between body size difference between species and the difference in their foraging sites we calculated an index of difference. For each of the four types of foraging site in a tree (trunk, branch, twig, leaves and needles pooled together as one category) we calculated the absolute value of the difference between the frequency (%) of its use by one species and such a frequency for another species. For each pair of species, we have added up these five differences to obtain an index of niche difference (possible values 0–200%, from identical to totally different niches). For each pair of species, we calculated absolute value of the difference in body size and calculated correlation between the difference in body size and the index of foraging site difference.

We also calculated a correlation between the difference in body size and the difference in the frequency of use of coniferous trees between each two species. For this analysis more observations were available (including those for which full information about foraging site was not available, and therefore they were not used in the foraging site analysis): 30 for *S. europae*a, 74 for *P. varius*, 241 for *P. major*, 290 for *P. palustris*, 256 for *P. ater*, and 84 for *A. caudatus*.

3. Results

There was a significant positive correlation (r = 0.959, n = 6, p = 0.0024) between body size and the frequency of use of trunks and branches: larger birds used branches and trunks more often than did smaller species (Fig. 1). After excluding *S. europea,* a species specialized in trunk and branch foraging, the correlation remained significant (r = 0.930, n = 5, p = 0.022).

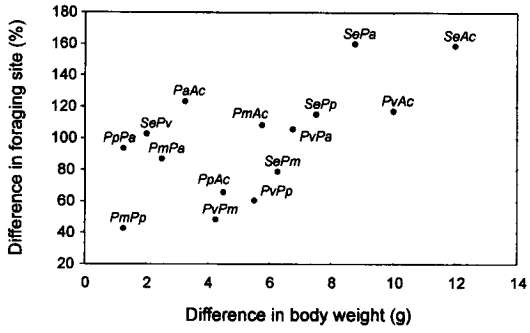

Fig. 2 . Relationship between difference in body size and the difference in the foraging site distribution for 15 pairs of species (all two-species combinations from the six species) in flocks near Seoul. Four-letter symbols denote pairs of species; two-letter code was used for each species: *Se = Sitta europaea; Pv = Parus varius; Pm = Parus major; Pp = Parus palustris; Pa = Parus ater; Ac = Aegithalos caudatus.*

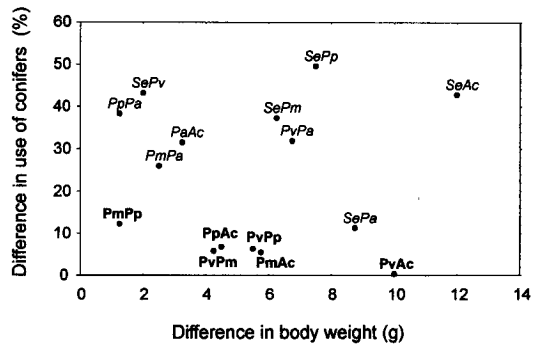

Fig. 3. Relationship between difference in body size and the difference in the use of coniferous trees for 15 pairs of species. The four-letter symbols denote pairs of species (*see* Fig. 2). Bold indicates pairs of species which are not specialized in using conifers exclusively.

The correlation between the differences in body size and the differences in the feeding site distribution was positive and significant ($r = 0.644$, $n = 15$, $P = 0.010$, Fig. 2). It means that foraging sites of species of similar body size overlap more than do sites of species of different body size. If species of similar body size share similar foraging sites in trees, do they avoid competition by using different types of trees? Two of the species, *S. europaea* and *P. ater*, showed high frequency (100% and 89%, respectively) of foraging in conifers. The remaining 4 species foraged in conifers less frequently: *P. major*, 63%; *P. varius* and *A. caudatus*, 57% each; *P. palustris*, 50%. There was no correlation between body size difference and the difference in the use of conifers ($r = -0.027$, $n = 15$, $p = 0.923$, Fig. 3). However, after excluding the two species specialized in using conifers (*P. ater* and *S. europaea*), the correlation was negative and significant ($r = -0.970$, $n = 6$, $p = 0.001$; Fig. 3, pairs marked in bold). It means that the smaller the difference in body size between any two species, the more the two species differ in their frequency of foraging in coniferous trees.

In 85% of interactions between *P. major* and *P. palustris* ($n = 15$), the heavier species (*P. major*) was the attacker (significantly more often, $\chi_1^2 = 6.23$, $P < 0.002$, than expected if *P. major* did not dominate *P. palustris*). All four interactions between *P. varius* and *P. major,* and four interactions between *P. major* and *P. ater* were attacks of the heavier species (binomial $P = 0.06$). The interactions took place between species which did not differ considerably in their body weights: 4.25 g for *P. varius–P. major*, 1.25g for *P. major–P. palustris* and 2.5 g for *P. major–P. ater,* in comparison to the maximum difference of 12 g (*S. europaea-A. caudatus*) . Among the remaining 3 interactions observed, two were of *P. varius* supplanting *P. palustris* and one of *P. varius* supplanting *P. ater.*

4. Discussion

Similarity of foraging site distributions between species of similar body sizes illustrates that morphology contributes to shaping the ecological niches and that competition is expected to be the most pronounced in pairs of species of similar body sizes. Accordingly, most of the aggressive interactions were observed between species which did not differ much in their body weights. The fact that species whose body sizes differed the least were the most divergent in their frequencies of foraging in conifers suggests that they may avoid each other by choosing different trees. This is consistent with the interpretation that among tits in Korea, the strength of competition between species is negatively correlated with the difference in their body size, a relationship documented in European guilds (Alatalo et al. 1986).

As in other studies carried out in Europe (e.g., Alatalo 1981, 1982, Alatalo et al. 1986, Alatalo et al. 1987, Dhondt 1989, Alatalo & Moreno 1987, Moreno 1981, Carrascal et al. 1990, Rolando 1983, Suhonen et al. 1992, Suhonen 1993, Suhonen et al. 1993, 1994), larger species in Korea used trunks and branches more often than did smaller species. The larger species dominated in interactions over the smaller ones in the studied flocks, which is the same as with tits in Europe (e.g., Gibb 1954, Hinde 1952, Morse 1978, Hogstad 1978). This suggests that, as in European tits, the positive correlation between body size and the use of inner tree parts may be related to dominance.

Why do birds compete for the inner tree parts? If food is more abundant in inner tree sections one should expect that dominant species would exclude the subordinate ones from inner parts of trees to gain better resources. We do not have evidence of such differences in resource abundance between inner and outer tree sections in Korea, but Suhonen et al. (1992) reported differently for northern Europe: higher arthropod abundance in outer than inner tree sections. It has been shown in Europe that differences in predation risk between inner and outer tree parts may better explain the differences between large and small species in distribution of their foraging sites (Ekman 1986, Suhonen et al. 1992, Suhonen 1993, Suhonen et al. 1993, 1994) . In general, European species avoid outer tree sections because doing so brings about better protection against predation from hawks and pygmy owls. Hawks (*Accipiter nisus*) were present in the study area. Smaller species in our study might have been forced by the larger ones to forage in outer tree sections because birds there are more exposed to predators.

In summary, we showed that differences of ecological niche between members of the mixed species flocks in Korea are positively related to body-size differences between species, just as in European guilds of tits and associated species. Our observations of aggressive interactions among these birds suggest a possible role of dominance in creating the relationship reported here. However, we do not have data to estimate the role of differences in food abundance and predation risk among sites in shaping foraging site differences among species in Korea. Hence, this report is important in that it shows, for the first time, foraging niche differences in a previously unstudied guild of tits, and that the differences are correlated with body-size differences just as in the well-studied guilds of tits in Europe. Foraging niche differences in a different guild of tits (excluding the Varied Tit) of temperate Asia were previously reported by Ogasawara (1970a, 1970b, 1975).

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Selostus: **Erot lajien ruokailutavassa korreloivat lajien kokoerojen kanssa tiaisten ja pähkinänakkelin sekaparvissa Koreassa**

Kirjoittajat tutkivat tiaiskillan lajien ruokailukäyttäytymistä talvella 1996/97 Koreassa. Kiltaan kuului 5 lajia (isoimmasta pieninpään): pähkinänakkeli, kirjotiainen (*Parus varius*), talitiainen, viitatiainen, kuusitiainen ja pyrstötiainen. Linnun ruumiin koko oli yhteydessä ruokailupaikkaan: suurikokoiset lajit ruokailivat enemmän puiden rungoilla ja paksuilla oksilla kuin pienikokoiset lajit (Kuva 1). Tämä tulos havaittiin riippumatta siitä, oliko pähkinänakkeli mukana analyysissä vai ei. Lajien välinen painoero korreloi positiivisesti ruokailupaikan eroavaisuuden kanssa (Kuva 2), mikä merkitsee sitä, että kooltaan samankaltaiset lajit ruokailivat samoissa osissa puuta. Lajien välinen kokoero ei ollut yhteydessä siihen kuinka paljon lajien ruokailupaikat poikkesivat havupuiden ja lehtipuiden käytön suhteen. Kuitenkin kun analyysistä jätettiin pois selkeästi havupuihin erikoistuneet lajit, pähkinänakkeli ja kuusitiainen, tämä korrelaatio osoittautui merkitseväksi ja negatiiviseksi (Kuva 3). Tulos viittaa siihen, että samankokoiset lajit pyrkivät välttämään ravintokilpailua ruokailemalla erilaisissa puissa (havu- vs. lehtipuissa).

Korealaisista talviparvista saadut tulokset lajien ruumiinkoon ja ruokailupaikkojen välisestä suhteesta ovat pitkälti samanlaisia kuin hyvin tutkituissa eurooppalaisissa tiaiskillan talvisekaparvissa. Kirjoittajat tutkivat myös lajien välisiä suoria vuorovaikutuksia. Tuloksissa havaittiin selvä säännönmukaisuus, missä suurikokoinen laji dominoi pienempää. Kirjoittajat päättelevät, että dominanssihierarkia talviparvissa on havaittujen ilmiöiden taustalla: suurikokoiset lajit ruokailevat lähempänä runkoa, missä ravintoa on runsaammin ja/tai riski joutua pedon saaliiksi on pienempi kuin ulompana puiden oksilla, pienikokoisten lajien joutuessa tyytymään oksiston ulompiin osiin.

References

Alatalo, R. V. 1981: Interspecific competition of tits Parus spp. and the goldcrest Regulus regulus: foraging shifts in multispecific flocks. — Oikos 37: 335–344.

Alatalo, R. V. 1982: Evidence for interspecific competition among European tits Parus spp: a review. — Ann. Zool. Fenn. 19: 309–317.

Alatalo, R. V. & Moreno, J. 1987: Body size, interspecific interactions and use of foraging sites in tits (Paridae). — Ecology 68: 1773–1777.

Alatalo, R. V., Gustafsson, L., Linden, M. & Lundberg, A. 1985: Interspecific competition and niche shifts in tits and the goldcrests: an experiment. — J. Anim. Ecol. 54: 977–984.

Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1986: Interspecific competition and niche changes in tits (Parus spp): an evaluation of nonexperimental data. — Am. Nat. 127: 819–834.

Alatalo, R. V., Eriksson, D., Gustafsson, L. & Larsson, K. 1987: Exploitation competition influences the use of foraging sites by tits: experimental evidence. — Ecology 68: 284–290.

Carascal, L. M., Moreno, E. & Telleria, J. L. 1990: Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. — Holarctic Ecology 13: 105–111.

Carascal, L. M. & Moreno, E. 1992: Proximal costs and benefits of heterospecific social foraging in the great tit, Parus major. — Can. J. Zool. 70: 1947–1952.

Carlson, A. 1992. Body size, prey handling efficiency, and choice of diet in three coniferous forests tits (Paridae). — Biol. J. Linn. Soc. 46: 299–308.

Cimprich, D. A. & Grubb, T. C. 1994: Consequences for carolina chickadees of foraging with tufted titmice in winter. — Ecology 75:1615–1625.

Cramp, S. 1993: Handbook of the birds of Europe the Middle East and North Africa. — The Birds of Western Palearctic. Vol 7. Oxford University Press, Oxford, New York.

Dhondt, A. A. 1989: Ecological and evolutionary effects of interspecific competition in tits. — Wilson Bull. 101: 198–216.

Dixon, K. L. 1965: Dominance-subordination relationships in the Mountain Chickadee (Parus gambeli). — Condor 67: 291–299.

Ekman, J. 1986: Tree use and predation vulnerability of wintering passerines. — Ornis Scandinavica. 17: 261–267.

Ekman, J. 1989: Ecology of non-breeding social systems of Parus. — Wilson Bull. 101: 263–288.

Ekman, J., Cederholm, G. & Askenmo, C. 1981: Spacing and survival in winter groups of willow tits Parus montanus and crested tits P. cristatus — a removal study. — J. Anim. Ecol. 50:1–9.

Gibb J. 1954: Feeding ecology of tits, with notes on treecreeper and goldcrest. — Ibis 96: 513–543.

Hamerstrom, F. 1942: Dominance in winter flocks of chickadees. — Wilson Bull. 54: 32–42.

Hartzler, J. E. 1970: Winter dominance relationships in Black-capped Chickadees. — Wilson Bull. 82: 427–434.

Herrera, C. M. 1978: Niche shift in the genus Parus in southern Spain. — Ibis 120: 236–240.

Hinde, R. A. 1952: The behavior of the great tit, Parus major, and some related species. — Behaviour suppl. 2: 1–201.

Hogstad, O. 1978: Differentiation of foraging niche among tits, Parus spp., in Norway during winter. — Ibis 120: 139–146.

Hogstad, O. 1989: Subordination in mixed-age bird flocks — a removal study. — Ibis 131: 128–134.

Krebs, C. J. 1994: Ecology. The Experimental Analysis of Distribution and Abundance. Fourth Edition. — Harper-Collins College Publishers.

Lack, D. 1954: The Natural Regulation of Animal Numbers. — Oxford University Press, New York.

Lee, S. D. & Jabłoński, P. G. (submitted) : Spatial segregation among tits in mixed species flocks wintering in forests near Seoul, Korea.

MacArthur, R. H. 1958: Population ecology of some warblers of northeastern coniferous forests. — Ecology 39: 599–619.

Moreno, J. 1981: Feeding niches of woodland birds in a montane coniferous forest in central Spain during winter. — Ornis Scand. 12: 148–159.

Morse, D. H. 1978: Structure and foraging patterns of flocks of tits and associated species in an english woodland during winter. — Ibis 120: 298–312.

Norberg, U. 1979: Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the tree creeper in relation to locomotor pattern and feeding station selection. — Phil. Trans. R. Soc. Lond. B 287: 131–165.

Ogasawara, K. 1970a: Analysis of mixed flocks of tits in the botanical garden of Tohoku University, Sendai. II. Foraging layers by species and their interrelations

within the mixed flock. — Misc. Rep. Yamashima Inst. Ornithol. 6: 170–178.

Ogasawara, K. 1970b: Analysis of mixed flocks of tits in the botanical garden of Tohoku University, Sendai. III. Flock behaviors and interspecific relations within the mixed flock. — Misc. Rep. Yamashima Inst. Ornithol. 6: 179–187.

Ogasawara, K. 1975: Analysis of mixed flocks of tits in the botanical garden of Tohoku University, Sendai. III. Foraging habits and supplanting attacks among species forming mixed flocks. — Misc. Rep. Yamashima Inst. Ornithol. 7: 638–651.

Partridge, L. 1976a: Field and laboratory observations on the foraging and feeding techniques of blue tits (Parus caeruleus) and coal tits (P. ater) in relation to their habitats. — Anim. Behav. 24: 534–544.

Partridge, L. 1976b: Some aspects of the morphology of blue tits (Parus caeruleus) and coal tits (P. ater) in relation to their behaviour. — Journal of Zoology 179: 121–133.

Rolando, A. 1983. Ecological segregation of tits and associated species in two coniferous woods of northern Italy. — Monitore Zool. Ital. 17: 1–18.

Sasvari, L. 1992: Great tits benefit from feeding in mixed-species flocks: A field experiment. — Anim. Behav. 43: 289–296.

Schoener, T. W. 1983: Field experiments on interspecific competition. — Am. Nat. 122: 240–285.

Siegel, S. & Castellan, N. J. 1988: Nonparametric statistics for the behavioral sciences. — McGraw-Hill, Inc. 399 pp.

Smith, S. M. 1967: An ecological study of winter flocks of Black-capped Chickadees and Chestnut-backed Chickadees. — Wilson Bull. 79: 200–207.

Snow, D. W. 1949: Jämförande studier över vara mesarters näringsokande. — Var Fagervärld 8: 159–169.

Suhonen, J. 1993a: Risk of predation and foraging sites of individuals in mixed-species tit flocks. — Anim. Behav. 45: 1193–1198.

Suhonen, J. 1993b: Predation risk influences the use of foraging sites by tits. — Ecology 74: 1197–1203.

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.

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. & Gustafsson, L. 1994: Evolution of foraging ecology in fennoscandian tits (Parus spp.). — Proc. R. Soc. Lond. B 258: 127–131.

Szekely, T., Szep, T. & Juhasz, T. 1989: Mixed species flocking of tits (Parus spp.): A field experiment. — Oecologia 78: 490–495.

Ulfstrand, S. 1962: On the nonbreeding ecology and migratory movements of the great tit Parus major and the blue tit Parus caeruleus in southern Sweden. — Var Fagervärld suppl 3: 1–145.

Won, P. O. 1981: Illustrated flora and fauna of Korea. vol 25. — Avifauna, Ministry of Education: 1–1126.

Yaukey, P. H. 1995: Effects of food supplementation and predator simulation on nuthatches and parids within mixed-species flocks. — Wilson Bull. 107: 542–547.