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Foraging niches of two passerines at their subarctic limit of distribution: the Siberian Tit *Parus cinctus* and the Pied Flycatcher *Ficedula hypoleuca*

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Foraging niches of a well-established native (Siberian Tit) and a southern migratory passerine (Pied Flycatcher) were studied at their northern limit of distribution in Finnish Lapland at 69°N. For both species, there were marked seasonal fluctuations in food availability, with peaks in late summer well after the breeding season. Overall, both species had wide and partially overlapping foraging niches during the breeding season. Extensive overlap of food niches is possible presumably because of the low density of birds in relation to their food resources. The overlap of foraging niches was lowest in late summer, at the time when food availability peaked. Niches were broadest in mid- (Siberian Tit) or late summer (Pied Flycatcher). A broad niche may be necessary for successful breeding since no single food source is available throughout the breeding season. This may make it impossible for truly specialized foragers to spread farther north because of the short period when its food sources are available.

1. Introduction

Food abundance is the most significant factor affecting foraging patterns of birds. It has been shown that insectivorous birds concentrate their search during periods of high prey densities (Royama 1970, Krebs 1978). However, intra- and interspecific competition, predation, morphology and life-histories of birds modify foraging behaviours (Alatalo 1982a, Alatalo et al. 1985, 1987, Ekman 1986, 1987, With & Morrison 1990, Suhonen 1993). To understand the mechanisms resulting in different foraging strategies, we need studies that clarify the effects of all these factors.

Most studies relating to foraging strategies in birds have been conducted in the temperate zone. In this paper we describe foraging niches of two passerines (a resident Siberian Tit, and a southern migrant Pied Flycatcher) in Finnish Lapland. This is an environment where food availability is seasonally very peaked, short and annually variable (Veistola et al. 1995). Furthermore, both the density and diversity of birds are low (Järvinen 1979), suggesting low competition especially during the short peak of maximum food availability. Of the two species, the breeding biology of the Pied Flycatcher has been extensively studied but only a few detailed studies have been made on the foraging tactics of this species (Lundberg & Alatalo 1992). As far as we know, only one earlier study concerned foraging behaviour of the Siberian Tit during its breeding season (Virkkala 1988, see Cramp & Perrins 1993).

Our aim in this paper is to report how the species react to fluctuating food conditions. In particular, we are interested in possible alterations of foraging patterns in relation to variable food availability. We propose that the species have different solutions for food fluctuation, because they differ in morphology and breeding history in northern areas (see Holmes & Schultz 1988, Moreno & Carrascal 1993, Suhonen et al. 1994). We expect that the overlap of the foraging niches of the species is possibly smaller during peaks in food abundance. This arises from the idea that morphology and foraging patterns of the species allow different solutions to use the maximum amount of food (MacArthur & Pianka 1966, Robinson & Holmes 1984).

2. Materials and methods

Data for this article were gathered from a long-term project on the ecology of hole-nesting passerines and on the abundance of their food in northern Finland, near the Kevo Subarctic Research Station (69°N) in the Utsjoki valley.

The forests in the study area consist mainly of tree-line birch forests or shrubs, dominated by the Mountain Birch (*Betula pubescens* spp. *czerepanovii*). Although the area is north of the forest line for the Scots Pine (*Pinus sylvestris*), individual pines and stands occur in river valleys (see details from Kallio et al. 1969). Thus, both birch and pine were common in our study area, and birds were able to use both tree species in every territory.

In an earlier study we looked at food availability in ground-layer vegetation, in forbs and bushes, and in trees (for details, see Veistola et al. 1995). These censuses covered the whole summer period, from the end of May to the end of August for two to six summers. Fig. 1 gives a short summary of the combined data for the years

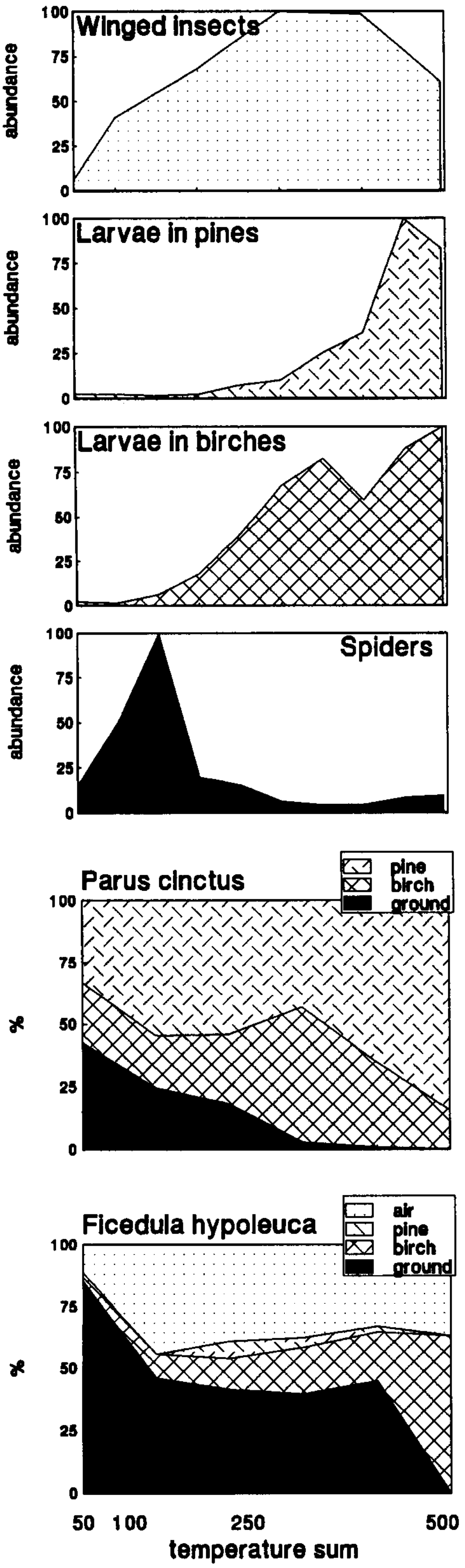

Fig. 1. Relative availability of different food sources in Kevo, and foraging-site use in the Siberian Tit (n = 160 observation periods) and the Pied Flycatcher (n = 143) during the breeding season. The figure gives relative alterations in availability of four food sources (larvae in pines, larvae in birches, winged insects and spiders) in relation to temperature sum (base of 5°C). The temperature sum 50 D° was reached on average 12 June (range 3 June–17 June), and 250 D° on average 10 July (range 1 July–21 July), respectively in 1986–1991.

1986–1991. At the end of May and in the beginning of June (temperature sum < 50 D°, when there were no leaves on birches and the ground was partly covered by snow), food resources were uniformly poor. The availability of spiders in the ground layer increased in June (temperature sum ca. 50–150 D°), but decreased steeply after that (Fig. 1). Winged insects were most abundant in July, and were still common in August (see details from Veistola et al. 1995). Larval abundance in birches and pines started to increase in July, and the peak occurred in August.

The foraging behaviour of the two species was studied by direct observation. This was done for the Siberian Tit (*Parus cinctus*) and the Pied Flycatcher (*Ficedula hypoleuca*) during 1986–1991 and 1994. Direct observation is easy, particularly for the tame Siberian Tit. Furthermore, the low and sparse vegetation makes for easy observation. Foraging observations were made in 25 territories of the Siberian Tit and 51 territories of the Pied Flycatcher, usually between 8 a.m. and 4 p.m. For the Siberian Tit, which regularly stayed longer periods at a site, one observation lasted less than a minute. In the Pied Flycatcher, which is less easy to observe, one successful catch of a food item was recorded as one observation. Our observation periods lasted on average one hour during which two to fifty observations per individual were recorded. Since the observations were not independent, we calculated average percentage distributions for observation periods, and used these in analyses. Because of time constraints and low densities of species, we had to observe some territories repeatedly. This leads to some unavoidable nonindependence in data. Our conclusions were not sensitive to possible nonindependence of some observation periods, because the sampling was well interspersed over the study area and weather conditions.

Prey items fed to the young were identified with the aid of binoculars and from videotapes made during 1986–1990 and 1994. Eleven nests of the Siberian Tit (72 study periods; the young 3–19 days old), and fifteen nests of the Pied Flycatcher (46 study periods; the young 3–14 days old) were observed for this part of the study.

We measured foraging niches at two levels. First, we analysed partial niches in the following separate 'niche axes':

1. Tree species or other niche (birch, pine, ground, air, later tree category);
2. Foraging height (two classes in birch (0–2 m, 2–6 m), three classes in pine (0–2 m, 2–6 m, > 6 m); and
3. Horizontal tree part (three classes, trunk, middle and outer zone of branches or twigs).

Second, we defined the combined feeding niche space to be all the seventeen niches: ground, air, six feeding sites in birch and nine in pine. The inverse of Simpson's index was used as the measure of niche breadth:

$$B = \frac{1}{\sum p_i 2} \tag{1}$$

where p_i is the proportion of the *i*th category.

The differences of niche breadths between the periods (Table 1) were tested by the Kruskal-Wallis test.

Niche overlaps between species were analysed by the specific niche overlap index (SO, see Ludwig & Reynolds 1988). SO_{ki} measures overlap of species k's niche with that of species i, and SO_{ik} *vice versa*. This index thus allows an asymmetric overlap situation.

To be able to classify the data based on phenological stages, we pooled foraging data collected during different years by temperature sums (base 5°C), at the time of each observation. To study seasonal changes in the foraging behaviour during the breeding season, we divided the foraging data into three periods according to the phenological stage (Table 1).

3. Results

The food taken by the Siberian Tit changed significantly with the seasons. During the pre-laying, laying and incubation periods (from mid-May to mid-June, Table 2, Fig. 1), the Siberian Tit preferred to forage on the ground layer. At this level, Siberian Tit avoided bare ground, but preferred patches of *Empetrum* and *Vaccinium* vegetation as a foraging niche (89% of the ground layer observations). Before the spiders emerged, the Siberian Tit mainly fed on *Tipula* larvae on the ground layer. In addition, the Siberian Tit used pines and birches even during peak spider abundance (Fig. 1). As the availability of food supplies increased in trees, and spider availability decreased on the ground layer, the Siberian Tit shifted to foraging in trees. In late summer, the Siberian Tit foraged more in pines than in birches (Table 2, Fig. 1).

The Pied Flycatcher foraged almost exclusively on the ground layer during the laying and incubation periods (in early June, Table 2, Fig. 1). When the number of flying insects increased (Fig. 1), the Pied Flycatcher caught them mostly on the ground layer or just above (Table 2). The Pied Flycatcher used birches to some extent only in late summer (almost exclusively foliage, Figs. 1 and 2), but it always avoided pines (Fig. 1, Table 2).

The Siberian Tit fed small Araneae and Diptera (own obs.) to small nestlings (1–3 days old). Older nestlings received larger food items, such as larger spiders and both larval and adult *Tipula* (Table 3). These large food items were collected from the ground layer. That is why the diet of the young consisted of fewer (small) food items caught in the trees, although the Siberian Tit used trees as a foraging niche most of the time (82%) during the nestling period (Table 2). Winged insects, spiders and larvae were the main diet of nestling Pied Flycatchers (Table 3).

Table 1. Three study periods and the breeding stage.

Period	Temperature sum (°C)	Breeding stage
1	< 50	Egg-laying and incubation period; from end of May to mid-June
2	100–250	Nestlings, the Siberian Tit young fledge; from end of June to beginning of July
3	251–500	Fledgling and independence period; from beginning of July to mid-August

Table 2. Variation of feeding site distribution of the Siberian Tit and Pied Flycatcher over four niches (pine, birch, ground layer, air). Average percentages, their standard errors (S. E.) for proportions of each niche within observation periods (n), and the number of different individuals studied (ind.) are given.

			Pine		Birch		Ground		Air	
	n	ind.	%	S. E.	%	S. E.	%	S. E.	%	S. E.
Siberian Tit										
Period 1	86	32	33	3.7	24	3.4	43	3.4	0	0.0
Period 2	45	28	55	5.2	27	4.6	18	3.8	1	0.3
Period 3	13	11	63	10.6	35	10.3	1	0.9	0	0.0
Pied Flycatcher										
Period 1	58	46	2	0.8	2	0.7	86	3.1	11	2.4
Period 2	38	34	7	1.7	13	2.7	42	4.2	38	4.2
Period 3	40	23	2	0.9	24	4.1	37	4.2	36	3.9

Table 3. The diet of Siberian Tit and Pied Flycatcher nestlings.

	Main niche of the taxon	Siberian Tit		Pied Flycatcher	
		Number	%	Number	%
Araneae	Ground	176	37.1	154	27.8
Tipula (larv.)	Ground	70	14.8	1	0.2
Tipula (ad.)	Ground/trees	66	13.9	30	5.4
Diptera (excl. Tipula)	Air/ground	4	0.8	23	4.1
Winged insects[1]	Air/ground	93	19.6	234	42.2
Larvae[2]	Foliage	65	13.7	112	20.3
Total		474	99.9	554	100.0

[1] Includes Ephemeroptera, Plecoptera, Coleoptera, Lepidoptera (ad.), Hymenoptera (Symphyta, ad.).
[2] Includes larvae of Lepidoptera and Hymenoptera (Symphyta).

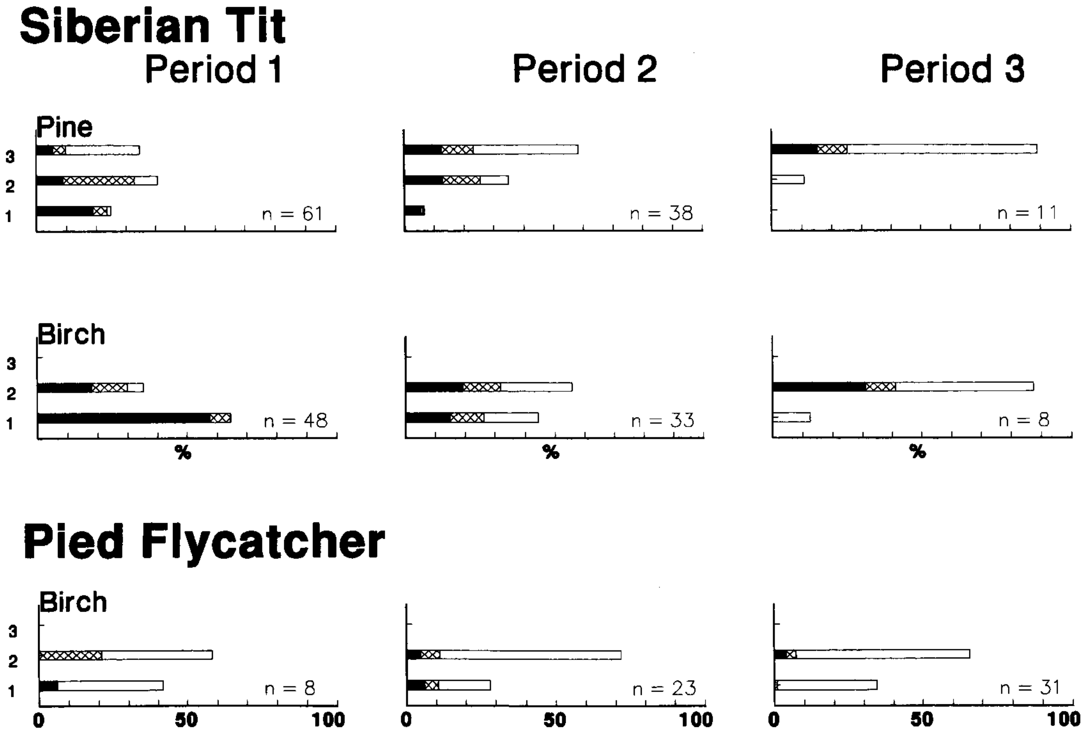

Fig. 2. Foraging of the Siberian Tit and Pied Flycatcher in trees in Periods 1–3 (see Table 1). Foraging height (y-axis): 1 = 0–2 m, 2 = 2–6 m, 3 = > 6 m. Horizontal tree part (x-axis): Solid bar = trunk, screened bar = middle zone, and empty bar = outer zone.

Generally, the Siberian Tit had a broader foraging niche than the Pied Flycatcher (Fig. 1, Table 4). At the beginning of the breeding season the Pied Flycatcher almost exclusively used the ground layer, but it used all feeding sites in mid- and late summer (Fig. 1, Tables 2 and 4).

All feeding niches overlapped especially in the beginning of the summer and in midsummer. The combined food niche of the Pied Flycatcher overlapped the Siberian Tit's food niche to a greater extent in all periods (Table 5). But there was little overlap in tree category, because the Pied Fly-

Table 4. Breadths of the combined and partial feeding niches of the Siberian Tit and the Pied Flycatcher. Kruskal-Wallis test for the breadth of feeding niches among periods (see Table 1). n = number of observation periods.

	Period 1			Period 2			Period 3			CHISQ	P
	B	S. E.	n	B	S. E.	n	B	S. E.	n		
Siberian Tit											
Combined	2.960	0.06	86	3.466	0.08	45	3.402	0.13	13	25.130	0.0001
Tree category	1.672	0.06	86	1.680	0.09	45	1.385	0.12	13	3.015	0.221
Birch	1.519	0.09	48	1.919	0.18	33	1.614	0.20	8	4.084	0.130
Pine	1.894	0.13	61	2.816	0.26	38	1.476	0.20	11	10.360	0.006
Pied Flycatcher											
Combined	2.032	0.02	58	2.240	0.08	38	2.329	0.09	40	11.307	0.004
Tree category	1.325	0.07	58	2.140	0.10	38	2.172	0.11	40	42.797	0.0001
Birch	1.477	0.26	8	1.495	0.13	23	1.334	0.08	31	1.925	0.382
Pine	1.335	0.21	6	1.453	0.14	16	1.226	0.15	8	2.656	0.265

catcher did not use pine very much and the Siberian Tit did not flycatch (Table 5, Fig. 1). In birches, the niches overlapped extensively in late summer (Table 5), when both species fed on larvae in the foliage (Figs. 1 and 2).

4. Discussion

Both species studied here shifted their foraging niches in response to changes in the abundance of food during the breeding season (also Gibb 1954, Alatalo & Alatalo 1979).

The study species forage on the ground layer or on the trunks of trees in the beginning of summer, because food resources are scarce in other niches (especially flying insects and arthropods in the foliage are not available). Later, the availability of spiders on the ground layer decreases, and birds have to shift their food niche. In July, food sources are plentiful in relation to the beginning of summer (e.g. Veistola et al. 1995), and birds have greater freedom to 'choose' their foraging niche according to their morphological abilities: Siberian Tits prefer pines to the ground layer, and Pied Flycatchers catch winged insects from the ground layer and from the air during the period of abundant food. As the numbers of energy-rich larvae increase, both species start to forage for them in the foliage, and the significance of other food niches diminishes (also Alatalo & Alatalo 1979).

Both study species used very broad foraging niches during the breeding season. We conclude that broad foraging niches are the result of adaptations to a seasonal environment (long-term shifting in foraging behaviour, e.g. Alatalo & Alatalo 1979, Sæther 1982, Laurent 1986). A broad food niche is necessary in high latitudes, since no single food source is available throughout the breeding season.

The species also had broad foraging niches within each study period, in which seasonal alterations in conditions were not remarkable. We suggest that there are two reasons for short-term shifting in the foraging behaviour of the birds. First, a large and rapid variation in food availability forced birds to alter their foraging methods. For instance, Pied Flycatchers forage in the air during favourable conditions, but they shift to foraging on the ground layer when the activity level of flying insects slows down because of low temperatures (Tuominen 1969, Alatalo & Alatalo 1979, Lennerstedt 1983, own obs.). Second, birds have to search for food in many different niches when the availability of food sources fluctuates rapidly (see MacArthur & Pianka 1966, cf. Yoccoz et al. 1993). Thus, we propose that the food-seeking niche is more extensive than the optimal foraging niche, because birds have to look for food in many different niches (Krebs & Inman 1992).

Rabenold (1978) stated that a broad foraging niche may be a consequence of a shortage of food or of less competition in harsh conditions. We cannot confirm that food shortages lead to broad foraging niches, because the sizes of the foraging niches of the study species were largest during periods of ample food supplies (also Alatalo 1980, Wagner 1981). For instance, the Siberian utilizes the largest niche in the middle of summer, when food supplies are available in many different niches, i.e., it forages in trees as well as on the ground level.

We suppose that birds are able to use a broad foraging niche without any disturbance by other birds (Rabenold 1978, Wagner 1981, Alatalo et al. 1987), because passerines do not necessarily compete in the north (Mönkkönen et al. 1990,

Table 5. The specific niche overlap ($SO_{k,i}$) of the study species (Ludwig & Reynolds 1988). The index $SO_{k,i} = 1$ means complete overlap of species *k* over species *i*, and $SO_{k,i} = 0$ means no overlap. The number of observation periods is given in Table 2.

	$SO_{ST,PF}$			$SO_{PF,ST}$		
	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3
Combined	0.371	0.592	0.083	0.804	0.820	0.670
Tree category	0.249	0.315	0.115	0.130	0.181	0.001
Birch	0.009	0.701	0.598	0.002	0.711	0.635
Pine	0.044	0.125	0.000	0.487	0.610	0.000

1996). The evidence for the lack of competition is difficult to present, but Mönkkönen et al. (1990) showed in their experiment that interspecific competition is only of minor importance in the feeding ecology of passerines in the north. Similarly, we observed aggressive behaviour rarely between our study species, and only in the vicinity of Siberian Tit's nest.

In many studies, the niche overlap between species is greatest during favourable food conditions (e.g. Rabenold 1978, Alatalo 1980, 1982b, Wagner 1981, Sæther 1982, Laurent 1986, Székely & Moskát 1991). In our study, the overlap of combined foraging niches is lowest in late summer, when food availability has peaked (also Ulfstrand 1977). We suggest that low overlap of niches in late summer is due to extensive differences between species' morphology and foraging strategies (e.g. Moreno & Carrascal 1993). We suppose that birds could concentrate on feeding by the most suitable methods and in the most suitable sites. The Siberian Tit forages mostly in trees in late summer, because it is able to pick food items from all parts of trees. Because the Pied Flycatcher is not able to forage in trees by clinging and hanging (see e.g. Cramp & Perrins 1993), it specializes in catching its food while flying just above the ground, although food is plentiful in trees. In early summer, when food availability is poor, both species are forced to seek food items from the same foraging niches leading to a large overlap of niches.

We propose that specialized foliage-gleaners may find it difficult to spread to the north, because food conditions in foraging niches fluctuate greatly. The combined feeding niche of the native Siberian Tit is broader than that of the migrant Pied Flycatcher in each study period. Similarly, Virkkala (1988) found that two native passerines (Siberian Tit and Siberian Jay *Perisoreus infaustus*) had broader niches than two migrant species (Willow Warbler *Phylloscopus trochilus* and Brambling *Fringilla montifringilla*) in the north. Thus, the adaptation of the Siberian Tit (or other native species) for northern conditions is readily evident from its abilities to use a very broad foraging niche (see also Virkkala 1988). The Siberian Tit can forage on the underside of leaves and on the top of twigs, which are signs of a specialized foliage insectivore (e.g. Nyström 1991). However, it is also a very skilful forager on the ground layer (e.g. Hannila 1987) and on the trunks of trees (Nilsson & Alerstam 1976, Virkkala 1988). The southern Pied Flycatcher with its flexible foraging methods and broad foraging niche could have spread to the northern parts of Fennoscandia during the last decades. However, the success of the Pied Flycatcher depends on favourable weather conditions (e.g. Järvinen & Väisänen 1984). The Pied Flycatcher finds it difficult to feed its young during cold and rainy periods, whereas the Siberian Tit can prey successfully on immobile arthropods (own obs.).

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Selostus: **Kahden varpuslintulajin ruokailukäyttäytyminen levinneisyyden pohjoisrajalla: lapintiainen ja kirjosieppo**

Vaikka kilpailun, predaation ja lajin morfologian on osoitettu vaikuttavan ruokailukäyttäytymiseen, ravinnon saatavuus on epäilemättä tärkein ruokailulokeron määräytymiseen vaikuttava tekijä. Tästä huolimatta ruokailulokeron suhdetta ravinnon määrään on tutkittu huomattavan vähän.

Tutkimme lapintiaisen ja kirjosiepon ruokailukäyttäytymistä suhteessa ravinnon määrään Utsjoella 1986–1991 ja 1994. Molemmilla lajeilla ravinnon saatavuus eri ravintokohteissa vaikutti selvästi ruokailukäyttäytymiseen (Kuva 1). Kun alkukesällä ravintoa oli niukasti tarjolla, molemmat lajit saalistivat erityisesti maasta. Keskikesällä lapintiainen siirtyi ruokailemaan erityisesti männylle. Kirjosieppo saalisti keski- ja loppukesällä eniten maasta ja ilmasta, mutta se napsi mm. toukkia myös koivun lehdiltä (Kuvat 2 ja 3).

Molemmilla lajeilla oli laaja ruokailulokero. Kummallakin lajilla ruokailulokero oli kapein alkukesällä. Lapintiaisen ruokailulokero oli laajin keskikesällä ja kirjosiepon loppukesällä. Laajan ruokailulokeron käyttö on välttämätöntä, koska mikään yksittäinen ruokailupaikka tai -tapa ei tarjoa riittävästi ravintoa koko pesimäkauden ajan.

Tästä syystä ruokailutavoiltaan erikoistuneen lajin on vaikeampaa levitä Lappiin kuin ravinnonhankintatavoiltaan joustavan lajin (esim. kirjosieppo).

Lajien ruokailulokerot olivat osittain päällekkäiset koko kesän ajan. Päällekkäisyys oli suurinta alkukesällä. Vaikka lajien ruokailulokerot olivat päällekkäiset, kirjoittajat eivät usko, että lajit kilpailisivat merkittävästi ruoasta tai ruokailulokeroista, koska lintutiheys pohjoisessa on hyvin alhainen.

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