Effects of temperature on foraging behaviour of small forest birds wintering in northern Finland

Rauno V. Alatalo

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Tits *Parus* spp., Goldcrests *Regulus regulus* and Treecreepers *Certhia familiaris* were studied during October 1975 — March 1976 in the mainly coniferous forests near the city of Oulu. The Goldcrest hovered less frequently at low ambient temperatures. Hanging upside down was equally common for tits at all temperatures. Less energy-consuming, non-horizontal feeding postures (head up or side up on twigs) were used more often at low temperatures. Niche breadth for foraging site decreased with decreasing ambient temperature, as did the foraging site overlap.

The changes in feeding postures and feeding sites may be interdependent and some reasons are suggested for the shifts. The physiological explanation might be that the energy costs of flying and hovering are greater at very low temperatures, so that the birds reduce the flying time and use foraging sites where less flying is needed. One ecological explanation might be that during warmer weather birds, to some degree, save their most profitable foraging sites for the more critical cold periods. The other is that in cold weather birds cannot devote much time to intraspecific aggressiveness, and all the individuals of the flock can forage at the most profitable sites.

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Introduction

Grubb (1975, 1977) considered that both air temperature and wind velocity affect the choice of the foraging sites of wintering birds. It is easy to explain the effect of wind velocity on foraging, since birds tend to look for shelter to reduce their heat loss (see Porter & Gates 1969, Calder & King 1974). However, it is not equally clear how changes in foraging sites can be caused by changes in ambient temperature. For this reason I studied whether tits and associated small passerine birds gleaning arthropods, etc., in trees changed their foraging sites with varying ambient temperature during winter in northern Finland.

Norberg's (1977) energetic model of optimal food searching does not provide for the possible necessity of altering foraging technique owing to increased energy needs in cold weather. Grubb (1978), however, noted that the movement patterns of foraging birds changed in cold weather. Therefore I also examined whether the postures used during feeding differed at different air temperatures. The two aspects of foraging behaviour studied are interdependent, since the feeding postures used by birds differ with the type of foraging site.
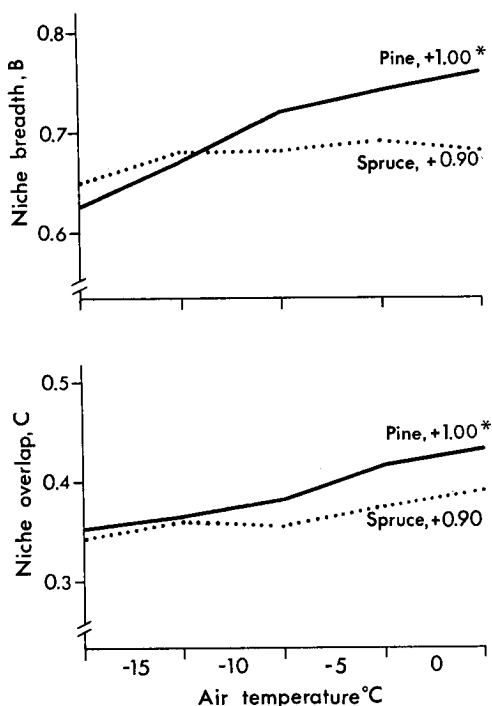
FIG. 1. The average niche breadths and overlaps for the use of tree parts in pine and spruce plotted against air temperature. Numbers after the names of the resource axes give the Spearman's rank correlation coefficient (r_s); asterisks indicate the statistical significance $(P < 0.05)$ of the trend.

Material and methods

I gathered data in the coniferous forests near the city of Oulu in northern Finland (main study area 64°57′N, 25°48′E) during October 1975 — March 1976. The same observations were used for other purposes in papers (Alatalo 1980, 1981, 1982) to which readers are referred for a more detailed description of the field methods and study area. Essentially, in each month the same areas in the forest were visited, and the foraging of birds was recorded in short series of observations (a record made every 15 seconds). The average number of records per series was 4 and the average number of series devoted to an individual bird at any one time was 2.6. Thus the observa-

tions are not fully independent, which restricts the use of statistical tests.

The foraging site dimension considered here is the part of the tree, since this proved to be the most important of the dimensions examined in studies of the niches of foliage-gleaners (Alatalo 1980, 1982). The feeding posture data are also included, since they illustrate the food-searching method. The air temperature was measured during the field work at intervals of one hour, in the shade 2 m above the ground.

The niche overlap (C) between species was measured as the sum of the minimum relative frequencies over all resource categories (Colwell & Futuyma 1971 Eq. 3, Hurlbert 1978 Eq. 1). Niche breadth (B) was measured by antilogarithmic Shannon's entropy $(ExpH')$, and standardized by dividing the niche breadths by the niche breadth values of the pooled annual data of the whole guild (tree 3.890, tree part 3.087, feeding posture 2.479; Alatalo 1980, 1982).

The species studied are (in order of abundance): the Willow Tit *Parus montanus*, Goldcrest *Regulus regulus*, Crested Tit *Parus cristatus*, Treecreeper *Certhia familiaris*, Great Tit *Parus major* and Coal Tit *Parus ater*.

Results

At the lowest temperatures, increased specialization in foraging sites was found with respect to the use of tree parts, especially in pines (Fig. 1). The positive correlation between the average niche breadth of foliage-gleaners and the air temperature was significant for the tree part in pine. There was also a linear decrease in foraging overlaps between species with decreasing temperature (Fig. 1).

The Willow and Crested Tits, and the Goldcrest increased their use of needled twigs as the temperature fell below zero (Tables 1, 2). The use of needled twigs is generally greater in winter (Alatalo 1980, 1982). Yet, as the temperature fell below —10°C, there was a tendency for the foliage-gleaners to move to bare twigs, with less use not only of needled twigs but also of branches. At the lowest tempe-

TABLE 1. Tree part use in spruce (height at least 5 m) at different air temperatures. The diameter limit between branch and twig is 8 mm. B = niche breadth.

	Trunk	Branch	Twig	Needled twig	B	N
Willow Tit						
— 0°C	0.00	0.22	0.41	0.37	0.96	325
0 — —5	0.01	0.22	0.33	0.44	0.99	320
—5 — —10	0.03	0.24	0.35	0.38	1.05	209
—10 — —15	0.03	0.21	0.56	0.20	0.95	325
—15 —	0.02	0.14	0.52	0.32	0.93	178
Goldcrest						
— 0°C	—	0.01	0.11	0.88	0.49	417
0 — —5	—	0.01	0.12	0.87	0.49	112
—5 — —10	—	—	0.01	0.99	0.35	69
—10 — —15	—	—	0.09	0.91	0.43	93
—15 —	—	—	0.13	0.87	0.47	78
Crested Tit						
— 0°C	—	0.12	0.59	0.30	0.82	215
0 — —5	—	0.14	0.60	0.26	0.82	250
—5 — —10	—	0.20	0.50	0.30	0.91	54
—10 — —15	—	0.11	0.64	0.25	0.78	226
—15 —	—	0.10	0.74	0.16	0.69	49
Treecreeper						
— 0°C	0.89	0.09	0.02	—	0.48	161
0 — —5	0.85	0.14	0.01	—	0.52	72
—5 — —10	0.95	0.05	—	—	0.39	62
—10 — —15	0.94	0.06	—	—	0.41	63
—15 —	0.98	0.02	—	—	0.36	49
Great Tit						
— 0°C	—	0.44	0.27	0.29	0.95	125
0 —	0.03	0.41	0.42	0.14	0.99	59
Coal Tit						
— 0°C	—	—	0.01	0.99	0.35	72
—5 — —10	—	—	0.03	0.97	0.37	33
—10 — —15	—	0.01	0.15	0.84	0.53	79
—15 —	—	—	0.09	0.91	0.44	33

ratures the Treecreeper stayed exclusively on the trunk, while in warmer weather it foraged to some extent on branches as well.

Since six months' data are used, the results might be obscured by some seasonal, temperature-independent, foraging shifts. Therefore I partitioned the observations into two-month periods. In December-January, there were enough observations to consider the niche breadth for the tree part in the three most abundant species over four categories of ambient temperature (Table 3). In both pine and spruce the average niche breadth was lowest at temperatures below —10°C, mainly as a consequence of the increased use of twigs by the Willow and Crested Tits. With four ordered

TABLE 2. Tree part use in pine (height over 5 m) and air temperature.

	Trunk	Branch	Twig	Needled twig	B	N
Willow Tit						
— 0°C	0.07	0.24	0.54	0.16	1.02	511
0 — —5	0.03	0.19	0.44	0.34	1.06	532
—5 — —10	0.04	0.19	0.48	0.28	1.04	180
—10 — —15	0.04	0.19	0.61	0.16	0.90	275
—15 —	0.01	0.14	0.73	0.12	0.72	116
Goldcrest						
— 0°C	—	0.01	0.38	0.61	0.67	450
0 — —5	—	0.01	0.29	0.70	0.61	276
—5 — —10	—	—	0.22	0.78	0.55	119
—10 — —15	—	0.01	0.27	0.72	0.60	360
—15 —	—	—	0.31	0.69	0.60	55
Crested Tit						
— 0°C	0.02	0.20	0.59	0.19	0.89	135
0 — —5	—	0.03	0.42	0.56	0.71	259
—5 — —10	—	0.05	0.30	0.65	0.71	84
—10 —	—	0.02	0.49	0.49	0.71	88
Treecreeper						
— 0°C	0.85	0.13	0.02	—	0.53	181
0 — —10	0.83	0.16	0.01	—	0.53	82
—10 —	0.99	0.01	—	—	0.35	145
Great Tit						
— 0°C	0.02	0.57	0.41	—	0.70	138
0 —	0.07	0.34	0.59	—	0.77	58

temperature categories, the probability that the two lowest average niche breadths will chance to be in the two lowest temperature categories is 1/6. Since this was found independently in both pine and spruce, the random probability of the observed pattern is <0.05. The specialization of foraging sites with decreasing ambient temperature seems to hold true within shorter periods as well.

Feeding posture. I have distinguished the following food-searching postures: horizontal (standing), head up (or seldom down), side up, hanging upside down, and hovering. Since feeding posture is dependent on the tree part and tree, I will present the feeding postures separately for pine and spruce, and also for bare twigs (Table 4) and needled twigs (Tables 5, 6). On twigs or branches without needles, in pine in particular, the proportion of non-horizontal postures was low, but they were used to a much greater extent on needled twigs. Posture diversity was least in the Great Tit and greatest in the Coal Tit. Only the Goldcrest hovered regularly, but on the other hand it seldom hung upside down.

Summarizing (Fig. 2), non-horizontal postures were used more at the lowest ambient temperatures in each foraging site. However, there are striking differences in the trends for different types of non-horizontal post-

ures. The general increase at low temperatures is due to the increase in the use of head-up and side-up postures. Hanging upside down is equally common (or equally rare) at all temperatures and hovering decreased with falling temperatures, particularly in the Goldcrest on needled twigs of pine and spruce. In general, the increased use of non-horizontal postures at low temperatures caused an increase in posture diversity as measured by niche breadth (B) (Tables 4, 5, 6).

The numbers of observations for each tree part become low when shorter time periods than the whole winter are considered, and the data could be divided only for the most numerous species (Willow Tit, Goldcrest, Crested Tit). For the Willow Tit, within a tree part (two categories) in a tree (two species) within a two-month

TABLE 3. The average niche breadth (B) for tree part use in pine and spruce during December 1975 — January 1976. Only the Willow Tit, Goldcrest and Crested Tit included.

Air temperature	Niche breadths	
	Pine	Spruce
0 — —5°C	0.75	0.69
—5 — —10	0.79	0.72
—10 — —15	0.70	0.64
—15 —	0.69	0.64

period (three periods), the use of non-horizontal feeding postures differed between temperature categories. In colder weather the percentage of non-horizontal postures was 5.6 (SD = 8.1, N = 12, paired t-test, P<0.05) higher than in the warmer weather. Similarly, Goldcrests used non-

TABLE 4. Frequency (%) of non-horizontal feeding postures (hanging, side up, head up, or rarely hovering) on branches or twigs at different air temperatures. Posture diversity as measured by niche breadth (B) and the number of observations (N).

|	Pine			Spruce		
	%	B	N	%	B	N
Willow Tit						
— 0°C	0.12	0.65	397	0.08	0.57	205
0 — —5	0.16	0.74	337	0.07	0.56	176
—5 — —10	0.18	0.75	121	0.15	0.69	123
—10 — —15	0.17	0.73	221	0.14	0.69	251
—15 —	0.15	0.68	101	0.20	0.81	117
Goldcrest						
— 0°C	0.02	0.45	176	0.32	0.92	50
0 — —10	0.01	0.42	108	0.48	1.23	33
—10 —	0.09	0.57	118			
Crested Tit						
— 0°C	0.04	0.47	107	0.22	0.86	151
0 — —5	0.07	0.54	115	0.13	0.69	186
—5 — —15				0.12	0.65	208
—15 —	0.04	0.49	74	0.37	1.07	41
Great Tit						
— 0°C	0.00	0.40	135	0.01	0.43	89
0 —	0.06	0.52	54	0.06	0.51	49
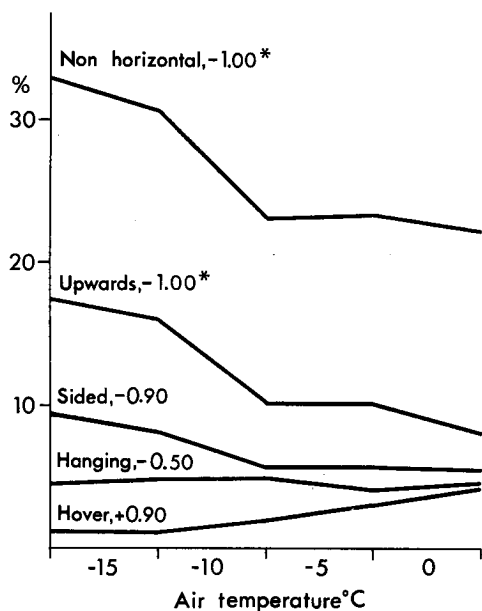
FIG. 2. The average (for all species and tree parts) percentage freguency of non-horizontal feeding postures at different ambient temperatures. Spearman's rank correlation coefficient (r_s) given after the posture (asterisk = the trend is significant with $P < 0.05$).

horizontal postures more in colder weather, if only observations of two-month periods are considered within each tree part (average difference in percentages = 11.5, SD = 9.0, t = 3.70, $P < 0.01$). For the Crested Tit, only seven comparisons could be made, and the difference (1.2, SD = 7.4) was not significant.

Discussion

Food-searching method. Why did the birds change their feeding postures, even on the same tree parts, using hovering less but increasing the total use of non-horizontal postures at low temperatures in winter?

Grubb (1978) showed that the speed of movement of wintering woodland birds, including two *Parus* species, decreased with lowered ambient temperature. More time was spent perching, the number of periods of inactivity increased and the distance travelled decreased. Odum (1942) reported a decrease in the average speed of movement in flocks of the Black-capped Chickadee *Parus atricapillus* on cold days. Hogstad (1970) found that the time spent per tree in the Goldcrest increased during midwinter, but this seemed to be more closely related to the snowcover of the trees than to fluctuations in temperature. In this study only a few observations, some in November, were made when there was snow on the twigs. Thus the effect of snow should not obscure the relation with temperature. Reduced flight on exposure to cold has been reported from hummingbirds by Beuchat et al. (1979). I did not measure the rates of movement or flying frequency directly, but there was a clear decrease in the hovering frequency of the Goldcrest at low ambient temperatures.

Norberg's (1977) energetic model of the optimal food-searching method does not give any changes in the search method due to increased metabolic needs in cold weather. The optimal food-searching method is the one which maximizes the net energy intake (energy gained minus energy costs of food-searching). The model is based on the assumption that the energy costs of the searching methods are independent of ambient temperature. If this is not valid, we might except changes in the food-searching method. Can the energy costs of food-searching, with or without hovering, vary with the temperature?

The heat production of flight may

TABLE 5. Feeding postures on needled pine twigs and ambient temperature.

	Horizontal	Head up	Side up	Hanging upside down	Hover-ing	B	N
Willow Tit							
— 0°C	0.54	0.29	0.06	0.05	0.05	1.29	79
0 — —5	0.58	0.26	0.07	0.09	0.01	1.23	175
—5 — —10	0.72	0.12	0.04	0.12	—	1.01	51
—10 —	0.50	0.38	0.09	0.03	—	1.14	58
Goldcrest							
— 0°C	0.57	0.08	0.02	0.00	0.33	1.08	274
0 — —5	0.65	0.08	0.03	0.01	0.24	1.05	194
—5 — —10	0.69	0.09	0.02	0.02	0.18	1.04	93
—10 —	0.45	0.26	0.09	0.04	0.16	1.56	297
Crested Tit							
— —5°C	0.67	0.19	0.05	0.08	0.01	1.09	170
—5 —	0.72	0.13	0.04	0.10	—	0.96	98

not substitute adequately for shivering at low temperatures, as much of the increase above the resting level is lost via the forced convention of the exercise (Calder & King 1974). Hence the energy costs of flight may increase with lowered temperature. In any case, Berger & Hart (1974) report that shivering, which is the only known source of regulatory thermogenesis in cold in birds (West 1965), is completely suppressed during flight (Hart 1960). During sustained flight the excess heat generated by the flight muscles eliminates the need for additional temperature regulation, so that the energy expenditure of birds is independent of ambient temperature (Kendeigh et al. 1977). However, the situation may be somewhat different for short flights (see Kendeigh et al. 1977). Information on this aspect of subneutral thermoregulation was recently supplied by Schuchmann (1979). He found that with decreasing ambient temperature, hovering hummingbirds increased their oxygen consumption at least as much as resting hummingbirds. Heat production by the wing muscles could not substitute for thermoregulatory heat production from other sources. Furthermore Kontogiannis (1968) showed with forced locomotion that the energy cost per unit of activity in *Zonotrichia albicollis* varies inversely with temperature.

Schuchmann's (1979) observations indicate that the energy costs of hovering increase with decreasing ambient temperature, but the same is true of food-searching without hovering, owing to the increase in the energy needed for thermoregulation. If the net energy intake is to be maximized in birds, hovering will be less beneficial than non-hovering (hopping etc.) at low temperatures only if the increase in the energy needed is greater in the case of hovering. Schuchmann (1979) did not find significant differences in the slopes of the regression lines for oxygen consumption plotted against temperature in hovering and resting hummingbirds, though in both *Amazilia cyanifrons* and *A. tzacatl* the line was slightly steeper for hovering birds.

TABLE 6. Feeding postures on needled spruce twigs and ambient temperature.

	Horizontal	Head up	Side up	Hanging upside down	Hover-ing	B	N
Willow Tit							
— 0°C	0.77	0.10	0.05	0.08	—	0.89	119
0 — —5	0.76	0.14	0.05	0.05	—	0.90	140
—5 — —10	0.69	0.14	0.06	0.11	—	1.04	80
—10 — —15	0.66	0.22	0.03	0.09	—	1.02	65
—15 —	0.46	0.35	0.12	0.07	—	1.30	57
Goldcrest							
— 0°C	0.61	0.13	0.14	0.00	0.12	1.25	367
0 — —5	0.63	0.11	0.12	0.01	0.12	1.21	98
—5 — —10	0.51	0.25	0.18	—	0.06	1.29	68
—10 — —15	0.31	0.31	0.36	0.01	0.01	1.34	85
—15 —	0.41	0.31	0.26	—	0.02	1.26	68
Crested Tit							
— 0°C	0.89	0.03	0.03	0.05	—	0.64	64
0 — —10	0.78	0.12	0.06	0.04	—	0.86	80
—10 —	0.75	0.14	0.06	0.05	—	0.90	64
Coal Tit							
— —10°C	0.61	0.13	0.15	0.12	—	1.27	103
—10 —	0.32	0.28	0.17	0.23	—	1.57	96

At the present stage of physiological knowledge we cannot say whether short flights are less beneficial at low temperatures owing to a sharper increase in energy costs than in other food-searching methods, but the clear decrease in hovering frequency in the Goldcrest in cold weather makes it possible to hypothesize that they are.

On the other hand, even if the relations between the net energy intakes with the different search methods are constant, and the only variable dependent on temperature is the absolute daily energy requirement for thermoregulation, differences may still be assumed to arise in the choice of search methods. It may be economical to use foraging sites where more flying is needed during warmer weather, and to save more profitable sites for cold weather, when it may be difficult to gather enough energy for the increased needs of thermoregulation (see next section). Goldcrests increased hovering on needled twigs during warmer weather, and it is very likely that they use the outermost parts of needled twigs more when hovering than when hopping.

The increased use of head-up and side-up postures on each tree part at low temperatures may be due to the need to compensate for the decreased amount of time spent flying. Furthermore the increased use of non-horizontal postures may indicate increased feeding intensity in general, which would be needed to cover the increased energy requirement for thermoregulation. Though this study included only observations on birds which were foraging, there may be differences in the level of foraging

activity. Activities closely related to foraging, such as inter- or intra-specific aggression (e.g. Hinde 1952, Gibb 1954, Ulfstrand 1962, Morse 1970, Glase 1973), may become less frequent at low temperatures as well, decreasing the flying time and increasing the actual feeding time. Caraco (1979b) found that *Junco phaeonotus* allocated less time to aggression in cold weather, and Beuchat et al. (1979) reported a decrease in the non-feeding flight activities of humming-birds with decreasing ambient temperature. In any case, this would offer only a partial explanation of my results at the most, as hovering (flying for active feeding) was less frequent at low temperatures.

Hanging upside down did not increase during cold weather. This feeding posture is likely to require more energy than being head up or side up on the twigs. Altogether, the most energy-consuming searching methods (hovering) are used less at low temperatures, whereas the least energy-consuming non-horizontal feeding postures are used more during the same period. Though intuitively this seems to be an expected result, the explicit background to these changes is far from clear, and physiological experiments on flight energetics at low temperatures are required to shed some light on these matters.

Foraging site. Niche breadth showed a decreasing trend at low temperatures, and this has also been reported by Grubb (1975). Interestingly, Ricklefs & Hainsworth (1968) found that *Campylorhynchus brunneicapillus* reduced the diversity of the foraging locations visited at the other extreme temperature stress, at very high temperatures.

Tits left the needled twigs, where more varied and energy-demanding search methods are needed, as the temperature fell. This shift could be expected if the energy costs of the food-searching methods vary with temperature as discussed in the previous section. The shift from needled to bare twigs also occurred to some extent in the Goldcrest, the specialist on needles, and led to a slight increase in its niche breadth. On the other hand there were also shifts which do not seem to be related to changes in preferred feeding posture; tits left branches in favour of twigs and on both sites the same feeding postures are used.

A kind of long-term optimal foraging strategy (see Katz 1974, Pyke et al. 1977) might also be the reason for the changes in foraging site. During winter the resources of these birds are generally not renewed, and consequently it might be profitable to use the foraging sites providing less energy under the less critical conditions at warmer temperatures. The best foraging sites could be saved to some degree for days when the energy need is maximal, and during the short days there may be hardly enough time for collecting the energy required for thermoregulation during the long winter nights. A condition of such 'saving behaviour' would be that the birds themselves obtain the benefit of the saved food (cf. Anderson & Krebs 1978 for hoarding), and this is quite probable as some of these birds hoard food (Haftorn 1956), and all of them stay in the same area the whole winter (Hinde 1952, Haftorn 1957, Hogstad 1970, Ekman 1979).

The choice of foraging sites may be influenced by other microclimatic factors (Porter & Gates 1969, Calder & King 1974), possibly related to ambient temperature. Grubb (1975, 1977) noted the effect of wind, but he

also found foraging shifts caused by temperature changes with constant wind conditions. The effects of wind were not studied in the present case, but during winter windy weather is more frequent at warmer temperatures. Thus it is unlikely that the shift from needled to bare twigs at the lowest temperatures was caused by increased wind, particularly since there were shifts in foraging sites in the inner parts of the trees as well. On the other hand, in cold weather birds should be more sensitive to the effects of wind, and the inner parts of trees provide shelter against it. In addition, the reflected thermal radiation might be greater there. In contrast, during sunny weather birds may expose themselves to sunlight (Lawrence 1958, Morse 1970, Hogstad 1970).

The low niche overlap in cold weather correlates with greater specialization in resource use, and may thus have the same explanation. It is attractive to assume that birds may tolerate more interspecific competition for food during warmer weather, when the food requirement is not so high. This could well be related to the food-saving hypothesis; e.g. tits could use needled twigs and compete with the Goldcrest at the highest temperatures, and at the same time they would save their best foraging sites for more severe weather. Moreover, Caraco (1979a, b) showed for *Junco phaeonotus* that intraspecific aggression, which is more common than interspecific aggression (see e.g. Hinde 1952, Gibb 1954, Morse 1970), was avoided at the lowest temperatures and that more time was allocated to feeding. Accordingly interference competition between individuals of the same species in foliage-gleaner flocks may relax in cold weather, allowing decreased niche breadths at the population level, as subordinates could join dominants in using the most profitable foraging sites. It is unlikely that foraging site shifts are due to movement of the prey. Much of the food is immobile (pupae, eggs, stored items), and adult insects or arthropods on twigs are not very active at the low temperatures (e.g. Huhta & Viramo 1979) at which the birds had foraging shifts.

In conclusion, it seems that less energy-consuming search methods, and foraging sites that allow less energy-consuming searching methods are used more in colder weather during the winter. This should decrease the energy required for feeding in periods when more energy is needed for thermoregulation. The reason why more energy-consuming searching methods are used during warmer weather is not clear. It may be that birds save their best foraging sites for the most critical cold periods, or that the decrease in intraspecific aggressiveness (all the time has to be devoted to feeding) makes it possible for all the individuals of a species to concentrate on the best foraging sites. The physiological explanation would be that as the ambient temperature decreases the energy cost of flying and hovering increases more rapidly than the cost of other foraging methods. Many factors may operate simultaneously, and shifts in foraging site and changes in searching method, though interrelated, may have partly different explanations.

Selostus: **Ilman lämpötilan vaikutus talvella tiaisten, hippiäisen ja puukiipijän ruokailukäyttäytymiseen Pohjois-Suomessa**

Talvella 1975—76 tutkittiin hömötiaisen, hippiäisen, töyhtötiaisen, talitiaisen, kuusitiaisen ja puukiipijän ruokailupaikkojen ja ruokailutekniikan riippuvuutta ilman lämpötilasta. Hömötiainen ja töyhtötiainen siirtyivät neulasoksilta neulasettomille oksille kovalla pakkasella (taul. 1, 2). Lajien käyttämien ruokailupaikkojen monipuolisuus (kuva 1, taul. 3) ja limittäisyys (kuva 1) vähenivät ilman lämpötilan laskiessa. Kovalla pakkasella linnut käyttivät suhteellisen usein ei-horisontaalisia ruokailuasentoja (pystysuorassa tai sivuttain oksalla), mutta oksien alapuolella riippuminen ei lisääntynyt ja neulasten edessä lentäen ruokailu väheni hippiäisellä (taul. 4, 5, 6, kuva 2).

Useita mahdollisia tekijöitä voi olla vaikuttamassa ruokailukäyttäytymisen muutoksiin. Fysiologinen selitys olisi, että lentäminen kuluttaa kovalla pakkasella enemmän energiaa kuin leudolla ilmalla, jolloin lentolihasten tuottama hukkalämpö ei pystyisi korvaamaan normaalia lämmönsäätelyn tarvittavaa aineenvaihduntaa näissä lyhytaikaisissa lennoissa. Siksi lintujen tulisi vähentää lentämistä ruokaillessaan ja ruokailla paikoissa, joissa lentämistä tarvitaan vähemmän.

Ekologinen selitys ruokailupaikkojen ja samalla ruokailutekniikan muutoksille voisi olla, että leudolla ilmalla linnut säästävät parhaita ruokailupaikkojaan jossakin määrin kriittisiä pakkaspäiviä varten. Samoin kovalla pakkasella tiiviin ruokailun vuoksi linnuilla ei ole aikaa lajinsisäiseen aggressioon, ja tällöin parvessa alistetussa asemassa olevat linnut voisivat myös ruokailla parhailla ruokailupaikoilla yhdessä sosiaalisesti dominoivien yksilöiden kanssa.

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