Foraging patterns in the male and female Redstart *Phoenicurus phoenicurus* during the nestling period

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Foraging site differences between males and females of the Redstart were studied in mountain birch forest in northern Finnish Lapland (69°N), and the results were compared with published records made further south (central Norway, 63°N, and South Wales, 52°N). The habitat variables studied were the foraging height (vertical dimension) and the structural foraging site, four site categories being distinguished: (1) ground, (2) inner parts of tree, (3) outer parts of tree and (4) air. In northern Lapland the overlap in the foraging sites of the sexes was almost complete both vertically and structurally. In central Norway and South Wales the sexual differences in the structural foraging site were also slight, but apparently more pronounced than in northern Lapland. The high feeding niche overlap in northern Lapland was presumably due to the highly seasonal and structurally simple and impoverished habitat, which does not allow the specialization observed in structurally more complex environments.

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Introduction

The division of feeding space or the occupancy of somewhat different niches within species may be based on sex. Sexual differences in foraging behaviour are often due to morphological differences between the sexes, although this is not always the case (e.g. the Red-cockaded Woodpecker *Dendrocopos borealis,* Ligon 1968; the Red-eyed Vireo, *Vireo olivaceus,* Williamson 1971). Sexual divergence in foraging patterns may also reflect the different roles played by the sexes during the breeding cycle. For instance, the Red-eyed Vireo males forage close to their singing perches and thus higher up in the trees than the females. In this way the males probably minimize the amount of energy spent on foraging and defence of the territory (Williamson 1971).

Cody (1974) presented models that predict the foraging patterns of birds under certain conditions. Generalists, with similar ways of foraging, seem to be favoured over specialists when (1) resources are scarce or the productivity is low, (2) when the canopy is open (crown size small), (3) when the resources are uniform, and (4) when the resources are highly seasonal.

In northernmost Europe plant resources are lower than further south since net primary productivity (dry matter) decreases progressively from about 2000 g $m^{-2}yr^{-1}$ in tropical forests, through about 1300 g $m^{-2}yr^{-1}$ in temperate forests and about 800 g $m^{-2}yr^{-1}$ in boreal forests, to about 140 g $m^{-2}yr^{-1}$ in tundra (Whittaker 1975). The number of plant species also decreases towards the poles (e.g. Hultén 1971). Evidence from the IBP projects suggests that both the number of invertebrate species and the biomass of invertebrates are relatively low in the north and at higher elevations (e.g. Solhøy et al. 1975, Wielgolaski 1975). Moreover, the forests in northern Fennoscandia are sparse and composed of a single tree species (birch, *Betula pubescens* ssp. *tortuosa;* Hämet-Ahti 1963), and the environment is highly seasonal (e.g. A. Järvinen 1983).

According to Cody's theory, in such an environment individuals are expected to have broad and overlapping feeding niches. Northern forest bird communities contain comparatively few species and individuals (O. Järvinen 1979), and this may further favour generalist feeding habits (for the effect of competitors on feeding habits, see e.g. Cody 1974: 78).

In this paper I document the foraging patterns of females and males in a species with little sexual size dimorphism, the Redstart *Phoenicurus phoenicurus.* According to Svensson (1984), the wing length of male Redstarts is 76–84 mm, and that of females 74–81 mm. My own data from northern Finnish Lapland are compared with published records made further south (Edington & Edington 1972, Hogstad 1977).

Study area, material and methods

The birch woods (alt. about 500 m) at Kilpisjärvi in NW Finnish Lapland (about 69°03′N, 20°50′E) are relatively barren and sparse with poorly developed shrub and herb layers. The mean height of the birches surrounding the Redstart nests studied was 4–5 m. In my area the total density of breeding birds in average mountain birch woods without nest-boxes is about 100 pairs/km^2, to which the Redstart contributes only about 0.7 pairs/km^2 (A. Järvinen 1983). In birch woods with nest-boxes the Redstart density is doubled (A. Järvinen 1983).

The Redstart winters in the southern Sahara and breeds in the whole of the western Palaearctic (Harrison 1982). This hole-nester occurs in subarctic birch forests, in boreal and temperate pine, broad-leaved and mixed forests and

Table 1. Sexual differences in foraging of the Redstart during the nestling period in Finnish Lapland, central Norway and South Wales. Number of observations (N) and relative frequencies (%) in each structural category.

	Northern Lapland				Central Norway				South Wales			
	♀		♂		♀		♂		♀		♂	
	N	%	N	%	N	%	N	%	N	%	N	%
Air	134	19.4	111	16.8	23	21.9	32	33.2	186	34.4	203	38.5
Outer parts of tree	128	18.5	110	16.7	35	32.9	35	36.5	156	28.9	137	26.0
Inner parts of tree	150	21.7	157	23.8	8	8.1	3	3.3	16	3.0	41	7.8
Ground	280	40.5	281	42.6	39	37.0	26	27.0	182	33.7	146	27.7
Total	692		659		105		96		540		527	

also in parkland and gardens. The Redstart density is clearly lower at Kilpisjärvi than in southern Finnish Lapland (A. Järvinen 1983). According to O. Järvinen & Väisänen (1976), the main reason for the depauperate bird communities of northern forests in Finland is presumably the combination of adverse climate and diminished resources (low maximum height of trees and thin forests, often with few bushes).

The data were collected near the Kilpisjärvi Biological Station during the periods 25 June–6 July 1980, 24 June–1 July 1981 and 8–12 July 1982. Altogether 1351 foraging records were made (692 of females, 659 of males) usually between 10.00 and 17.00 hours (range 09.00–20.00) on calm and dry days. The weather conditions are severe at Kilpisjärvi. During the study periods the mean daily air temperature at 480 m was +10.8 ± 2.3 °C (SD, n = 15 days). The long-term (1966–1980) mean temperature in June is + 8.0 °C and in July +10.9 °C.

About 80 % of the records were made by AJ and Leena Järvinen, about 20 % by AJ and students of the Subarctic Animal Ecology Course of the Department of Zoology at the University of Helsinki in 1980–1981. Foraging parents were watched with binoculars by the observer (AJ), another person acting as a secretary. Only one record was scored as long as the bird stayed in the same foraging site. The foraging of the Redstart consists of fly-catching, during which it is stationed on a perch and makes rapid darts after its prey. The observations stem from five different nestboxes with 2–13 days old young.

The following structural foraging sites were distinguished: (1) ground (includes 10–20 cm high *Empetrum hermaphroditum, Vaccinium myrtillus* and herbs), (2) trunk of tree, (3) branches (naked inner parts of tree), (4) outer parts of tree (foliage and occasional records in bushes), and (5) air. Later the records from sites (2) and (3) were lumped in the category "Inner parts of tree". These categories were chosen partly because they allowed comparisons with other studies. Within each structural category the foraging height (or vertical category) was estimated by eye to the nearest 0.5 m.

The mean foraging height was calculated as follows:

$$h = \sum m_i p_i,$$

where m_i is the mean height above the ground in the interval i, and p_i the proportion of feeding records in that interval. As an estimate of the breadth of the feeding niche I have used the inverse of Simpson's index (Colwell & Futuyma 1971):

$$B = 1/\sum p_i^2,$$

where p_i is the frequency of observations in the ith category. B was standardized as follows (Hespenheide 1975):

$$B_s = (B-1)/(n-1).$$

B_s increases as feeding habits become more generalized, and reaches unity when all feeding categories are exploited equally. An index of niche overlap is given by the formula (Schoener 1968):

$$O = 1-0.5\sum | p_{ij}-p_{ik} |,$$

where j and k refer to the two sexes and p_i has the same meaning as above. This measure of overlap ranges from 0 (no overlap) to 1 (complete overlap).

Hogstad (1977) studied the foraging behaviour of Redstarts in central Norway (about 63°10′N, 10°20′E) in 1972–1975. The habitat was oligotrophic mountain birch forest. There are no data on the density of Redstarts in the area, but in other mountain areas in southern and central Norway Meidell (1961) and Moksnes (1973) have reported higher Redstart densities than at Kilpisjärvi. However, their results are probably not comparable with newer ones from the Kilpisjärvi area, since the Redstart numbers have declined in many areas in recent decades (A. Järvinen 1981). As a basis for comparisons I have used data from the nestling period derived from Hogstad's (1977) Table 1 and Fig. 1 (105 and 96 obs. for females and males, respectively).

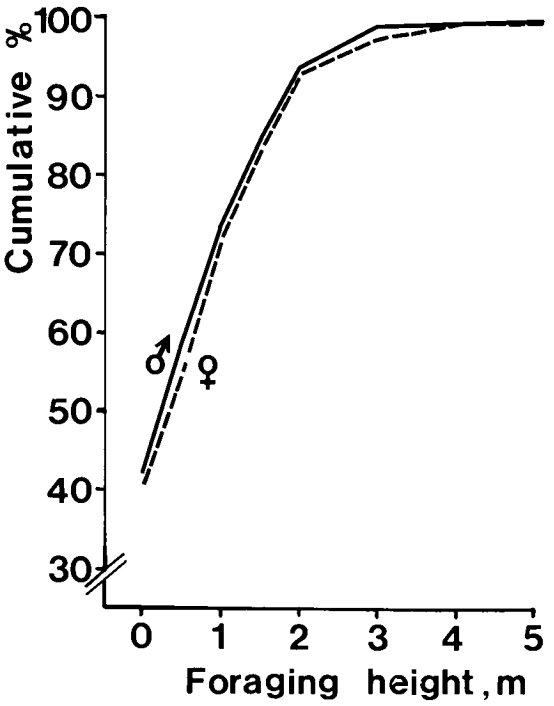

Fig. 1. Cumulative foraging height distributions of female (broken line) and male (continuous line) Redstarts in northern Finnish Lapland in 1980–1982.

Edington & Edington (1972) present data on the Redstart from mixed broad-leaved woodland 300–450 m above sea level in South Wales (about 52°N, 3°30′W) in 1968–1970. In this study area several tree species occur and the canopy is well developed (Edington & Edington 1972, Plate 1), although due to heavy browsing by sheep, foliage is usually present only above 1.25 m. As a basis for comparisons I have used their Table 1 (540 and 527 obs. made during the nestling period for females and males, respectively), but combined all cases in which food was taken from tree trunks or branches in the new category "Inner parts of tree" and all cases in which food was taken from leaves in the new category "Outer parts of tree". Thus the structural foraging categories are the same as at Kilpisjärvi and in central Norway. According to Edington & Edington (1972; their Fig. 1), the Redstart density in their study area is high (11 pairs in a forest belt of about 20 ha in 1968).

Results

Foraging patterns in northern Lapland. In northern Lapland both sexes foraged within a relatively narrow zone around the nest (radius about 50 m) and used overlapping areas. Thus there was apparently no local or habitat separation between the sexes in the foraging pattern.

There was almost complete overlap (0.95) between the sexes in the foraging height (Fig. 1; the foraging height distributions of the sexes did not differ from each other, $X^2 = 2.45$, df = 5, $P > 0.75$, data in categories 2.5–5.0 m combined). The mean foraging height was 0.8 m in both sexes; about 40 % of foraging took place on the ground and nearly 95 % of the food was collected below or at 2 m. The foraging height niche was thus relatively narrow ($B_s = 0.32$ and 0.33 for females and males, respectively).

Compared with their use of the vertical dimension, the birds in northern Lapland were more versatile in their structural habitat utilization ($B_s = 0.85$ and 0.80 for females and males, respectively; Table 1). However, the overlap between the sexes in the structural dimension (0.96) was as great as in the vertical dimension.

Comparisons with other studies. The B_s values for structural habitat utilization were almost the same in South Wales (0.72 and 0.78 for females and males, respectively) and central Norway (0.78 and 0.72), but in both cases were somewhat lower than in northern Finnish Lapland (Table 1). According to G-tests (with Williams' correction; Sokal & Rohlf 1981), the distributions of the female and male records among the foraging sites did not differ significantly in northern Lapland (Table 1; G = 2.87, df = 3, $P >> 0.1$), but in central Norway (G = 5.92, P = 0.1) and South Wales (G = 17.05, $P < 0.001$) the differences were greater.

The differences were statistically significant in all the other comparisons, except central Norway males vs. South Wales females (G = 2.59, $P >> 0.1$) and vs. South Wales males (G = 6.54, $P < 0.1$). It may be noted that the sample sizes are largest in northern Finnish Lapland, which increases the power of the statistical test to detect any difference between the sexes, and yet no significant differences appeared.

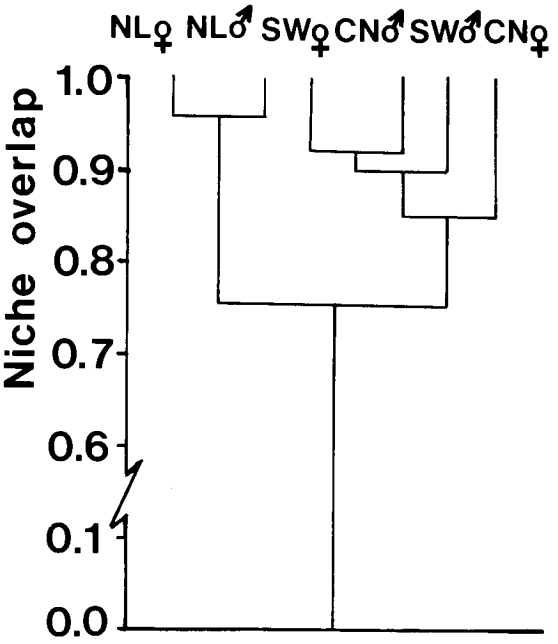

Fig. 2. A dendrogram showing the affinities of foraging patterns in the Redstart in different study areas. NL = northern Finnish Lapland, CN = central Norway, and SW = South Wales.

The dendrogram in Fig. 2, based on matrices of niche overlap values, illustrates the relationships of the different study areas and sexes. The dendrogram suggests that the foraging patterns of the Redstart in northern Lapland are different from those in central Norway and South Wales.

Discussion

In northern Lapland, both sexes of the Redstart foraged mainly on the ground. In central Norway females also foraged most often on the ground, but males preferred the outer parts of trees and the air. In South Wales, the females used the ground and air equally frequently, whereas the air was most often used by the males (Table 1). Earlier Buxton (1950) reported that in Central Europe the Redstart female feeds more on the ground than the male.

In central Finland (64°57'N, 25°48'E), Alatalo & Alatalo (1979) observed significant sexual differences in the foraging sites of the Redstart, the male using trees more and the ground less than the female. However, their observations (n = 55 for males and n = 36 for females) were made in May–July and thus include records from outside the nestling period. The foraging records from different phases of the breeding cycle are best treated separately, since sexual differences in the feeding sites of the Redstart seem to be more pronounced in early than in late summer (Hogstad 1977; feeding sites of males are affected by singing sites).

The feeding niche overlap between the sexes apparently increases from South Wales to northern Lapland, although sexual feeding differences were relatively slight in all areas. Mountain birch forests are structurally monotonous and the greater scarcity and uniformity of resources in the north probably do not allow structural or vertical spacing of feeding activity (Cody 1974: 59, Angell-Jacobsen 1980). As the differences between resource patches decrease, the advantage of being generalized increases (Pianka 1983: 277).

At higher latitudes, where the climate is harsh and unpredictable, selection favours organisms that tolerate wide variation in the physical environment and have more generalized feeding habits (Fischer 1960, Connell & Orias 1964). A low degree of specialization is in harmony with adversity selection, which seems to operate in harsh conditions (Greenslade 1983). In the north birds usually have flexible habits because the range of opportunities permitting the specializations observed at lower latitudes is not present (Southwood 1977). Generalized foraging patterns are presumably part of this flexibility.

It appears that in favourable, biologically controlled (southern) environments both inter- and intraspecific competition for space and nourishment is more pronounced than in unfavourable, physically controlled (northern) environments (e.g. Salomonsen 1972, Connell 1980, Greenslade 1983, A. Järvinen 1984). Under extremely severe conditions, Connell (1980) suggests, populations may even be depressed below levels of resource competition. Thus, in the north there is apparently relatively little selection pressure to drive individuals to partition the environment, which may lead to almost identical foraging patterns. However, sexual foraging differences were not studied in the Redstart after the young had left the nest. A division of feeding sites might occur between parents feeding fledged young, as in the Song Sparrow *Melospiza melodia* and the Wheatear *Oenanthe oenanthe* (Smith 1978, Moreno 1984).

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Selostus: **Leppälintukoiraan ja -naaraan saalistustapojen eroista pesäpoikasaikana**

Leppälintukoiraan ja -naaraan saalistustapoja tutkittiin pesäpoikasaikana Kilpisjärven tunturikoivikoissa 1980–1982 ja tuloksia verrattiin Keski-Norjasta (Hogstad 1977) ja Walesista (Edington & Edington 1972) julkaistuihin tietoihin. Saalistuskohteet luokiteltiin seuraavasti 1) maa, 2) puun sisäosat, 3) puun ulko-osat ja 4) ilma (taulukko 1). Lisäksi määritettiin kunkin saalistuskohteen korkeus maanpinnasta (kuva 1).

Kaikilla alueilla sukupuolten väliset saalistustapojen erot olivat melko vähäiset joskin erot näyttivät supistuvan minimiin Kilpisjärvellä (taulukko 1, kuvat 1–2). Saalistustapojen samankaltaisuus Kilpisjärvellä johtunee tunturikoivikon yksinkertaisesta rakenteesta ja karuudesta, mikä ei edistä sukupuolten välisten saalistustapojen syntymistä.

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