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Food supply and reproduction in the common treecreeper (*Certhia familiaris*)

Markku Kuitunen

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The relationship of the food supply to avian reproduction was studied in the common treecreeper *Certhia familiaris*. Special attention was paid to the seasonal change in both the potential food supply and reproductive success. Food supply samples collected from the surface of tree trunks included 55 taxa (family or order) and provided on average 4.7 mg dry weight food for the treecreeper per m^2 of tree trunk surface. A seasonal increase followed by a decrease in October was found to be the primary cause of variation in the food supply. The seasonal development in reproductive success at first increases, but then begins to decrease long before the potential food supply does. According to these results the increasing food supply could account for the increasing reproductive success, but this cannot be the reason for the subsequent rapid decrease in reproductive success. The diet of treecreeper nestlings was found to be taxonomically very similar to the food supply. However, adult treecreepers preferred larger food items than expected. From the quantitative food supply results the foraging area for one breeding pair was predicted, which was also found to agree well with the observed home range size and the smallest forest islands used by treecreepers.

M. Kuitunen Department of Biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100 Jyväskylä, Finland.

1. Introduction

Reproductive tactics have been found to evolve responses to the environment (Stearns 1976, Southwood 1977). In avian species food supply has been supposed to constitute the ultimate check on population growth (e.g. Newton 1980). In particular the importance of the food has been emphasized in the timing of the reproductive period (Perrins 1969), which has been assumed to coincide with the increasing food supply during the spring.This hypothesis has also been supported by experimental extra food studies (see as review Davies & Lundberg 1985).

However, the discussion about the relationship between food supply and reproduction has most frequently been based on avian species that have either evolved a seasonal decrease in the reproductive effort during the breeding season or which have a strongly fluctuating food supply. However, there exists a group of passerine bird species whose seasonal reproductive pattern is based on an initial increase with time and an eventual decrease (e.g. Klomp 1970). Studies on this group could provide a novel insight into the relationship between reproduction and food supply (however, see Bryant 1988).

The relationship has most often been based on Lack's (1954, 1966) famous hypothesis concerning the most common clutch size, which is also the most productive clutch size. This widely accepted hypothesis (see the last experiments by Gustafsson & Sutherland 1988, Pettifor et al. 1988) has also been criticized by the so called trade-off hypothesis (e.g. Nur 1984), which emphasizes the trade-off between the two fitness components, viability and fecundity. Criticism is based on the observation that quite often the largest clutch size is the most productive and not the most frequent (see the last major reviews on the subject: Murphy & Haukioja 1986, Martin 1987).

In this study I describe the food supply of the common treecreeper (*Certhia familiaris*, later treecreeper) and compare its seasonal development to the seasonal development in the reproductive effort in terms of clutch size, brood size and number of fledglings. I also compare the food supply and the nestling diet and predict how large the actual home range for the treecreeper should be. The treecreeper is a suitable species for this, because it has a long breeding period, with the above-mentioned pattern observable in the reproductive effort, which first increases with time and afterwards decreases.

If there exists a relationship between the food supply and the seasonal change in reproductive effort, then the food supply should correspondingly first increase and later decrease, as does the reproductive effort in the treecreeper (see Kuitunen 1987). Three specific questions are raised:

1) Does there exist a similar seasonal trend in the food supply as has been observed in the reproduction of the treecreeper?

2) How similar are the potential food supply and the diet of treecreeper nestlings?

3) How does the home range size observed fit the foraging area required for breeding according to the food supply results?

The treecreeper offers an excellent opportunity for answering this question since the species is specialized in gleaning arthropods from large tree trunks (e.g. Nilsson & Alerstam 1976, Alatalo 1982, Suhonen & Kuitunen unpubl.). Such habits permit relatively easy estimation of the available food supply in comparison to foliage or ground foraging species.

2. Study area and methods

The field work was carried out in three 10 ha coniferous forest sites in southern Finland (Hauho, 61°10′N, 24°40′E). The sampling of food was performed from 15 April to 28 October 1984.

During the main breeding season (15.4.–4.7.) samples were collected weekly, and later in alternate weeks, making a total of 18 times. One sample included the tree trunk surface between the heights of 0.5 m and 1.5 m, which represents the foraging site most preferred by the treecreeper (Suhonen & Kuitunen unpubl.). The bark was first covered by a special plastic tarpaulin which was equipped with six zippers. The animals were sucked from the trunk with a battery-operated vacuum cleaner by opening the zippers. The sucking capacity was increased by means of a crevice tool. If some animals dropped down, they were later sucked into the sample from the bottom of the tarpaulin.

On each sampling occasion four samples were taken in each of the three study sites. The sampled trunks were Norwegian spruces (*Picea abies*). Each trunk was sampled only once. Each site had a treecreeper nest box, and the nearest 72 spruce trunks (dph > 20 cm) were sampled. Four plus four samples from pine (*Pinus sylvestris*) and birch (*Betula* sp.) trunks were also taken on 2 June because the treecreeper also uses these trees for foraging. Below, all the tree species are pooled because there were no observable differences in their potential food supply.

During the study period the nest boxes (sites) number 1 and 3 were occupied by the treecreeper. The pair in number one produced 5 fledglings, which were in the nest from 14 May to about 2 June. The breeding attempt in box number three was unsuccessful. Box number two remained empty throughout the entire breeding period.

The 222 samples (two were lost) contained 1115 arthropods picked off and preserved in 70% ethanol. Only 16 of the samples were devoid of specimens. The arthropods were mainly determined to the family level, measured to the nearest millimetre (body length) and weighed with a microbalance after drying in an oven (60°C) for 24 hours. To compensate for losses caused by preservation in alcohol, 20% was added to the weights. The most common Aranea species were determined to the species level. Data on breeding success has been collected since 1974 (for details see Kuitunen 1987).

3. Results

3.1. Arthropod assemblage on the surface of tree trunks

Trunk samples consisted solely of arthropods and 55 taxa (family or order) were represented (Table 1). A Detrended Correspondence Analysis (Hill & Gauch 1980) for the invertebrate assemblages on the bark was performed. The first axis is affected by seasonal differences explaining not less than 87.9% of the variance, and the loadings of the axis correlated with the sample dates ($r^2=-0.27$, $df=206$, $P<0.001$). Because the second axis is also affected by the seasonal variation explaining 87.2% ($r^2=0.27$, $df=206$, $P<0.001$), the date appears to be of great importance. This could be explained by the seasonal variation in both biomass and taxons. During the spring the variance in the second axis seems to be higher than in autumn (Fig. 1).

The contribution of most families to the total number or biomass was low. On average, a sample contained only 5.0 specimens ($n=222$, $SD=4.6$, the maximum was 38 and the minimum 0). The length of the arthropods ranged from 1 to 20 mm and the dry weight from 0.01 mg to 27.98 mg (Fig. 2). The longest specimen was the larva of a lepidopteron and the heaviest one was a spider (*Gibbaranea omoedus*).

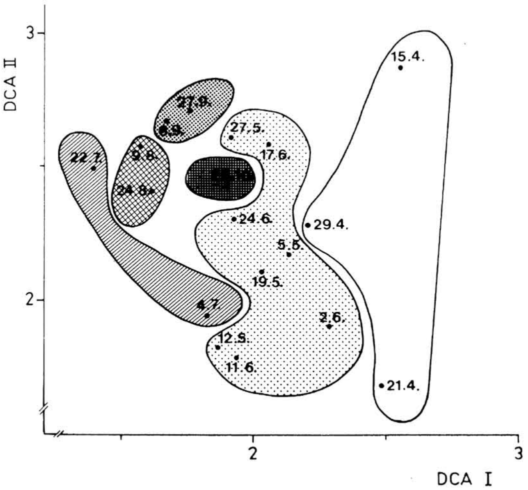

Fig. 1. Detrended Correspondence Analysis (Hill & Gauch 1980) for the arthropod assemblages on spruce trunks in southern Finland from 15 April to 28 October 1984. The figures represent the means for each sample collecting date.

The most important contribution (70.8%) to the biomass and energy supply content was made by spiders and harvestmen. Small spiders (1–2 mm) were the most abundant items (35.6% of the numbers, 9.4% of the biomass). Their contribution to the biomass and energy content was small compared with that of larger (3–9 mm) and equally numerous spiders (35.0 of the numbers and 56.7% of the biomass). Among spider families the most numerous were the Linyphiidae (49.1%).

Spiders in general were also the most frequent (86.0%) items in the samples. The mean length and mean weight for the whole material was 2.7 mm (n=1115, SD=1.8) and 1.4 mg (SD=2.9), respectively. 72.9% of the arthropods sampled were running. Flying (17.4%), jumping (6.6%) and slow-moving or sessile animals (e.g. Coleoptera and Lepidoptera larvae, 3.1%) were less numerous.

3.2. Variation in food supply due to season and habitat

The variation between sampling dates (Table 2) was statistically highly significant (ANOVA, F=14.8, df_1=201, df_2=6, P<0.001), while the variation between sites was significant (ANOVA, F=4.0, df_3=2, P<0.05). Log-transformation for arthropod numbers was carried out prior to statistical analysis, since the

Table 1. Composition of food supply in Hauho, southern Finland. The numbers represent the totals for 222 samplings (1115 items and 1047.6 mg altogether) made by the suction method from 15 April to 28 October 1984.

Taxon	Percentages by number	Percentages by weight	Frequency in samplings %
Opilionida	2.0	6.7	8.1
Clubionidae	2.6	3.7	9.9
Thomisidae	0.6	3.0	2.3
Salticidae	0.4	0.8	1.8
Agelenidae	11.7	4.8	32.0
Theridiidae	1.6	1.3	6.8
Araneidae	1.8	4.7	7.2
Linyphiidae	49.6	45.4	73.0
Egg coccoons	0.5	0.3	2.7
Collembola	4.8	0.2	11.3
Ephemeroptera	0.1	0.3	0.5
Psocoptera	0.4	0.2	2.3
Nabidae	0.4	0.7	1.8
Miridae	0.1	0.1	0.5
Heteroptera nymph	0.2	0.1	0.9
Cercopidae	1.2	5.6	3.6
Cicadellidae	0.3	0.1	0.9
Aphididae	0.1	0.0	0.5
Tineidae	0.3	0.7	1.4
Tortricidae	1.1	2.4	2.7
Geometridae	0.3	1.9	0.9
Lepidoptera larvae	0.2	0.9	0.9
Tipulidae	0.3	0.3	1.4
Psychodidae	0.4	0.0	0.9
Culicidae	1.0	1.5	5.0
Ceratopogonidae	0.1	0.0	0.5
Bibionidae	0.2	0.3	0.9
Mycetophilidae	0.4	0.2	1.8
Cecidomyidae	0.5	0.0	2.3
Rhagionidae	0.1	0.3	0.5
Empididae	0.7	0.3	2.7
Phoridae	1.8	0.5	8.1
Drosophilidae	0.1	0.0	0.5
Chloropidae	0.1	0.0	0.5
Muscidae	0.1	0.1	0.5
Calliphoridae	0.1	0.8	0.5
Lauxanidae	0.2	0.1	0.9
Hippoboscidae	0.1	0.2	0.5
Diptera larvae	0.2	0.3	0.9
Ichneumonidae	0.7	0.9	3.6
Chalcidoidea	0.4	0.0	1.8
Proctotrupoidea	1.3	0.0	5.0
Chrysididae	0.1	0.0	0.5
Vespidae	0.1	1.3	0.5
Formicidae	2.9	4.9	8.1
Hymenoptera larvae	0.3	1.0	1.4
Staphylinidae	0.5	0.2	2.3
Nitidulidae	0.1	0.1	0.5
Cryptophagidae	0.2	0.0	0.9
Lathridiidae	5.8	1.1	17.1
Chrysomelidae	0.1	0.1	0.5
Curculionidae	0.2	1.0	0.9
Coleoptera larvae	1.2	0.6	5.9
Total	100.0	100.0	

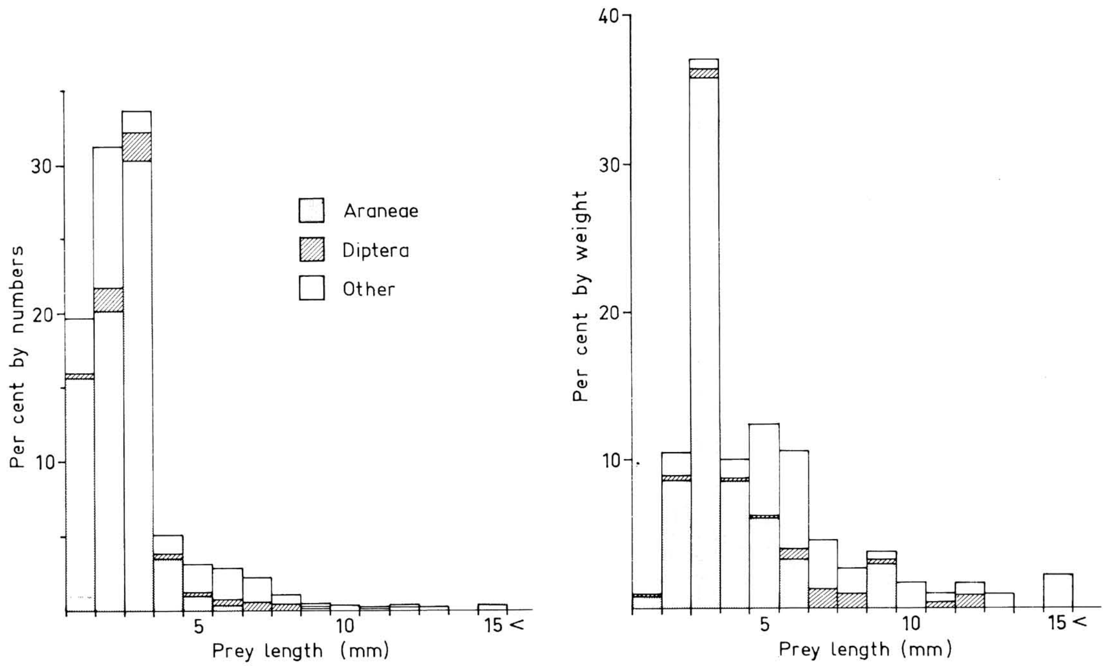

Fig. 2. Contribution of different size classes to the numbers and weight of the food supply of treecreepers in southern Finland.

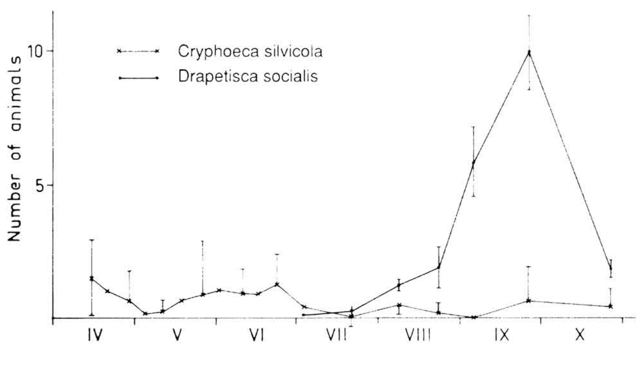

Fig. 3. The seasonal variation in the distribution numbers of the two most common arachnid species *Drapetisca socialis* (Linyphiidae) and *Cryphoeca silvicola* (Agelenidae) on spruce trunks in southern Finland.

Table 2. Seasonal variation in the potential food supply of the treecreeper (dry weight mg/m^2; mean±*SD* and *n*) in the study sites. The results of Cheffe's average test between the months are indicated by symbols under the numbers. The symbols for the months are Ap = April, My = May, Jn = June, Jy = July, Ag = August, Sp = September, Oc = October.

Site	April	May	June	July	August	September	October	Total
1	5.2±8.7 (10)	0.8±0.9 (15)	2.5±3.3 (17)	6.1±3.8 (8)	3.9±2.4 (7)	12.1±7.5 (8)	2.5±0.9 (4)	4.2±5.7 (69)
2	2.0±2.5 (14)	2.3±2.8 (16)	3.8±7.0 (23)	6.4±6.0 (8)	2.7±1.6 (9)	10.4±4.7 (8)	3.9±1.1 (4)	4.0±5.2 (82)
3	2.5±2.1 (11)	3.2±4.3 (16)	6.8±6.5 (16)	3.8±3.3 (8)	10.2±6.5 (8)	13.0±5.6 (8)	6.0±4.8 (4)	6.1±6.0 (71)
Total	3.0±5.0 (35)	2.1±3.2 (47)	4.3±6.1 (56)	5.7±4.5 (24)	5.6±5.2 (24)	11.8±5.9 (24)	4.1±3.0 (12)	4.7±5.6 (222)
P<0.05	Jy,Ag,Sp	Jy,Ag,Sp,Oc	Jy,Sp	Ap,My,Jn,Sp	Ap,My,Sp	Ap,My,Jn,Jy,Ag	My	

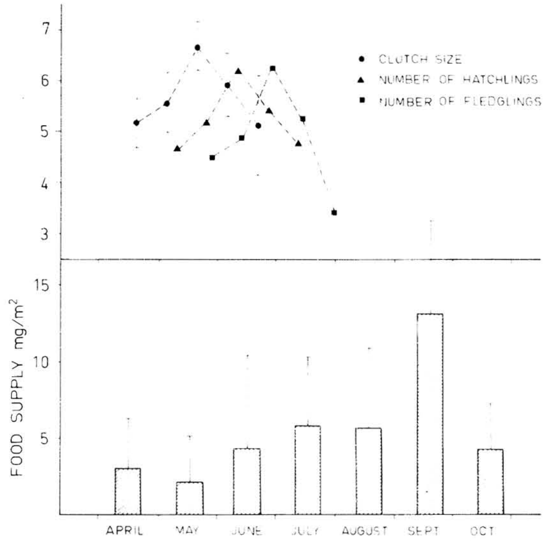

Fig. 4. Clutch size, brood size and number of fledglings of the treecreeper in relation to the laying date and seasonal variation of the potential food supply (mg/m^2). The vertical line is the standard deviation.

Table 3. Clutch size, number of hatchlings and number of fledglings (mean±*SD* and *n*) in relation to the time of laying in southern Finland in 1975–1978 and 1981–1983. ***= *P*<0.001.

Laying period	Clutch size	Hatchlings	Fledglings
12.4–26.4	5.16±0.54 (104)	4.63±1.09 (114)	4.48±1.28 (97)
27.4–11.5	5.55±0.61 (83)	5.13±0.85 (92)	4.85±1.19 (78)
12.5–26.5	6.67±0.52 (6)	6.17±0.75 (6)	6.25±0.50 (4)
27.5–10.6	5.91±0.64 (32)	5.40±1.01 (35)	5.26±1.00 (31)
11.6–25.6	5.13±0.99 (24)	4.76±1.09 (25)	3.39±2.00 (18)
All periods	5.42±0.71 (249)	4.94±0.99 (272)	4.66±1.36 (228)
F	17.1***	7.9***	8.6***

Table 4. The proportions (%) of the major prey taxa in the potential food supply and diet of nestling treecreepers (Kuitunen & Törmälä 1983) in southern Finland; based on dry weight biomass.

	Supply	Diet
Spiders and Harvestmen	71	75
Diptera	5	8
Hymenoptera	8	0
Coleoptera	3	3
Others	13	15

standard deviations differed. The results of Scheffe's average test between the sampling dates are given in Table 2.

The two most frequent spider species *Drapetisca socialis* (Linyphiidae) and *Cryphoeca silvicola* (Agelenidae) contributed 27.6% and 4.8% of the whole biomass respectively, and collectively 40.9% of the spider biomass, which forms a substantial proportion of the whole material. The seasonal variation in these species was diametrically opposite (Fig. 3). The former species caused the abundance peak in September, so it cannot be very important to the breeding treecreepers. The latter spider species is obviously more important, because its population maximum was in June.

3.3. Comparison between the food supply and reproduction

The seasonal clutch size trend in the treecreeper typically first increases and then decreases. The same trend exists in brood size and in the number of fledglings (Table 3, see also Kuitunen 1987). During the nestling period of the treecreeper (about 15.5.–1.8.) the seasonal change in the food supply increases over two-fold. However, it continues to increase after this period, achieving the maximum in September long after the seasonal trend in the reproductive effort of the treecreeper has started to decrease (Fig. 4).

3.3. Comparison between the food supply and the diet

The mean potential food supply for the whole material was 4.7 mg per m^2. 71% of this consisted of spiders and harvestmen, 5% of Diptera, 8% of Hymenoptera, 3% of beetles and 13% of others. The percentage similarity between the trunk samples and the diet of treecreeper nestlings reported from the same area (Kuitunen & Törmälä 1983) was 92 when a division was made into the taxonomic groups mentioned above (Table 4).

On average, treecreepers selected larger items than the supply included (t=7.1, df=1414, P<0.001; Fig. 5).

3.4. Predicted foraging area for breeding

Based on the results of the available food supply it is possible to estimate how large the home range area should be for one treecreeper pair:

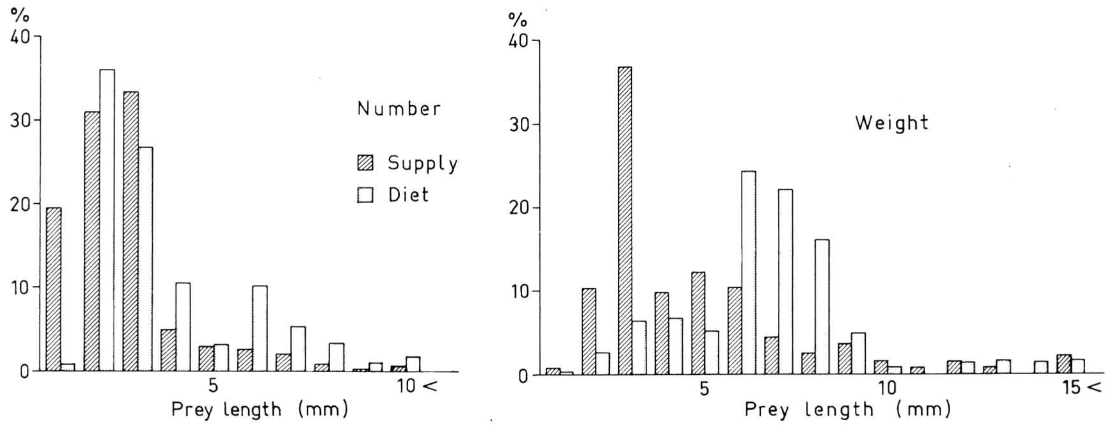

Fig. 5. Size distribution of arthropods. Potential food of the treecreeper sampled on spruce trunks, and the diet of the species (Kuitunen & Törmälä 1983) in southern Finland.

The average load carried to nestlings has been reported as 23.5 mg (Kuitunen & Törmälä 1983). The trunk surface area needed for a load is on average 5.0 m^2. Because treecreeper adults feed the nestlings on average 13 times per hour and 219 times per day (Kuitunen & Suhonen 1989), the adult birds need 65 m^2 trunk surface for one hour's feeding and 1095 m^2 for one day's feeding, respectively, assuming that they clean the area completely. Since the average nestling time is 16 days, adult birds need a trunk surface area of 17 520 m^2 in order to feed the nestlings. According to Ilvessalo's (1965) modification tables, this figure is equivalent to 764 m^3.

The stand characteristics were estimated in 25 stand compartments occupied by a nesting treecreeper. The mean solid volume was 304.5 m^3/ha (SD=82.2, range 148–490 m^3/ha). Based on these figures a treecreeper pair for just one breeding needs a home range amounting on average to at least 2.5 ha (SD=0.8, minimum 1.6 and maximum 5.2 ha, Fig. 6). These calculations do not take into account the seasonal variation of the food supply, the renewal rate of the food supply, the foraging rate of the treecreepers, or the diet of adults.

It is, however, possible to estimate the energy and foraging area requirements of the adult birds for feeding themselves during the nestling period. Willow tit (*Parus montanus*), crested tit (*P. cristatus*) and coal tit (*P. ater*) were estimated as using energy equivalent to about 40 kJ/d (Moreno et al 1988). The treecreeper is roughly the same size as these species. Norberg (1978) quotes 24.0 kJ/g dry biomass as the spider energy content.

The food supply for the treecreeper was 4.7 mg/m^2 (0.11 kJ) and the digestive coefficient, according to Weiner & Glowacinski (1975) for this kind of bird, is 0.75. On the basis of these numbers two adult treecreepers need a habitat of average size 2.2 ha for their own feeding purposes, which means an 88% increase on the home range size. Together with the area required by the adult birds for feeding the nestlings, the home range for one pair on average exceeds 4.7 ha.

4. Discussion

4.1. Reproductive effort

The seasonal change in the reproductive effort in terms of clutch size, brood size and number of fledglings (Table 3) agrees partly with the observed seasonal change in the food supply (Table 2, and Fig. 4). During the springtime the increasing food supply might affect the growing number of nestlings, but the food supply maximum does not coincide with the period when the nestlings of the largest clutches are near the fledgling stage at the end of June. Also against the direct relationship between the number of nestlings and food supply are the several experimental studies on the extra food (e.g. Källander 1974, Högstedt 1981, but see Perrins & Moss 1975). In most

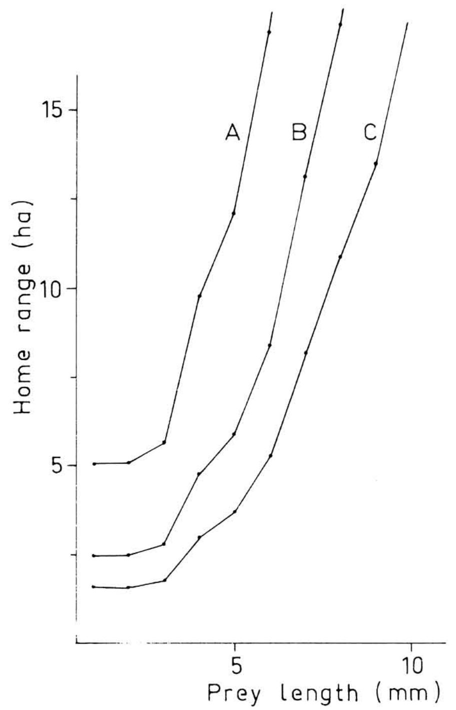

Fig. 6. Contribution of the different size classes of food in relation to the predicted size of the home range of the treecreeper. The numbers are based on stand characteristics, quantitative estimates of food supply and feeding activity. The lines represent the average (B), minimum (A) and maximum (C) habitat. The first point represents the situation in which treecreepers forage on all size classes (100% foraging efficiency) of the food supply. The second point represents situations in which treecreepers do not forage on 1 mm long prey items and so on. The model is generalized and assumes that both the total foraging rate (assumed to be 100%) and the renewal rate of the food supply (assumed to be 0%) remain stable.

of these papers the clutch size has not increased after an increased food supply. Besides, the manipulation has advanced the laying date (see Davies & Lundberg 1985). This is especially true in larger avian species (James & McCulloch 1985). However, this relationship probably depends a great deal on the predictability of the food supply between years. If the food supply is sufficiently predictable, the clutch size to evolve responses of this without doubt the bird has advantage to fit its clutch size to correspond the food supply.

If great variation exists in the food supply between years as is the case e.g. with the caterpillar food (Perrins 1965), there is no advantage in adjusting the clutch size to this. The food of the treecreeper consists of spiders, which are not as variable in numbers between years (Huhta 1965) and there might be a closer relationship between the food resource and clutch size.

The maximum densities of the most common spider species occur after the breeding season (Fig. 3) and increase the total biomass of potential food more than two-fold compared to that of June. After all, there probably exists a trade off between the reproduction and moulting period (see e.g. Pietiäinen et al 1984) and preparation for the wintertime. This spider species (*Drapetisca socialis*), which is abundant in September, might be essential in enabling the treecreeper to built up winter reserves. Winter has often been observed to be the most critical time for the so called tit guild, which includes the treecreeper (e.g. Ekman & Askenmo 1986). This hypothesis is supported by the high proportion of recruits in clutches laid at the very beginning of the reproductive period (Kuitunen 1987). Probably the early fledglings have morechance of surviving over the winter than later ones.

4.2. Food supply and diet

The comparison between food supply and diet gives a high similarity. Most likely the treecreeper is a generalist feeder, displaying no pattern for selectivity as regards the species in its food. This phenomenon has been observed previously in regard to spiders and Parus species (Norberg 1978). The most important difference between the diet and supply is the exclusive lack of Hymenoptera. The food supply contained items from six Hymenoptera families, ants being the most frequent. The observed difference between the available and selected size classes was noteworthy (Fig. 5): treecreeper adults consumed on average larger items than the average offered as a potential food supply.

The impact of predation by the treecreeper is not obvious in the observed differences between the sample sites occupied by a treecreeper pair or not occupied by one. Experimental evidence has been presented for the impact of bird predation during the wintertime (Askenmo et al 1977, Gunnarsson 1983. In this study the third site with a treecreeper pair which was unable to incubate the eggs included the highest biomass supply. This site was also the richest in terms of vegetation, resembling a dry herb rich forest. It was more open and well-lighted than other sites, as indicated by the presence of plant species preferring manmade habitats.

The food of nestlings consists mainly of predatory spiders (Kuitunen & Törmälä 1983), which are a fairly predictable food resource compared to the caterpillars consumed by foliage gleaners (see e.g. Huhta 1965, Perrins 1965). In addition the food density is relatively low and the large trunked spruces are well spaced in the forest. This situation forces the treecreeper to utilise a relatively large foraging area incomparison with foliage gleaners.

4.3. Foraging area

The calculations respecting the foraging area required for onebreeding agree well with the observations made by Kuitunen & Helle (1988) on the geographical variation in the minimum forest area the treecreeper will accept as its breeding site. In Central Finland the average home range size has been calculated as 3.3 ha (SD=0.6, N=7, Suhonen & Kuitunen unpubl). The relatively large observed and estimated home range size indicates that the treecreeper needs a relatively large amounty of foraging and flying time between the tree trunks and its nest. Hanski & Haila (1988) showed by means of the radio-tracking method that the home ranges of chaffinches were 4–8 times larger than their singing territories. This agrees well with the indication here that the home range required for breeding could be larger than the visually observed territory.

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