Ornis Fennica 87:77–92. 2010

Determination of clutch size in Treecreepers *Certhia familiaris* under food and time constraints

Teija Aho, Markku Kuitunen*, Jukka Suhonen & Ari Jäntti

T. Aho, Swedish Board of Fisheries, Institute of Coastal Research, Box 109, SE-74071 Öregrund, Sweden
*M. Kuitunen & A. Jäntti, Department of Biological and Environmental Sciences, P.O. Box 35, FI-40014 University of Jyväskylä, Finland. * Correspondent author's e-mail: markku.kuitunen@jyu.fi*
J. Suhonen, Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland

Received 3 September 2009, accepted 17 May 2010

Brood size of Eurasian Treecreepers *Certhia familiaris* was manipulated in three years that differed in food abundance in order to detect factors that limit clutch size. The Treecreeper parents were able to successfully raise enlarged broods only in a year with good food availability, but even then, the nestlings were of lower body weight than in reduced broods. Among the enlarged broods, the lowest breeding success was observed in a year with the lowest food abundance. Treecreepers with enlarged broods depleted their food supply in a year with scarce food, but not when food was abundant, and changes in foraging behaviour were observed only when food was scarce. Females and males did not increase their provisioning rates with brood size, but the responses of the sexes differed between years. Our results support Lack's hypothesis of clutch-size regulation: when food was scarce, Treecreepers laid the maximal number of eggs that they were able to raise successfully to fledging. However, trade-offs between current and future reproduction may also be important in clutch size determination of this species. Food abundance and limited foraging time seem to play major roles in limiting the clutch size of Treecreepers, but the importance of these factors differs among years.

1. Introduction

Life-history theory views reproduction as a problem of optimization with trade-offs between costs and benefits of reproductive effort (Roff 1992, Stearns 1992). In altricial birds, this optimization includes the determination of clutch size. David Lack (1947) initially suggested that clutch size is set by the number of young parents can adequately provision. Subsequent experiments using manipulation of brood size have shown that parents are frequently able to raise a larger brood than their original brood size, but often at the expense of their own residual reproductive value (Gustafsson & Sutherland 1988, Pettifor *et al.* 1988, 2001, Dijkstra *et al.* 1990, Lessells 1991, Roff 1992, Stearns 1992).

Despite the extensive effort devoted to brood size manipulation experiments (Lindén & Møller 1989, Dijkstra *et al.* 1990, Lessells 1991) in order to reveal the costs of reproduction (Williams 1966), the mechanisms that limit clutch size and through which the trade-off between current and future reproduction comes about are still poorly understood. One possible mechanism for the negative effects of brood enlargements is food depletion in the territory during the nestling period (Martin 1987). If food majorly constrains the ability of parents to feed their young, the parents should adjust their clutch size according to the availability of food in the territory. Thus, an experimental increase of brood size should result in a decrease in either the amount or quality of food during the nestling stage. However, direct evidence for such food depletion is lacking.

In order to affect reproductive success, food limitation must act through changes in individual body condition, foraging behaviour or parental care. If food depletes in the territory, the profitability of food patches decreases, which should lead to changes in individual foraging behaviour (Stephens & Krebs 1986). Food scarcity may thus limit the ability of the parents to find enough food of sufficiently high quality to their nestlings. On the other hand, parental feeding frequency may reflect a trade-off between fledgling and parental survival (Nur 1984, 1987). Because parental investment is related to the reproductive value of the brood, theoretical models of optimal allocation strategies predict that the total parental effort should increase with brood size up to an asymptote, whilst effort per young should decrease (Houston & Davies 1985, Winkler 1987). In addition, the magnitude of a parent's response to a reduction in its partner's contribution should increase, and the parental response per young should decrease, as brood size increases.

Some investigations of the relationship between parental effort and reproductive output of manipulated broods have found parents to increase their effort and thereby compensate for the increased food demand in the enlarged broods (e.g., Wright & Cuthill 1990, Cucco & Malacarne 1995, Moreno *et al.* 1995, Orell *et al.* 1996). Conversely, other studies have shown that parents may not respond to the brood manipulation by adjusting effort to nestling demand (e.g., Korpimäki 1988, Smith *et al.* 1988, Tolonen & Korpimäki 1994), probably in order to avoid survival costs during reproduction (Tuomi 1990). However, only few studies have documented the effects of brood size manipulation on the foraging behaviour of the parents, together with measurements of parental care and food supply (e.g., Cucco & Malacarne 1995, Tolonen & Korpimäki 1996).

In the present experiment, our aim was to find factors that limit reproduction in different environmental conditions, and to explore mechanisms behind fitness consequences caused by brood enlargements. We manipulated the brood size of the Eurasian Treecreeper (*Certhia familiaris*) in three years differing in food conditions. We aimed to test the effects of brood enlargement on foraging behaviour and parental care of parents, and on the subsequent breeding success and available food supply in the territory. If food depletion is the mechanism that limits clutch size in Treecreepers, brood enlargement should result in decreased abundance and/or quality of food at the end of the nestling period. The Eurasian Treecreeper forages exclusively on tree trunks; thus, altered food availability should result in changes in foraging behaviour on these foraging patches. Finally, we tested whether Treecreeper parents are able to increase their feeding rates in response to brood enlargement.

2. Material and methods

2.1. Study species and site

The Eurasian Treecreeper is a cavity-nesting, double-brooded and insectivorous passerine that breeds throughout the northern coniferous zone (Suhonen & Kuitunen 1991a). It is specialized to search for its food on tree trunks and prefers the largest tree trunks in the forest (Suhonen & Kuitunen 1991b). Its foraging behaviour is therefore easy to observe and the abundance of the available food supply can be measured easily (Kuitunen 1989).

The fieldwork was done at the vicinity of the Konnevesi Research Station, Central Finland (62°37' N, 26°20' E) during the summers of 1991, 1992 and 1995. The study area is mainly covered by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) forests, mixed with birches (*Betula pendula* and *B. pubescens*) and other deciduous tree species. In our study area, Treecreepers often breed in specifically designed nest boxes (Fig. 1). Each breeding pair had access to extra

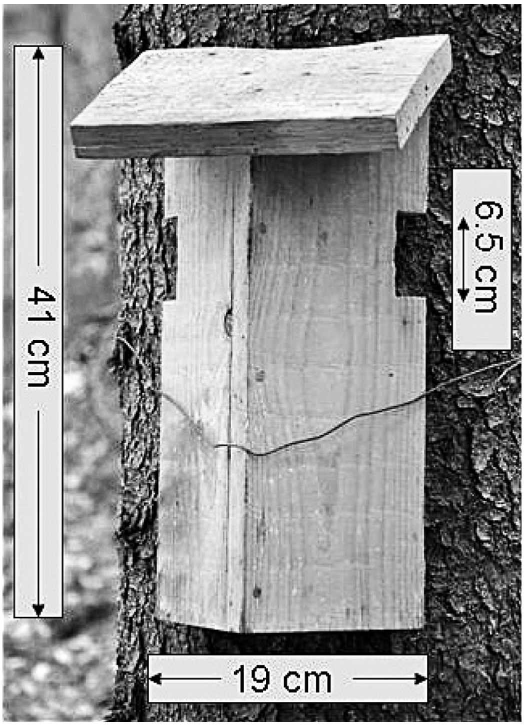

Fig. 1. Nest box design for the treecreepers used e.g. in this study (*Certhia familiaris*, *C. brachydactyla*, and *C. americana*) (© Markku T. Kuitunen)

nest boxes for a second breeding attempt. Food abundance at the breeding sites of Treecreepers was highest in 1995 and lowest in 1992, and was low also in 1991 (e.g., Jäntti *et al.* 2001, 2007a, 2007b).

2.2. Basic data collecting and experimental design

Data on laying date, clutch size, date of hatching, nestling mortality and number of fledglings were collected for each nesting attempt in each study year. We caught breeding females and males during the early nestling stage and marked them individually with aluminium and colour rings. Morphological characteristics, such as wing, tarsus, and bill lengths and body mass, were measured. Study nests were randomly assigned into three treatment categories: (1) an increase in the number of nestlings (hereafter enlarged broods); (2) a decrease in the number of nestlings (reduced broods); and (3) an unaltered number of nestlings (control broods; see below). Twelve nests (four per treatment) were studied in 1991 and 1995 and fifteen nests (five per treatment) in 1992. The randomization was done as follows: nests with the same hatching date either became untouched controls, or one of the two types of manipulated nests: the number of nestlings was either increased or decreased by adding (from an adjacent, to-be-reduced brood nest) or removing one two-day old nestling (to be moved to an adjacent, to-be-enlarged brood nest). No nestling mortality was involved, and we did not observe parents to discriminate between their own and foster young. Because the diameter of spruce trunks determines the Treecreeper foraging site selection (Suhonen & Kuitunen 1991b), we applied several criteria (the proportions of different tree species, density of trees, and size distribution of trees) in order to obtain similar Treecreeper territories for control and experimental nests. The treatments did not significantly differ in any of these variables between each of the study years. This is a predictable outcome because the forests in the study area, used for the nest box experiment, are generally quite homogenous. The number of wood ants per tree trunk did not significantly vary between the territories of each of the different treatment groups (see Aho *et al.* 1997, 1998, 1999, 2009).

2.3. Behavioural observations

The foraging behaviour of Treecreeper parents feeding their 12–14 days old nestlings were observed in 1991 and 1995. For each observed individual we recorded four foraging variables: tree species used for foraging, diameter of tree trunks at the height of one meter, foraging distance from the nest, and time spent on each tree. We used tree-specific visiting frequencies and mean values of the foraging variables of each individual bird (at least 30 spruce trees foraged on per individual) as independent observations for statistical tests.

We collected data on parental care in 1991 and 1992. In 1991, feeding activity was determined by counting the feeding frequency of the parents for one hour between 10 AM and 6 PM, until the nestlings were 12 days old, by direct observations. In 1992, feeding frequencies and load sizes were measured using a small video camera installed beside the nest entrance. The size of each load was determined in relation to the bill length of the feeding parent from the video tapes. From a total time of two hours that each nest was video taped, we used the period of one hour (beginning 30 minutes after the start of the tape) for the determination of both feeding frequencies and load sizes.

We experienced occasional data losses. In one experimentally enlarged brood in 1991, all the nestlings died at the age of 8 days and therefore we could not obtain behavioural data for this nest (hence $N = 11$ pairs). In two experimental nests in 1995, we did not get enough foraging observations for males (hence $N = 12$ females and 10 males). In 1992, we obtained no video data for one control and one enlarged brood. In addition, one control female, one control male and three males of enlarged broods did not feed the nestlings at all, and therefore data on load sizes and foraging times per bout are missing for these individuals. The sample sizes in 1992 are thus 13 females and 13 males (feeding frequencies), and 12 females and 9 males (load sizes and foraging times/bout).

2.4. Breeding success and food abundance

Reproductive success of each nest was determined each year by weighing the nestlings just before fledging (at the age of 12–13 days) and recording the number of nestlings that died or survived to fledge. We visited all the nest boxes regularly throughout the breeding seasons in order to check the initiation and fate of the second clutches.

We gathered data on food abundance in the territories after the experiments in 1991 and 1995. Just after fledging, we collected arthropod samples from six randomly-selected tree trunks that were larger than 30 cm in diameter at breast height (trunks of this size are preferred by foraging Treecreepers; Suhonen & Kuitunen 1991b) within 20–30 m range from the nest in each territory. The trunk surface at the height of 0.5–1.5 m was vacuum-cleaned for invertebrates by a 12 V battery-operated vacuum cleaner (see Kuitunen 1989), the diameter of each trunk was measured, and the results were afterwards transformed to correspond to a trunk area of one m^2. Invertebrates larger than 1 mm in size were identified to the family level. The mean number and body length of the food items on six trunks in each territory were used as indicators of the amount of food remaining on tree trunks in each territory. The vacuum-cleaning was always done during good weather conditions. Differences in food abundance between each of the treatment groups were analysed separately for years 1991 and 1995, because the variances differed remarkably between years. Within years, the original data was log-transformed to equalize the variances.

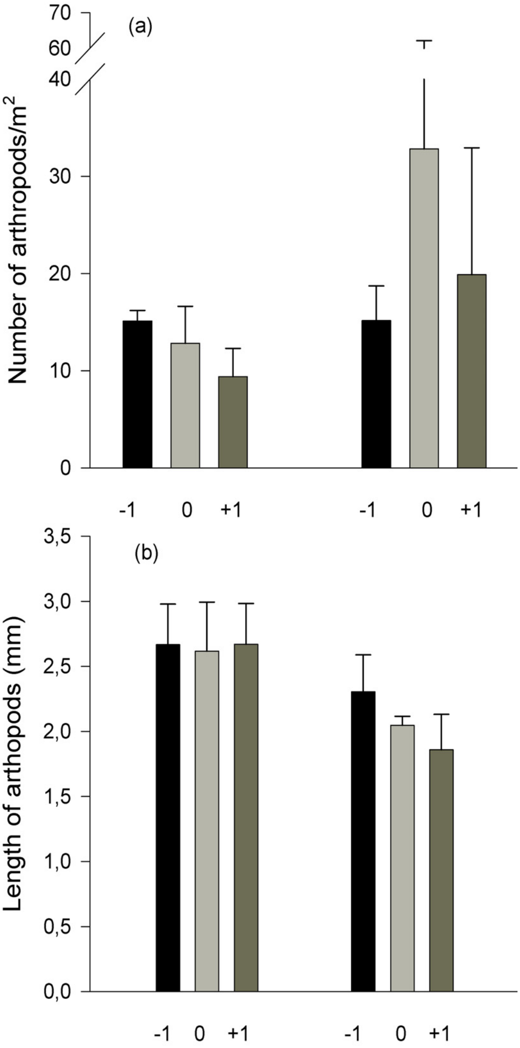

Fig. 2. Mean number (a) and body length (b) of arthropods in Treecreeper territories of reduced (–1), control (0) and enlarged (+1) broods after fledging in 1991 and 1995. Vertical lines denote standard deviations.

Table 1. Mean ± SD of clutch size and number of hatched young prior to manipulation, and nestling mortality (% nestlings that died), frequency of second broods, and total number of fledglings produced in a breeding season (first and second broods pooled) after the manipulation among brood-size treatments and study years (see text).

	1991			1992			1995		
Treatment	Reduced	Control	Enlarged	Reduced	Control	Enlarged	Reduced	Control	Enlarged
N	4	4	4	5	5	5	4	4	4
Prior to manipulation									
Clutch size	5.8 ± 0.5	5.0 ± 0.0	5.5 ±0.6	5.2 ± 0.8	5.6 ± 0.5	5.4 ± 0.5	5.0 ± 0.8	5.8 ± 0.5	5.3 ± 1.0
No. hatchlings	5.0 ± 1.4	4.5 ± 0.6	5.0 ± 0.8	5.0 ± 0.7	5.0 ± 1.0	5.0 ± 1.2	4.8 ± 1.0	5.3 ± 0.5	4.8 ± 0.5
After manipulation									
Brood size	4.0 ± 1.4	4.5 ± 0.6	6.0 ± 0.8	4.0 ± 0.7	5.0 ± 1.0	6.0 ± 1.2	3.8 ± 1.0	5.3 ± 0.5	5.8 ± 0.5
Nestling mortality (%)	15.0 ± 30.0	20.0 ± 23.1	47.1 ± 42.9	4.0 ± 8.9	4.0 ± 8.9	36.9 ± 38.5	0.0 ± 0.0	12.5 ± 25.0	0.0 ± 0.0
Second broods	75.0	50.0	0.0	40.0	20.0	20.0	100.0	25.0	50.0
Fledglings	7.5 ± 2.1	5.5 ± 2.6	3.3 ± 2.8	5.8 ±2.6	6.0 ± 2.4	4.6 ± 3.7	8.5 ± 3.7	6.3 ± 2.5	8.5 ± 3.5

2.5. Statistical testing

The differences in foraging and parental behaviour were analysed using Kruskal-Wallis tests, because many variables were not normally distributed or the compared variances were different. The effects of the foraging behaviour (the four variables; see above) were analysed separately for years 1991 and 1995, on the feeding frequency for years 1991 and 1992, and on the load size and foraging time on each bout for 1992 only.

The differences in original clutch sizes and number of hatched young, and number of nestlings after their manipulation among brood treatments were analysed using two-way ANOVA with the treatment and year as factors. The effects of brood-size manipulation on the mean body mass and number of fledglings, produced from the first and second broods, were also analysed by two-way ANOVA.

The fledgling success among years and brood treatments was analysed using logistic regression. Two models were used, and year 1995 was selected to represent the year to which the comparisons were made. The first model evaluated differences among the brood treatments over the three years, and compared the success of the broods in 1991 and 1992 to the success of the broods in 1995. The second model included interaction terms between treatments and years, and this model was also used to test treatment effects on fledging success in 1995.

Data on the frequency of second broods were pooled over the three years due to the scarcity of observations, and analysed using Chi-square test. The number of broods included in the analysis of reproductive parameters was 39 (12 in 1991, 15 in 1992 and 12 in 1995) except in the analysis of nestling body mass, where the number of broods was 34 (11 in 1991, 12 in 1992 and 11 in 1995). In two of the enlarged broods all the nestlings died before the age of 12 days, and in four other nests we did not obtain data on nestling weights.

3. Results

3.1. Food abundance

In 1991, the brood-size manipulation affected the number of invertebrates on tree trunks ($F_{2,9} = 4.46$, $P = 0.045$; Fig. 2a). Tukey's a posteriori comparison revealed that there were fewer food items left on the largest tree trunks in territories of enlarged broods compared with reduced broods (df = 9, $P = 0.038$). The average size of food items did not significantly differ among the treatments ($F_{2,9} = 0.04$, $P = 0.96$; Fig. 2b). In 1995, we did not find significant effects of the manipulation on the number of invertebrates ($F_{2,9} = 0.45$, $P = 0.65$; Fig. 2a), but the manipulation had a marginally significant effect on the mean body length of the food items ($F_{2,9} = 3.98$, $P = 0.058$; Fig 2b). Tukey's a posteriori comparison revealed that the food items were on

Table 2. Two-way ANOVA for Treecreeper clutch size and brood size at hatching prior to manipulation, and for brood size after manipulation. Treatment = control, enlarged or reduced brood, and Year = 1991, 1992 or 1995. *N* = 39 broods.

	Clutch size				Brood size at hatching				Brood size after manipulation			
Source	df	SS	*F*	*p*	df	SS	*F*	*p*	df	SS	*F*	*p*
Treatment	2	0.114	0.138	0.872	2	0.000	0.000	1.000	2	25.71	15.28	0.000
Year	2	0.047	0.057	0.945	2	0.186	0.110	0.896	2	0.186	0.110	0.896
Treat*Year	4	2.579	1.554	0.212	4	1.333	0.396	0.810	4	1.333	0.396	0.810
Error	30	12.45			30	25.25			30	25.25		

average smaller at sites of enlarged broods compared with sites with reduced broods (df = 9, *P* = 0.049).

3.2. Breeding success

The original clutch size and the mean original number of nestlings did not differ significantly among the treatments or study years (Tables 1–2). Mean nestling weight, however, differed both among treatments and years, and the interaction between treatment and year was significant (Table 3, Fig. 3).

For mean nestling weight, Tukey's multiple comparisons showed that the years 1991 and 1992 differed from 1995 (df = 25, *P* = 0.024 and *P* = 0.004, respectively). To detect pair-wise differences between each of the treatments in each year, we applied sequential Bonferroni tests (Sokal & Rohlf 1995). In 1991, there were no differences in mean nestling weight between each of the treatments. However, in 1992, the nestlings of the enlarged broods had significantly lower body weight than had nestlings of the control or reduced broods (df = 25, *P* = 0.001 for both comparisons). In 1995 the only significant difference was that nestlings in the reduced broods were heavier than nestlings in the enlarged broods (df = 25, *P* = 0.005; Fig. 3).

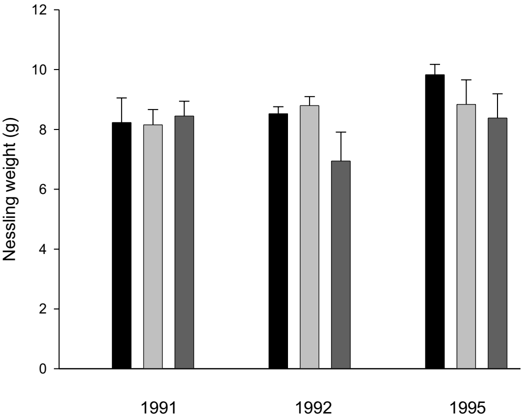

Fig. 3. The effect of brood-size manipulation on the mean nestling weight of Treecreepers in 1991, 1992 and 1995. Vertical lines denote standard deviations.

A logistic regression for the relationship in the proportions of fledglings and nestlings showed that, over all years, reduced broods were as successful as control broods (coefficient = 0.60, P =

Table 3. Two-way ANOVA for the effects of brood size manipulation (Treatment) and year (1991, 1992 or 1995) on the body mass of nestlings (*N* = 34) and number of fledglings (*N* = 39) of Treecreepers.

	Mean nestling mass				Number of fledglings			
Source	df	SS	*F*	*p*	df	SS	*F*	*p*
Treatment	2	5.144	6.745	0.005	2	2.781	0.642	0.533
Year	2	5.449	7.144	0.004	2	10.83	2.499	0.099
Treat*Year	4	5.878	3.853	0.014	4	9.400	1.085	0.382
Error	25	9.534			30	65.00		

Table 4. Effects of brood-size manipulation on the observed feeding rates (FR) of Treecreeper females, males and both parents summed in 1991 and 1992, and on the load size (LS; mm^2) and foraging time/bout (FT; min) of females and males in 1992. Mean ± SD values and Kruskal-Wallis statistics (*H* and *p*) are shown. Numbers of females and males (f/m) are shown below each figure.

	1991					1992				
Treatment	Reduced	Control	Enlarged	*H*	*p*	Reduced	Control	Enlarged	*H*	*p*
FR, female	13.5 ± 2.5	8.00 ± 6.2	10.7 ± 4.0	1.70	0.43	7.60 ± 1.1	11.0 ± 8.0	17.0 ± 9.7	3.10	0.21
FR, male	8.75 ± 5.6	10.8 ± 4.6	10.3 ± 3.5	0.91	0.64	8.60 ± 3.8	7.75 ± 7.0	1.50 ± 3.0	4.92	0.09
FR, sum	22.3 ± 6.7	18.8 ± 10.5	21.0 ± 6.1	0.33	0.85	16.2 ± 4.0	18.8 ± 9.0	18.5 ± 8.9	0.65	0.72
N(f/m)	4/4	4/4	3/3			5/5	4/4	4/4		
LS, female						75.7 ± 23.5	112.8 ± 51.0	92.9 ± 17.2	2.39	0.30
LS, male						156.7 ± 69.6	162.2 ± 95.7	84.0	1.35	0.51
FT, female						6.9 ± 1.3	3.7 ± 0.6	4.0 ± 2.0	7.19	0.028
FT, male						8.9 ± 6.0	6.0 ± 3.5	7.7	0.34	0.84
N (f/m)						5/5	3/3	4/1		

0.36), but the success of enlarged broods was significantly lower than the control broods (coefficient = –1.13, *P* = 0.016; Fig. 4). However, the success of the broods in 1991 and 1992 differed from the success of the broods in 1995 (coefficient$_{1991}$ = –2.23, *P* = 0.0009; coefficient$_{1992}$ = –1.51, *P* = 0.025; Fig. 4). The second regression model with interaction terms included revealed no differences in fledging success among the treatments in 1995. Comparisons of the two models showed that the interactions between years and treatments were significant (log likelihood ratio statistic: $\chi^2 = 13.4$, df = 4, *P* = 0.009). Thus, fledging success was significantly lower in the enlarged than in the control or reduced broods in 1991 and 1992, but this difference was non-significant in 1995.

Over all years, the probability of laying a second clutch during the same breeding season decreased as the brood size increased ($\chi^2 = 6.57$, df = 2, *P* = 0.037; Table 1). However, the total number of fledglings produced in one breeding season did not significantly differ among treatments or years (Tables 1 and 3).

3.3. Parental care

In 1991, the brood-size manipulation did not significantly affect the observed feeding frequencies of parents (Table 4). However, in terms of relative feeding rate (feeding rate/hour/chick), the feeding rate in females marginally decreased as the brood size increased ($H_{2,8} = 5.21$, $P = 0.07$; Fig. 5). Males did not significantly change their relative feeding frequencies ($H_{2,8} = 0.38$, $P = 0.83$; Fig. 5). Consequently, chicks were fed at approximately equal rates in different treatments (Table 4; relative feeding frequency: $H_{2,8} = 1.96$, $P = 0.37$; Fig. 5).

In 1992, the manipulation did not significantly affect the observed (Table 4) or the relative feeding frequencies of females ($H_{2,10} = 0.47$, $P = 0.82$; Fig. 5). Males, however, fed the nestlings of enlarged broods marginally less than control or reduced broods, both in absolute numbers (Table 4) and per chick ($H_{2,10} = 5.64$, $P = 0.06$; Fig. 5). In 1992,

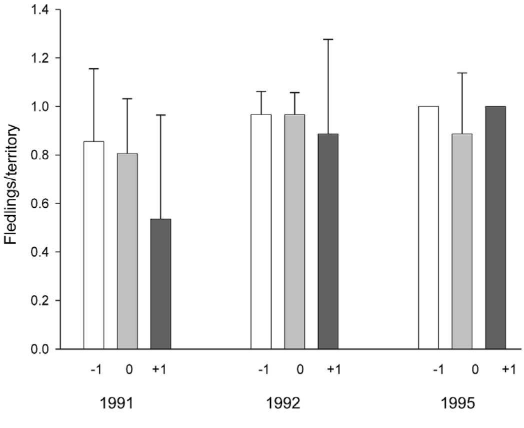

Fig. 4. Mean number of Treecreeper fledglings produced in territories of reduced (–1), control (0) and enlarged (+1) broods in 1991, 1992 and 1995. Vertical lines denote standard deviations.

Table 5. The effects of brood-size manipulation on the frequency of spruce usage, foraging distance from the nest and inter-patch distance of female and male Treecreepers. Values are mean ± SD.

	1991			1995		
Treatment	Reduced	Control	Enlarged	Reduced	Control	Enlarged
N, females/males	4/4	4/4	3/3	4/4	4/4	4/2
% spruce, female	86.9 ± 12.6	92.4 ± 5.49	83.4 ± 25.0	85.3 ± 10.0	95.3 ± 7.2	78.8 ± 14.2
% spruce, male	53.4 ± 30.8	59.4 ± 21.6	55.9 ± 44.4	86.1 ± 5.18	91.5 ± 8.5	74.8 ± 29.6
Foraging distance (m)						
Female	18.5 ± 6.47	25.5 ± 6.18	27.4 ± 10.9	22.0 ± 11.0	17.6 ± 8.91	12.6 ± 6.10
Male	35.1 ± 12.9	42.3 ± 25.1	19.3 ± 5.76	23.3 ± 6.36	20.9 ± 11.9	17.4 ± 8.34
Inter-patch distance (m)						
Female	9.86 ± 1.7	10.3 ± 1.6	11.3 ± 2.1	6.78 ± 2.2	10.2 ± 2.7	8.19 ± 2.5
Male	10.4 ± 2.1	11.6 ± 3.6	9.64 ± 0.3	6.52 ± 2.1	8.81 ± 2.5	8.73 ± 3.5

chicks of different treatments were fed at nearly equal rates (Table 4; relative feeding frequency: $H_{2,10} = 0.77$, $P = 0.68$; Fig. 5). We found no differences in mean load sizes of females or males (Table 4). Time that male treecreepers spent foraging on each bout did not differ was constant among treatments, but females of reduced broods seemed to spend more time per each bout as compared with control and enlarged-brood females (Table 4), although the a posteriori comparison of mean ranks did not detect significant differences between each of the treatments.

3.4. Foraging behaviour

In 1991, spruce was the most frequently used tree species by female and male treecreepers in all treatments (Table 5). Spruce usage among the treatment groups was quite similar for females and males ($H_{2,8} = 0.84$, $P = 0.65$ and $H_{2,8} = 0.05$, $P = 0.97$, respectively). Females of enlarged broods foraged on thinner spruce trunks than did females of the reduced broods ($H_{2,8} = 7.48$, $P = 0.024$, pairwise comparisons of mean ranks; Fig. 6a). Females of enlarged broods spent on average less

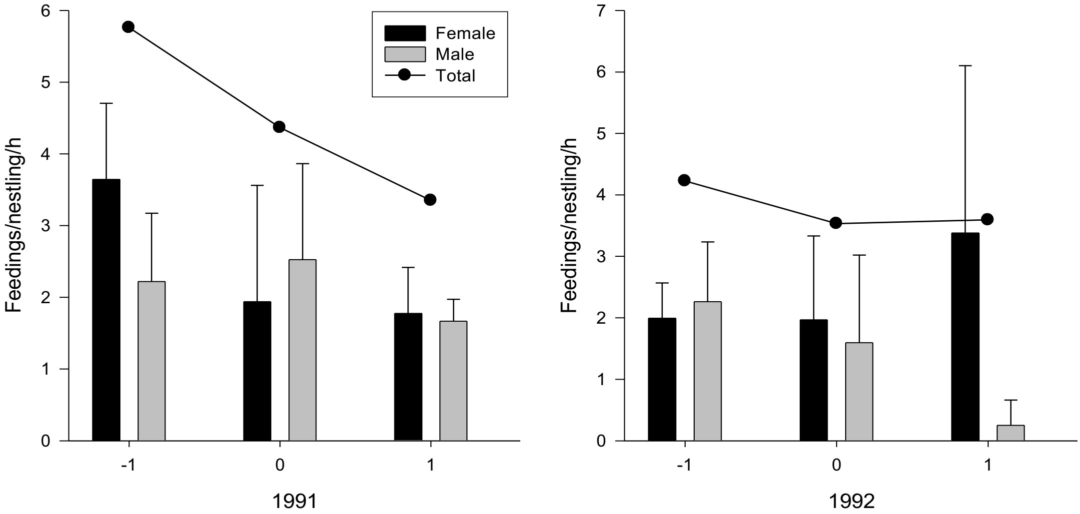

Fig. 5. The effects of Treecreeper brood-size manipulation on the relative hourly feeding rate (feedings/chick/h) of females and males in 1991 and 1992. Vertical lines denote standard deviation, and the horizontal line above bars denotes the combined relative feeding rate of females and males.

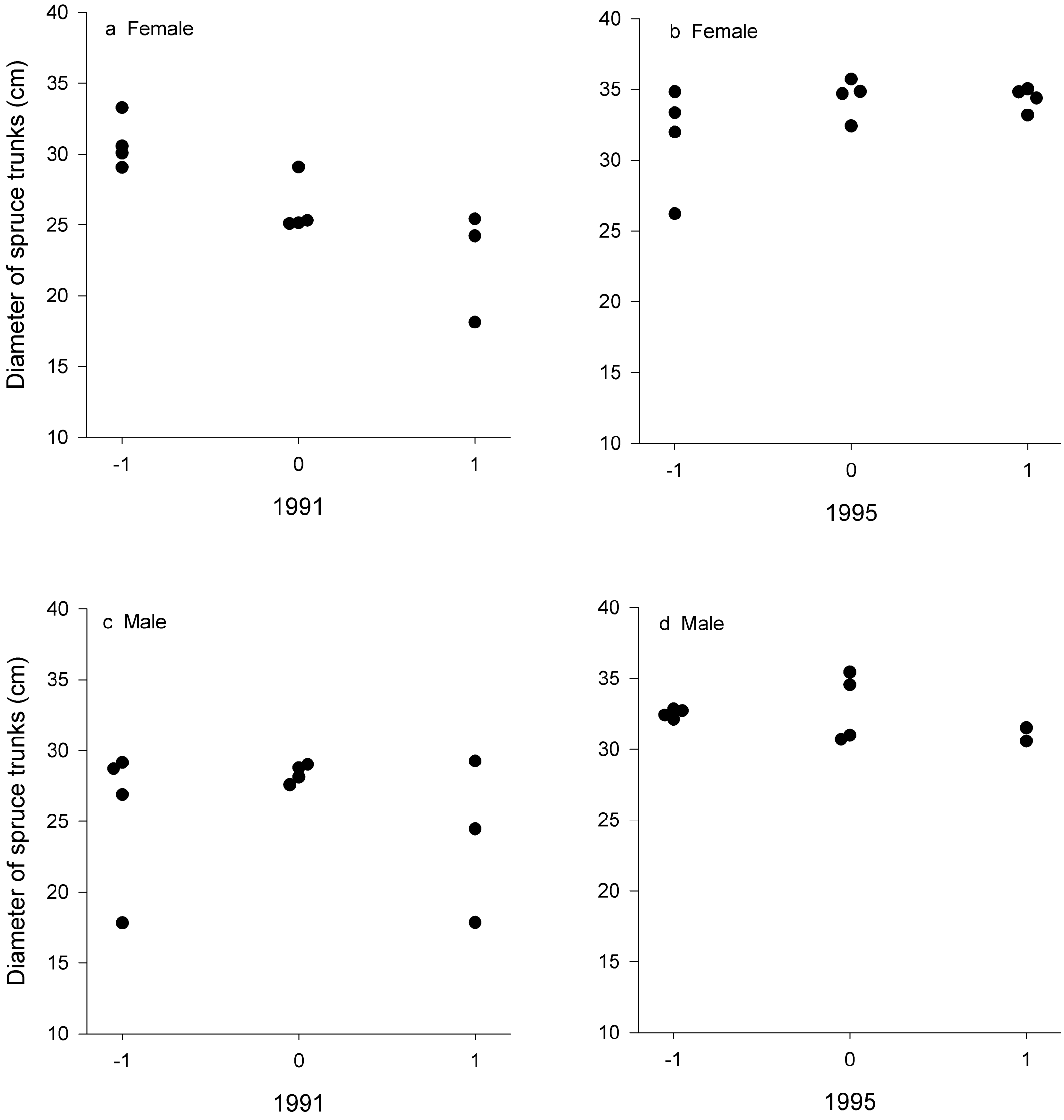

Fig. 6. The effects of Treecreeper brood-size manipulation on the foraging-site selection of (a) females in 1991, (b) females in 1995, (c) males in 1991, and (d) males in 1995.

time in foraging per trunk, while the females of reduced broods foraged longer ($H_{2,8}$ = 6.14, P = 0.046; Fig. 7a), although a posterior comparisons of mean ranks did not detect significant differences between each of the treatments. Males, however, did not change their foraging strategy in response to the brood-size manipulation ($H_{2,8}$ = 0.40, P = 0.82; Fig. 6c), but males of enlarged broods spent less time on each tree than did the control males ($H_{2,8}$ = 6.55, P = 0.038; Fig. 7c). There were no significant differences in the distance between foraging trees and the nest for females ($H_{2,8}$ = 1.75, P = 0.42; Table 5), but males of enlarged broods foraged on average slightly closer to the nest than did males of control and reduced broods ($H_{2,8}$ = 4.21, P = 0.12; Table 5). We did not find significant differences in the inter-patch travelling distance among treatments either in females or males ($H_{2,8}$ = 1.55, P = 0.46 and $H_{2,8}$ = 0.18, P = 0.91, respectively; Table 5).

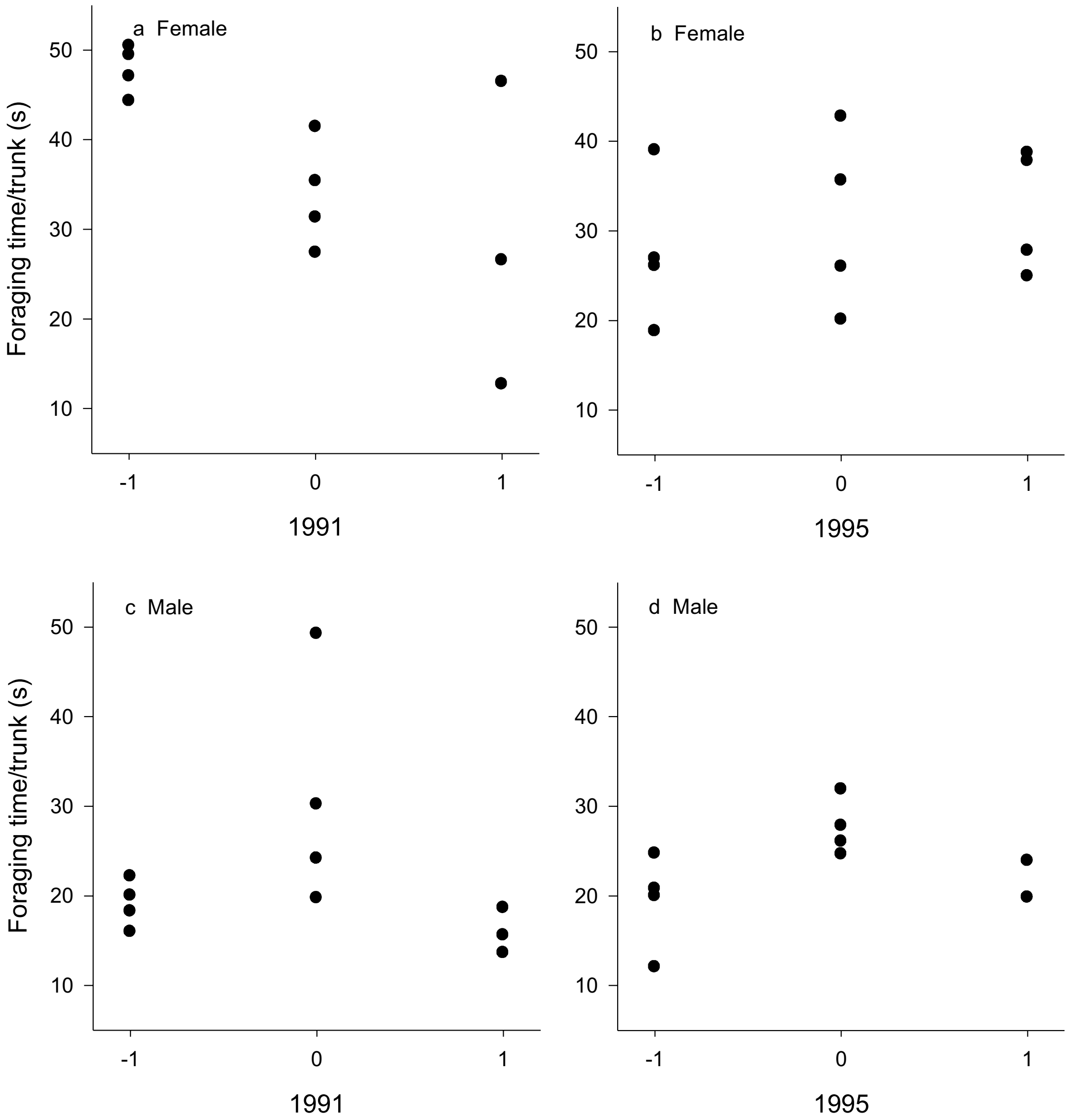

Fig. 7. The effects of Treecreeper brood-size manipulation on the foraging time per trunk of (a) females in 1991, (b) females in 1995, (c) males in 1991, and (d) males in 1995.

In 1995, the brood-size manipulation did not significantly affect the foraging behaviour of parent Treecreepers. Spruce was the most frequently used tree species of both sexes in all treatments ($H_{2,9} = 4.54$, $P = 0.10$ and $H_{2,7} = 0.74$, $P = 0.69$; respectively; Table 5) and the diameter of the trunks used for foraging did not differ significantly either (females: $H_{2,9} = 2.35$, $P = 0.31$; males: $H_{2,7} = 2.51$, $P = 0.29$; Figs. 6b, 6d). Foraging times per trunk of females did not significantly differ among treatments ($H_{2,9} = 0.50$, $P = 0.78$; Fig. 7b). Control-brood males spent on average the longest time foraging per trunk, but the difference was not statistically significant ($H_{2,7} = 4.55$, $P = 0.10$; Fig. 7d). The manipulation did not significantly affect the foraging distances of females or males ($H_{2,9} = 2.0$, $P = 0.37$ and $H_{2,7} = 0.74$, $P = 0.69$, respectively; Table 5) or the inter-patch travelling distances (females: $H_{2,9} = 3.5$, $P = 0.17$; males: $H_{2,9} = 1.72$, $P = 0.42$; Table 5).

3.5. Observational data on the relationships between food abundance, foraging behaviour and breeding success

We did not obtain data on food abundance in the territories of the manipulated nests in 1992, but data from other territories during that year (mean number ± SD of arthropods/trunk over 14 territories: 9.1 ± 4.7) suggests that food abundance was as low as in 1991 (mean number ± SD of arthropods in the enlarged group: 9.1 ± 2.9, Fig. 2a; Jäntti *et al.* 2001). In 1992, the success of enlarged broods was also the lowest: parents could not raise added nestlings, and the nestlings of enlarged broods were also of lower body weight than other broods. In 1991, parents were unable to successfully raise enlarged broods to fledging, but the manipulation did not affect nestling body mass. In 1991 with low food abundance, parents apparently depleted their food supply and changed their foraging behaviour.

In 1995, a year with higher food abundance, parents were able to raise enlarged broods to fledging, but the nestlings of these broods weighed less than did nestlings of reduced broods. Food abundance in the territories with enlarged broods did not markedly deplete, but food items were on average smaller in these territories as compared with territories with control or reduced broods. Foraging behaviour of parents did not significantly differ among treatments that year.

4. Discussion

4.1. Food abundance and breeding success

Our results revealed that the brood-size manipulation had differential effects on the reproductive success and behaviour of Treecreepers in different years. These differences may be related to food abundance, which varied between years. In 1991, when food abundance was relatively low, Treecreepers could not raise the extra nestlings to the fledgling stage, but the body weights of the nestlings were approximately equal between each of the three treatments. In 1995, when food abundance was higher, Treecreepers were able to raise also the extra nestlings, but the average weight of the nestlings was lower in enlarged than in reduced broods. Also in 1992, when food was most scarce, Treecreepers with enlarged broods could not raise the additional nestlings to the fledging stage, and the mean nestling weight was also lowest in the enlarged broods. Thus, in the year with good food conditions, the offspring in the enlarged broods did generally better than in the years with low food abundance, but were still of lower body weight than in the reduced broods. There might be a trade-off between the number and quality of offspring, with the outcome varying from the inability to raise extra young to the production of lower-quality fledglings across years. However, generally our results support Lack's (1947) hypothesis of clutch-size regulation; Treecreepers apparently laid the maximal number of eggs they were able to raise successfully to fledging.

4.2. Food abundance and foraging behaviour

In 1991, when food abundance was low, Treecreepers raising enlarged broods seemed to deplete their food supply, as we observed fewer food items per trunk area than we observed in the control or reduced-brood territories. This food depletion in the largest trunks may have forced females of enlarged broods to forage also on thinner trunks, which they do not usually prefer (Suhonen & Kuitunen 1991b). In 1995, when food was more abundant, the number of arthropods did not significantly differ among the treatments, but the mean size of items was smaller in the territories with enlarged broods. Thus, in poor food conditions the brood-size manipulation apparently made Treecreepers to deplete their food supply and forced the females to switch to smaller foraging trees, whereas in better food conditions the brood-size manipulation did not markedly affect food abundance or foraging behaviour of the parents, but the largest food items seemed to have depleted from the territories of enlarged broods.

In 1991, females with the enlarged broods also foraged for shorter time periods per trunk than did females with reduced broods. This may be a result of optimal foraging considerations in a situation with low food abundance and greater food demand of the nestlings (Stephens & Krebs 1986). Reduced time available for foraging, may have forced the parents with enlarged broods to become less selective, that is, to include also smaller prey in their diets. On the other hand, reducing handling time by switching prey type (Houston 1985a, 1985b) or being less selective and increasing the frequency of feeding events can be optimal strategies in reducing the probability of starvation, despite an overall decrease in biomass delivered (Houston & McNamara 1985a, 1985b). In treecreepers, both strategies would lead to short patch residence times observed in the territories with enlarged broods. A laboratory experiment in Zebra Finches (*Taeniopygia guttata*) found a cost of reproduction in modification of reproductive interval under unrestricted access to food, which showed that factors other than food may also restrain reproduction (Deerenberg *et al.* 1996). The authors suggested that the available foraging time potentially limits the amount of food that can be collected and transported to the young, and thereby restrict brood size. Although the time constraint did not seem to apply for Zebra Finches, it may apply in field conditions where other ecological factors, such as predation risk (e.g., Lima 1987), also affect individual behaviour. In Treecreepers, the relatively short residence times in foraging patches by parents with enlarged broods suggest that the time available for foraging may be limited with large broods, at least if food abundance is low. In addition, females rearing reduced broods in 1992 spent clearly the longest time on each foraging bout, suggesting that foraging time is limited only with larger broods or in conditions of low food abundance.

The response of males to the brood-size manipulation was somewhat different than that of females. Males of both enlarged and reduced broods tended to spend a shorter time per trunk than did control males both in 1991 and 1995. For the males with enlarged broods, the greater food demand of nestlings may have contributed to the short foraging times and distances from the nest, as discussed earlier for females. Conversely, due to the lower food demands of nestlings of reduced broods, males may have allocated more time to other activities, such as territory or nest defence, and thus reduced their foraging times on each patch.

4.3. Parental care in different years

There were no differences in the patterns of male parental care among treatment groups in 1991, suggesting that males contributed equally in nestling feeding regardless of brood size. Females did not change their observed feeding rates either, but the resulting feeding rate per chick decreased as brood size increased. This suggests that females were not able or willing to increase their effort in order to meet the demands of the enlarged brood. This may have resulted from food scarcity and consequent changes in foraging behaviour of females. The summed contribution of each pair to a chick was thus lowest (albeit statistically non-significant) in the enlarged broods, and this is likely to have contributed to the inability of raising all the chicks from enlarged broods to fledging.

In 1992, males decreased their feeding rates as brood size increased, thus investing less in the chicks of enlarged broods. In fact, three males with enlarged broods did not feed their nestlings at all during our observation periods, whereas only one control male and none of the males with reduced broods did not care for young. Parental feeding frequency is supposed to reflect a trade-off between fledgling and parental survival (Nur 1984, 1987). However, optimal levels of parental effort of each sex may vary according to the value of the brood (Houston & Davies 1985, Winkler 1987), which may differ owing to the degree of relatedness to the brood (e.g., Houston & Davies 1985, Alatalo *et al.* 1988) or to the different costs of feeding nestlings due to sexual dimorphism (e.g., Hughes & Hughes 1986). Also, when food is scarce, males may invest relatively more in self-maintenance and less in the offspring than females (e.g., Jones 1987). In 1992, food abundance in the studied Treecreeper territories was low, and the optimal strategy for males may have been to invest less in the care of the enlarged brood, whose value may be less than that of control and reduced broods (indicated by the lower number and body mass of fledglings), and perhaps in that way be able to survive to the a new breeding attempt under more favourable conditions (second broods; Kuitunen 1987, 1989, Kuitunen *et al.* 1996). Renesting and raising a second brood during the same breeding season is costly (e.g., Antczak *et al.* 2009) and not so productive even in Treecreepers

(Kuitunen 1987). In conditions with very low food abundance, it may also be more costly for larger than for smaller males to feed nestlings (e.g., Hughes & Hughes 1986), although the size dimorphism in this species is small.

Females showed no significant differences in feeding rate between each of the three treatments in 1992, although they showed slightly higher feeding rates per chick in enlarged broods. This way the females may have compensated for the reduced amount of care by males, and consequently the chicks may have achieved roughly equal amounts of care in all treatments. Nevertheless, the lower breeding success of the enlarged broods in 1992 than in 1991 or 1995, suggests differences in the quality of parental care. Although we did not find differences in the amount of food brought by the females, the smaller average prey size in territories with enlarged broods may have affected the quality of the food loads and thereby reduced the condition of nestlings (see Aho *et al.* 1997, Jäntti *et al.* 2001). Apparently the care given by females was not sufficient to fully compensate for the reduced level of paternal care given to the enlarged broods.

Our results support the models of evolutionary stable or optimal investment strategies (Houston & Davies 1985, Winkler 1987) which predict that a member of a pair should compensate for the loss of parental care by its partner, and that the compensation is usually incomplete. We have earlier documented such incomplete compensation in Treecreepers in a male removal experiment (Aho *et al.* 1997, 2009). However, the optimal level of investment by each sex seems to differ among years, and may be related to the value of the current brood, food abundance, and consequent abilities to produce a second clutch during the same breeding season. Male contribution to caring for the young in the enlarged broods was lowest in 1992, when food abundance and frequency of second broods were low, and when the brood enlargement had most detrimental effects on the reproductive success of Treecreepers.

The reproductive success was lower in the enlarged than in the control or reduced broods also in 1995, when food was abundant and no changes in foraging behaviour were detected. However, although food was plentiful in numbers, depletion may have occurred in the quality of food, since the food items sampled in the territories after fledging of enlarged broods were on average smaller than in the other treatments. The amount and quality of parental care may have differed among the treatments also in this year. Also, the actual produced brood size may already be at the physiological limits of the parents' ability to care for young, and therefore the maximum working capacity of parents may limit brood size even if food is plentiful (e.g., Drent & Daan 1980, Deerenberg *et al.* 1996).

4.4. Conclusions

Our results support Lack's (1947) hypothesis that clutch size is set by the number of young the parents can adequately provision: when food was scarce, Treecreepers laid the maximum number of eggs they were able to raise successfully to fledging. However, trade-offs between current and future reproduction may also be important determinants of clutch size in this species. We also found some support for our prediction of food limitation; Treecreepers raising enlarged broods depleted their food supply, whereas in better food conditions some depletion occurred only in the size of potential food items. When food was scarce, parent birds changed their foraging behaviour in a predictable way, but with abundant food no changes in foraging behaviour was observed. In conditions with low food abundance, parent Treecreepers did not increase their feeding rate with respect to brood size, indicating that they were either already working at their maximal capacity with their normal-sized broods, or that they traded off the survival of their fledglings to that of their own. The latter seems to be a more plausible explanation, because there were changes in the relative contributions of each sex to the parental duties.

To sum up, in years with scarce food, the factors that limit clutch size seem to be food depletion and possibly also limited foraging time, whereas in better food conditions the quality of food, limited time and parental working capacity may play major roles. Our results support the earlier findings that factors limiting clutch size may vary in different environmental conditions (e.g., Korpimäki 1988), although in Treecreepers these seem to be more predictable than in the birds of prey, or passerines gleaning the hardwood foliage.

Acknowledgements. We thank R. Alatalo, N. B. Davies, E. Korpimäki, A. Laurila, and M. Orell for their comments on the manuscript, and H. Huhtanen for invaluable assistance in the laboratory. The study was supported by the Jenny and Antti Wihuri foundation, the University of Jyväskylä (to TA) and the Academy of Finland (to MK and JS). The staffs of the Konnevesi Research Station, the Natural Resources Research Institute at the University of Minnesota, Duluth, USA, and the School of Environmental Science at the Murdoch University, WA, Australia are especially acknowledged, the latter two for providing comfortable working facilities for MK in 1996, 2005, and 2006.

Pesyekoon määräytyminen ravinto- ja aikarajoitteisella puukiipijällä

Tutkimuksessa muutettiin puukiipijän (*Certhia familiaris*) poikuekokoa kokeellisesti kolmena vuonna siten, että samanaikaisilla poikueilla siirrettiin yksittäisiä poikasia pesästä toiseen joko lisäämällä poikueita yhdellä poikasella tai vähentämällä niitä yhdellä poikasella. Kontrollipesissä toteutettiin vain normaalit tutkimustoimenpiteet. Tutkimuksen tarkoituksena oli selvittää pesyekokoa rajoittavien ympäristötekijöiden merkitystä jälkeläisten kelpoisuuteen. Tällä lajilla on aiemmissa vertailevissa tutkimuksissa todettu, että keskeisiä selittäviä tekijöitä lajin pesyekoon taustalla ovat ravinnon saatavuus ja ravinnonhankintaan käytettävissä oleva aika. Käytännössä siirrettävä poikanen siirrettiin samanaikaiseen toiseen poikueeseen. Yhden poikasen siirtäminen katsottiin riittäväksi, koska aiempien tutkimusten perusteella tiedetään, että selkärangattomien määrät ovat niukkoja puiden rungoilla touko–kesäkuussa, jolloin puukiipijä tuottaa ensimmäistä poikuettaan.

Tutkimuksessa käytettiin erikoisvalmisteisia pesäpönttöjä. Parien pesintäaikataulu selvitettiin ja kaikki linnut sekä merkittiin että mitattiin. Emolintujen ravinnonhankinta- ja ruokintakäyttäytyminen määritettiin seuraamalla emolintuja ja videoimalla ruokintakerrat. Videoilta määritettiin myös ravintolastin koko. Lopuksi kerättiin pesinnän jälkeen ravintonäytteet puiden rungoilta imuroimalla jokaiselta reviiriltä systemaattisesti kuusi satunnaista kuusen runkoa. Selkärangattomat määritettiin heimotasolle.

Saadut tulokset olivat jonkin verran vaihtelevia eri vuosina, mutta lisätyt poikueet näyttivät menestyvän vain niinä vuosina, jolloin ravintoa oli riittävästi tarjolla. Pesintämenestystä arvioitiin poikasten painon, lentokykyisten poikasten ja toisten pesyeiden määrän avulla. Poikasten keskipaino erosi merkitsevästi sekä koeryhmien että vuosien välillä. Sekä kokeen että vuoden yhteisvaikutus oli myös merkitsevä. Kaikkina tutkimusvuosina todennäköisyys munia toinen poikue samana vuonna laski poikuekoon kasvaessa.

Naaraiden ruokintamäärät myös kasvoivat suuremmilla poikueilla, mutta koiraan ruokintakäyttäytymisessä ei havaittu vastaavaa käyttäytymismuutosta. Poikasille kannettavan ravintolastin suuruudessa ei havaittu eroja, mutta naaraan ravinnonhankinta-ajat pitenivät vähennetyillä poikueilla. Ravinnonhankinta käyttäytymisessä havaittiin, että suosituin ruokailupuu oli kuusi sekä koiraalla että naaraalla. Sekä koiras että naaras myös ruokailivat ohuemmilla rungoilla ja lyhyemmän aikaa per runko silloin, kun poikuekokoa oli kasvatettu. Ravinnontarjonta puiden rungoilla oli vähäisempää vuosina 1991 ja 1992 kuin vuonna 1995. Lisätyn poikueen huonoin pesintämenestys olikin niinä vuosina, jolloin ravintoa oli vähiten saatavilla. Näissä tilanteissa havaittiin myös muutoksia emojen ravinnonhankintakäyttäytymisessä.

Tulokset tukevat David Lack’ in hypoteesia pesyekoon säätelystä. Puukiipijät munivat maksimaalisen pesyekoon, jonka ne myös kykenevät saamaan lentokykyisiksi. Kuitenkin voimavarojen allokoinnin vaihtelu nykyisen ja tulevan lisääntymismahdollisuuden välillä voi olla tärkeä tekijä pesyekoon määrittäjänä. Saatavilla olevan ravinnon määrä ja rajallinen ruokailuaika näyttävät olevan merkittävimmät tekijät, jotka rajoittavat puukiipijän pesyekokoa, vaikka näiden tekijöiden merkittävyys vaihtelee jonkin verran vuosien välillä riippuen tarjolla olevan ravinnon määrästä.

References

Aho, T., Kuitunen, M., Hakkari, T., Suhonen, J. & Jäntti, A. 1997: Effects of male removal on reproductive success and food supply of the Eurasian treecreeper. — Behavioural Ecology and Sociobiology 41: 49–53.

Aho, T., Kuitunen, M., Suhonen, J. Jäntti, A. & Hakkari, T. 1998: Behavioural responses of Eurasian treecreepers, *Certhia familiaris*, to competition with ants. — Animal Behaviour 54: 1283–1290.

Aho, T., Kuitunen, M., Suhonen, J., Jäntti, A. & Hakkari, T. 1999: Fitness consequences of Eurasian Treecreepers, *Certhia familiaris*, on resource competition with ants. — Ecology 80: 998–1007.

Aho, T., Kuitunen, M., Hakkari, T., Suhonen, J. & Jäntti, A. 2009: Effects of male removal on reproductive success and food supply of the Eurasian Treecreeper. — Ornis Fennica 86: 1–10.

Alatalo, R. V., Gottlander, K. & Lundberg, A. 1988: Conflict or co-operation between parents in feeding nestlings in the pied flycatcher *Ficedula hypoleuca*. — Ornis Scandinavica 19: 31–34.

Antczak, M., Golawski, A., Kuzniak, S. & Tryjanowski, P. 2009: Costly replacement: how do different stages of nest failure affect clutch replacement in the red-backed shrikes *Lanius collurio*. — Ethology, Ecology and Evolution 21: 127–136.

Cucco, M. & Malacarne G. 1995: Increase of parental effort in experimentally enlarged broods of Pallid Swifts. — Canadian Journal of Zoology 73: 1387–1395.

Deerenberg, C., de Kogel, C.H. & Overkamp, G.F.J. 1996: Costs of reproduction in the Zebra Finch *Taeniopygia guttata*: manipulation of brood size in the laboratory. — Journal of Avian Biology 27: 321–326.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990: Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. — Journal of Animal Ecology 59: 269–285.

Drent, R.H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — Ardea 68: 225–252.

Gustafsson, L. &. Sutherland, W.J. 1988: The cost of reproduction in the collared flycatcher *Ficedula albicollis*. — Nature 335: 813–815.

Houston, A.I. 1985: Central place foraging: some aspects of prey choice for multiple prey loaders. — The American Naturalist 125: 811–826.

Houston, A.I. & Davies, N. B. 1985: The evolution of cooperation and life history in the dunnock, *Prunella modularis*. — In Behavioural Ecology: The Ecological Consequences of Adaptive Behaviour (eds. Sibley, R.M. & Smith, R.H.): 471–487. Blackwell Scientific Publ., Oxford.

Houston, A. I. & McNamara, J. M. 1985a: The choice of prey types that minimizes the probability of starvation. — Behavioural Ecology and Sociobiology 17: 135–141.

Houston, A. I. & McNamara, J. M. 1985b: A general theory of central place foraging for single prey loaders. — Theoretical Population Biology 28: 233–262.

Hughes, A. L. & Hughes, M. K. 1986: Paternal investment and sexual size dimorphism in North American passerines. — Oikos 46: 171–175.

Jäntti, A., Aho, T., Hakkarinen, H., Kuitunen, M. & Suhonen, J. 2001: Prey depletion by the foraging of Eurasian treecreeper, *Certhia familiaris*, on tree trunk arthropods. — Oecologia 128: 488–491.

Jäntti, A., Suorsa, P., Hakkarainen, H., Sorvari, J., Huhta, E., and Kuitunen, M. 2007a: Within territory abundance of red wood ants *Formica rufa* is associated with the body condition of the Eurasian treecreeper *Certhia familiaris*. — Journal of Avian Biology 38: 619–624.

Jäntti, A., Hakkarainen, H., Kuitunen, M. & Suhonen, J. 2007b: The importance of landscape structure for nest defence in the Eurasian Treecreeper *Certhia familiaris*. — Ornis Fennica 84: 145–154.

Jones, G. 1987: Parent-offspring resource allocation in swallows during nestling rearing: an experimental study. — Ardea 75: 145–168.

Korpimäki, E. 1988: Costs of reproduction and success of manipulated broods under varying food conditions in Tengmalm's owl. — Journal of Animal Ecology 57: 1027–1040.

Kuitunen, M. 1989: Food supply and reproduction in the common treecreeper (*Certhia familiaris*). — Annales Zoologici Fennici 26: 25–33.

Kuitunen, M. 1987: Seasonal and geographical variation in the clutch size of the Common Treecreeper *Certhia familiaris*. — Ornis Fennica 64: 125–136.

Kuitunen, M., Jäntti, A., Suhonen, J. & Aho, T. 1996: Food availability and male's role in parental care in the double-brooded common treecreeper. — Ibis 138: 638–643.

Lack, D. 1947: The significance of clutch size. I. Intraspecific variation. — Ibis 89: 302–352.

Lessells, C. M. 1991: The evolution of life histories. — In Behavioural Ecology, An Evolutionary Approach (eds. J. R. Krebs & N. B. Davies): 32–68. Blackwell Scientific Publications, Oxford.

Lima, S. L. 1987: Clutch size in birds: a predation perspective. — Ecology 68: 1062–1070.

Lindén, M. & Møller, A. P. 1989: Cost of reproduction and covariation of life history traits in birds. — Trends in Ecology and Evolution 4: 367–371.

Martin, T. E. 1987: Food as a limit on breeding birds: a life-history perspective. — Annual Review of Ecology and Systematics 18: 453–87.

Moreno, J., Cowie, R.J., Sanz, J.J. & Williams, R.S.R. 1995: Differential response by males and females to brood manipulations in the pied flycatcher: energy expenditure and nestling diet. — Journal of Animal Ecology 64: 721–732.

Nur, N. 1984: Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. — Oecologia 65: 125–137.

Nur, N. 1987: Parents, nestlings and feeding frequency: a model of optimal parental investment and implications for avian reproductive strategies. — In Foraging Behavior (eds. Kamil, A., Krebs, J. R. & Pulliam, H. R.): 49–77. Plenum Press, New York.

Orell, M., Rytkönen, S., Koivula, K., Ronkainen, M. & Rahiala, M. 1996: Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the Willow Tit *Parus montanus*. — Ibis 138: 630–637.

Pettifor, R.A., Perrins, C.M. & McCleery, R.H. 1988: Individual optimization of clutch size in Great Tits. — Nature 336: 160–162.

Pettifor, R.A., Perrins, C.M. & McCleery, R.H. 2001: The individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. — Journal of Animal Ecology 70: 62–79.

Roff, P.A. 1992: The Evolution of Life Histories. — Chapman & Hall, New York.

Smith, H.G., Källander, H., Fontell, K. & Ljungström, M. 1988. Feeding frequency and parental division of labour in the double-brooded great tit *Parus major*. — Behavioural Ecology and Sociobiology 22: 447–453.

Stearns, S.C. 1992: The Evolution of Life Histories. — Oxford University Press, Oxford.

Stephens, D.W. & Krebs, J.R. 1986: Foraging theory. — Princeton University Press, Princeton.

Suhonen, J. & Kuitunen, M. 1991a: Food choice and feeding by male and female common treecreeper (*Certhia familiaris*) during the nestling period. — Ornis Fennica 68: 17–25.

Suhonen, J. & Kuitunen, M. 1991b: Intersexual foraging niche differentiation within the breeding pair in the common treecreeper *Certhia familiaris*. — Ornis Scandinavica 22: 313–318.

Tolonen, P. & Korpimäki, E. 1994: Determinants of parental effort: a behavioural study in the Kestrel, *Falco tinnunculus*. — Behavioural Ecology and Sociobiology 35: 355–362.

Tolonen, P. & Korpimäki, E. 1996: Do kestrels adjust their parental effort to current or future temporally varying environment? — Ecoscience 3: 165–172.

Tuomi, J. 1990: On clutch size and parental survival. — Oikos 58: 387–389.

Williams, G.C. 1966: Natural selection, the costs of reproduction, and a refinement of Lack's principle. — The American Naturalist 100: 687–690.

Winkler, D.W. 1987: A general model for parental care. — American Naturalist 130: 526–543.

Wright, J. & Cuthill, I. 1990: Manipulation of sex differences in parental care: the effect of brood size. — Animal Behaviour 40: 462–471.