

Markku Kuitunen

Food, space and time
constraints on reproduction
in the common treecreeper
(*Certhia familiaris* L.)

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1989

Markku Kuitunen

Food, space and time constraints on
reproduction in the common treecreeper
(*Certhia familiaris* L.)

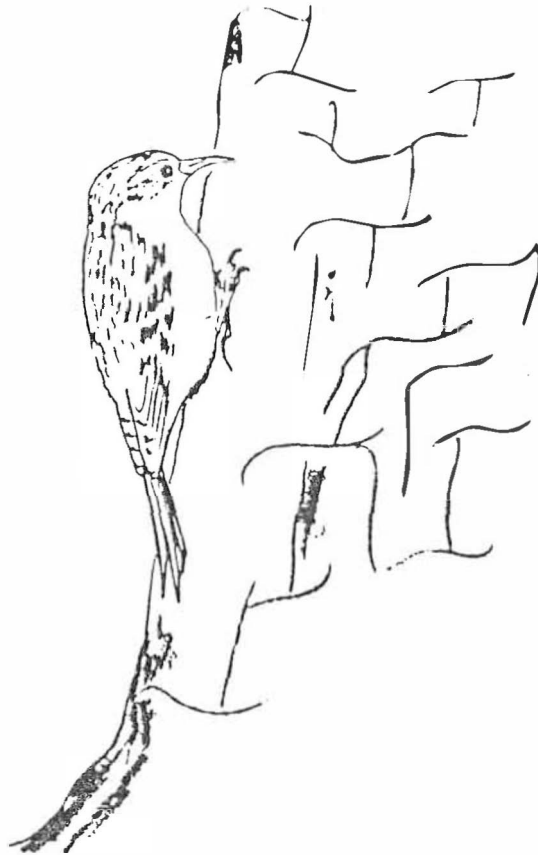
Academic Dissertation

*To be presented, with the permission of the Faculty of Mathematics and
Natural Sciences of the University of Jyväskylä, for public criticism
in Auditorium S 212, on June 3, 1989, at 12 o'clock noon.*



UNIVERSITY OF JYVÄSKYLÄ, JYVÄSKYLÄ 1989

To Juho-Pekka and Selja



URN:ISBN:971-951-39-9018-3
ISBN 971-951-39-9018-3 (PDF)
ISSN 0356-1062

Jyväskylän yliopisto, 2022

ISBN 951-680-107-2
ISSN 0356-1062

Copyright © 1989, by Markku
Kuitunen and University of Jyväskylä

Biol. Res. Rep. Univ. Jyväskylä 15: 3-22. 1989

FOOD, SPACE AND TIME CONSTRAINTS ON REPRODUCTION IN THE
COMMON TREECREEPER (*CERTHIA FAMILIARIS* L.)

Markku Kuitunen

Kuitunen, M. 1989: Food, space and time constraints on reproduction in the common treecreeper (*Certhia familiaris* L.). - Biol. Res. Rep. Univ. Jyväskylä 15: 3 - 22. ISSN 0356-1062.

The effects of food supply and day length on the reproductive success of the common treecreeper were studied comparatively and experimentally, with particular attention to seasonal changes in these factors. Data are presented and analysed from a long term study of treecreepers breeding in special nest boxes mostly in Southern Finland (1973 - 1988) and Central Finland (1983 - 1988).

The seasonal reproductive pattern was based on an initial increase in clutch size with time, eventually followed by a decrease. A similar seasonal trend was also found in the number of hatchlings and fledglings, but the recruits were observed to survive better the earlier they had hatched.

The potential food supply was observed to increase during the spring, as did the clutch size. The diet of the nestlings was as variable as the food supply, with both of them including 72 % spiders by biomass. The treecreepers seemed to favour relatively large food items, however.

The home range averaged 3.3 hectares in Central Finland. The minimum forest size accepted by a breeding treecreeper pair agreed well with this figure and increased markedly northwards. The treecreeper favoured large, uniform forest stands in southern Finland.

The feeding rate and time budget of the adult birds during the breeding season were also studied, and their response to the seasonal change in day length was assessed. They were observed to change their behaviour in parallel with day length, foraging and feeding nestlings more the longer the day was. They did not seem to be able to increase their hourly feeding rate when the brood size was higher, but

they could increase the feeding rate per day, which agrees well with the observations on seasonal variation in clutch size and brood size. Experiments were conducted by preventing feeding of the nestlings for three hours each day over a period of six days. These nestlings developed significantly more slowly than those in control nests. The time budget analysis proved that the adult birds used most of their time during the breeding season for foraging and feeding the nestlings.

The environmental circumstances under which treecreepers live are relatively predictable (food supply, day length, mature spruce forest), and this may allow the population to develop in a closer response to the environmental conditions and resources than most foliage-gleaning passerine birds studied. The results support the idea that day length is also of some importance in determining the feeding capacity of treecreepers. Nevertheless the major factor governing reproduction seems to be the food supply.

Key words: Reproductive effort, food supply, diet, time allocation, day length, forest fragmentation.

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

Contents

1. Introduction	6
2. Study areas, material and methods	8
3. Results and discussion	10
3.1. Reproductive effort in terms of clutch size, brood size, number of fledglings and number of recruits	10
3.2. Food supply	12
3.3. Diet related to the availability of food	13
3.4. Home range size	14
3.5. Day length and time allocation	15
3.6. Effects of day length variation: an experiment	16
4. Conclusions	17
Acknowledgements	18
Selostus	19
References	20

1. Introduction

One of the most exciting challenges of modern ecology is to try to understand the correspondence between life cycles and environments (Southwood 1977). In a heavily seasonal environment the predictability of external circumstances, which limits reproduction, plays the most crucial role. This is related to the degree to which the environmental resources or conditions can be utilized by an organism in order to maximize the number of recruits produced for the next generation. By definition, a resource represents quantities that can be reduced by the activity of the organism, whereas conditions are not consumed or used up by the organism or made unavailable or less available to others (Begon et al. 1986).

The possibility of a population being limited in the non-breeding season in a seasonal environment has often been emphasized (Fretwell 1972), although emphasis has also been placed on the importance of saturated breeding populations and inter-specific interactions (e.g. Cody 1985, but see Wiens 1983). Both of these viewpoints have been greatly criticized. The present investigation is focused on the reproductive period and how the essential resources or conditions influence reproductive success in passerine birds of the temperate zone. The most important resources usually studied are food, space and nest sites (e.g. Lack 1966, Newton 1980, Martin 1987) and the most common conditions the seasonal variation in temperature, rainfall (e.g. Biebach 1981, 1984, Mertens 1987, Coleman &

Whittall 1988) and day length (Lack 1954, 1966). These factors have seldom been quantified, nor have many attempts been made to study how they affect the number of recruits produced (see, however, Bryant 1975, Bryant 1988).

A search is made here for the constraints governing reproduction in the common treecreeper *Certhia familiaris* (referred to below simply as the treecreeper), concentrating chiefly on seasonal changes in potential food supply, available home range size and day length and their effects on reproductive success, relationships which are studied here both comparatively and experimentally.

The highly specialized treecreeper prefers mature forests as its habitat and tree trunks as its microhabitat. This may be assumed to be a more predictable environment than that of the most commonly studied small foliage gleaning passerines, e.g. the *Parus* and *Ficedula* species. If this is so, it may as a consequence be possible for a treecreeper population to evolve in closer response to the available resources and conditions than for those species living in a more unpredictable environment. In this respect, long term study of a species like the treecreeper could contribute new ideas to the discussion of the reproductive effort and clutch size evolution in avian species.

This thesis is based on the following articles, which will be referred to by their Roman numerals:

- I Kuitunen, M. 1987: Seasonal and geographical variation in the clutch size of the Common Treecreeper Certhia familiaris. - Ornis Fennica 64:125-136.
- II Kuitunen, M. 1989: Food supply and reproduction in the common treecreeper Certhia familiaris. - Ann. Zool. Fennici 26 (In press).
- III Kuitunen, M. & Törmälä T. 1983: The food of Treecreeper Certhia f. familiaris nestlings in southern Finland. - Ornis Fennica 60:42-44.
- IV Kuitunen, M. & Helle P. 1988: Relationship of the Common Treecreeper Certhia familiaris to edge effect and forest fragmentation. - Ornis Fennica 65:150-155.
- V Kuitunen, M. & Suhonen, J. 1989: Daylength and time allocation in relation to reproductive effort in the Common Treecreeper Certhia familiaris. - Ornis Fennica 66 (In press).
- VI Kuitunen, M. & Suhonen, J. 1989: Reproductive success and day length in the Common Treecreeper (Certhia familiaris): an experimental approach. - Manuscript (submitted).

2. Study areas, material and methods

The research was conducted in southern Finland (61°10'N, 24°40'E) during 1973-1987 and in central Finland (62°37'N, 26°20'E) during 1983-1988. Additional material was collected from Hungary (47°40'N, 18°20'E) during 1982-1986. All of the areas concerned are dominated by mature forests, those in Finland mainly of spruce (*Picea abies*), and those in Hungary mixed deciduous stands of oak (*Quercus petraea* and *Q. cerris*) and beech (*Fagus silvatica* and *Carpinus betulinus*). For detailed descriptions of the areas see I, and Kuitunen (1985 and 1989).

The data collected in southern Finland apply to a population of about 30-80 pairs breeding yearly in 156

special nest boxes (for details, see Kuitunen 1985). In central Finland and Hungary 50 and 220 nest boxes were set up, respectively, being spread out in order to maximize the numbers of pairs breeding in them.

The treecreeper forages almost exclusively on tree trunks, and its potential food supply was studied by taking invertebrate samples from the trunks of trees, mostly Norwegian spruce (*Picea abies*). The bark was first covered with a special plastic sheet equipped with six zip fasteners, which were opened in turn and the animals sucked from the trunk with a battery-operated vacuum cleaner (II).

Food samples of nestlings were collected when an adult bird visited a nest box. A plastic bag was attached to the other entrance of the box, and one of the investigators, rushing from a hide, flushed the bird into the bag, from which the food it had gathered could be collected (III).

The edge effect was studied by measuring the distance of every nest-box from the nearest clearing or other open habitat. The results were classified into six categories (for details, see IV), in which the breeding results were compared. The minimum area of forest supporting a breeding pair was checked by comparing the data collected in southern Finland with three published series of observations from groups of islands and four reports on the occurrence of the treecreeper in forest 'islands' (IV).

The feeding rate of adult birds was determined in Central Finland in 1985 and 1986 using a photocell device in which the beam from a light emitting diode (LED) was broken each

time a bird entered or left the nest box, these interruptions being logged by an automatic recorder (V).

The time budget analysis was performed simultaneously with the feeding rate analysis, the behaviour of the breeding adult treecreepers being observed throughout the period and categorized into 14 distinct activities at 10 seconds' intervals (V).

Field experiments were carried out in Central Finland in which the feeding of the nestlings in five experimental nests was prevented for three hours each day over a period of six days. The feeding rates of the adult birds was determined by the automatic recorders and all the nestlings were weighed daily and their wing lengths measured (VI).

3. Results and discussion

3.1. Reproductive effort in terms of clutch size, brood size, number of fledglings and number of recruits.

The treecreeper began laying its first clutch on 27 April on average (SD = 5.8 days, N = 236) in southern Finland and 26 April (SD = 5.1 days, N = 48) in Central Finland. The breeding period is long and a second clutch is usually produced. 37 % of the pairs in southern Finland laid a genuine second clutch after a successful first breeding attempt.

The average clutch size was 5.43 (SD = 0.71, N = 299) in southern Finland, varying between three and seven eggs. The

variation was almost exclusively related to the laying date (I). The clutch size increased from the beginning of the breeding season to 20 May, followed by a decrease to the end of the breeding period. This variation also included the "calendar effect" (see v. Haartman 1982 and I).

All the data from Europe (A: Central Finland (Kuitunen & Suhonen, unpubl.), B: II, C: British nest-card material, D: Finnish nest-card material, E: Lithuania (Aleknonis unpubl.), F: DDR (Schönfeld 1983) and G: South-western Sweden (Enemar pers. comm.) show a very similar single-peaked trend in clutch size with time. Geographically, the curve is lower and the peak is located earlier the more southerly or south-westerly the locality (I).

Although breeding success was primarily studied in terms of the number of offspring recruited, it was found that the number of hatchlings and fledglings per breeding attempt showed a positive correlation with clutch size. This seems to contradict the suggestion of Lack (1966, 1968) that the most common clutch size is the most productive one. This is probably due to seasonal differences in breeding success, and does not imply acceptance of the 'trade-off hypothesis' (for a discussion see Nur 1984, Murphy & Haukioja 1986, Martin 1987, Bouce & Perrins 1987, Gustafsson & Sutherland 1988, Pettifor et al. 1988 and Alatalo & Lundberg 1989). Investigations in which the clutch or brood size has been manipulated (e.g. Gustafsson & Sutherland 1988, Korpimäki & Lagerström 1988 and Pettifor et al. 1988; for a review, see Lessells 1986) the most frequent clutch size is usually also

observed to be the most productive. These studies also provide evidence that the energy required for the incubation does not seem to limit the clutch size, but the resources or other conditions in the environment during the nestling time do so (cf. Biebach 1981, 1984).

A total of 33 breeding attempts produced at least one local recruit in the F1 generation. It is interesting that the early breeding attempts produced more recruits than would be expected assuming that offspring dispersal is independent of laying date (I). This agrees well with earlier observations in *Parus* species (e.g. Ekman & Askenmo 1986 and McCleery & Perrins 1988, however, see Dhondt & Huble 1968). The low production of treecreeper fledglings in late breeding attempts supports this observation.

3.2. Food supply

The trunk samples consisted only of arthropods, and 55 taxa (families or orders) were represented (II). The contribution of most families to the total number or biomass was low. The most important contribution to the biomass and energy content (70.8 %) was made by spiders and harvestmen. Small spiders (1-2 mm) were the most abundant items (36 % by number, 9 % by biomass). Spiders were also the most frequent in the samples (86.0 %).

The most noteworthy variation in the arthropod assemblage on the tree trunks was found between the sampling dates (ANOVA, $F = 14.8$, $df_1 = 201$, $df_2 = 6$, $P < 0.001$, Fig. 2; II).

Many experiments have been conducted in which the amount of food available to the feeding adult birds has been increased, because in the most cases food represents the most important environmental resource (e.g. Källander 1974, Högstedt 1981, Arcese & Smith 1988). The clutch size has not usually increased significantly as compared with control nests, however (Davies & Lundberg 1985).

3.3. Diet related to the availability of food

The nestling food consisted almost entirely of arthropods. The most significant contribution to the biomass and energy content (77 %) was made by spiders and harvestmen. One load carried by an adult bird to the nestlings included on average 9.6 items and weighed 23.5 mg (dry biomass, III). Food load size did not correlate with feeding date or nestling age nor did it vary between brood sizes (V).

The similarity between the trunk samples (II) and the diet of treecreeper nestlings (III) was 92 % at the order level. The adult treecreepers seemed to select larger food items than the average for the food supply, which agrees well with the earlier observations (e.g. Stephens & Krebs 1986).

3.4. Home range size

The treecreeper prefers old forests as its breeding habitat in all the areas studied. In southern Finland it preferred

large forest stands of > 50 ha (Mann-Whitney U-test, $z = 2.0$, $P < 0.025$, IV), but the distance to the nearest forest edge did not play any role. No differences in laying date, clutch size or the size of breeding adults were found in relation to the proximity of the forest edge (IV).

The minimum area of forest supporting a breeding pair of treecreepers seems to increase from about 1 ha in Britain to about 20 ha in northern Finland. In southern Finland it is about 2 hectares, as judged from several sets of Finnish data. The home range of the treecreeper in Central Finland averaged 3.3 ha ($SD = 0.6$, $N = 7$, II), which also agreed well with the estimates made from the food supply and forest structure used by treecreepers (II).

The geographical trend found in the minimum area requirement for the treecreeper probably also applies to forest tits. If so, this supports the hypothesis put forward by Järvinen et al. (1977) that widespread forest fragmentation and not only the reduction in the area of old forest (Helle & Järvinen 1986) has been responsible for the crash in the population of forest tits in Finland during recent decades.

3.5. Day length and time allocation

Both the peak-like seasonal change and the "calendar effect" in the clutch size (I) give us reason to study the importance of day length for reproduction. treecreeper parents were observed to change their behaviour in relation

to the seasonal change in the time between sunset and sunrise during the breeding season in order to take advantage of the increasing foraging opportunities provided by the prolonged day length. The adult birds could not increase their hourly feeding rate, but they could increase the number of visits per day and in consequence feed a larger brood and produce more offspring when the day was longer (V). There may be some advantage in a longer day for the adult birds and their nestlings, in that the food of the treecreepers is distributed patchily, forcing them to consume energy and time in 'unnecessary' flying between the tree trunks and the nest.

Day length varies in the same way year after year, and the difference between the longest and shortest day during the nestling period of the treecreeper is two hours and two minutes in southern Finland:

		15.4.	15.5	21.6.
		<hr/>	<hr/>	<hr/>
Central Finland	61o	14 h 32 min	17 h 33 min	19 h 45 min
Southern Finland	62o	14 h 33 min	17 h 17 min	19 h 19 min
	%	73.6	88.9	100.0
		73.7	87.5	97.8

3.6. Effects of day length variation: an experiment

Since the comparative results suggested that day length could be an important factor (V), a shortened day was

simulated experimentally by preventing feeding of the nestlings for a certain time each day. The nestlings concerned were then seen to grow significantly more slowly than those in control nests (VI), which confirms the importance of day length as implying an increase in foraging time. The feeding rate of the parents varied greatly during the experiments, however, and did not give the impression that the birds were particularly busy, and they were probably able to make up at least part of the lost feeding time (VI). The brood sizes in the experimental nests were not always maximal for the environment compared with the clutch size variations seen in natural populations, however. Although no trend was found for the load size to increase with nestling age, brood size or date (V), the parents probably did change their behaviour and fed the nestlings either with smaller loads or with loads of lower energy content.

4. Conclusions

The results point out a probability that treecreepers may begin laying early because the snow and ice melt from the tree trunks early in the spring. The species thus has a long breeding period, which enables it to produce two broods during the same year. The clutch size increases during the early part of the breeding period because the potential food supply increases at that time in parallel with the growth of the nestlings in the nests. The calendar effect may indicate

a timing system for this. The environment of the treecreeper may be sufficiently predictable for the length of the day to be of some importance for the feeding of more nestlings later in the breeding season, although success may be hindered by bad weather conditions (e.g. Hildén et al 1982). The decrease in the clutch size and reproductive success later in the season is evidently independent of food supply, which is still increasing at the time when the reproductive effort is already decreasing. The length of the day does begin to decrease at the same time as the number of hatchlings, however. Since the treecreeper has a short life-span, the results do not support the hypothesis of a trade-off between the two components of fitness (see Nur 1984, Murphy & Haukioja 1986, Martin 1987, Gustafsson & Sutherland 1988, Pettifor et al. 1988). Treecreepers seem to produce as many recruits as they can feed during a breeding season. The rapid decrease in the reproductive effort during the late part of the breeding period, however, is probably a trade-off between reproduction and moulting (see e.g. Orell & Ojanen 1980, Pietiäinen et al. 1984), in which preparation for winter is emphasized. This is also supported by the results which suggest that the recruits obtained during the beginning part of the breeding period are more valuable to the species, just as they are also favoured by the parents themselves. In general the results support the ideas of Lack (1954, 1966) on the importance of food supply and geographical change in the day length as factors enabling the birds to produce as many offspring as they can feed at the given breeding site. They also provide evidence for

Ashmole's hypothesis (1963) regarding variation in the reproductive effort in relation to the geographical and seasonal rationality of the outcome (see also Ricklefs 1980).

Acknowledgements. This work was mostly carried out at the Department of Biology, University of Jyväskylä. I am grateful to the staff of the department, and especially to Mikko Raatikainen for providing me with working facilities and much practical advice. It has taken 15 years to complete the work and it owes much to the help of other people. I thank them all, but I can mention only the most important by name. Pertti Saurola was the first who encouraged me to begin this project. My wife Pirjo Kuitunen, my parents Irene and Pauli Kuitunen, my brother Tuomo Kuitunen, my sister Leena Moilanen and the Friend Timo Saloranta have helped me to keep my courage up to continue this work. The staff and stimulating atmosphere at the Konnevesi Research Station have been very important, for which I thank Jussi Viitala. My friends Pekka Pouttu, Aarto Tuominen, Markku Mäkinen, Jukka Suhonen, Markku Saarekas, Szekrényi György and Zágón András have been unreplaceable in the fieldwork. Rauno V. Alatalo and Pekka Helle have helped in many ways, including fruitful discussions, constructive criticism and valuable comments on scientific questions. I would also like to thank all those persons who have given valuable comments in discussions or on the original manuscripts, including Erkki Haukioja, Antero Järvinen, Olli Järvinen, Ilpo Kojola, Pirjo Kuitunen, Lövei Gábor, Juan Moreno, Mikko Raatikainen, Esko Rossi, Jukka Suhonen, Juha Tiainen, Timo Törmälä and Török János. Comments made by Erkki Korpimäki and Markku Orell have been profitable to this synthesis. The work has been supported financially by the Emil Aaltonen Foundation, the Finnish Academy, the Ministry of Agriculture and Forestry, the Ministry of Labour, the Institute of International Culture in Hungary, the British Council, the Ministry of Education, the Committee for Scientific, Technical and Educational Co-operation between the Soviet Union and Finland, the Nordic Council for Ecology and the Jyväskylä University Society.

Selostus

Ravinto, tila ja aika puukiipijän (*Certhia familiaris*) lisääntymistä rajoittavina tekijöinä.

Puukiipijän lisääntymistä rajoittavia tekijöitä tutkittiin vuodesta 1973 lähtien Hauholla Etelä-Suomessa ja vuodesta 1983 sekä Konnevedellä Keski-Suomessa että Pilis-vuoristossa Unkarissa. Merkittävin tekijä, jonka havaittiin aiheuttavan vaihtelua puukiipijän lisääntymispanokseen, on muninta-ajan vaikutus pesyekokoon. Pesyekoko kasvoi aluksi pesimäkauden alussa saavuttaen huippunsa hiukan toukokuun puolivälin jälkeen, josta lähtien se väheni lisääntymiskauden loppua kohden. Havaitun vaihtelun syitä etsittiin puukiipijän pesimäympäristön asettamista ehdoista muistaen, että talvi voi puukiipijäpopulaation kannalta olla ennustamattoman vaikea.

Ravinnon tarjontaa ja sen käyttöä sekä vaikutusta liikkuma-alan kokoon ja lisääntymiseen tarkasteltiin. Tarjolla oleva ravinto lisääntyi pesimäkauden kuluessa samoin kuin pesyekoko ja poikastuotto. Samanaikaisesti poikasten energiatarve väheni ilman keskilämpötilan noustessa. Puukiipijän tarjolla oleva ravinto koostui biomassaltaan noin 70 %:sesti hämähäkeistä. Puukiipijä tarjosi poikasilleen hämähäkkejä samassa suhteessa, mutta valikoi selvästi suurimpia yksilöitä.

Ravinnon lisäksi tutkittiin, mikä vaikutus puukiipijän pesintätulokseen on päivän pituuden vaihtelulla pesimäkauden aikana. Tähän antoi aiheutta pesyekoossa havaittu niin sanottu kalenteriefekti, jonka mukaan puukiipijät munivat keskimäärin samalla päivämäärällä samankokoisia pesyeitä vuodesta riippumatta.

Päivänpituuden merkitystä selvitetttiin aineistolla emojen ruokinta-aktiivisuudesta eri-ikäisten, erikokoisten ja eriaikaisten poikueiden suhteen. Isommilla poikueilla emot eivät nostaneet ruokinta-aktiivisuuttaan tuntia kohden, mutta lisäsivät sitä vuorokautta kohden. Tämä havainto antoi aiheen olettaa, että päivän pituuden kasvulla on merkitystä puukiipijän poikastuoton vuodenaikaisessa vaihtelussa. Samaa asiaa selvitetttiin myös kokeellisesti, jolloin saatiin tulokseksi, että puukiipijän pesäpoikaset kehittyivät hitaammin verrattuina kontrollipesiin, jos emojen ruokintamahdollisuuksia rajoitettiin. Ruokinta-aktiivisuudessa ei kuitenkaan havaittu eroa kontrollipesiin. Emojen poikasille tuoman ravintolastin koko ei näyttänyt riippuvan poikasten iästä, poikuekoosta tai vuodenaajasta. Pesimäkauden kuluessa tapahtunut ympäristön lämpötilan nousu kuitenkin vähensi ilmeisesti poikasten energian tarvetta ja helpotti emojen ruokintapaineita. Näin ollen ravinnon tarjonnan kasvu, päivänpituuden kasvu ja lämpötilan nousu pesimäkauden kuluessa vaikuttivat samansuuntaisesti nostaen puukiipijäemojen mahdollisuuksia tuottaa jälkeläisiä. Pesimäkauden lopussa lisääntymispanos näytti vähenevän, vaikka ulkoiset olosuhteet olisivat säilyneet kohtalaisina. Tämän tulkitttiin johtuvan valmistautumisesta talveen.

Puukiipijä elää Suomessa vanhoissa kuusimetsissä ja hakee ravintonsa puiden rungoilta. Näissä mahdollisesti verraten ennustettavissa olosuhteissa pesivä

puukiipijäpopulaatio on saattanut geneettiseltä rakenteeltaan kehittyä suuntaan, jossa yksilöt voivat reagoida vähäisempiinkin lisäyksiin ympäristön tarjoamissa mahdollisuuksissa tuottaa enemmän jälkeläisiä. Näin puukiipijäpopulaatio on saattanut kehittyä käyttämään hyödykseen myös päivänpituuden vaihtelussa tapahtuvia muutoksia. Ravinnon tarjonta ja sen lisääntyminen pesimäakuden kuluessa on kuitenkin epäilemättä tärkein lisääntymistä säätelevä tekijä.

References

- Alatalo, R.V. & Lundberg, A. 1989: Clutch size of the pied flycatcher *Ficedula hypoleuca* - an experiment. - *Ornis Fennica* 66 (In press).
- Arcese, P. & Smith, J.N.M. Effects of population density and supplemental food on reproduction in song sparrows. - *J. Anim. Ecol.* 57:119-136.
- Ashmole, N.P. 1963: The regulation of numbers of tropical oceanic birds. - *Ibis* 103:458-473.
- Begon, M., Harper, J.L. & Townsend, C.R. 1986: Ecology, individuals, populations and communities. - 876 pp. Oxford.
- Biebach, H. 1981: Energetic costs of incubation on different clutch sizes in starlings (*Sturnus vulgaris*). - *Ardea* 69:141-142.
- Biebach, H. 1984: Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sturnus vulgaris*). - *Physiol. Zool.* 57:26-31.
- Boyce, M.S. & Perrins, C.M. 1987: Optimizing great tit clutch size in a fluctuating environment. - *Ecology* 68:142-153.
- Bryant, D.M. 1975: Breeding biology of house martins in relation to aerial insect abundance. - *Ibis* 117:180-216.
- Bryant, D.M. 1988: Lifetime reproductive success of house martins. - In: Clutton-Brock, T.H. (ed.): Reproductive success - studies of individual variation in contrasting breeding systems. pp. 173-188. Chicago and London.
- Cody, M. 1985: An introduction to habitat selection in birds. - In: Cody, M. (ed.): Habitat selection in birds. pp. 3-56. New York.
- Coleman, R.M. & Whittall, R.D. 1988: Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata* var. *domestica*). - *Behav. Ecol. Sociobiol.* 23:367-372.
- Davies, N.B. & Lundberg, A. 1985: The influence of food on time budgets and timing of breeding of the dunnoek *Prunella modularis*. - *Ibis* 127:100-110.
- Dhondt, A.A. & Huble, J. 1968: Fledgling date and sex in relation to dispersal in young Great Tits. - *Bird Study* 15:127-134.
- Ekman, J. & Askenmo, C. 1986: Reproductive cost, age-specific survival and a comparison of the reproductive strategy in two European tits (genus *Parus*). - *Evolution* 40:159-168.
- Fretwell, S.D. 1972: Populations in a seasonal environment.

- 217pp. Princeton.
- Gustafsson, L. & Sutherland, W.J. 1988: The costs of reproduction in the collared flycatcher *Ficedula albicollis*. - *Nature* 335:813-815.
- v.Haartman, L. 1982: Two models of clutch size determination in passerine birds. - *J. Yamashina Inst. Ornithol.* 14:214-219.
- Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. - *Oikos* 46:107-115.
- Hildén, O., Järvinen, A., Lehtonen, L. & Soikkeli, M. 1982: Breeding success of Finnish birds in the bad summer of 1981. - *Ornis Fennica* 59:20-31.
- Högestedt, G. 1981: Effect of additional food on reproductive success in the magpie *Pica pica*. - *J. Anim. Ecol.* 50:219-229.
- Järvinen, O., Kuusela, K. & Väisänen, R.A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945-1975 (in Finnish with English summary). - *Silva Fennica* 11:284-294.
- Källander, H. 1974: Advancement of laying of great tits by the provision of food. - *Ibis* 118:547-574.
- Korpimäki, E. & Lagerström, M. 1988: Survival and natal dispersal of fledglings of tengmalm's owl in relation to fluctuating food conditions and hatching date. - *J. Anim. Ecol.* 57:433-441.
- Kuitunen, M. 1985: Is the common treecreeper (*Certhia familiaris* L.) more widespread in Hungary than has been previously believed. - *Aquila* 92:255-262.
- Kuitunen, M. 1989: What I have learned about the treecreepers in Hungary? - *Proc. II ornithol. Congr. of Hungary* (In press).
- Lack, D. 1954: *The Natural regulation of Animal Numbers*. - 323pp. Oxford.
- Lack, D. 1966: *Population studies of birds*. - 366pp. Oxford.
- Lessells, C.M. 1986: Brood size in Canada Geese: A manipulation experiment. - *J. Anim. Ecol.* 55:669-689.
- McCleery, R.H. & Perrins C.M. 1988: Lifetime reproductive success in the Great Tit *Parus major*. - In: Clutton-Brock, T.H. (ed.): *Reproductive success - studies of individual variation in contrasting breeding systems*. pp.136-153. London.
- Martin, T.E. 1987: Food as a limit on breeding birds: A life-history perspective. - *Ann. Ecol. Syst.* 18:453-487.
- Mertens, J.A.L. 1987: The influence on temperature on the energy reserves of female great tits during the breeding season. - *Ardea* 75:73-80.
- Murphy, E.C. & Haukioja, E. 1986: Clutch size in nidicolous birds. - *Current Ornithol.* 4:141-180.
- Nur, N. 1984: The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. - *J. Anim. Ecol.* 53:497-517.
- Orell, M. & Ojanen, M. 1980: Overlap between breeding and moulting in the great tit *Parus major* and willow tit *P. montanus* in northern Finland. - *Ornis Scand.* 11:43-49.
- Pettifor, R.A., Perrins, C.M. & McCleery, R.H. 1988: Individual optimization of clutch size in great tits. -

- Nature 336:160-162.
- Pietiäinen, H., Saurola, P. & Kolunen, H. 1984: The reproductive constraints on moult in the Ural Owl *Strix uralensis*. - *Ann. Zool. Fennici* 21:277-281.
- Ricklefs, R.E. 1980: Geographical variation in clutch-size among passerine birds: Ashmole's hypothesis. - *Auk* 97:38-49.
- Southwood, T.R.E. 1977: Habitat, the templet for ecological strategies. - *J. Anim. Ecol.* 46:337-365.
- Stephens, D.W. & Krebs, J.R. 1986: *Foraging theory*. - 248pp. Princeton.
- Wiens, J.A. 1983: Avian community ecology: an iconoclastic view. - In: Brush, A.H. & Clark Jr. G.A. (eds): *Perspectives in ornithology*. pp. 355-403. Cambridge.

ORIGINAL PAPERS

I

SEASONAL AND GEOGRAPHICAL VARIATION IN THE CLUTCH
SIZE OF THE COMMON TREECREEPER *CERTHIA FAMILIARIS*.

Ornis Fennica 64:125-136

by

Markku Kuitunen

<https://www.researchgate.net/publication/35460956>

[https://lintulehti.birdlife.fi:8443/pdf/artikkelit/651/
tiedosto/of_64_125-136_artikkelit_651.pdf](https://lintulehti.birdlife.fi:8443/pdf/artikkelit/651/tiedosto/of_64_125-136_artikkelit_651.pdf)

II

FOOD SUPPLY AND REPRODUCTION IN THE COMMON TREECREEPER
CERTHIA FAMILIARIS

Annales Zoologici Fennici 26 (In press)

by

Markku Kuitunen

<https://www.researchgate.net/publication/279938335>

III

THE FOOD OF TREECREEPER *CERTHIA F. FAMILIARIS* NESTLINGS
IN SOUTHERN FINLAND.

Ornis Fennica 60:42-44.

by

Markku Kuitunen & Timo Törmälä

<https://www.researchgate.net/publication/292666199>

[https://lintulehti.birdlife.fi:8443/pdf/artikkelit/772/tiedosto/
of_60_42-44_artikkelit_772.pdf](https://lintulehti.birdlife.fi:8443/pdf/artikkelit/772/tiedosto/of_60_42-44_artikkelit_772.pdf)

IV

RELATIONSHIP OF THE COMMON TREECREEPER *CERTHIA FAMILIARIS*
TO EDGE EFFECT AND FOREST FRAGMENTATION.

Ornis Fennica 65:150-155

by

Markku Kuitunen & Pekka Helle

<https://www.researchgate.net/publication/284969122>

v

DAYLENGTH AND TIME ALLOCATION IN RELATION TO REPRODUCTIVE
EFFORT IN THE COMMON TREECREEPER *CERTHIA FAMILIARIS*.

Ornis Fennica 66 (In press)

by

Markku Kuitunen & Jukka Suhonen

[https://lintulehti.birdlife.fi:8443/pdf/artikkelit/618/
tiedosto/of_66_53-61_artikkelit_618.pdf](https://lintulehti.birdlife.fi:8443/pdf/artikkelit/618/tiedosto/of_66_53-61_artikkelit_618.pdf)

VI

REPRODUCTIVE SUCCESS AND DAY LENGTH IN THE COMMON
TREECREEPER *CERTHIA FAMILIARIS*: AN EXPERIMENTAL
APPROACH

Manuscript (Submitted)

by

Markku Kuitunen & Jukka Suhonen

<https://doi.org/10.1093/auk/108.1.180>