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Teija Aho

Determinants of Breeding  
Performance of  
the Eurasian Treecreeper



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1997

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston Musica-salissa (M103)  
toukokuun 10. päivänä 1997 kello 12.

Academic dissertation to be publicly discussed, by permission of  
the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä,  
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Publishing Unit, University Library of Jyväskylä

URN:ISBN:978-951-39-9050-3  
ISBN 978-951-39-9050-3 (PDF)  
ISSN 0356-1062

Jyväskylän yliopisto, 2022

ISBN 951-34-0980-5  
ISSN 0356-1062

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Jyväskylä University Printing House,  
Jyväskylä and ER-Paino, Lievestuore 1997

*for Aksu*

## ABSTRACT

Aho, Teija

Determinants of breeding performance of the Eurasian treecreeper

Jyväskylä: University of Jyväskylä, 1997, 22 p.

(Biological Research Reports from the University of Jyväskylä, ISSN 0356-1062; 58)

ISBN 951-34-0980-5

Yhteenveto: Puukiipijän lisääntymismenestykseen vaikuttavat tekijät

Diss.

The aim of this thesis was to study the determinants of clutch size and reproductive success of the Eurasian treecreepers (*Certhia familiaris*). The emphasis is on individual foraging behaviour and parental care, and how they relate to reproductive success and food abundance. Clutch size seems to be limited by available food. When food was scarce, parents forced to raise larger brood than their original clutch size changed their foraging behaviour and depleted the food supply in their territory. Parental care was affected by the varying environmental conditions during the first and second broods. Male care was found to be most important in conditions with low food abundance. Females, whose mates were removed during the first broods, compensated for the mate loss by increasing their provisioning rate, but the compensation was incomplete, since the reproductive success of the widowed females was lower than of paired birds. Widowed females also changed their foraging behaviour to be more male-like, which indicates, that the niche separation between the sexes in this species is a result of behavioural plasticity. Experimental manipulation of the number of wood ants on tree trunks in treecreeper territories revealed, that ants are able to deplete the food resources of the treecreepers. Treecreepers also avoided trunks with ants, and foraged for a shorter time on trunks with ants present. Reproductive success of the treecreeper pairs that bred in territories with ants was lower than of pairs breeding in territories without ants; birds in ant-territories produced less fledglings that were also of lower body weight than pairs in territories without ants. Studies of this thesis show, that food abundance is an important determinant of individual foraging behaviour and reproductive success. In addition, the profound effects of ants on treecreepers point out, that competition between organisms in different phyla can be effective in determining individual behaviour and life-history traits.

Key words: Eurasian treecreeper; competition; food abundance; foraging behaviour; parental care; reproductive success; *Formica rufa* -group.

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## List of original publications

This thesis is based on the following articles, which will be referred to by their Roman numerals. I have personally written, analysed the data and gathered a considerable proportion of the data of papers I and III-VI, and been involved in gathering the data for and writing the paper II.

- I Aho, T., Jäntti, A., Kuitunen, M. & Suhonen, J. 1997: Determination of clutch size in treecreepers under food constraint. Manuscript.
- II Kuitunen, M., Jäntti, A., Suhonen, J. & Aho, T. 1996: Food availability and male's role in parental care in the double-brooded Common Treecreeper, *Certhia familiaris*. - Ibis 138:638-643.
- III Aho, T., Kuitunen, M., Suhonen, J., Hakkari, T. & Jäntti, A. 1997: Effects of male removal on reproductive success and food supply of the Eurasian treecreeper. - Manuscript.
- IV Aho, T., Kuitunen, M., Suhonen, J., Hakkari, T. & Jäntti, A. 1997: Effects of male removal on female foraging behavior in the Eurasian treecreeper. - Behavioral Ecology and Sociobiology (in press).
- V Aho, T., Kuitunen, M., Suhonen, J., Jäntti, A. & Hakkari, T. 1997: Behavioural responses of Eurasian Treecreepers, *Certhia familiaris*, to competition with ants. - Animal Behaviour (in press).
- VI Aho, T., Kuitunen, M., Suhonen, J., Jäntti, A. & Hakkari, T. 1997: Interphylum competition with ants lowers reproductive success of Eurasian treecreepers. - Manuscript.

## 1 INTRODUCTION

Among the most important determinants of an animal's fitness is the amount and quality of food available during reproduction (Martin 1987). Especially in altricial birds, increased food supply has been found to improve both current and future reproductive success. In terms of current success, good food conditions can advance laying date, increase clutch and egg sizes, and improve hatching, growth and survival rates of the nestlings. In terms of future success, scarce food may reduce adult survival and reduce their subsequent abilities to produce young (reviewed by Reznick 1985, Partridge & Harvey 1988, Nur 1990, Stearns 1992).

Lack (1947) argued that clutch size in altricial birds is limited by the number of nestlings that parents can adequately feed. Increased parental effort expended to meet the food requirements of nestlings may also affect future reproductive output of parents (Williams 1966, Charnov & Krebs 1974, Martin 1987). This cost of reproduction has been used to explain the discrepancy between Lack's theory and the results of brood-enlargement experiments, which have shown that parents can frequently rear more young than the number of eggs they lay (Linden & Møller 1989, Dijkstra et al. 1990, Godfray et al. 1991, Lessells 1991, Roff 1992, Stearns 1992). Many hypotheses have been advanced since the original propositions of Lack, and they generally assume, that foraging requirements for nestlings are an important limit on present and future reproduction (e.g. Cody 1966, Williams 1966, Högstedt 1980, Ricklefs 1980, Slagsvold 1982, 1984, Martin 1987). However, the mechanisms affecting the reproductive effort and mediating subsequent costs of reproduction are still poorly understood.

In altricial birds, significant proportion of the parental effort during each nesting attempt consists of parental care. Feeding young has especially heavy energetic costs (Drent & Daan 1980), and parents' ability to find and collect food commonly constrains the number of young they can rear (Clutton-Brock 1991). Obviously, the amount of available food plays an important role in determining the costs and benefits of foraging and

consequent abilities to rear the young. In fact, the amount of energy transferred by parents to their offspring commonly declines as the availability of resources declines (Clutton-Brock 1991). The costs and benefits of parental care to each sex may also differ, often leading to conflicts of interest between care-givers (Clutton-Brock 1991). In many circumstances, the benefits of investing to the offspring fitness will decline in relation to expenditure by the other parent (Chase 1980), and consequently, the predicted response of a parent to reductions in the care of its partner is to increase its own effort (Houston & Davies 1985). At its extreme, a parent is likely to desert its mate when the potential payoffs of desertion are high, when reductions in care have relatively little effect on the fitness of its brood, or when its partner is not likely to desert in response (Lazarus 1989). Food abundance is likely to affect the value of the care, and consequently alter the patterns of parental care. For example, the frequency of deserting the brood by one of the parents has been found to increase when food is plentiful (e.g. Beissinger & Snyder 1987).

Since food abundance has strong influence on fitness traits, we can assume that selection favours individuals which forage in a way that maximizes benefits and minimizes costs. It is assumed, that behavioural actions which affects the acquisition of food, such as patch choice for example, also ultimately affect fitness. This is the basic assumption of optimal foraging theory (e.g. Stephens & Krebs 1986), which has been extensively tested both in laboratory and field conditions (for reviews see e.g. Stephens & Krebs 1986, Krebs & Kacelnik 1991). The need to test the linkage between foraging patterns and fitness has been identified as one of the major requirements for investigating optimal foraging ideas (e.g. Stearns & Schmid-Hempel 1987, Ward 1992). Nevertheless, few field studies have shown connections between foraging behaviour, its short-term costs and benefits in terms of food intake, and its long-term fitness consequences (e.g. Blanckenhorn 1991, Frey-Roos et al. 1995).

One important ecological factor that may affect individual foraging behaviour and reproductive success is competition for food. Competition is likely to arise in situations where food occurs in discrete patches in the habitat, and several individuals utilizes the same resources (e.g. Milinski & Parker 1991). Traditionally, competition has been presumed to be most intense between individuals of the same species, or alternatively, between closely related species, which frequently share similar ecological constraints. However, if food, space, or other resources are sufficiently limiting to result in competition among closely related species, then these organisms also should compete with distantly related organisms which use the same resources (e.g. Brown et al. 1979). Few studies have found evidence for competition between organisms even from different phyla (reviewed by e.g. Hochberg & Lawton 1990). Some studies have reported on the negative effects of interphylum competitive interactions on the abundance of competing species and on the foraging behaviour of the individuals (e.g. Brown et al. 1979, Laverty & Plowright 1985, Haemig 1996). Nevertheless, frequently the effects of competitive interactions on the

reproductive success are not studied, and the link between behaviour and fitness is not established.

In this thesis I attempt to demonstrate a link between food abundance, foraging behaviour, parental care and reproductive success of individual birds. I focus on the evolution of clutch size, foraging behaviour and parental care, and the relationship between these behavioural traits and breeding success of Eurasian treecreepers (*Certhia familiaris*) with respect to food abundance. In order to find out the factors that limit clutch size in treecreepers, I examine the effects of brood size manipulation on the foraging behaviour, parental care, and food supply together with reproductive success. I also study the importance of male parental care in conditions with varying food abundance, and by experimental removal of male birds in conditions with scarce food. Furthermore, I investigate the evolution of sex-specific foraging behaviour of the treecreepers, and the effects of interphylum competition with wood ants (*Formica rufa* -group) on the food supply, foraging behaviour and reproductive success of the treecreepers.

## 2 MATERIAL AND METHODS

### 2.1 The species

The study species, the Eurasian treecreeper is a hole-nesting, monogamous, double-brooded and insectivorous (Suhonen & Kuitunen 1991a) passerine that breeds throughout the northern coniferous zone. It is specialized to search for its food on tree trunk and prefers the largest trunks in the forest (Suhonen & Kuitunen 1991b). Part of the treecreeper population overwinters in our study area as a member of mixed-species flocks of tits, and the rest of the population migrates. Treecreepers start to breed very early in the spring, usually in late April (Kuitunen 1987). Approximately one third of the breeding females rear a second brood with the same male, and usually in the same territory as the first brood (Kuitunen 1987). The Eurasian treecreeper is the only bird species belonging to the bark foraging guild in our study area (with the exception of woodpeckers *Dendrocopos major* and *Picoides tridactylus* which have very different diets and foraging patterns). There is, therefore, no avian interspecific competition affecting treecreeper foraging behavior at this site.

### 2.2 The study area

The data presented in this thesis have been collected between 1990 and 1995 in the vicinity of the Konnevesi Research Station in Central Finland (62°37'N, 26°20'E). The study area is covered mainly with coniferous forest of spruce (*Picea abies*) and pine (*Pinus sylvestris*), with occasional birches

(*Betula pubescens* and *B. pendula*) and other deciduous trees. In our study area treecreepers prefer to breed in specially-designed nest boxes (Kuitunen 1987). Each breeding pair of treecreepers had access to extra nest-boxes for a second breeding attempt.

## 2.3 General methods

### 2.3.1 Routines at each nest

All the nestboxes were visited regularly throughout the breeding season to collect data on clutch initiation, clutch size, date of hatching and the fate of broods both for the first and second breeding attempts. Breeding females and males were caught during the nestling stage and marked individually with aluminum and coloured rings. Morphological characters such as wing, tarsus and bill lengths and body mass were measured and the approximate age of the parent birds was determined by plumage coloration. The body mass of the nestlings was measured either once or twice, and their subsequent fate was monitored by regular visits to the nests throughout the nestling period.

The data on food abundance on tree trunks in each territory was gathered just after fledging by vacuum-cleaners. The diameter of spruce trunks has been shown to be a critical determinant of treecreeper foraging site selection (Suhonen & Kuitunen 1991b). Therefore, several measures of territory characteristics were measured (the proportions of different tree species, density of trees, size distribution of trees and presence or absence of wood ants) in order to choose similar treecreeper territories for different treatment groups in each experiment.

### 2.3.2 Observations on foraging behaviour (I, IV, V)

To gather data on the foraging behavior of parent birds, I followed female and male treecreepers in the vicinity of their nest for approximately three hours during one day when the nestlings were 12-14 days old. I recorded foraging behaviour after the bird left the nest and started to collect food. Birds were followed for as long as possible during the time they collected food in each foraging bout. The observations were made during clear weather between 0800 and 1700 hours, which is the period of most active feeding behaviour of treecreepers (Kuitunen & Suhonen 1989). For each foraging observation I recorded the tree species that was used for foraging, diameter of the tree trunk, foraging height (only in IV), foraging distance from the nest and time spent on each tree using a stop-watch. Data were recorded into a dictaphone and later transcribed.

### **2.3.3 Observations on parental care (I, II, III)**

In 1990 and 1991, feeding activity was determined by direct observation by counting the feeding frequency of the parents for one hour between 10 a.m. and 6 p.m., when the nestlings were 12 days old. In 1992, feeding frequencies and load sizes were measured using a small videocamera installed beside the nest entrance. The size of each load was determined in relation to the bill length of the parent from the video tapes. From a total time of two hours that each nest was video taped, the period of one hour (beginning 30 minutes after the start of the tape) was used for the determination of both feeding frequencies and load sizes.

## **2.4 Clutch size manipulation (I)**

To study the determination of clutch size and mechanisms that may affect reproductive effort, brood size was manipulated in twelve nests (four in each treatment) in 1991 and 1995, and in fifteen nests (five in each treatment) in 1992. In nests with the same hatching date, the number of newly hatched nestlings was randomly increased or decreased by adding or removing one two-day old nestling, or the nest was left untouched as a control. When the nestlings were 12-14 days old, I observed the behaviour of the parent birds and weighted the nestlings.

## **2.5 Male removal (III, IV)**

Male removal experiment was carried out to study the determination of sex-specific foraging behaviour and importance of parental care in treecreepers. For the experiment we chose sixteen territories, which formed eight pairs of control and experimental territories in which the nestlings had hatched on the same day. In the experimental territories we caught breeding females during incubation and removed males (Permission of the Environmental Agency in Central Finland no LA-208/0995L0156/25) when the nestlings were five days old and females did not brood them any more. The males were transported approximately 100 kilometers and released. None of the males returned to their breeding sites. The control birds in the eight other territories were caught at the same time but the females were left with their mates. When the nestlings were 12-14 days old, I observed the foraging behaviour and parental care of widowed females and paired birds.

## **2.6 Ant reduction experiment (V)**

To study the effects of wood ants on the foraging behaviour and food supply of the treecreepers, I carried out an experiment, where ants were prevented to

enter part of the tree trunks in treecreeper territories. In four territories in 1993 and in two other territories in 1995 I reduced the number of ants on 30 spruce trunks in each territory by applying a ring of a chemical repellent (trademark Fluon) to the lower tree trunk. Spruce trunks were used in the experiment because spruce is the most preferred tree species used by foraging treecreepers in our study area (Suhonen & Kuitunen 1991b). Spruce trunks which were used by foraging ants and spruce trunks which completely lacked ants formed the two other groups. As a result I had three treatment groups in each territory: (i) trunks with ants, (ii) trunks with a reduced number of ants and (iii) trunks without ants. Five days after applying Fluon to the trunks (when the nestlings were 12-14 days old) I observed the foraging behaviour of parent treecreepers.



## **3 RESULTS AND DISCUSSION**

### **3.1 Factors influencing clutch size (I)**

Experimental manipulation of brood size is an extensively used method in the analysis of clutch size determination in birds. It has the advantage of eliminating the confounding influences from individual tuning of efforts by intrinsic and extrinsic circumstances, because parent birds are forced to deal with a different commitment from what they had 'decided' themselves (e.g. Lessells 1991).

Brood size manipulation clearly had effects on the behaviour and reproductive success of treecreepers. However, the birds differentially responded to the reduction or enlargement of their broods in different years. Parents were not able to successfully raise the enlarged broods to fledging in the years with the lowest food abundance (1991, 1992). In 1992, when food abundance was the lowest of all years studied, the nestlings in the enlarged broods also weighted less than nestlings in the control and reduced broods. In 1995, when food abundance was substantially higher, the parents could raise the enlarged broods to fledging, but the nestlings suffered from lower body weight than in the reduced group. Since body weight is a good predictor of future survival of the young (e.g. Perrins 1965), the success of the enlarged broods in terms of number of recruits produced may in fact be lower than in the other treatment groups also in 1995. Thus, at least in years with scarce food, the results support the Lack's (1947) suggestion, that clutch size is set by the number of young parents can adequately provision.

Despite the extensive effort devoted to experiments using brood size manipulations (in order to study the individual optimization of clutch size and the existence of reproductive costs), the factors that limit the abilities of the parents to raise their offspring and mediate the costs of reproduction are

not well documented. In study I, I sought the mechanisms, that may have limited the clutch size of the treecreepers. In 1991, when food was scarce, the food abundance after fledging of the young was lowest in the territories of enlarged broods. This indicates, that the parents raising additional young depleted their food resources during the nestling stage. Consequently, parents also changed their foraging behaviour; females in the enlarged group switched their foraging site and reduced their foraging time on each tree trunk, and males in the reduced and enlarged groups foraged shorter time on each patch than control males. In 1995, when food was abundant in numbers, but the invertebrates were smaller in size than in 1991, the average size, but not the number, of food items was lowest in the territories of enlarged broods. Thus, treecreepers in the enlarged group seemed to deplete only the largest food items in the territory, and did not change their foraging behaviour.

These findings suggest, that when food is scarce, the amount of food and possibly also the available time for foraging limit clutch size in treecreepers, but when food is abundant, the quality rather than the amount of food may constrain the abilities of parents to feed the young.

### **3.2 The importance of male parental care (II, III)**

The need for male care has traditionally been used to explain the prevalence of social monogamy in birds (Lack 1968, Wittenberger 1979). Many studies have found biparental care to appreciably improve reproductive success, while some studies have shown, that females may be able to care for their young alone (e.g. Bart & Tornes 1989). It has been suggested, that male care may be less important at times of good food supply (e.g. Wittenberger 1982, Bart & Tornes 1989).

We studied differences in male and female parental care in treecreepers between first and second broods in relation to food availability (II). Higher food availability was associated with reduced male care in the second broods. The offspring also fledged heavier in the second than first broods, although the females were in most cases raising the second broods alone. In the first broods, when the food abundance was lower, the mean fledgling mass increased with the feeding rate of the males.

Male removal experiment in the first broods revealed, that the reproductive success of widowed females was lower than of paired birds (III). Widowed females were found to increase their provisioning rates so that the total feeding rate was on average the same in the control and experimental broods. Hence, although females tried to compensate for mate loss, they were not able to raise their young alone in conditions with low food availability. The lower breeding success of widowed females may be due to changes in the composition of loads, since widowed females carried spiders and dipterans to the nestlings less often than control birds. These

differences are likely to be a result of changes in the foraging behaviour of widowed females (IV, 'Sex-specific foraging behaviour' below).

These results support the predictions of theoretical models of evolutionary stable strategies of parental care, which state that in monogamy the expected response to reduced parental care by one parent is incomplete compensation by its partner (Houston & Davies 1985). In treecreepers, male parental care seems to be most important at times of low food abundance, and the need for two parents to successfully raise the brood may favour monogamy during the first broods.

### **3.3 Sex-specific foraging behaviour (IV)**

Earlier studies show, that treecreepers have sex-specific foraging niches so that females forage on the higher parts of trees while males consistently use the lower parts of tree trunks (Suhonen & Kuitunen 1991b). It has been suggested, that dissimilar foraging niches may be either genetically determined or a result of behavioural plasticity (Werner & Hall 1976). We carried out a male removal experiment in order to study the mechanism of niche partitioning between the sexes of the treecreepers, together with the analysis of the importance of male parental care.

Widowed females foraged at lower heights and spent less time on each tree thus behaving more as paired males. These females also spent less time on each foraging bout than did the paired females. Male removal thus caused a change in a female's foraging niche and foraging time at the trees. Behavioural plasticity seems therefore to be the mechanism of niche partitioning between the sexes of Eurasian treecreepers. This might be partly due to male dominance in the territory, as has been found in woodpeckers (e.g. Peters & Grubb 1983, Matthysen et al. 1991) and tits (Ekman & Askenmo 1984) during wintertime. However, male treecreepers did not exclude paired females from their preferred foraging sites, which suggest that male dominance is of minor importance in determining the foraging behaviour of females. Reduced foraging times and shift in foraging site of widowed females suggest, that these females may have re-optimized their foraging strategies in the absence of male parental care, to be able to compensate for the mate loss.

### **3.4 The effects of interphylum competition on the foraging behaviour and breeding success (V, VI)**

Although interspecific competition has widely been shown to affect individual behaviour, the existence of competition between animals in different phyla has been a subject of much controversy. In study V we found, that wood ants (*Formica rufa* -group), which use the same foraging

sites as treecreepers, are able to deplete the food supply available to treecreepers on tree trunks. The magnitude of this depletion extends beyond the microhabitat (tree trunks), so that the food abundance in the whole treecreeper territories, that are occupied by ants, is decreased. Parent treecreepers were found to avoid trunks with ants and to forage for a shorter time on these trunks than on ones without ants. Experimental reduction of ant numbers allowed food resources to recover and led to longer foraging times of male treecreepers on these trunks compared with the trunks with ants present. The longest treecreeper visits were found on trunks without ants. These results show, that competition between two very different taxa can be effective in determining the behaviour of foraging individuals.

For the changes in food availability and foraging behaviour to be important in terms of individual fitness, they need to be reflected by reduced reproductive success or poorer survival in at least one of the competing species (Stephens & Krebs 1986, Martin 1987, 1995). In study VI, we found that the reproductive success of treecreepers breeding in territories with ants was considerably lower than in territories without ants. Treecreepers start to breed earlier in territories without ants and are able to increase the size of their second clutch, whereas birds breeding in territories with ants have similar clutch sizes in the first and second breeding attempts. In addition to later hatching, nestlings produced in territories with ants are of lower body weight and suffer from increased mortality compared to the nestlings in territories without ants. Consequently, those treecreeper pairs, that reared two broods in territories without ants during the same breeding season, produced more fledglings, that were also of higher quality, than pairs in territories with ants. Since there were no differences in the territory characteristics other than food abundance during the second brood, it seems, that ants are responsible for the deterioration of the territory quality of the treecreepers, and thus are able to negatively influence the breeding success of the birds.

These results show, that competition even between organisms in different phyla can be effective in determining individual behaviour and reproductive success. The plausible mechanism that causes the changes in reproductive parameters seems to be food depletion, that acts through changes in foraging behaviour and parental care. However, it is easy to believe, that when foraging on the same tree trunk, ants and treecreepers also directly interfere with each others, which probably also reflects to their behaviour. Nevertheless, the strong impact of ants on the reproductive success of the treecreepers is hard to explain by pure interference. Most likely the competitive interactions between these two dissimilar organisms share features of both exploitation of resources and interference.

## 4 CONCLUSIONS

In this thesis I studied the evolution of clutch size and parental behaviour and attempted to establish links between food abundance, behavioural traits and fitness. The results show that clutch size seems to be largely determined by the capacity of the parents to successfully rear a brood in given breeding conditions (Lack 1947). Possible factors, that limit clutch size in treecreepers are food depletion in the territory during the nestling period and limited time available for foraging. An additional factor, that seems to be important in clutch size determination of the treecreepers is the presence of wood ants in the territory. Because treecreepers start to breed very early in the spring, when the ants are not yet active, the birds may not know the presence of ants in their territory, and thus it may be impossible for them to predict the forthcoming effects of ants on the territory quality. On the other hand, at the egg-laying time of the second clutches, the birds are aware of the territory quality, and are better able to adjust the brood size to their feeding abilities by the number of eggs laid. Although in a short-lived species like the Eurasian treecreeper the investment in current breeding may be more important than investment in future reproduction, the trade-offs between current and future reproduction may also affect the evolution of clutch size.

Food depletion due to the enlarged brood or the actions of wood ants on trunks led to changes in foraging behaviour of the treecreeper parents, and differences in food availability was reflected in parental care. Food availability thus also affects behavioural traits. Furthermore, behavioural changes caused by brood enlargement, male removal, or competition between ants were associated with changes in reproductive success of the treecreepers. Thus, behavioural traits, which by large were affected by food availability, were also connected to the individual breeding success, and thus fitness.

The link between food abundance, foraging behaviour and reproductive success was especially obvious when competitive interactions with ants were involved. The fact that ants, which indeed differ a lot from birds in respect to behavioural and life-history characteristics (except to their resource use), can have such a strong influence on behaviour and reproduction of treecreepers, gives us a sign of the complex interactions between organisms that share the same breeding environment.

### *Acknowledgements*

I owe my deepest gratitude to my friends in our treecreeper-project: Tomi Hakkari, Ari Jääntti, Markku Kuitunen and Jukka Suhonen. Without you this work would have been impossible to carry out. Especially I want to thank you for bringing lots of joy to the field work in the dimp woods of Konnevesi. My warmest thanks to my supervisors Markku and Jukka, who have patiently encouraged and advised me. I am also thankful for professor Rauno Alatalo for his support and guidance on the road of science. My warm thanks are due to all the people in our department, especially "the downfloor ecologists" with whom I have shared many memorable moments: Matti Halonen, Taina Horne, Matti Hovi, Esa Huhta, Esa Koskela, Janne Kotiaho, Jonna Mappes, Tapio Mappes, Silja Parri, Jyrki Pusenius, Pekka Rintamäki, Osmo Rätti and Pirkko Siikamäki. Especial thanks to Janne for his practical advice during the last weeks of 'processing' the thesis. The Konnevesi Research Station has provided the most inspiring environment for field work and supported my study also financially; especial thanks to Jussi Viitala and Hannu Ylönen. Antti Sirkka and Risto Latvanen have solved many practical problems and Mirja Poikolainen has been very helpful both in the laboratory and field.

I thank the Department of Ecology and Systematics in the University of Helsinki for providing me the most comfortable working facilities during the past few years. I owe my deepest gratitude to my friends in the Integrative Ecology Unit (IKP): Heikki Hirvonen, Hanna Kokko, Katriina Lahti, Anssi Laurila, Jan Lindström, Susanna Pakkasmaa, Nina Peuhkuri, Esa Ranta, Hannu Rita and Teija Seppä. You have created very stimulating and warm environment to work with. Your advice at work has facilitated my work practically and your friendship has been essential for my mental welfare. Also, I want to thank Tvärminne Zoological Station for providing working facilities during many springs and summers. Antti Nevalainen kindly helped me in many 'computing problems'.

Many thanks for Erkki Korpimäki and Markku Orell for constructive comments on this thesis. Financially I have been supported by the University of Jyväskylä and Jenny and Antti Wihuri foundation.

Finally, I want to thank the ones whom I love the most, my family. My own parents Irene and Veikko, and Anssi's mother Sirkka and Martti have helped me in many ways, and provided me opportunities to relax and to

forget about the science for some moments. I warmly appreciate Anssi for increasing his share of parental care, while I wrote my thesis. Our son Aksu has taught me many important things of being a mother, and helped me to keep balance between science and the 'real world'.

## YHTEENVETO

### **Puukiipijän lisääntymismenestykseen vaikuttavat tekijät**

Väitöskirjassani tutkin tekijöitä, jotka rajoittavat pesyekokoa ja vaikuttavat yksilöiden lisääntymismenestykseen. Erityisesti halusin selvittää yksilöiden ravinnonhankintakäyttäytymisen ja jälkeläishuollon määräytymistä ja näiden yhteyttä lisääntymismenestykseen ja tarjolla olevan ravinnon määrään. Tutkimuskohteenani käytin puukiipijää (*Certhia familiaris*), joka on erikoistunut ruokailemaan puiden rungoilla, ja näinollen sen ravinnonhankintakäyttäytymistä on helppo mitata.

Lintujen pesyekoon määräytymistä on tutkittu paljon pesye- tai poikuekokoa manipuloimalla, mutta pesyekokoa rajoittavia tekijöitä on harvemmin selvitetty. Tutkin kokeellisesti, kuinka lintuemojen käyttäytyminen ja reviirillä olevan ravinnon määrä muuttuu poikuekoon manipuloinnin seurauksena eri vuosina. Vuosina, jolloin ravinnon määrä reviirillä oli vähäinen, suurennettuja poikueita kasvattavien emojen lisääntymismenestys oli heikompi kuin ravintotilanteeltaan hyvinä vuosina, mutta jopa hyvässä ravintotilanteessa suurennettujen poikueiden poikaset olivat keskimäärin kevyempiä kuin muissa pesissä. Puukiipijät siis näyttävät munivan niin suuren pesyeen, kuin ne kussakin ravintotilanteessa pystyvät ruokkimaan. Ravintotilanteeltaan huonoina vuosina suurennettua poikuetta ruokkivat lintuemot vähensivät saatavilla olevan ravinnon määrää reviirillään ja muuttivat ruokailukäyttäytymistään. Ravinnontarjonnaltaan hyvänä vuonna näitä muutoksia ei havaittu. Poikuekokomanipulaation aiheuttamat muutokset ravinnon määrässä ja käyttäytymisessä osoittavat, että saatavilla olevan ravinnon määrä ja käytettävissä oleva ruokailuaika näyttäisivät rajoittavan puukiipijöiden pesyekokoa.

Tutkin puukiipijäemojen jälkeläishoidon merkitystä sekä vertailemalla koiraiden jälkeläishoitoa ensimmäisten ja toisten pesyeiden



aikana että kokeellisesti poistamalla koiraita reviireiltään. Pesimäkauden alussa ensimmäisten pesyeiden aikaan havaitsin molempien emojen ruokkivan poikasiaan, kun taas paremman ravintotilanteen aikaisilla toisilla pesyeillä usein vain naaraat osallistuivat jälkeläisten hoitoon. Koiraiden poistaminen osoitti, että molempien emojen panostus jälkeläishoitoon on tärkeää etenkin ravintotilanteen ollessa huono, koska leskinaaraiden lisääntymismenestys oli selvästi heikompi kuin parien.

Puukiipijäkoiraat ja -naaraat ruokailevat normaalisti eri osissa reviirinsä puunrunkoja. On ehdotettu, että tällainen ekolokeroiden jakaminen on joko geneettisesti määräytynyt käyttäytymispiirre, tai seurausta yksilöiden joustavasta käyttäytymisestä erilaisissa ekologisissa tilanteissa. Puukiipijänaaraat, joiden koiraat oli poistettu reviireiltään, muuttivat ruokailukäyttäytymistään enemmän koiraiden kaltaiseksi, mikä osoittaa, että puukiipijänaaraiden ruokailupaikan valinta perustuu ennemminkin yksilölliseen käyttäytymisen optimointiin kuin geneettisiin tekijöihin.

Lajienvälisen kilpailun tiedetään vaikuttavan eläinyhteisöjen rakenteeseen ja yksilöiden käyttäytymiseen. Lajienvälisen kilpailun vaikutusten tutkimus on kuitenkin keskittynyt lähinnä lähisukuisten lajien välille, toisiaan vähän muistuttavien lajien välisestä kilpailusta tiedetään huomattavasti vähemmän. Etenkin eri pääjaksoihin kuuluvien lajien välistä kilpailua on tutkittu hyvin vähän, ja tällaisen kilpailun vaikutuksista yksilöiden lisääntymismenestykseen ei ole julkaistua tietoa. Tutkin samoja ravintoresursseja hyödyntävien puukiipijöiden ja kekomuurahaisten (*Formica rufa* -ryhmä) välistä kilpailua sekä kokeellisesti vähentämällä muurahaisten määrää rungoilla, että vertailemalla puukiipijöiden pesintämenestystä muurahaisten kolonisoimien ja muurahaisettomien reviirien välillä. Muurahaisten läsnäolo puunrungoilla vaikutti selvästi rungoilla elävien selkärangattomien eläinten määriin ja puukiipijöiden ruokailukäyttäytymiseen. Puukiipijöiden pesintämenestys oli myös huonompi muurahaisreviireillä. Muurahaisreviirien emot tuottivat vähemmän ja huonompilaatuisia jälkeläisiä kuin muurahaisettomilla reviireillä pesivät parit. Nämä tulokset osoittavat, että kilpailua voi esiintyä myös hyvin kaukaista sukua olevien lajien kesken, ja kilpailun vaikutukset voivat ulottua käyttäytymismuutosten ohella jopa yksilöiden lisääntymismenestyksen heikentymiseen.

## REFERENCES

- Bart, J. & Tornes, A. 1989: Importance of monogamous male birds in determining reproductive success - Evidence for house wrens and a review of male-removal studies. - *Behav. Ecol. Sociobiol.* 24: 109-116.
- Beissinger, S. R. & Snyder, N. F. R. 1987: Mate desertion in the snail kite. - *Anim. Behav.* 35: 477-487.
- Blanckenhorn, W. V. 1991: Fitness consequences of foraging success in water striders. - *Behav. Ecol.* 2: 46-55.
- Brown, J. H., Reichman, O. J. & Davidson, D. W. 1979: An Experimental Study of Competition Between Seed-eating Desert Rodents and Ants. - *Amer. Zool.* 19: 1129-1143.
- Charnov, E. L. & Krebs, J. R. 1974: On clutch size and fitness. - *Ibis* 116: 217-219.
- Chase, I. 1980: Cooperative and noncooperative behaviour in animals. - *Am. Nat.* 115: 827-857.
- Clutton-Brock, T. H. 1991: The evolution of parental care. - Princeton Univ. Press, Princeton.
- Cody, M. L. 1966: A general theory of clutch size. - *Evolution* 20: 174-184.
- 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. - *J. Anim. Ecol.* 59: 269-285.
- Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. - *Ardea* 68: 225-252.
- Ekman, J. B. & Askenmo, C. E. H. 1984: Social rank and habitat use in Willow Tit groups. - *Anim. Behav.* 32: 508-514.
- Frey-Roos, F., Brodmann, P. A. & Reyer, H.-U. 1995: Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. spinoletta*. - *Behav. Ecol.* 6: 287-295.
- Godfray, H. C. J., Partridge, L. & Harvey, P. H. 1991: Clutch size. - *Annu. Rev. Ecol.* 22: 409-429.

- Haemig, P. D. 1996: Interference from ants alters foraging ecology of great tits. - *Behav. Ecol. Sociobiol.* 38: 25-29.
- Hochberg, M. E., & Lawton, J. H. 1990: Competition Between Kingdoms. - *Trends Ecol. Evol.* 5: 367-371.
- Högstedt, G. 1980: Evolution of clutch size in birds: adaptive variation in relation to territory quality. - *Science* 210: 1148-1150.
- Houston, A. I. & Davies, N. B. 1985: The evolution of cooperation and life history in the dunnock *Prunella modularis*. - In: Sibley, R. M. & Smith, R. H. (eds), *Behavioural Ecology: The Ecological Consequences of Adaptive Behaviour*: 471-487. Blackwell, Oxford.
- Krebs, J. R. & Kacelnik, A. 1991: Decision-making. - In: Krebs, J. R. & Davies, N. B. (eds), *Behavioural Ecology: An Evolutionary Approach*: 105-136. - Blackwell, Oxford.
- Kuitunen, M. 1987: Seasonal and geographical variation in the clutch size of the Common Treecreeper *Certhia familiaris*. - *Ornis Fennica* 64: 125-136.
- Kuitunen, M. & Suhonen, J. 1989: Daylength and time allocation in relation to reproductive effort in the Common Treecreeper *Certhia familiaris*. - *Ornis Fennica* 66: 53-61.
- Lack, D. 1947: The significance of clutch size. I. Intraspecific variation. - *Ibis* 89: 302-352.
- Lack, D. 1968: Ecological adaptations for breeding in birds. - Chapman & Hall, London
- Laverty, T. M. & Plowright, R. C. 1985: Competition between hummingbirds and bumble bees for nectar in flowers of *Impatiens biflora*. - *Oecologia* 66: 25-32.
- Lazarus, J. 1989: The logic of mate desertion. - *Anim. Behav.* 39: 657-671.
- Lessells, C. M. 1991: The evolution of life histories. - In: Krebs, J. R. & Davies, N. B. (eds), *Behavioural Ecology: An Evolutionary Approach*: 32-68. Blackwell, Oxford.
- Lindén, M. & Møller, A. P. 1989: Cost of reproduction and covariation of life history traits in birds. - *Trends Ecol. Evol.* 4: 367-371.
- Martin, T. E. 1987: Food as a limit on breeding birds: a life-history perspective. - *Ann. Rev. Ecol. Syst.* 18: 453-487.
- Martin, T. E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. - *Ecol. Monogr.* 65: 101-127.
- Matthysen, E., Grubb, T. C. Jr & Cimprich, D. 1991: Social control of sex-specific foraging behaviour in downy woodpeckers, *Picoides pubescens*. - *Anim. Behav.* 42: 515-517.
- Milinski, M. & Parker, G. A. 1991: Competition for resources. In: Krebs, J. R. & Davies, N. B. (eds), *Behavioural Ecology: An Evolutionary Approach*: 137-168. - Blackwell, Oxford.
- Nur, N. 1990: The costs of reproduction in birds: evaluating the evidence from manipulative and non-manipulative studies. - In: Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery R. H. (eds), *Population biology of passerine birds: an integrated approach*: 281-296. Springer-Verlag, Berlin.

- Partridge, L. & Harvey, P. H. 1988: The ecological context of life history evolution. - *Science* 241: 1449-1455.
- Perrins, C. M. 1965: Population fluctuations and clutch-size in the great tit, *Parus major* L. - *J. Anim. Ecol.* 34: 601-647.
- Peters, W. M. D. & Grubb, T. C. 1983: An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. - *Ecology* 64: 1437-1443.
- Reznick, D. 1985: Cost of reproduction: an evaluation of the empirical evidence. - *Oikos* 44: 257-267.
- Ricklefs, R. E. 1980: Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. - *Auk* 97: 38-49.
- Roff, P. A. 1992: The evolution of life histories. - Chapman & Hall, New York.
- Slagsvold, T. 1982: Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus pilaris*). - *Ecology* 63: 1389-1399.
- Slagsvold, T. 1984: Clutch size variation of birds in relation to nest predation: on the cost of reproduction. - *J. Anim. Ecol.* 53: 945-953.
- Stearns, S. C. 1992: The evolution of life histories. - Oxford University Press, Oxford.
- Stearns, S. C. & Schmid-Hempel, P. 1987: Evolutionary insights should not be wasted. - *Oikos* 49: 118-125.
- 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 Scand.* 22: 313-318.
- Ward, D. 1992: The role of satisficing in foraging theory. - *Oikos* 63: 312-317.
- Werner, E. E. & Hall, D. J. 1976: Niche shifts in sunfishes: experimental evidence and significance. - *Science* 191: 404-406.
- Williams, G. C. 1966: Natural selection, the costs of reproduction, and a refinement of Lack's principle. - *Am. Nat.* 100: 687-690.
- Wittenberger, J. F. 1979: The evolution of mating systems in birds and mammals. - In: Marler, P. & Vandenbergh, J. (eds), *Handbook of Behavioral Neurobiology*: 271-349. Plenum Press, New York.
- Wittenberger, J. F. 1982: Factors affecting how male and female bobolinks apportion parental investment. - *Condor* 84: 22-39.

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