









*For My "Butterflies": Aurora, Vanessa & Helinä*

## ABSTRACT

Jäntti, Ari

Effects of interspecific relationships in forested landscapes on breeding success in Eurasian treecreeper

Jyväskylä, University of Jyväskylä, 2005, 41 p.

(Jyväskylä Studies in Biological and Environmental Science,

ISSN 1456-9701; 150)

ISBN 951-39-2046-1

Yhteenveto: Lajienvälisten suhteiden vaikutus puukiipijän pesintämenestykseen metsäympäristössä

Diss.

This study is focused on the effects of predation to the breeding success of Eurasian treecreeper and resource competition between red wood ants, *Formica rufa* -group and treecreepers. One of the most important factors in competition between ants and treecreepers seems to be limited food resources on tree trunks. Treecreeper could consume a significant amount of arthropods on tree trunks near the nest during nesting period. Nests of treecreeper suffer from heavy nest predation from the great spotted woodpecker and from mustelids. Nest defence behaviour of parents is quite mild and composed mostly from high-pitched alarm calls that silence hungry nestlings in the nest. I used a moulted great spotted woodpecker as a predator model. Nest defence was similar between female and male on the first brood, but on the second, later brood male is mostly absent. Treecreepers are sensitive to modern forestry. Parents have to take more risk in their nest defence in smaller forest patches keeping the hungry nestlings quiet. It is more difficult to noisy offspring to hear alarm-calls of parents. The land-use and forest resource data of Landsat within two hundred meter radii around the nest boxes were used in GIS. Breeding success of treecreeper was greater and less variable in mature forest areas and lower in young forest areas. Nest predation rate was higher in territories with high proportion of young sapling stands. The territories of red wood ant were counted and each territory was classified as being either with ants, if the territory contained at least one ant mound or without ants. Treecreepers breeding in territories with ants laid their first clutches later and produced fewer fledglings with lower body mass at the nestling stage compared to the pairs breeding in territories without ants. Comparing the pairs that bred twice in the same territory during the same breeding season, I found that those breeding in territories with ants laid smaller second clutches than pairs in territories without ants. Food abundance was higher during the second broods, but the overall availability of food was lower in territories with ants. Additionally, I found associated evidence that the quality of treecreepers nestlings were affected by amount of red wood ants. Morphological characters of nestlings like body mass were lighter, subcutaneous fat contents were thinner and tarsus lengths were shorter when the quantity of red wood ants was higher. The amount of wood ants had no significant effect on morphological characters like wing length and also there was no significant relationship between the wood ant level and nest-box occupancy, fecundity (clutch size) or physiological stress of nestlings. The survival and fecundity of treecreepers' chicks fledging from ant territories may be further reduced by their low fledging mass.

Key words: Body condition; Eurasian treecreeper; landscape structure; nest defence; predation; prey depletion; reproductive success; wood ants.

Ari Jäntti, Department of Biological and Environmental Science, P. O. Box 35, FI-40014, University of Jyväskylä, Finland.

**Author's address** Ari Jäntti  
Department of Biological and Environmental Science  
P.O. Box 35  
FI-40014 University of Jyväskylä , Finland  
e-mail: [arijujantti@hotmail.com](mailto:arijujantti@hotmail.com)

**Supervisors** Professor Markku Kuitunen  
Department of Biological and Environmental Science  
P.O. Box 35  
FI-40014 University of Jyväskylä, Finland

Docent Harri Hakkarainen  
Section of Ecology  
Department of Biology  
FI-20014 University of Turku, Finland

**Reviewers** Professor Anders Pape Møller  
Laboratoire de Parasitologie Evolutive  
CNRS UMR 7103  
Université Pierre et Marie Curie  
Bâtiment A, 7ème étage  
7quai St. Bernard  
Case 237  
FR-75252 Paris Cedex 05, France

Professor and director Gerald J. Niemi  
Department of Biology and the Environment Natural  
Resources Research Institute  
University of Minnesota  
5013 Miller Trunk Highway  
Duluth, MN 44811-1442, USA

**Opponent** Professor Hannu Pöysä  
Game and Fisheries Research Institute  
Yliopistokatu 6  
FI-80100 Joensuu, Finland

# CONTENTS

ABSTRACT

LIST OF ORIGINAL PUBLICATIONS

1	INTRODUCTION .....	9
2	MATERIALS AND METHODS.....	14
2.1	The passerine species .....	14
2.2	The study area.....	14
2.3	General methods.....	15
2.3.1	Routines at territories (I-VI) .....	15
2.3.2	Breeding data of seven years (IV) .....	15
2.3.3	Quality and physiological stress of nestlings (VI).....	15
2.3.4	Food abundance on tree trunks.....	16
2.3.5	Food abundance after prey depletion (I).....	16
2.3.6	Ant levels of territories (II) .....	16
2.3.7	Ant levels of territories (VI) .....	16
2.3.8	Nest defence (III, V) .....	17
2.3.9	Landscape structure (IV, V) .....	17
3	RESULTS AND DISCUSSION .....	19
3.1	Prey depletion made by treecreeper .....	19
3.2	Breeding time, clutch size and territory quality.....	19
3.3	Effects of ants on breeding success .....	20
3.4	Breeding success and habitat structure .....	20
3.5	Nest defence behaviour of adult treecreepers .....	21
3.6	Nest defence and habitat loss.....	23
3.7	Red wood ants and the body condition of treecreeper nestlings .....	24
4	CONCLUSIONS.....	27
	<i>Acknowledgements</i> .....	29
	YHTEENVETO.....	31
	REFERENCES.....	33

## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which will be referred to by their Roman numerals. I have personally performed a significant proportion of the work in gathering data (I-VI), analysing data (I, III, V & VI) and writing papers (I-VI).

- I Jänntti, A., Aho, T., Hakkarainen, H., Kuitunen, M. & Suhonen, J. 2001: Prey depletion by the foraging of the Eurasian treecreeper, *Certhia familiaris*, on tree-trunk arthropods. *Oecologia* 128 (4): 488-491.
- II Aho, T., Kuitunen, M., Suhonen, J., Jänntti, A. & Hakkari, T. 1999. Reproduction success of Eurasian Treecreepers, *Certhia familiaris*, is lower in territories with wood ants. *Ecology* 80(3): 998-1007.
- III Jänntti, A., Suhonen, J., Kuitunen, M. & Aho, T. 2003. Nest defence of Eurasian Treecreeper *Certhia familiaris* against the Great Spotted Woodpecker *Dendrocopos major*: Only one parent is needed. *Ornis Fennica* 80: 31-37.
- IV Huhta, E., Aho, T., Jänntti, A., Suorsa, P., Hakkarainen, H., Kuitunen, M. & Nikula, A. 2003. Habitat-related nest predation effect on the breeding success of the Eurasian treecreeper. *Ecoscience* 10: 283-288.
- V Jänntti, A., Hakkarainen, H., Kuitunen, M., & Suhonen, J. 2004. Importance of landscape structure on nest defence in the Eurasian treecreeper, *Certhia familiaris*. (Submitted)
- VI Jänntti, A., Suorsa, P., Hakkarainen, H., Sorvari, J., Huhta, E. & Kuitunen, M. 2004. Within territory amount of red wood ants is associated with the body condition of nestlings in the Eurasian treecreeper (Manuscript)

# 1 INTRODUCTION

One species does not exist alone in nature, but it lives within a wider matrix of other species and different individuals of same species. Some species will be affected by the presence of another species in the same area, but in many cases two or more species will interact. Thus the population of one species can change the presence of a second species. Interactions between populations can be classified on the basis of either the mechanism of interaction (competition, predation, herbivory, parasitism, disease, mutualism, Abrams 1987) or the effects of the interactions (0, +, - effects on population growth, Odum 1983). My study is focused on the effects of predation on the breeding success of Eurasian treecreeper, *Certhia familiaris* and resource competition between red wood ants, *Formica rufa* -group, and treecreepers.

The most intensive interspecific competitions in natural populations are principally documented between closely related species with similar niche (Connell 1983, Schoener 1983, Gustafsson 1987, Korpimäki 1987, Punttila et al. 1994, Confer et al. 2003). Taxonomically very distant species may have interspecific competition for limiting resources (Hochberg & Lawton 1990, Aho et al. 1997, Haemig 1996, 1999). Negative effects of interphylum competitive interactions on the abundance of competing species, the foraging behaviour of individuals, and on common food resources are found between frogs and insects (Morin et al. 1988), between birds and insects (Carperter 1979, Kodric-Brown & Brown 1979, Gill et al. 1982, Laverly & Plowright 1985), between ants and rodents (Brown et al. 1979) and between ants and birds (Haemig 1992, 1994, 1996, Aho et al. 1997). Competition between species occurs in two major ways: exploitative and interference competition (Amarasekare 2002, Hawes et al. 2002). Exploitative competition, also called scramble of resource competition, are indirect negative interactions arising from the use of a common resource by each consumer of same or of different species (Birch 2001, Haemig 1992, 1994). In interference competition, also called contest competition (Birch 2001), direct interactions arising from territoriality, overgrowth, undercutting, predation or chemical competition, can negatively alter the foraging behaviour of the other species (Haemig 1996).

In I article, I examined to what extent breeding treecreepers affect the abundance and mean size of their prey population on the surface on trunks near the nest in their territories. Some studies have revealed a negative impact of insectivorous bird guilds on populations of spider and insects outside the breeding season (e.g. Askenmo et al. 1977). The role of food limitation is especially important when studying competitive interactions and resource partitioning in animal assemblages (e.g. Martin 1986; Wiens 1989). Limited food resources have also been considered to be one of the important determinants of breeding time, clutch size and reproductive success in birds (e.g. Svensson & Nilsson 1995, Brodmann et al. 1997, Hakkarainen et al. 1997). My prediction was that treecreeper consume more food close to the nest than further away according to the prey depletion hypothesis, and so the expectation was that treecreepers select larger invertebrates from territories on the basis of optimal foraging theory (Begon et al. 1990).

In II article, the effects of red wood ant abundance on the reproductive parameters of treecreeper were analysed. How the amount of red wood ants affected the food abundance of treecreeper was also analysed. Predictions were that a higher amount of ants could depress invertebrate abundance on treecreeper territories; a higher amount of ants could depress clutch size of treecreeper; a higher quantity of ants could depress the fledging success of treecreepers.

In article III, I studied the nest defence behaviour of treecreeper against great spotted woodpecker, *Dendrocopos major*, which is a potential predator of treecreepers' nests. Nest defence is an important factor impacting fitness in many bird species (see especially Montgomerie & Weatherhead 1988). Especially treecreeper nests in natural cavities suffer from heavy nest predation from the great spotted woodpecker and from mustelids (*Mustelidae*) such as the least weasel (*Mustela nivalis*) and the stoat (*Mustela erminea*) (Kuitunen & Aleknonis 1992). Treecreepers' nests in artificial boxes also suffer from nest predation (Huhta et al. 2004). Additionally, mustelids pose a threat to treecreeper adults, but woodpeckers do not. I used a woodpecker model to observe how monogamous treecreeper parents shared nest defence duties during the first and second broods. In III article, I tested two separate hypotheses. The "effectiveness hypothesis" predicts that one parent does not take part in the nest defence, when the other parent is as effective as both parents together in defending the nest (Winkler 1992). According to this hypothesis, male or female treecreepers alone could silence their nestlings without the investment of the other parent. This hypothesis is closely related to the second one. The "silence hypothesis" predicts that the high-pitched warning calls of treecreepers should silence nestlings and that this is enough to protect the cryptic nest. This is important, especially when the brood gets older and louder, thus making it more vulnerable to predation. Many bird species use a special call to silence their nestlings rather than immediately engaging in nest defence in the presence of a predator (East 1981, Knight & Temple 1986).

Treecreeper is known to be sensitive to forest management because it is absent from clear-cuts and saplings and its breeding densities are three times

higher in old-growth forest than in managed forests (Virkkala et al. 1994, Haila et al. 1989). In article IV, I examined the effects of landscape, especially forest structure on breeding success of treecreeper over seven years. In Finland, the rather intensive human land use has led to diminished quality of environment as living habitat for many forest species. For instance, habitat patches differing in size as a result of the subdivision of natural habitats can vary in terms of their resource abundance for animals (e.g. Cody 1985, Wiens 1989, Møller 1991). This reduction of resources can have several fitness consequences, e.g. increased energetic and physiological costs, and reduction in time and energy used for other functions such as reproduction (Suorsa et al. 2003). Reproductive success is one of the most important factors affecting the persistence of populations in an environment (e.g. Martin 1995). In fragmented environments, behaviour, breeding success and other fitness-related consequences are influenced by patch size, habitat within patches, variable food supply, and harmful edge effects such as poorer climatic conditions, negative interspecific interactions like predation and changes in vegetation structure close to the edge (Gates & Gysel 1978, Møller 1988, Robinson et al. 1995, Burke & Nol 2000, Zanette et al. 2000). When there is relative low variability in breeding population densities most high-quality territories are occupied every year and they are characterised by high and stable reproductive success in relation to mortality. In poor quality habitats, year-to-year variability in reproduction success is high and mortality exceeds reproduction and the impacts of environmental fluctuations on reproduction success are more severe (Pulliam 1988). Reproductive surpluses from productive source habitats can maintain populations in sink habitats, where local reproductive success fails to keep pace with local mortality.

Destruction of natural habitats involves habitat loss and fragmentation-like edge effects and habitat isolation (Andrén 1994, Fahrig 1997, Schmiegelow & Mönkkönen 2002), which can have several harmful biological and ecological effects (Andrén 1994). Modern forestry usually diminishes the quality of forest environments as a living habitat for forest dwelling species. It especially causes the loss of mature forest habitats, particularly in boreal forest ecosystems. As a result of this rational forest planning, the forest blocks are fragmented by large clear-cuts and dense sapling stands (Mykrä et al. 2000). This ecosystem alteration increases the harmful effects on species that are dependent on continuous and homogeneous wood and forest cover (Niemelä 1999, Kouki & Väänänen 2000). These species could have restricted ability to disperse between suitable habitat patches (Hansson 1992), and the energy expenditure of food and mate searching may fail in strongly fragmented landscapes (e.g. Rolstad & Wegge 1989). The increased predation pressure in fragmented forest landscapes is extensively documented (e.g. Kuitunen & Helle 1988, Andrén 1992, Kurki & Linden 1995, Huhta 1995, Huhta et al. 2004).

In V article, I examined the effects of forest structure on the nest defence behaviour of treecreeper parents. Because treecreepers use a warning call to silence the nestlings in the nest (see article III), we would expect that parents have to take more risk in their nest defence in low quality environment keep the hungry nestling quiet. As a consequence the call rate and the direct mobbing

rate are expected to be higher in smaller forest fragments. The distance of the defending parents from the predator should be shorter in lower quality forest patches, because noisy offspring have to hear parents' callings.

The Eurasian treecreeper tries to avoid physical contact with biting and acid spraying red wood ants, which also forage on tree trunks and wander tree trunks to their aphid cattle (the sub-order *Aphidodea*) to the top of trees. Red wood ants use partly the same food resources as treecreepers: invertebrates on tree trunks (e.g. Rosenberg & Sundström 1991). Both wood ants (Haemig 1994) and treecreepers (Kuitunen et al. 1996) consume the biomass invertebrates on tree trunks. Such interspecific competition for the same food sources have been shown to cause negative effects on the breeding performance of birds (Aho et al. 1997).

Therefore, interspecific competition with wood ants could have especially harmful effects on the physiology and body condition of treecreeper, because lack of food may result in chronic physiological stress (Nunez-de la Mora et al. 1996, Kitaysky et al. 1999). Further the stress from different environmental conditions experienced during ontogeny may have permanent consequences for morphological (e.g. Boag 1987, Newton 1989, Larsson & Forslund 1991, Haywood & Perrins 1992, Hõrak 1994, Potti & Merino 1996, de Kogel 1997) and life-history traits (Haywood & Perrins 1992, Bernardo 1993, Hõrak 1994, 2003, Gustafsson et al. 1995, Lindström 1999). Nutritionally based chronic stress may further decrease survival by decreasing growth and suppressing the immune system, gluconeogenesis and neuronal cell death (Wasser et al. 1997, Wingfield et al. 1997, Romero & Wikelski 2001). Especially in young vertebrates, chronically elevated physiological stress may impair growth and development (see reviews of Martin 1985, Sapolsky 1987).

In general, birds with high energy reserves may have higher fitness than birds with low energy reserves and the energy limitation of birds could influence life-history traits like body condition, reproductive investment, survivorship, parasite loads, or sexual displays (Green 2001 and referees within). Fat reserves are the most important source of stored energy of passerines (Blem 1990). An increase in fat reserves during cold periods may provide energy to stay warm overnight or during winter storms thereby reducing risk of starvation (e.g. Lahti et al. 1998). Alternatively, extremely high fat reserves may increase risk of predation through reduced manoeuvrability or increased exposure time (Lima 1986, Witter et al. 1994).

Fledging weight is considered to correlate with physical condition in avian species (Perrins 1991, Verboten & Visser 1998, Both et al. 1998, Saino et al. 1999; Redfern et al. 2000) and high body mass is known to be related to high nestling quality (Martin 1987). Heritability estimates of nestling weight are low and therefore nestling weight can be regarded as an estimator of a complex of traits affected by malnutrition. Low weight nestlings of great tits, *Parus major*, had low recapture rates and a lower chance of acquiring a territory (Tinbergen & Boerlijst 1990 and referees within).

In article VI, I explored the relationship between the amount of red wood ants and different life-history components of treecreepers by providing nest-

boxes in forest patches characterised by a gradient of red wood ant quantities. My purpose was to assess whether the red wood ant levels are related to nest-box occupancy rate, fecundity, individual body condition, and individually measured physiological stress in chicks. I expected that a high quantity of red wood ants near the nest box of treecreeper would decrease occupancy rate, fecundity, individual body condition of treecreepers and increases the physiological stress of nestlings.

## 2 MATERIALS AND METHODS

### 2.1 The passerine species

The Eurasian Treecreeper is a slit- or hole-nesting, monogamous, double-brooded and insectivorous (Suhonen & Kuitunen 1991a) passerine species (weight 9 g) that breeds throughout the northern coniferous zone. It prefers old-growth forest and its territory is rather large (10-20 ha) (Kuitunen & Helle 1988, Suorsa et al. 2004). It is specialised to search for its food on tree trunk and prefers the largest trunks in the forest (Suhonen & Kuitunen 1991b). In pale-arctic coniferous forests, the treecreeper is the only bird species belonging to the bark-foraging guild, with the exception of woodpeckers, (*Dendrocopos major*, *Dryocopus martius* and *Picoides tridactylus*). These species, however, differ greatly from treecreepers in their foraging pattern and preferred food items.

### 2.2 The study area

The materials presented in this thesis have been collected between 1990 and 1995 in the vicinity of Konnevesi Research Station in Central Finland (62°37'N, 26°20'E). In 1999-2003 we expanded the study area to the rural district of Laukaa. Treecreeper territories are covered mainly with coniferous forest of spruce *Picea abies* and pine *Pinus sylvestris*, with occasional birches *Betula pubescens* and *B. pendula*, aspen *Populus tremula*, grey alder *Alnus incana*, rowan *Sorbus aucuparia* and Goat willow *Salix caprea*. In our study area, treecreepers prefer to breed in specially-designed nest boxes (Kuitunen 1987). Each breeding pair of treecreeper had access to extra nest-boxes for a second breeding attempt.

## **2.3 General methods**

### **2.3.1 Routines at territories (I-VI)**

All the nest-boxes in territories were visited regularly throughout the breeding season to collect data on clutch initiation, clutch size, brood size, date of hatching and the fate of broods both for the first and second/late breeding attempts. Breeding males and females were caught during the early nestling stage and parents were marked individually with aluminium rings and their breasts were marked. Morphological characteristics such as wing, tarsus and bill lengths and body mass were measured. The approximate age of the parent birds was determined by plumage coloration and the sex of parents was established by incubation patch. The body mass of the nestling was measured and their subsequent fate was monitored by regular visits to the nest throughout the nesting period. In article II, the body mass of nestlings was measured twice, at 6-8 and at 12-14 d old.

### **2.3.2 Breeding data of seven years (IV)**

Breeding data was collected during the summer in each of seven years: 1990-1993, 1995, 1999, and 2000. The data was collected repeatedly from the same forest patches and thus individual forest patches were used as sampling units. Data on clutch size, brood, and the fate of the nest were collected for each nesting attempt. Some breeding pairs had two broods per year. We summed, on an annual basis, the total numbers of eggs laid, nestlings, fledglings, and destroyed nests for each forest patch. Then we calculated the mean fledgling production per year, the mean number of nestlings fledged per nesting attempt and year, the mean number of nestlings fledged per successful nesting attempt and year, and the proportion of nests destroyed by predators per forest patch over the 7-year study period.

### **2.3.3 Quality and physiological stress of nestlings (VI)**

The nestlings about to fledge were handled at the age of 14 days. Wing length was measured to 0.1 mm by the maximum method (Svensson 1992). Body mass was also measured. Subcutaneous fat in the abdomen and tracheal pit as well as the condition of the pectoral muscle were recorded on a five-point scale (0-4) (Gosler 1991, Kaiser 1993). The physiological stress in 9-day-old nestlings was measured by way of the Amersham radioimmunoassay of plasma corticosterone (RIA) kits (Biotrak rat corticosterone [<sup>125</sup>I]; Amersham, UK) in the summer of 2000 (see details in Suorsa et al. 2003).

### 2.3.4 Food abundance (II)

In article II, the data on food abundance, arthropods, on randomly selected tree trunks heights of 0, 5 - 1, 5 m in territories was gathered just after the first fledging by vacuum-cleaners (see Kuitunen 1989). The diameter of tree trunks has been shown to be a critical determinant of treecreeper foraging site selection (Suhonen & Kuitunen 1991b). Gleaning distance was about 50 m from the nest. Invertebrates >1 mm in size were identified to the family level. The mean number and body length of the food items on gleaned trees were used as an indicator of the amount of food on tree trunks in each territory. The diameters of the trunks were measured and the results later were subsequently summarized as prey per square meter.

### 2.3.5 Food abundance after prey depletion

In order to determine foraging pressure on tree trunks, we observed the parent birds foraging behaviour in marked squares (25 x 25 m) at a short (10m) and long distance (90 m) from the nest, when the nestlings were near fledging. Immediately after fledging, we measured the remaining food abundance on a sample of tree trunks near (10 m) and far (90 m) from the nest. All arthropods, mostly spiders, longer than 1 mm were collected and identified to family level and their length was measured.

### 2.3.6 Ant levels of territories (II)

We counted the number of *Formica* -ant mounds that exceeded a height of 25 cm within 100 m of the treecreepers' nest boxes in each breeding territory. Each territory was classified as being either (1) with ants, if the territory contained at least one ant mound or (2) without ants.

### 2.3.7 Ant levels of territories (VI)

In Finland, the *Formica rufa*-group includes the species of *F.aquilonia*, *F. lugubris*, *F. polyclena* and *F. rufa*. Identification of species was made with the key of Collinwood (1979) based on the relative abundance of hairs on different body parts. The red wood ant levels were measured around 146 nest-box pairs. We located all the nest mounds and measured their basal diameter to the nearest 0.01 m within a radius of 50 m from the treecreepers nest. The total basal areas of the nest mounds ( $\Sigma$  m<sup>2</sup> varying from 0 to 12.41, mean  $1.95 \pm 2.74$  s. d., n = 146) were used as an estimate of the red wood ant abundance around the nest-boxes. The basal area of a nest mound has been shown to correlate well with the number of worker ants in *Formica* species (Deslippe & Savolainen 1994, Liautard et al. 2003).

### 2.3.8 Nest defence (III, V)

Treecreeper nest defence behaviour was studied using 15 pairs of the early brood (17 May–3 June, 1991) and 17 pairs of the late brood (14 June–14 July, 1991). Only seven of the pairs altogether bred twice during the same breeding period. In 1992 we studied seven new pairs of the early brood (4–8 June) and six new pairs of the late brood (7–13 July). In article V, I used data from only 15 early brood pairs.

Nest defence measurements were done when the nestlings were 13–15 days old, i.e. a few of days before fledging. At this age nestlings are quite vulnerable to predators, because they are generally noisy (personal observation). The predator model, great spotted woodpecker, was wired to a one-metre-long wood stick and put up at the front of the nest box about 20 cm away from the two side entrance holes. Observations were made from a shelter with the naked eye or binoculars at a distance of 10–40 m from the nest on sunny or cloudy days, but not on rainy days. Data were recorded into a dictaphone and later transcribed. We started each measurement period (trial) as soon as we saw or heard one of the parents was calling, to be sure that it had noticed the predator. The tape-recorded measurement period lasted for 5 minutes. Generally, the arrival time was different for the male and female, so the trial was performed separately for both parents. Arrival time was the time from setting up the predator model until the parent arrived and started to display.

### 2.3.9 Landscape structure (IV, V)

The land-use and forest data of the study area and location of each treecreeper territory were imported to a Geographical Information System (GIS). The landscape structure was measured within 500 m radii when the breeding success in seven years was studied and within two hundred meters radii around the nest-boxes when the nest defence was studied. We used classified Landsat TM five satellite images produced by National Land Survey of Finland (NLS) from the year 1990 as the land-use and forest-resource data (Vuorela 1997). Pixels originally measuring 30 m × 30 m were re-sampled to measure 25 m × 25 m by NLS. Digital maps of roads, agricultural land, etc. were used to separate forest and non-forest land from each other. Each pixel in NLS classification can initially belong to one of 50 land use and forest classes. In the case of forested areas, each pixel was classified according to the total timber volume (mainly applying 50 m<sup>3</sup>/ha intervals) before being further classified according to the main tree species or mixed species composition.

Clear cuts and sapling stands were separated as distinct classes by allowing a maximum timber volume of 4 m<sup>3</sup>/ha for clear-cuts and 12 m<sup>3</sup>/ha for sapling stands (Vuorela 1997). According to the national forest inventory, this definition refers to sapling stands of 1–20 years old. Mature forest area was calculated by combining the area of forest land where total timber volume was > 151 m<sup>3</sup>/ha (Tomppo et al. 1999). Thus, the identification of mature forest stand

is based on the timber volume and not, for example, on the management status of the stand. However, we find this criterion reasonable since, according to the national forest inventory, forests in the age class of 101-120 years have an average timber volume of 201 m<sup>3</sup>/ha in the study area. Further, an intensive forest management in this area with clear-cutting as the main regeneration method mainly concerns forests >100 m<sup>3</sup>/ha in timber volume.

The habitat classes used in the analyses to describe the landscape structure at the radii of 200 m were lake (3.5%), open mire (0.0%), agricultural field (11.1%), clear-cut (4.8%), open land (combined to forestless habitat, 22.8%), wet spruce forest (1.3%), pine mires (0.7%), sapling stands (3.3%), pine forest (14.5%), spruce forest (34.8%), deciduous forest (2.1%) and mixed forest (20.5%). We also measured the forest patch density (7.4/100 ha), mean patch size (16.3 ha), mean shape of forest patches (1.99), mean nearest-neighbour distance of patches (35.0 m), forest-open land edge density (119.8 m/ha), and the size of a home patch (forest patch where nest-boxes were situated, 43.9 ha) using FRAGSTATS (McGarigal & Marks 1995).

## **3 RESULTS AND DISCUSSION**

### **3.1 Prey depletion made by treecreeper**

Treecreepers removed about half of their prey stock (mostly spiders) from tree trunks near the nest during the first brood, but on less frequently used tree trunks far from the nest (90m), prey depletion was not as strong. On the contrary, food abundance on tree trunks should generally increase in territories of treecreepers as the breeding season progresses (Kuitunen et al. 1996, Suorsa et al. 2003). Furthermore, the number of red wood ants had a negative effect on the number of other invertebrates on a single tree. Amount of ants, however, can not explain the difference in arthropod numbers near and far from the treecreepers nest as the mean number of ants did not differ between within distance from the nest.

### **3.2 Breeding time, clutch size and territory quality**

According to my study, red wood ants affect the breeding performance of Eurasian treecreepers. Treecreepers breeding in territories with ants laid their first clutches later, and produced fewer fledglings with lower body mass at the nestling stage compared to pairs breeding in territories without ants. The second clutches in territories with ants were smaller. The clutch size of treecreeper is largest when laid around mid-May (Kuitunen 1987), and thereafter the mean clutch size decreases. Thus, clutch size varied throughout the season and follows a concave quadratic distribution. Food abundance of treecreeper was higher during the second clutch, but the overall availability of food was lower in territories with ants. Earlier laying date of second clutches in territories without ants may be an affect of more abundant food in these territories than in ones with ants. Delayed breeding can cause negative fitness consequences, e.g. it could lower post-fledging survival (e.g. Perrins 1979,

Verhulst & Tinbergen 1991). Survival prospects of treecreeper young produced in no-ants territories may be better than for those young born later in territories with ants.

### **3.3 Effects of ants on breeding success**

Single-brooded pairs in territories with ants and poor food conditions produced nestlings with lower body mass than pair in territories without ants. Seasonal change in food supply was mostly a result of an increase in the invertebrate abundance in territories without ants, whereas in territories with ants the food abundance was constantly at a low level during the whole breeding season. Thus, nestling growth was poorer in ant territories irrespective of hatching date. In our earlier experiments, it was shown that ants can alter the foraging behaviour of treecreepers by excluding them from the best foraging sites (Aho et al. 1997). Ants may decrease the body mass of treecreeper offspring indirectly through food depletion and, furthermore, direct interference by ants can change the foraging behaviour of parent treecreepers.

### **3.4 Breeding success and habitat structure**

The long-term breeding success of the Eurasian treecreeper (seven years) was dependent on habitat structure. Breeding success was greater and less variable in mature forest areas and lower and more variable in areas with high proportions of young saplings stands. This difference was due to the high nest predation rate in territories with low proportions of mature forest. Nest predation was the major source of nestling mortality and explained about half of the between-year variation in breeding success. Nest predation is the major cause of nest failures in passerines and it can significantly affect an individual's fitness, survival rate and lifetime reproductive success (e.g. Martin 1995). In the case of short-lived species such as the treecreeper, the role of a safe breeding territory, with low probability of predation, for successful breeding is especially important.

Small mustelids especially are responsible for the high nest predation rate for increased year-to-year variability in the breeding success of the treecreeper. Nest predation is observed to be an important component when separating source-sink habitats (Pulliam 1988, Vierling 2000). Habitats that suffer from human related fragmentation likely function as sinks with high mortality due to nest predation, whereas large undamaged habitats could represent source populations with high breeding success.

In territories where the proportions of mature forest in the landscape were over 60%, nest predation was significantly lesser, and correspondingly,

breeding success was higher than in the nest sites in territories below this threshold. Thus, it seems that the intensity of harmful interspecific interactions, such as nest predation, may depend on degree of habitat alteration.

Reproductive success plays an essential role in the long-term persistence of animal populations in the environment. There is evidence that populations of old-forest bird species, including the Eurasian treecreeper, can show marked temporal variation in abundance even in moderately fragmented forest landscapes (Jokimäki et al. 2000). High quality habitats can improve the chances of population persistence by favouring large and less variable reproductive success, reducing mortality and creating population surplus.

### **3.5 Nest defence behaviour of adult treecreeper**

Nest defence behaviour of treecreeper does not appear to be very active. The most important trait of their nest defence is a high-pitched narrow frequency "tjii"-alarm call, which silences the nestlings in the cryptic nest normally located in a tree crevice or between the bark and the tree trunk. Consequently, it could be assumed that birds with cryptic nests should defend their offspring less than birds with open nests (Montgomerie & Weatherhead 1988). The alarm-calls of treecreepers are difficult to detect and, in addition, the tree-trunk coloured treecreeper is hard to observe in thick spruce forest. Treecreeper use these alarm calls to silence nestlings, like many other bird species (Grieg-Smith 1980, East 1981, Knight & Temple 1986) rather than immediately engaging in active nest defence. Parents with high-pitched alarm-calls do not expose the nest or themselves to a predator nearby. Over 90% of nests were silenced by the calls of one or both treecreeper parents. Thus, parents have done enough to defend their nest, if they can silence their offspring from far away before a predator gets too close to the nest and finds it.

My nest defence study was done during the nestling phase when nest defence activity was assumed to be the strongest and the nestlings are most valuable because of their age (Andersson et al. 1980, Grieg-Smith 1980, Montgomerie & Weatherhead 1988). Two weeks old nestlings of treecreepers are very noisy and almost ready to fledge. As a consequence, they are most vulnerable to predators like stoat, least weasel and great spotted woodpecker at this age. Thus in this phase of breeding, effective nest defence by parents is required.

Male and female treecreepers defended their nest in the same pattern for the first, early brood according to the monogamous biparental care predictions, but on the second, late brood the male was absent in 83% of cases. The monogamous female treecreeper incubates eggs alone (Kuitunen 1987) and also feed nestlings more than the male (Kuitunen et al. 1996). We found only one significant difference in nest defence between mates, if both of them had taken part in the nest defence. The average distance of females to the predator model

was shorter than that of males for the early brood. Males and females arrived near the nest at about the same time.

The nest defence intensity of an individual bird compared to two birds could influence the risk taking of parent birds. If a pair is twice as effective as one bird alone, then the parents, or perhaps even more individuals of the same species, should work together. If a pair is less effective than one bird, then one member of the pair could invest its energy elsewhere e.g. to foraging. This situation has been observed in tree swallows *Tachycineta bicolor* (Winkler 1992). One parent could be absent, when the needed intensity of nest defence is mild. Predators can indirectly decrease nest defenders' fitness, for example, if there is an energy or time cost or if the disturbance by the predator decreases the survival of nestlings or the defender itself (Wheelwright & Dorsey 1991). There is a limited amount of food on tree trunks early in spring during the first brood (Kuitunen 1989, Kuitunen et al. 1996). Females can not find enough living spiders and insects to feed the brood alone. This could be the most important reason for the presence of males during the first brood. The increased amount of food enables females to be unaided in feeding the young later in summer.

The earliest produced offspring in treecreepers are likely to be the most valuable based on recruits (Kuitunen 1987). Earlier produced offspring may have a better possibility to survive to the next breeding season than the later ones, which do not have enough time to grow before migration or a cold winter period. This could also be a reason, why male are absent for the second and the late brood. Also, males might join the first fledged broods and protect these more valuable offspring by giving alarm calls and also lead fledglings to better foraging areas.

Females showed few differences in their nest defence behaviour between the early and the late brood. The only exception was the minimum approach distance from the predator model was on average shorter for the early brood than for the late brood. The arriving time of females for nest defence for the early brood was an average 83 seconds longer than on the late brood. The differences in arriving time of females between broods could be explained by the longer foraging time in May when the food supply was lower than later in summer. The nest defence behaviour of males did not differ between the broods if the male was present.

### 3.6 Nest defence and habitat loss

Noiseless, well-fed nestlings in larger forest environments could be easier to silence when this could be done from a longer distance from the nest than in poor quality small forest fragments with hungry and stressed nestlings (see also Suorsa et al. 2003). There were some effects of landscape structure. Treecreeper females had longer calling distance in larger forest patches and when there were more fledged offspring. Treecreepers use warning calls to silence their nestlings (see article III) as I expected parents have to take more risk in their nest defence in smaller forest patches to keep hungry nestlings quiet because it is more difficult for noisy offspring to hear the alarm-calls of their parents. Accordingly, I found that in larger forest patches females had a longer average distance from the nest with more fledglings than females in a smaller forest fragment with fewer fledglings.

Many larger old-growth forest-dwelling bird species, for example goshawk *Accipiter gentilis* and black woodpecker *Dryocopus martius*, can survive in fragmented fine-grained habitats by having large territories with many patches of forest per territory (Widen 1989, Tjernberg et al. 1993, see also Forsman et al. 1984, Wegge & Rolstad 1986). Treecreeper, however, seldom flies over wide open areas (>100 m) during the breeding season and large territories could be very costly to defend and control, especially for males, in fragmented, fine-grained forest habitats (Suhonen & Kuitunen 1991ab, Kuitunen et al. 1996, Aho et al. 1997, Suorsa et al. 2003, Huhta et al. 2004).

Within populations of passerine ovenbird *Seiurus aurocapillus*, males paired better in a contiguous forest farther from edges than in fragments created by agriculture and forestry (Bayne & Hobson 2001). Female ovenbirds seem to avoid pairing with males near edges, because nest predation and brood parasitism near edges in small farm land fragments is higher than continuous and larger forest areas (Van Horn et al. 1995, Burke & Nol 1998, Bayne 2000, Hobson & Bayne 2000).

The greatest weakness of this study was that treecreeper territories were in similar kinds of coniferous and mixed forest patches in our study area, and forest fragmentation was about the start in our study area in 1990. Also, the anxious calls of nestlings should surely increase the nest defence, for example the mobbing rates. We sometimes noticed that treecreeper parents displayed injury feigning if the nestling screamed in our hands. But silence alarm calls of treecreeper could partly explain why landscape structure had only minor effects on direct nest defence behaviour of treecreepers.

### 3.7 Red wood ants and body condition of treecreeper nestlings

We found evidence that the quality of treecreeper nestlings was affected by the amount of red wood ants. The body mass of nestlings were lighter, subcutaneous fat content was thinner and tarsus length was shorter when the quantity of red wood ants was higher. On the other hand, the amount of wood ants had no significant effect on wing length. Also, there was no significant relationship between the wood ant level and nest-box occupancy, fecundity (clutch size) or physiological stress of nestlings.

Fat reserves are considered to be the most important source of stored energy of passerines (Blem 1990), and fat reserves can dynamically change throughout the day (Cresswell 1998). Great tits with a relatively, rather than absolutely, higher mass at fledging stage have a higher probability of recruiting into the breeding population (Both et al. 1998). Light fledgling condition can affect future reproductive effort. For example, smaller blue tits *Parus caeruleus* lost more mass during breeding than larger ones, and females with low incubation masses deserted their clutches more often than heavier ones (Merilä & Wiggins 1997). Potti et al. (2002) showed that natural selection on fledging viability in a population of pied flycatcher *Ficedula hypoleuca* acted directionally on weight but not on tarsus length, a measure of skeletal size (Senar & Parcial 1997), or on hatching date. Lombardo et al. (1996) found a negative correlation in tree swallow *Tachycineta bicolor* between both tarsus length and mass with the presence of *Salmonella shigell* and other enteric bacteria.

In coal tits *Parus ater* some morphological characters, like relative tarsus length, developed early in life were significantly associated with juvenile recruitment, so early developmental conditions may influence individual fitness well beyond the post-fledging period. Further, relative tarsus length and body condition were positively associated with the probability of individuals becoming residents within the native area during winter. This indirectly shows that morphology may affect the social status of juvenile during winter (Brotons & Broggi 2003).

Body mass is partly a measure of body size and partly a measure of condition, and seems to be more sensitive than tarsus length to environmental variation (Keller & van Noorwijk 1991 and references therein). In great tits nestling, body mass and condition were significantly reduced at heavily polluted site when nestlings were exposed to large amount of heavy metals (Janssens et al. 2003). In European starling *Sturnus vulgaris*, the growth rate of an offspring feather character, but not final mass or tarsus length, tended to be related to the availability of pasture, the loss of which seems to be one reason for the decline of starlings' populations (Smith & Bruun 2002).

In titmice *Parus sp.*, the reproductive system is considered to be adapted mainly to the quick seasonal changes in food availability (the so called the caterpillar peak), since energy supply is a very important determinant of nestling growth and condition (e. g. Perrins 1991, Naef-Daenzer & Keller 1999,

Naef-Daenzer et al. 2001). But treecreepers are independent from this kind of caterpillar peak, because the number of arthropods on tree trunks increases as the summer advanced (Kuitunen et al. 1996).

In the collared flycatcher *Ficedula albicollis*, mass at fledging is determined to a great extent by the environment and not by the additive effects of genes (Alatalo et al. 1990). Fledging mass in the great tit may show heritability of a moderate but significant magnitude (van Noordwijk et al. 1988, Linden et al. 1992). Larger males (as determined by tarsus length) had larger song type repertoires, and males with longer wing chords fledged more young (Dussourd & Ritchison 2003).

France young flamingos *Phoenicopterus ruber roseus* with higher mass and longer tarsus length have higher dispersal probabilities than individuals in poor condition (Barbraud et al. 2003). Shmutz (1993) showed that heavy goslings of emperor geese, *Chen canagicus* had significantly higher survival than goslings of smaller mass between late pre-fledging and arrival on fall staging areas. Therefore, consideration of fledging success alone might be insufficient to predict demographic patterns correctly as inter-annual variation in body condition at fledging can affect demographic parameters. It was also found that pre-fledging body mass of barnacle geese *Branta leucopsis* was positively related to juvenile survival in the winter (Owen & Black 1989).

Suorsa et al. (2003) found evidence that the concentration of plasma corticosterone nestlings of Eurasian treecreepers were higher with a poor food supply in a dense, young forest than in a sparse, old forest. In addition, the nestlings in large forest patches had lower corticosterone levels and a better body condition than in small forest patches. In this study we did not find that nestlings of treecreeper were more stressed with a higher amount of red wood ants near the nest. Thus, we can infer that forest quality has stronger effect on the physiological condition of nestlings than wood ants have.

The ecological role of red wood ants and their long-lasting societies is especially remarkable in northern forests, and is exemplified by their ecological importance in mature taiga (Rosengren et al. 1979, Savolainen & Vepsäläinen 1988, Savolainen et al. 1989, Puntila et al. 1991, 1994, Laakso & Setälä 2000). Haemig (1996) compared the effects of interference competition on the foraging behaviour of distantly-related taxa, *Formica aquilonia* and great tits, and he found that great tits visited trees without ants more frequently and for longer time than trees with biting ants. Biomass of arthropod prey for birds is greater in trees from which wood ants have been excluded (Haemig 1994, Skinner & Whittaker 1981), and the numbers of arthropods increases with distance from the ant mound as wood ant density decreases (Laine & Niemelä 1980).

Treecreeper tries to avoid physical contact with red wood ants on tree trunks (personal observation). Thus, ants are able to interfere with treecreepers, yet treecreepers are unable to exclude ants from tree trunks. Here I can conclude that the quality of treecreepers nestlings, measured with body mass, subcutaneous fat and tarsus length (skeletal size), was negatively affected by the amount of red wood ants. Thus the presence of ants could decrease the fitness and survival of young treecreepers. The poorer body condition of these

treecreepers could decrease the probability of an individual being recruited into the breeding population, its future reproductive effort, and its probability of becoming a resident within the native area during winter. Thus early conditions may simply have an influence on individual fitness extending beyond the post-fledging period. On the other hand, the amount of wood ants had no significant effect on morphological characters like wing length and there were also no significant relationships between the wood ant level and nest-box occupancy, fecundity (clutch size) or physiological stress of nestlings. A reason for this could be that the natural amount of red wood ants in the forest is seldom so high enough to deplete all invertebrate resources from other insectivores.

The time of laying eggs in a season is one of the most important determinants of reproductive success and fitness in birds (for example Svensson 1997, Visser & Verboten 1999). When treecreepers choose their territories in winter or early in spring, they likely cannot determine the abundance of wood ants under snow cover. Treecreepers lay eggs especially early for an insectivorous passerine species. Early breeding could be one way to avoid competition with wood ants, because wood ants can not climb trees when air temperatures within the forest are at low levels early in May.

To conclude, the amount of red wood ants (radius of 50 m) was not associated with the occupancy rate of nest-boxes over the five-year study period. Similarly, neither the clutch size nor the number of fledged young was related to the amount of wood ants during 1999-2000. By contrast, the high wood ant levels were adversely associated to some individual quality measurements such as body mass, subcutaneous fat content and tarsus length at fledging. The condition of pectoral muscle seemed to be related to the quantity of wood ants differently between the study years 1999-2000. Yet, when the years were analysed separately no significant effect of wood ant was found on muscle condition. Additionally, wing length and physiological stress, assessed by way of plasma corticosterone, have not affected by wood ants.

## 4 CONCLUSIONS

There exists interspecific, mainly exploitative, competition even between such dissimilar taxa as ants and birds (see also Aho et al. 1997). This interphylum competition can lower the reproductive success of birds, in our case Eurasian treecreepers. One of the most important mechanisms by which this occurs seems to be food depletion on tree trunks. Treecreepers begin their breeding very early in the spring, when the forest floor is covered by snow and the ants are not yet active. Therefore, treecreeper may not be able to detect the presence of ants in their territory, and thus it may be impossible for them to predict the impact of ants on the territory quality.

There was a significant difference in the remaining arthropod abundance between trees frequently and seldom-visited. On tree trunks close to the nest, treecreepers removed about half of the prey stock, especially spiders and other small arthropods, compared to the less frequently used tree trunks located far from the nest. However, the arthropod consumption by treecreepers was not size selective and this seems to be meaningful in limited food conditions when the chances for being selective are limited, and prey choice may be costly in terms of energy expenditure and time loss (e.g. Martin 1987, 1995; Hakkarainen et al. 1997)

Treecreepers breeding in territories with ants laid their first clutches later and produced fewer fledglings with lower body mass at the nestling stage compared to the pairs breeding in territories without ants. In addition, of the pairs that bred twice in the same territory during the same breeding season, those breeding in territories with ants laid smaller second clutches than pairs in territories without ants. Food abundance was higher during the second broods, but the overall availability of food was lower in territories with ants. The inter-brood interval was 2, 5 d longer in territories with ants than ones without ants, which explains the significant difference in the laying dates of second broods. The survival and fecundity of treecreeper offspring from ant territories may be further reduced by their low fledging mass. Lower food abundance may have mediated higher nestling mortality via malnutrition in territories with ants.

Direct nest predation, eating or harassing treecreeper nestlings by ants is rarely observed.

Forest landscape can have an impact on the interactions between birds and nest predators. There is evidence that populations of old-forest bird species like Eurasian treecreeper can show marked temporal variation in abundance even in moderately fragmented landscapes. Breeding success of treecreepers was greater and less variable in areas with a high proportion of mature forest and more variable in woodland. The high proportion persistence was favoured through large and less variable reproductive success, reducing mortality, and creating population surplus.

Male and female treecreepers defended their nests in the same pattern during trials on the first or early broods according to the monogamous biparental care predictions, but during trials on the second or late broods, males were absent in 83% of the cases. The nest defence of treecreepers consists of high-pitched, narrow frequency alarm calls. These calls are difficult to locate, and treecreepers are hard to observe in thick spruce forests. At the same time, the nestlings in the cryptic nest become quiet. I have shown that over 90% of nests were silenced by one or both parent treecreepers. The male Eurasian treecreeper seems to be mostly useless in nest defence on the second, late brood, because one parent is enough to silence offspring in the nest for this brood. Because one parent is enough to silence offspring in the nest, this observation is in accordance with the silence and the effectiveness hypotheses. The actual reason for the absence of males during the second, late brood could be increasing food quantity on tree trunks during this time.

There were some effects of landscape structure on the direct nest defence behaviour of female treecreeper. In larger forest patches, females have a longer average distance from the nest with more fledglings than female in a smaller forest fragment with fewer fledglings. This is because noisy and hungry nestlings may not hear the alarm calls of parents in the long distances in the smaller, lower quality forest fragments.

Exploitative competition between ants and treecreepers may have considerable and adverse influences on the nestling quality as measured by body mass, subcutaneous fat and tarsus length. On tree trunks, foraging red wood ants may decrease the fitness of treecreepers since the poorer body condition of nestlings has the potential to impair recruitment into the breeding population and thus negatively affect their future reproduction.

## *Acknowledgements*

It was great honour and pleasure for me working with birds in the forest of my home landscapes and nearby in Konnevesi. Since I was seven I always liked to be in wooden areas of Rautalampi searching for bird nests and late in summer searching for ordinary and less-ordinary "caterpillars" or other insects. Without interest in birds and other living animals and plants, I would hardly have had the interest to take this hard professional journey. So I deeply hope that the knowledge of this study will be profitable in protecting and conserving of Finnish and other parts of boreal forests and in research of interspecific relationships. First, I want to thank local birdwatchers of Rautalampi: Hannu Siikavirta, Esko Vesanen, Kauko Sikström and Jorma Knuutinen from the great motivation to my hobby. And special thanks to my biology teacher Eila Karki, who educated and supported me in early in my career.

Let's go to the beginning of this project. At first, I want to thank my friend Päivi Lundvall (Palokangas) who introduced me to my supervisor Markku Kuitunen, who needed a birdwatcher for his treecreeper project. It was good for me that Markku made my interest in birds more scientific. Without Markku's patience and humanity my thesis was undone during these years. I started in Markku's team in the spring of 1990 at the Konnevesi Research Station, which provided an excellent environment for the field work. Early in 1990, the mature forest areas in Konnevesi were much larger than today. The Research Station also had very friendly personnel: Jussi Viitala, Antti Sirkka, Helvi and Mirja Poikolainen, Risto Latvanen ... and so many other persons that I can't remember all their names. Personnel were always helpful when I needed any help in the field and the laboratory or when I needed someone to talk to. Then, I want to give the great thanks to the other member of Markku's group in years 1990-95: Teija Aho, Tomi Hakkari and Jukka Suhonen. The work was sometimes heavy, and so were the evening parties and nights too, but nowadays these are only old good memories. And thanks to everyone who was there when it happened most. There are so many names that writing them down that I would have to waste "hundreds of pages".

Some years went by without working on this project. In 1999, Harri Hakkarainen from the University of Turku wanted to give some lights to my doctoral thesis and so started the Academy project with forest fragmentation and treecreepers. This work is done partly with Esa Huhta and Petri Suorsa from the University of Turku. Working with these guys was not easy, but many thanks to them anyway. Then, I want to thank Ari Nikula and Outi Lehtinen, who kindly helped us with the use of Landsat-data and Fragstat-program. I have to give some special thanks to the field workers Heikki Helle and Jouni Sorvari during past years. I thank also the Academy of Finland and the University of Jyväskylä for financial support. Many thanks for Anders Møller and Gerald Niemi for constructive comments of on my thesis.

I owe my greatest thanks to my close relatives and family: Anna Bagge, Aurora, Vanessa and Helinä. Then I want to thank my relatives (mum-Helga,

Olavi, Tuula, Hannu, Henna & Virpi), "parents-in law" Barbro & Pauli, all neighbours during these years, especially Anu & Hannu, and friends for taking care of my children during these years.

## YHTEENVETO

### **Lajienvälisten suhteiden vaikutus puukiipijän pesintämenestykseen metsäympäristössä**

Lajienvälistä kilpailua on tutkittu jo pitkään. Tässä väitöskirjassa selvitetään pääosin ravinnosta johtuvaa lajienvälistä kilpailua kekomuurahaisten ja puukiipijän välillä. Toisena teemana on predaation eli petojen, lähinnä karpän, lumikon ja käpytikän, aiheuttama rasite puukiipijän pesintämenestykseen. Tärkeimpänä kilpailuun vaikuttavana tekijänä näyttää olevan ravinnon riittävyys puun rungoilla. Puukiipijä aloittaa pesinnän "hyönteissyöjäksi" poikkeuksellisen varhain keväällä huhtikuussa lumen ollessa vielä maassa. Tällöin muurahaiset ovat vielä hangenkuoren alla, eikä lyhytikäinen puukiipijä luultavimmin tiedä, kuinka suuri määrä muurahaisia hangen alla talvehtii kullakin metsäkuviolla.

Muiden aikaisempien tutkimusten perusteella muurahaiset vähentävät oleellisesti puissa ja maassa liikkuvia muita selkärangattomia. Väitöskirjani I artikkelissa olen osoittanut myös puukiipijöiden vähentävän pesinnän aikaan ensimmäisellä poikueella oleellisesti selkärangattomia, etenkin hämähäkkejä, puiden rungoilla pesän lähetyvillä (alle 50 m). Puukiipijän ravinnon hankinta ei ollut kokovalikoivaa, mikä onkin rationaalista olosuhteissa, joissa ravinnon määrä on rajallista. Aiemmin on myös osoitettu, että selkärangatonmäärät puiden rungoilla ensimmäisen poikueen aikaan ovat vähäisempiä kuin myöhemmin kesällä.

Toisessa artikkelissa nähdään, että puukiipijän pesintä alkaa muurahaisreviireillä muutamaa päivää myöhemmin, lentopoikasia tuotetaan vähemmän ja poikaset ovat kevyempiä kuin reviireillä, joilla ei ole kekomuurahaisia. Poikasten pienempi paino voi vähentää poikasten hengissä säilymistä ja hedelmällisyyttä, kuten monilla varpuslinnuilla on osoitettu.

Metsärakenteella voi olla suuri vaikutus lajienvälisiin suhteisiin pesivien lintujen ja petojen välillä. Puukiipijän pesintämenestys on suurempi ja vähemmän vaihteleva suurissa yhtenäisissä metsäsaarekkeissa kuin pirstoutuneessa ja pienemmissä metsäsaarekkeissa, joten puukiipijäkannan säilymiseksi yhtenäiset ja laajat metsäalueet ovat pitkällä aikavälillä tärkeitä, ja ne muodostavat perustan myös pienempien saarekkeiden puukiipijäpopulaation uusiutumiselle.

Puukiipijäemojen pesäpuolustuskäyttäytymistä tutkittiin petomallikokeilla, jossa petona toimi täytetty käpytikka. Käpytikka on puukiipijän pesärosvo ja kykenee tuhoamaan myös kokonaisia pönttöjä pesimäkelvottomiksi puhumattakaan luonnonpesistä kaarnanrakosissa. Puukiipijän pesän puolustus koostuu enimmäkseen korkeista varoitusäänistä, joiden tarkoitus on hiljentää poikaset pesässä. Kevään ensimmäisellä poikueella koiras ja naaras puolustavat pesää pääsääntöisesti samalla tavalla. Toisella ja myöhemmällä poikueella koiras ei osallistunut pesäpuolustukseen suurimmassa osassa tapauksista.

Syynä tähän on olettavimmin parantunut ravintotilanne pesimäajan edetessä, jolloin naaras pärjää yksin ilman koiraan apua myös ruokinnassa, kuten aikaisemmissakin tutkimuksissa on todettu.

Metsämaisemarakenne vaikuttaa naaraan varoitteletäisyyteen. Naaraan etäisyys pedosta oli pidempi laajemmissa metsälaikuissa, koska pienimmissä laikuissa nälkäisten poikasten hiljentäminen oli vaikeampaa ja naaraan täytyy mennä lähemmäksi pesää, jotta poikaset kuulevat varoituksen.

Tutkimusteni ravintoresurssikilpailua (exploitative competition) esiintyy kekomuurahaisten ja puukiipijän välillä. Puiden rungoilla liikkuvat ja ruokailevat muurahaismäärät vähentävät puukiipijälle tärkeitä selkärangattomia puiden rungoilla ja näin heikentävät puukiipijän poikasten elinkelpoisuutta. Reviireillä, joilla oli paljon kekomuurahaisia, poikaset olivat kevyempiä, ihonalaista rasvaa oli vähemmän ja nilkat olivat lyhyempiä.

## REFERENCES

- Abrams, P. A. 1987. On classifying interactions between populations. *Oecologia* 73: 272-281.
- Aho, T., Kuitunen, M., Suhonen, J., Jäntti, A. & Hakkari, T. 1997. Behavioural responses of Eurasian Treecreepers, *Certhia familiaris*, to competition with ants. *Animal Behaviour* 54: 1283-1290.
- Alatalo, R.V., Eriksson, D., Gustafsson, L. & Lundberg, A. 1990. Hybridization between pied and collared flycatchers - sexual selection and speciation theory. *Journal of Evolutionary Biology* 3: 375-389.
- Amarasekare, P. 2002. Interference competition and species coexistence. *Proceedings of the Royal Society of London B* 269: 2541-2550.
- Andersson, M. Wiklund, C. G. & Rundgren, H. 1980. Parental defence of offspring a model and example. *Animal Behaviour* 28: 536-542.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794-804.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: a review. *Oikos* 71: 355-366.
- Askenmo, C., Brömssen, A. von, Ekman, J. & Jansson C. 1977. Impact of some wintering birds on spider abundance in spruce. *Oikos* 28: 90-94.
- Barnbaud, C., Johnson, A. R. & Bertault, G. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the Importance of body condition. *Journal of Animal Ecology* 72: 246-257.
- Bayne, E. M. 2000. Effects of forest fragmentation on the demography of Ovenbirds (*Seiurus aurocapillus*) in the boreal forest. Ph. D. dissertation, University of Saskatchewan, Saskatoon.
- Bayne, E. M. & Hobson, K. A. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: Importance of male age and floater behavior. *Auk* 188: 380-388.
- Begon, M., Harper, J. L. & Townsend C. R. 1990. *Ecology, individuals, populations and communities*. Blackwell, Oxford.
- Bernardo, J. 1993. Determinants of maturation in animals. *Trends in Ecology and Evolution* 8: 166-173.
- Birch, L. C. 2001. Classification of species interactions. In: C. J. Krebs (ed.) *Ecology: The experimental analysis of distribution and abundance*. 5th Edition. The University of British Columbia, - Benjamin Cumming, San Francisco, USA, 179-180.
- Blem, C. R. Avian energy storage. *Current Ornithology* 7: 59-113.
- Boag, P. T. 1987. Effects of nestlings' diet on growth and adult size of zebra finches (*Poephila guttata*). *Auk* 104: 155-166.
- Both, C., Visser, M. E. & Verboven, N. 1998. Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings Royal Society of London B* 266: 465-469.

- Brodmann, P. A., Reyer, H. U., Bollman, K., Schläpfer A. R. & Rauter C. 1997. The importance of food quantity and quality for reproductive performance in alpine water pipits (*Anthus spinoletta*). *Oecologia* 109: 200-208.
- Brotons, L. & J. Broggi. 2003. Influence of morphology on winter residence and recruitment in juvenile coal tits (*Parus ater*) after the post-fledging period. *Ecoscience* 10: 273-282.
- Brown, J. H., Reichman, O. J. & Davidson, D. W. 1979. Carnivory in desert ecosystem. *Annual Review of Ecology and Systematics* 10: 201-227.
- Burke, D. M. & Nol, E. 1998. Influence of abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115: 96-104.
- Burke, D. M. & Nol, E. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* 10: 1749-1761.
- Carpenter, F. L. 1979. Competition between hummingbirds and insects for nectar. *American Zoologist* 19: 1105-1114.
- Cody, M. L. (ed.) 1985. *Habitat selection of birds*. Academic Press, Orlando, Florida.
- Collinwood, C. A. 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 8: 1-174.
- Confer, J. L., Larkin, J. L. & Allen, P. E. 2003. Effects of vegetation, interspecific competition, and brood parasitism on golden winged warbler (*Vermivora chrysoptera*) nesting success. *Auk* 120: 138-144.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*. 122: 661-696.
- Cresswell, W. 1998. Diurnal and seasonal mass variation in blackbirds, *Turdus merula*: consequences for mass-dependent predation risk. *Journal of Animal Ecology* 67: 78-90.
- Deslippe, R. J. & Savolainen, R. 1994. Role of food supply in structuring a population of Formica-ants. *Journal of Animal Ecology* 63: 756-764.
- Dussourd, N. & Ritchison, G. 2003. Singing behavior of male yellow-crested chats: repertoires, rates, reproductive success, and a comparison with other wood-warblers. *Wilson Bulletin* 115: 52-57.
- East, M. 1981. Alarm calling and parental investment in the Robin *Erithacus rubecula*. *Ibis* 123: 223-230.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.
- Forsman, E. D., Meslow, E. C. & Wright, H. M. 1984. Distribution and biology of spotted owl in Oregon. *Wildlife Monograph* 87: 1-64.
- Gates & Gysel 1978. Gates, J. E. & Gysel, L. W. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology* 59, 871-883.
- Gill, F. B., Mack, A. L. & Ray, R. T. 1982. Competition between Hermit hummingbirds Phaethorninae and insects for nectar in a Costa Rica rain forest. *Ibis* 124: 44-49.

- Gosler, A. G. 1991. On the use of greater covert molt and pectoral muscle as measures of condition in passerines with data for the Great Tits *Parus major*. *Bird Study* 38: 1-9.
- Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82, 1473-1483.
- Grieg-Smith, S. W. 1980. Parental investment in nest defence by Stonechats (*Saxicola torquata*). *Journal of Biogeography* 17: 561-568.
- Gustafsson, L. 1987. Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis* an experimental demonstration. *Ecology* 68: 291-296.
- Gustafsson, L., Qvarnström, A. & Seldon, B. C. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature* 375: 311-313.
- Haemig, P. D. 1992. Competition between ants and birds in a Swedish forest. *Oikos* 65: 479 - 483.
- Haemig, P. D. 1994. Effects of ants on the foraging of birds in spruce trees. *Oecologia* 97: 35-40.
- Haemig, P. D. 1996. Interference from ants alters foraging ecology of great tits. *Behavioral Ecology and Sociobiology* 38: 25-29.
- Haemig, P. D. 1999. Predation risk alters interactions among species: competition and facilitation between ants and nesting birds in a boreal forest. *Ecology Letters* 2: 178-184.
- Haila, Y., Hanski, I. K. & Raivio, S. 1989. Methodology for studying the minimum habitat requirements of forest birds. *Annales Zoologici Fennici* 26: 173-180.
- Hakkarainen, H., Koivunen, V. & Korpimäki, E. 1997. Reproductive success and parental effort of Tengmalm's owls: effects of spatial and temporal variation in habitat quality. *Ecoscience* 4: 35-42.
- Hansson, L. 1992. Landscape ecology of boreal forests. *Trends in Ecology and Evolution* 7: 299-302.
- Hawes, C., Stewart, A. J. A. & Evans, H. F. 2002. The impact of wood ants (*Formica rufa*) on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in a Scots pine plantation. *Oecologia* 131: 612-619.
- Haywood, S. & Perrins, C. M. 1992. Is clutch size in birds affected by environmental conditions during growth? *Proceedings of Royal Society of London* 249: 195-197.
- Hobson, K. A. & Bayne, E. M. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed-wood of western Canada. *Wilson Bulletin* 112: 373-387.
- Hochberg, M. E. & Lawton, J. H. 1990. Competition between kingdoms. *Trends in Ecology and Evolution* 5: 367-371.
- Hörak, P. 1994. Effects of nestling history on adult size and reproduction in the great tit. - *Ornis Fennica* 71: 47-57.
- Hörak, P. 2003. When to pay the cost of reproduction? A brood size manipulation experiment in great tits (*Parus major*). *Behavioral Ecology and Sociobiology* 54: 105-122.

- Horn, M. A. van, Gentry, P. R. & Faaborg, J. 1995. Patterns of Ovenbird (*Seiurus aurocabillus*) pairing success in Missouri forest tracts. *Auk* 112: 98-106.
- Huhta, E. 1995. Effects of spatial scale and vegetation cover on predation of artificial ground nests. *Wildlife Biology* 1: 73-80.
- Huhta, E., Aho, T., Jäntti, A., Suorsa, P., Kuitunen, M., Nikula, A. & Hakkarainen, H. 2004. Forest fragmentation increases nest predation in the Eurasian Treecreeper. *Conservation Biology* 18: 148-155.
- Janssens, E., Dauwe, T., Pinxten, R., Bervoets, L., Blust, E. & Eens, M. 2003. Effects of heavy metal exposure on the condition and health of nestling of the great tit (*Parus major*), a small songbird species. *Environmental Pollution* 126: 267-274.
- Jokimäki, J., Huhta, E., Mönkkönen, M. & Nikula, A. 2000. Temporal variation of bird assemblages in moderately fragmented and less-fragmented boreal forest landscapes: A multi-scale approach. *Ecoscience* 7: 256-266.
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64: 246-255.
- Keller, L. F. & van Noorwijk, A. J. 1991. A method to isolate environmental effects on nestling growth, illustrated with examples from the great tit (*Parus major*). *Functional Ecology* 7: 493-502.
- Kitaysky, A. S., Piatt, J. F., Wingfield, J. C. & Romano, M. 1999. The adrenocortical stress-response of black-legged kittiwake chicks in relation to dietary restrictions. *Journal of Comparative Physiology B* 169: 303-310.
- Knight, R. L. & Temple, S. A. 1986. Why does intensity of avian nest defence increase during the nesting cycle. *Auk* 103: 318-327.
- Kodric-Brown, A. & Brown, J. H. 1979. Competition between distantly related taxa in the coevolution of plants and pollinators. *American Zoologist* 19: 1115-1127.
- Kogel, C. H. de. 1997. Long-term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. *Journal of Animal Ecology* 66: 167-178.
- Korpimäki, E. 1987. Dietary shifts, niche relationships and reproductive output of coexisting Kestrels and Long-eared Owls. *Oecologia* 74: 277-285.
- Kouki, J. & Väänänen, A. 2000. Impoverishment of resident old-growth forest bird assemblages along an isolation gradient of protected areas in eastern Finland. *Ornis Fennica* 77: 145-154.
- Kuitunen, M. 1987. Seasonal and geographical variation in the clutch size of Common Treecreeper *Certhia familiaris*. *Ornis Fennica* 64: 125-136.
- Kuitunen, M. 1989. Food supply and reproduction in the common treecreeper (*Certhia familiaris*). *Annales Zoologici Fennici* 26: 25-33.
- Kuitunen, M. & Aleknonis, A. 1992. Nest predation and breeding success on common treecreepers nesting in boxes and natural cavities. *Ornis Fennica* 67: 7-12.
- Kuitunen, M. & Helle, P. 1988. Relationships of the common treecreeper *Certhia familiaris* to edge and forest fragmentation. *Ornis Fennica* 65: 150-155.

- 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.
- Kurki, S. & Linden, H. 1995. Forest fragmentation due to agriculture affects the reproductive success of the ground-nesting black grouse *Tetrao tetrix*. *Ecography* 18: 109-113.
- Laakso, J. & Setälä, H. 2000. Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of boreal floor. *Annales Zoologici Fennici* 37: 93-100.
- Lahti, K., Orell, M., Rytönen, S. & Koivula, K. 1998. Time and food dependence in willow tit winter survival. *Ecology* 79: 2904-2916.
- Laine, K. J. & Niemelä, P. 1980. The influence of ants on survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. *Oecologia* 47: 39-42.
- Larsson, K. & Forslund, P. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. *Journal of Evolutionary Biology* 4: 619-636.
- Laverty, T. M., & Plowright R. C. 1985. Competition between hummingbirds and bumble bees for nectar in flowers of *Impatiens biflora*. *Oecologia* 66: 25-32.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67: 377-385.
- Linden, M., Gustafsson, L. & Pärt, T. 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology* 73: 336-343.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14: 343-348.
- Lombardo, M. P., Thorpe, P. A., Cichewicz, R., Henshaw, M., Millard, C., Steen, C. & Zeller, T. K. 1996. Communities of cloacal bacteria in Tree Swallow families. *Condor* 98: 167-172.
- Litauard, C., Brown, W. D., Helms, K. R. & Keller, L. 2003. Temporal and spatial variations of gyne production in the ant *Formica exsecta*. *Oecologia* 136: 558-564.
- Martin, C. R. 1985. *Endocrine physiology*. New York: Oxford University Press.
- Martin, T. E. 1986. Competition in breeding birds. On the importance of considering processes at level of the individual. *Current Ornithology* 4: 181-210.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review Ecological Systematics* 18: 453-487.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monograph* 65: 101-127.
- McGarigal, K. & Marks, B. J. 1995 FRAGTATS: Spatial pattern analysis program for quantifying landscape structure. General Technical Reports PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Merilä, J. & Wiggins, D. A. 1997. Mass loss in breeding blue tits: the role of energetic stress. *Journal of Animal Ecology* 66: 452-460.

- Møller, A. P. 1988: Nest predation and nest site choice in passerine birds in habitat patches of size; a study of magpies and blackbirds. *Oikos* 53: 215-221.
- Møller, A. P. 1991: Clutch size, nest predation, and distribution of avian unequal competitors in patchy environment. *Ecology* 72: 1336-1349.
- Montgomerie, R. D. & Weatherhead, P. J. 1988: Risk and rewards of nest defence by parent birds. *Quarterly Review of Biology* 63: 167-187.
- Morin, P. J., Lawler, S. P. & Johnson, E. A. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* 69: 1401-1409.
- Mykrä, S., Kurki, S. & Nikula, A. 2000. The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland. *Annales Zoologici Fennici* 37: 79-91.
- Naef-Daenzer, B. & Keller, L. 1999. The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology* 68: 708-718.
- Naef-Daenzer, B., Widmer, F. & Nuber, M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70: 730-738.
- Newton, I. 1989. *Lifetime Reproduction in Birds*. Academic Press, London.
- Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology and Management* 115: 127-134.
- Noorwijk, A. van, Balen, J. H. van & Scharloo, H. 1988. Heritability of body size in natural population of great tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genetical Research (Cambridge)* 51: 149-162.
- Nuez-de la Mora, A., Drummond, H. & Wingfield, J. C. 1996. Hormonal correlates of dominance and starvation-induced aggression in chicks of the blue-footed booby. *Ethology* 102: 748-761.
- Odum, H. T. 1983. *Systems Ecology: An Introduction*. Wiley, New York.
- Owen, M. & Black, J. M. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal of Animal Ecology* 60: 335-351.
- Perrins, C. M. 1979. *British Tits*. New Naturalist, Collins.
- Perrins, C. M. 1991. Tits and their caterpillar food supply. *Ibis* 133: 49-54.
- Potti, J. & Merino, S. 1996. Parasites and the ontogeny of sexual size dimorphism in passerine bird. *Proceedings of the Royal Society of London* 263: 9-12.
- Potti, J., Dávida, J. A., Tella, J. L., Frias, Ó. Villar, S. 2002. Gender and viability selection on morphology in fledgling pied flycatchers. *Molecular Ecology* 11: 1317-1326.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.

- Punttila, P., Haila, Y., Pajunen, T. & Tukia, H. 1991. Colonisation of clearcut forest by ants in the southern Finnish taiga: a quantitative survey. *Oikos* 61: 250-262.
- Punttila, P., Haila, Y., Niemelä, J. & Pajunen, T. 1994. Ant communities in fragments of old-growth taiga and managed surroundings. *Annales Zoologici Fennici* 31: 131-144.
- Redfern, C. P. F., Slough, A. E. J., Dean, B., Brice, J. L. & Hope, J. P. 2000. Fat and body condition in migrating Redwings *Turdus iliacus*. *Journal of Animal Ecology* 31: 197-205.
- Robinson, S. K., Thompson III, F. R., Donovan, D. R., Whitehead, D. R. & Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Rolstad, J. & Wegge, P. 1989. Capercallie *Tetrao urocallus* populations and modern forestry - a case for landscape ecological studies. *Finnish Game Research* 46: 43-52.
- Romero, L. M. & Wikelski, M. 2001. Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Niño events. *Proc. Natl. Acad. Science USA*. 98: 7366-7370.
- Rosengren, R. & Sundström, L. 1991. The interaction between red wood ants, *Cinara* aphids and pines. A ghost of mutualism past? In: C.R. Huxley, C. R. & Cutler, D.F.(eds), *Ant-plant interactions*: 80-91. Oxford University Press, Oxford, UK.
- Rosengren, R., Vepsäläinen, K. & Wuorenrinne, H. 1979. Distribution, nest densities, and ecological significance of wood ants (the *Formica rufa*-group) in Finland. *O. I. L. B. Bulletin SROP II*, 3: 181-213.
- Saino, N., Calza, S., Ninni, P. & Møller, A. P. 1999. Barn Swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* 68: 999-1009.
- Sapolsky, R. 1987. Stress, social status and reproductive physiology in free-living baboons. In: Crews, D. (ed.), *Psychobiology of reproductive behavior: an evolutionary perspective*: 291-322. Englewood Cliffs, NJ: Prentice-Hall.
- Savolainen, R. & Vepsäläinen, K. 1988. A competition hierarchy among boreal ants: Impacts on resource partitioning and community structure. *Oikos* 51: 135-155.
- Savolainen, R., Vepsäläinen, K. & Wuorenrinne, H. 1989. Ant assemblages in taiga biome: testing the role of territorial wood ants. *Oecologia* 81: 481-486.
- Schmiegelow, F. K. A. & Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* 12: 225-273.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122: 240-285.
- Senar, J. C. & Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea* 85: 269-274.
- Shmutz, J. A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. *Condor* 95: 222-225.

- Skinner, G. J. & Whittaker, J. B. 1981. An experimental investigation of inter-relationships between the wood-and (*Formica rufa*) and some tree-canopy herbivores. *Journal of Animal Ecology* 50: 313-326.
- Smith, H. G. & Bruun, M. 2002. The effect of pasture on starling (*Sturnus vulgaris*) Breeding success and population density in a heterogeneous agricultural landscape in southern Sweden. *Agric., Ecosyst. Environment*. 92: 107-114
- 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.
- Suorsa, P., Huhta, E., Nikula, A., Nikinmaa, M., Jäntti, A., Helle, H. & Hakkarainen, H. 2003. Forest management is associated with physiological stress in an old-growth forest passerine. *Proceedings of Royal Society of London B* 270: 963-969.
- Suorsa, P., Helle, H., Koivunen, V., Huhta, E., Nikula, A. and Hakkarainen, H. 2004. Effects of forest patch size on physiological stress and immunocompetence in an area-sensitive passerine, the Eurasian treecreeper (*Certhia familiaris*): an experiment. *Proceedings of the Royal Society of London B* 271: 435-440.
- Svensson, E. 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. *Evolution* 51: 1276-1283.
- Svensson, E. & Nilsson, J. Å. 1995. Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology* 60: 269-282.
- Svensson, L. 1992 Identification guide to European passerines. Södertälje, Sweden: Fingraf AB.
- Tinbergen, J. M. & Boerlijst, M. C. 1990. Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology* 59: 1113-1127.
- Tjernberg, M., Johnsson, K. & Nilsson, S. G. 1993. Density variation and breeding success of the black woodpecker *Dryocopus martius* in relation to forest fragmentation. *Ornis Fennica* 70: 155-162.
- Tomppo, E., Henttonen, H., Korhonen, K., Aarnio, A., Ahola, A., Ihalainen, A., Heikkinen, J. & Tuomainen, T. 1999. Forest resources and their development in central Finland, 1967-1996. *Metsätieteen aikakauskirja, Folia Forestalia* 2B/1999, 309-388. ( In Finnish).
- Verboven, N. & Visser, M. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81: 511-524.
- Verhulst, S. & Tinbergen, J. M. 1991. Experimental evidence for a causal relationship between timing and success of reproductive in the great tit (*Parus major*). *Journal of Animal Ecology* 60: 269-282.
- Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. *Ecological Applications* 10: 1211-1218.

- Virkkala, R., Rajasärkkä, A., Väisänen, R. A. Vickholm, M. & Virolainen, E. 1994. Conservation value of nature reserves: Do hole-nesting birds prefer protected forest in southern Finland? *Annales Zoologici Fennici* 31: 173-186.
- Visser M. E. & Verboten, N. 1999. Long-term fitness effects of fledging date in great tits. *Oikos* 85: 445-450.
- Vuorela, A. 1997. Satellite image-based land cover and forest classification of Finland. In: Kuittinen, R. (ed.) Finnish-Russian seminar on remote sensing, 29 August-1 September 1994: 41-51, Reports of the Geodetic Institute 97(2).
- Wasser, S. K., Bevis, K., King, G. & Hanson, E. 1997. Noninvasive Physiological Measures of Disturbance in the Northern Spotted Owl. *Conservation Biology* 11: 1019-1022.
- Wegge, P. & Rolstad, J. 1986. Size and spacing of capercallie leks in relation to social behaviour and habitat. *Behavioral Ecology and Sociobiology* 19: 401-408.
- Wheelwright, N. T. & Dorsey, F. B. 1991. Short-term and long-term consequences of predator avoidance by tree swallows (*Tachycineta bicolor*). *Auk* 108: 719-723.
- Widen, P. 1989: The hunting habitats of goshawk *Accipiter gentilis* in boreal forests of central Sweden. *Ibis* 131: 205-213.
- Wiens, J. A. 1989. *The Ecology of Bird Communities*, vol 2. Process and Variations. Cambridge University Press, Cambridge.
- Wingfield, J. C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G.S., Freed, L. & Lepson, J. 1997. Environmental stress, field endocrinology, and conservation biology. In: Clemmons, J. R. & Buchholz, R. (eds), *Behavioural Approaches to Conservation in the Wild*: 95-131. Cambridge: Cambridge University Press.
- Winkler, D. W. 1992: Causes and consequences of variation in parental defence behavior by Tree Swallows. *Condor* 94: 502-520.
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. 1994. Experimental investigation of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour* 48: 210-222.
- Zanette, L., Doyle, P. & Tremont, S. M. 2000. Food shortage in small fragments: evidence from an area sensitive passerine. *Ecology* 81: 1654-1666.