

Pirkko Siikamäki

Determinants of Clutch Size  
and Reproductive Success  
in the Pied Flycatcher

UNIVERSITY OF JYVÄSKYLÄ

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston vanhassa juhlasalissa (S212)  
tammikuun 21. päivänä 1995 kello 12.

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URN:ISBN:978-951-39-9100-5  
ISBN 978-951-39-9100-5 (PDF)  
ISSN 0356-1062

Jyväskylän yliopisto, 2022

ISBN 951-34-0408-0  
ISSN 0356-1062

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Jyväskylä University Printing House  
and Sisäsuomi Oy, Jyväskylä 1995

# ABSTRACT

Siikamäki, Pirkko

Determinants of clutch size and reproductive success in the pied flycatcher

Jyväskylä: University of Jyväskylä, 1995, 35 p.

(Biological Research Reports from the University of Jyväskylä, ISSN 0356-1062; 41)

ISBN 951-34-0408-0

Yhteenvedo: Kirjosiepon pesyekoon ja lisääntymismenestyksen määräytyminen

Diss.

This thesis deals with the mechanisms that influence optimization of clutch size. The studies were mainly carried out with experiments in a population of the Pied Flycatcher (*Ficedula hypoleuca*) breeding in central Finland. The adjustment of clutch size was affected by habitat quality. Females that were forced to breed in a habitat of poorer quality than where they had initially settled, laid smaller clutches than control females. Seasonal decline in the clutch size seemed to be an adaptation to both the deteriorating food supplies and temporally changing trade-off between resources allocated to breeding and maintenance of parents (i.e. moult). The trade-off documented here between the current reproduction and moult of parents is suggested to be a link between two successive breeding attempts and thus a mechanism causing costs of reproduction. Although females seem to adjust their clutches to correspond to the approximate number of young they can raise, the effect of unpredictable and varying weather on the growth and mortality of young weakens the ability of females to adjust the clutch at the egg-laying time. Consequently, during adverse conditions brood reduction is a strategy for adjusting the brood size to the level parents can rear. In all, studies of this thesis suggested that the most important factor influencing the optimization of clutch size in this species is the amount of food available to nestlings that largely depends on the habitat quality and the time of season. Additionally, the trade-offs between the current breeding attempt and future reproduction also mould the evolution of clutch size.

Key words: Pied flycatcher; clutch size; food limitation, individual optimization; reproductive success; trade-off.

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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 Siikamäki, P. 1994: Habitat quality and reproductive traits in the Pied Flycatcher - an experiment. - Ecology (in press).
- II Siikamäki, P. 1994: Clutch size limitation by food availability and breeding time. - Manuscript (submitted).
- III Siikamäki, P. 1994: Are large clutches costly to incubate - the case of the Pied Flycatcher. - Journal of Avian Biology (in press).
- IV Siikamäki, P., Hovi, M & Rätti, O. 1994: A trade-off between current reproduction and moult in the Pied Flycatcher - An experiment. - Functional Ecology 8: 587-593.
- V Siikamäki, P. 1994: Unpredictable environment and nestling growth and mortality in the Pied Flycatcher. - Manuscript (submitted).
- VI Siikamäki, P., Rätti, O., Hovi, M. & Bennett, G. F. 1994: Association between haematozoan infections and reproduction in the Pied Flycatcher. - Manuscript.

## CONTENTS

1	Introduction	
2	Material and methods	10
2.1	The species	10
2.2	The study area	11
2.3	General methods	11
2.4	Clutch size manipulation ( III, IV, V, VI)	12
2.5	Relocation experiment (I)	12
2.6	Delaying and feeding experiment (II)	13
2.7	Recording the state of moult (II, IV)	13
2.8	Sampling of blood parasites (VI)	14
3	Results and discussion	15
3.1	Factors influencing clutch size	15
3.1.1	Territory quality (I)	15
3.1.2	Breeding time (II)	16
3.1.3	Costs of incubation (III)	19
3.2	Trade-off between reproduction and moult (II, IV)	20
3.3	Effects of external environment on reproduction	21
3.3.1	Impact of weather (III, IV, V)	21
3.3.2	Blood parasites (VI)	23
4	Conclusions	24
	Acknowledgements	25
	Yhteenveto	27
	References	29



# 1 INTRODUCTION

Clutch size is one of the most critical life-history traits (e.g. Stearns 1976, Godfray et al. 1991), and its variation and determination has been the object of wide scientific interest after the pioneering works of Lack (1947, 1954, 1966, 1968). He hypothesized that the modal clutch size in the population is also the most productive one in terms of the number of recruited young. According to his hypothesis the ultimate factor limiting clutch size is the feeding capacity of parents.

Several studies, however, have confirmed that the clutch size producing the largest number of fledglings tends to be larger than the modal clutch size of the population (e.g. Partridge 1989). This discrepancy has evoked continued interest, and many factors and mechanisms that may influence selection on clutch size have been raised (Murphy & Haukioja 1986).

One factor contributing to the difference between the most productive and the modal clutch size is the fact that there is no single optimal clutch size for a population, since the breeding conditions vary both spatially and temporally. According to the individual optimization hypothesis females are able to lay optimal clutches that maximize the recruitment rate (Perrins & Moss 1975). The number of eggs laid by a female corresponds to the ability of parents to rear offspring that is either based on the quality of parents (Perrins & Moss 1975, Drent & Daan 1980, Coulson & Porter 1985) or the food resources and territory quality available to parents (Högstedt 1980, 1981).

The majority of studies, where brood size has been manipulated, have proved that parents are capable of raising experimentally enlarged clutches (Murphy & Haukioja 1986, Godfray et al. 1991, VanderWerf 1992). Then why birds do not seem to maximize the production of offspring? This could be related to the fact that Lack's hypothesis assumes

that maximizing fitness per clutch will also maximize lifetime fitness. However, this is not the case, if high reproductive effort in one breeding attempt lowers the future fitness of the parent (Williams 1966, Charnov & Krebs 1974). A number of experimental studies on birds have indeed found evidence for costs of reproduction in terms of reduced parental survival (e.g. Askenmo 1979, Reid 1987) or lower future fecundity of parents (Gustafsson & Sutherland 1988, Nur 1988, Gustafsson & Pärt 1990). Thus, if there are costs of reproduction, a clutch size smaller than the most productive could maximize lifetime fitness (Williams 1966, Charnov & Krebs 1974).

Both clutch size and timing of breeding are probably constrained by parental condition (Perrins 1970, Jones & Ward 1976). Food requirements for laying females may constrain the timing of breeding and the production of optimal clutch resulting in a lower brood size than parents can feed. The best empirical evidence that parental condition affects determination of clutch size and laying dates comes from experiments in which parents were provided with extra-food prior to egg-laying (for reviews see Martin 1987, Arcese & Smith 1988, Daan et al. 1989, Meijer et al. 1990). In most of these studies females have responded to food provisioning by advancing the onset of egg-laying and/or by slightly (usually non-significantly) increasing their clutch sizes.

In addition to the above mentioned factors, several other ecological and environmental factors have been demonstrated to influence clutch size in altricial (see reviews by Murphy & Haukioja 1986, Godfray et al. 1991) including, for example, predation (Slagsvold 1984, Lima 1987) and incubation capacity (e.g. Coleman & Whittall, 1988, Moreno & Carlson 1989). All these explanations assume that the clutch size can be adaptively modified by a laying female. A considerable amount of variation in clutch size has indeed been found to be genetically determined (Perrins & Jones 1974, van Noordwijk et al. 1980) thus enabling a response to selection. This genetically based variability could be maintained by temporally and spatially varying selection pressures (van Noordwijk et al. 1981, Dhondt et al. 1990).

Numerous experiments in a wide array of bird species have been performed to study whether parents are able to optimize their reproductive effort. Yet, the mechanisms influencing the determination of clutch size as well as costs of reproduction have not evoked so much scientific interest, and consequently, are not so well understood. In this thesis I emphasize to examine the mechanisms underlying the selective processes that affect the evolution of clutch size in altricial birds using the pied flycatcher (*Ficedula hypoleuca* Pallas) as a study object. In particular, I focus on the role of habitat quality, food availability and trade-offs in the determination of reproductive effort. I investigate whether and how birds

are able take into account spatially and temporally varying environment during one breeding attempt. Finally, I discuss the results and their generality from the perspective of the hypotheses proposed to account for the evolution of clutch size.

## 2 MATERIAL AND METHODS

### 2.1 The species

The pied flycatcher is a small (12-13 g) migratory passerine of northern and central Europe. It is a single-brooded hole-nester that prefers nest-boxes to natural cavities as breeding sites. Therefore, it is quite easy to attract a large part of the breeding population to breed in nest-boxes. Additionally, the pied flycatcher is very abundant and not very sensitive to disturbances. Because of these features, it is a very suitable study organism for many purposes. (Lundberg & Alatalo 1992).

Pied flycatchers are found in a wide array of forest habitats if there are nest-holes available, but they prefer deciduous habitats to coniferous ones. The probable reason for this preference is more abundant food supplies in deciduous forests (Lundberg et al. 1981). As the name suggests, flying insects are the main food items of the pied flycatcher. However, many prey items are also caught from the ground and trees which to some extent depends on the habitat. Food given to nestlings differs somewhat from that of adults, being predominantly caterpillars and spiders (Lundberg & Alatalo 1992, Cramp & Perrins 1993).

Pied flycatchers overwinter in tropical West Africa. In spring the first pied flycatcher males arrive to central Finland during the first week of May about one week ahead of females. Immediately after their arrival males establish a territory and start to advertise it by singing (Lundberg & Alatalo 1992). Females start nest-building soon after their mating decision, and it takes, on average, 11 days to complete the nest-building. In southern Finland the first eggs are usually laid around 21 May (von Haartman 1990). The timing of the onset of egg-laying is presumably

determined by both the capacity of females to lay and the need to match the nestling period with the time of highest availability of food.

The clutch size of the pied flycatcher declines continuously throughout the breeding season (von Haartman 1967, Crick et al. 1993). The reduction of clutch size is particularly rapid in this species being 0.05-0.1 eggs for each successive day of delayed breeding (Lundberg & Alatalo 1992). Additionally, the clutch size of pied flycatcher is also influenced by age, size and mass of a female and the characteristics of breeding site (altitude, habitat quality). Clutches of six eggs are the most frequent, and natural variation in clutch size ranges from three to eight eggs.

Incubation starts usually when the last egg is laid and is done by the female alone. The length of incubation period is about 13-16 days. After the hatching of young the female spends a considerable amount of time brooding. Nestlings are fed by both parents, and they normally leave the nest at 15 or 16 days after the hatching. Parents take care of young about one week after the fledging before the independence. Adults start a complete summer moult just after breeding or during the late nestling stage (Ginn & Melville 1983), while juveniles moult only the body feathers before the autumn migration.

## 2.2 The study area

The data presented in this thesis have been collected between 1991 and 1994 in the vicinity of the Konnevesi Research Station (62°37'N, 26°20'E). Study plots were mainly coniferous forests dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) or mixed coniferous forests with varying number of deciduous trees. Study area consists of 20 separate study plots. In all study plots nest-boxes have been provided in excess, containing up to 40 nest-boxes per plot.

## 2.3 General methods

All the study plots were visited in the early May and at the same time old nest material was removed from the nest boxes. After the first visit the nest-boxes were checked regularly to find new breeding pairs and to determine the initiation of egg-laying. Data on clutch size was obtained during the incubation at the same time when females were caught. The nests were inspected daily around the estimated hatching day until the first egg hatched. The growth of young was monitored during the nestling period by weighing them and measuring several morphological

characteristics. The fledging success was determined by visiting the nests until the fate of every nestling was known. Most of the breeding females were caught during the incubation or feeding period, whereas most of the males were trapped either just after their arrival or during the nestling feeding period. Adult birds were ringed with numbered aluminium rings, aged and several morphological characteristics were measured. Birds were separated into yearlings or older birds on the basis of their moult patterns and weariness of feathers (Kalsson et al. 1986).

Weather data were gathered at the Konnevesi Research Station and at the Jyväskylä Airport by the Finnish Meteorological Institute. Two-tailed statistical tests were used throughout, and when the assumptions of parametric tests were not met, non-parametric tests were performed.

## **2.4 Clutch size manipulation ( III, IV, V, VI)**

We carried out clutch size manipulations in 1991, 1992 and 1993 to investigate the determination of clutch size, and in particular the mechanisms that affect the optimum reproductive effort. Clutches with the same laying date were manipulated by removing or adding eggs during the egg-laying period before the start of incubation. The treatment for a pair of clutches was randomized and either one or two eggs were moved from one nest to the other. In the treatment control group, one or two eggs were exchanged between the nests. In the pure control group no manipulations were done. Because no side-effects of the manipulation on the hatching success or the length of incubation were found in 1991 and 1992, the use of treatment control group was considered unnecessary in 1993.

## **2.5 Relocation experiment (I)**

With the experimental relocations of simultaneously paired females I was able to focus on direct effects of habitat quality on determination of clutch size and reproductive success. I erected new nest-boxes in boundaries between deciduous and coniferous forest and checked them daily to find newly arrived, singing males and newly paired females. When two females had arrived simultaneously and started nest-building on the same day, I assigned one of them to the control group and the other to the experimental group. Immediately after a female had started nest-building, I put up two additional nest-boxes in the direction I intended to move the birds. In a few hours I transferred the original nest-box to the

site of first additional nest-box. Females commonly continued the nest-building at the new nest site shortly after movements, when a further movement was performed and so forth.

I moved the control females within the deciduous habitat, where they had initially settled and the experimental females to a coniferous habitat. As a result of these gradual movements I had pairs of females with the same arrival time and similar original habitat selection from whom one came to breed in deciduous and the other in coniferous habitat.

## 2.6 Delaying and feeding experiment (II)

I manipulated the breeding time and the amount of food during the nestling period to test different hypotheses proposed to account for the seasonal decline of avian clutch size. I randomly assigned females that had started egg-laying simultaneously to one of three treatment groups. One group was an unmanipulated control group, the second an experimental group where the breeding was delayed by one week and the third was an experimental group whose breeding was delayed by one week and food provisioned during nestling period. To change the breeding time of females, I delayed the onset of incubation by replacing the newly laid eggs as they were laid with dummy eggs. I stored the eggs in a refrigerator at 8°C and returned them into the nests after 7 days.

After the hatching I started food provisioning that continued over the whole nestling period. The food consisted of live mealworms (*Tenebrio* sp.) and pupae of red ant (*Formica rufa*) offered in a feeding tray. The parents used extra food both themselves and they also fed their nestlings with extra food, especially so in the end of the nestling period.

## 2.7 Recording the state of moult (II, IV)

The timing of moult in relation to breeding was studied by recording the state of moult of parents when their nestlings were 13 or 14 days old. Moult usually starts by shedding of the innermost primaries (Svensson, 1992), thus the state of primary moult has traditionally been used as an indicator of the whole moult (Newton 1966). The degree of moult was scored on a scale from 0 (old feather) to 5 (fully grown, new feather) for each primary of both wings. A sum of scores assigned to the individual primaries was then used as an index of the general progress of the moult.

## **2.8 Sampling of blood parasites (VI)**

We captured males for blood sampling soon after their arrival to the breeding grounds or when they were feeding the nestlings. Most females were sampled during their incubation. Blood was taken from the brachial or tarsus vein and smeared on glass slide. Blood smears were air-dried and fixed with absolute methanol. The Giemsa stain solution was used to stain the samples. Blood smears were microscopically examined by counting the numbers of different genera of blood parasites.



## 3 RESULTS AND DISCUSSION

### 3.1 Factors influencing clutch size

#### 3.1.1 Territory quality (I)

Habitat quality clearly affected the adjustment of clutch size in the pied flycatcher. Females, who were moved to breed in a habitat of poorer quality than where they had initially settled, responded by laying a lower clutch size than control females ( $6.4 \pm 0.62$  eggs ( $\bar{x} \pm SD$ )  $N=17$  and  $7.3 \pm 0.48$  eggs,  $N=13$ , respectively; Mann-Whitney U-test:  $U=187.5$ ,  $P<.001$ ). With the procedure used, it was possible to control many factors that are known to influence the determination of clutch size such as laying date (e.g. Klomp 1970, Drent & Daan 1980) and age as well as the condition of a female (e.g. Harvey et al. 1989, Sæther 1990).

The lower clutch size of experimental females could imply that they were proximately constrained by a poorer habitat and could not find enough food for egg formation. Alternatively, they could have adjusted clutches to correspond their ability to raise a brood in this particular breeding situation. Control and experimental females did not differ in the time from the onset of nest-building to the initiation of egg-laying and they were of the same mass when incubating. Both these facts suggest that experimental females were not more constrained to lay clutches than control ones. Instead, lower clutch in the poorer habitat is more likely to represent females' decision to adjust clutch size on the basis of territory quality as predicted by the individual optimization (Perrins & Moss 1975) and Högstedt's hypotheses (1980).

### 3.1.2 Breeding time (II)

The onset of egg-laying commonly affects the clutch size: the later a female starts egg-laying the fewer eggs she will lay (Klomp 1970, Drent & Daan 1980, Murphy & Haukioja 1986). This seasonal decline in clutch size could be due to seasonal variation in the parental or territory quality with high quality parents breeding early and occupying good territories whereas lower quality parents later have to take poorer territories (Price et al. 1988). Alternatively, the environment may become progressively less suitable throughout the breeding season causing the decline (Verhulst & Tinbergen 1991). The deteriorating food supplies have commonly been suggested to be the changing property in the environment (Perrins 1970, Murphy 1986). Moreover, late-breeding parents may reduce clutch size because reproduction is costly and value of extra offspring decreases over the season (Hussell 1972, Murphy 1986, Hochachka 1992).

In study II the causes of seasonal decline of clutch size and reproductive success were experimentally examined by manipulating both the breeding time and the amount of food during the nestling period. I found that for both the fledging weight and fledglings per hatched young, the success of non-food supplemented nests with delayed (hereafter D) breeding was lower than that of control nests (hereafter C) or food supplemented nests with delayed breeding (hereafter EF) (Fig. 1 a & b). Because mass of 13 d nestlings reflects fledging mass, and post-fledgling survival is greatly influenced by condition of fledglings (Perrins 1965, Lundberg & Alatalo 1992, Lindén et al. 1992), fledglings of control and food provisioned nests are more likely to have better survival prospect than young of nests with delayed breeding.

Had the parental or territory quality been the most critical factor, no difference between the breeding success of C and D broods would have been found. If the changing property in the environment would have been something else than the amount of food, the breeding success of D and EF should have been the same. Thus, these results on fledging success suggest that the deteriorating food supplies limit the breeding success of late breeders.

The progress and timing of moult was affected by manipulation of both breeding date and amount of food. Overlap between moult and breeding was most pronounced among EF parents (Fig. 2 a & b), whereas among C parents very few individuals had started moulting, and D parents were intermediate between these two. This indicates that parents with delayed breeding had to start their moult to complete it in time before autumn migration. In addition, timing and progress of moult was influenced by food provisioning. These results imply that the trade-off between breeding and moult (e.g. Pietiäinen et al. 1984, Bensch et al.

1985, Lessells 1986) is, indeed, due to competition for energy between these two activities. Additionally, the time available for breeding and moulting is clearly restricted causing an overlap between them.

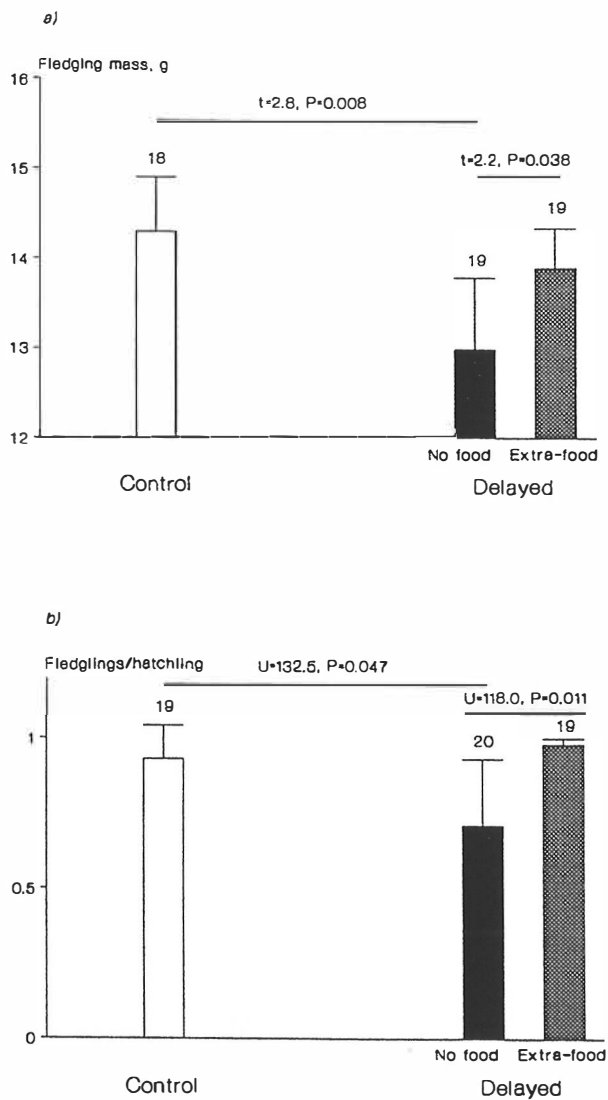
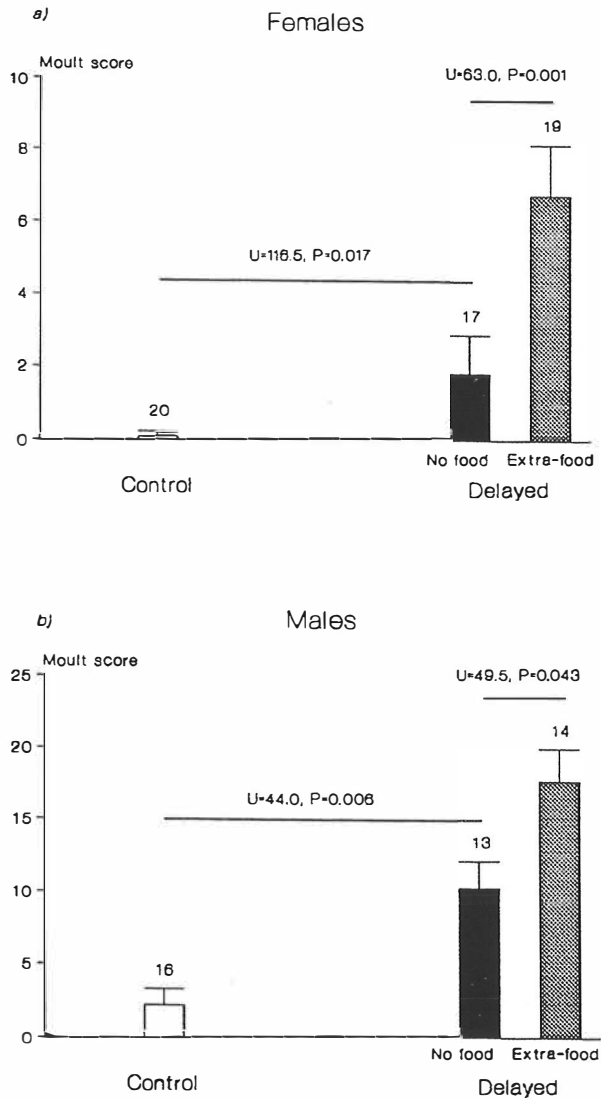


FIGURE 1 Mean nestling mass (a) and fledging success (b) in C, D and EF nests. Horizontal lines above the bars refer to the pairwise comparisons. The numbers above bars refer to the sample sizes.

These results suggest that both the deteriorating food supplies and the increasing energy consumption of parents due to moult explain the seasonal decline in the clutch size. Some studies have earlier documented that the timing of breeding and fledging success and offspring survival are causally related (Verhulst & Tinbergen 1991, Norris 1993, Brinkhof et al. 1993). However, the mechanisms underlying this relationship have not been tested before.



**FIGURE 2** Mean moult scores of females (a) and males (b) in C, D and EF nests. Horizontal lines above the bars refer to the pairwise comparisons, and the numbers to the sample sizes.

### 3.1.3 Costs of incubation (III)

The role of incubation cost in the evolution of clutch size in birds has been a subject of much controversy (e.g. Moreno & Carlson 1989). However, the incubation capacities of parents have been found to depend on clutch size and affect reproductive performance in many ways. For instance, the oxygen consumption of incubating females has been reported to increase with increasing clutch size (e.g. Biebach, 1981, 1984, Haftorn & Reinertsen 1985, Moreno et al. 1991) indicating higher energy expenditure of females with large clutches. On the other hand, some studies have found no apparent fitness costs of incubation suggesting that clutch size is limited by other than incubation constraints (e.g. Jones 1987).

One possible factor that could account for this discrepancy is that most studies on incubation have been conducted during one season only. Clutch size manipulation carried out during three consecutive years reveals that clutch size dependent costs of incubation are indeed consistent between the seasons (III). The mean duration of incubation differed between both the treatment groups and years (two-way ANOVA: treatment:  $F_{2,195}=16.0$ ,  $P<0.001$ , year:  $F_{2,195}=26.9$ ,  $P<0.001$ ). Clutch size manipulation affected the duration of incubation in a similar way in the three years (interaction term treatment\*year:  $F_{4,195}=1.7$ ,  $P=0.145$ ) (Table 1). Females incubated enlarged clutches, on average, for 0.8 d longer than females with unaltered or reduced clutches. Hatching success differed between treatments in 1992 and 1993 but not statistically significantly in 1991 (Table 1). However, every year hatching success was highest among reduced clutches, intermediate among control clutches and lowest among enlarged clutches.

These results of a 3-year study on incubation patterns corroborate earlier findings on clutch size related costs of incubation (e.g. Moreno & Carlson 1989, Smith 1989, Moreno et al. 1991). It seems that incubation is a period of energetic stress that depends on clutch size. Consequently, it could affect the overall reproductive success in terms of prolonged incubation and poorer hatchability. A longer duration of incubation leads to a later hatching, which has been found to reduce future survival prospects (Perrins 1965, Kluyver et al. 1977, Arcese & Smith 1985). In all, clutch-size dependent effects during incubation are likely to be an additional factor in the determination of clutch size.

TABLE 1 Mean values $\pm$ SD (sample size) of the length of incubation and hatching success of fertilized eggs (%) in different treatment groups and years. Kruskal-Wallis test refers to comparisons between hatching success in different treatments.

	1991	1992	1993
Length of incubation (d)			
Reduced	13.4 $\pm$ 0.8 (19)	12.8 $\pm$ 0.5 (19)	13.8 $\pm$ 0.8 (13)
Control	13.4 $\pm$ 2.2 (41)	12.8 $\pm$ 2.1 (44)	13.9 $\pm$ 0.8 (14)
Enlarged	13.9 $\pm$ 1.0 (19)	13.4 $\pm$ 1.1 (20)	15.2 $\pm$ 1.7 (15)
Hatching success (%)			
Reduced	98.2 $\pm$ 7.6 (19)	98.2 $\pm$ 7.6 (19)	98.1 $\pm$ 6.9 (15)
Control	96.3 $\pm$ 7.7 (41)	98.0 $\pm$ 4.9 (44)	95.4 $\pm$ 8.1 (14)
Enlarged	95.2 $\pm$ 8.7 (19)	95.2 $\pm$ 7.1 (20)	91.2 $\pm$ 9.0 (14)
Kruskal-Wallis test:			
H	2.6	6.4	9.4
P	0.279	0.041	0.009

### 3.2 Trade-off between reproduction and moult (II, IV)

One of the most critical life-history decisions of an individual is the amount of effort it should expend during one breeding attempt (e.g. Stearns 1989, 1992, Roff 1992). Reproductive effort is moulded by trade-offs that an organism is faced with during each breeding attempt and the whole life cycle. Selection should favour such individuals who are able to find the optimal solutions between competitive activities i.e. those that maximize life-time fitness.

The relationship between the reproductive effort in one breeding attempt and feather renewal of parents (i.e. moult) has been quite a neglected topic in the study of birds' breeding ecology. They have traditionally been studied as independent events in the annual cycle of birds. We found, however, that the timing of moult and reproductive effort were in a close connection (II, IV). The stage of moult among females correlated negatively with clutch and brood size (IV). This association may indicate that females with larger broods began moulting later in relation to breeding schedule than females with smaller broods. Additional evidence for this interpretation is obtained from the

experiments where either the reproductive effort (IV) or the breeding time and the amount of food (II) were manipulated.

The stage of female moult was affected by the clutch size manipulation, so that the females with enlarged clutches delayed their moult. The manipulation of clutch did not have any statistically detectable effects on the timing of male moult. However, when the timing of breeding and food availability during the nestling period were manipulated, parallel results among females and males were found (see chapter 3.1.2 and Fig. 2 a & b for detailed results). When the parents were food provisioned they started moulting earlier than parents without extrafood. This implies that parents trade between their moult and breeding, and that current reproduction is by far the most important activity for them. In addition to energy constraints, the timing of moult also is moulded by restricted time for breeding and moulting. Breeding and moulting has actually been found to overlap to a greater extent among late than early breeders in two tit species (Orell & Ojanen 1980).

Since moulting and parental care have been documented to overlap in several species (e.g. Pitelka 1958, Haukioja 1971; Ojanen & Orell 1982; Zaias & Breitwisch 1990), and additionally, regulation of moult has also been found to depend on brood size (Pietiäinen et al. 1984; Bensch et al. 1985, Lessells 1986), a trade-off between these activities is presumably quite common in birds. A delayed moult is very likely to be disadvantageous (Bensch et al. 1985). Thus, it is likely to be the main physiological link between the two breeding attempts and a possible mechanism (IV) causing the costs of reproduction that have been documented in birds (e.g. Askenmo 1979, Reid 1987, Gustafsson & Sutherland 1988, Nur 1988, Gustafsson & Pärt 1990).

### **3.3 Effects of external environment on reproduction**

#### **3.3.1 Impact of weather (III, IV, V)**

As documented also in other species (e.g. Kluyver 1951, van Balen 1973, Perrins 1979, Perrins & McCleery 1989, Perrins 1990), spring temperature influences markedly the laying date of pied flycatchers (Slagsvold 1976, von Haartman 1990, Lundberg & Alatalo 1992, IV). The timing of breeding is ultimately balanced by the advantages and disadvantages of early breeding (Drent & Daan 1980). Yet, the weather of spring determines proximately the initiation of egg-laying by affecting the amount of food available to females for egg-formation (e.g. Perrins 1970).

The incubation patterns were also affected by weather (III). The prolonged incubation, lower hatching success and death of some females

in 1993 were most likely due to the adverse weather during that season. The duration of incubation was negatively correlated with the mean temperature of incubation period ( $r_s = -0.499$ ,  $n = 136$ ,  $P < 0.001$ ). Low hatching success during poor weather is due to the fact that the risk of chilling and anomalies in the development of embryos increases with decreasing ambient temperature (White and Kinney 1974). Additionally, incubation may require production of additional heat when the air temperature falls below the lower critical value of the thermoneutral zone (e.g. Kendeigh 1963, Biebach 1981, 1984 and Vleck 1981).

In the study V the growth and mortality of pied flycatcher young were investigated in relation to weather conditions. In control broods where parents were allowed to reproduce at their own rate, masses of nestlings correlated with temperature and precipitation during the later parts of nesting. Analyses of the whole data set on the effects of manipulation of clutch size and weather conditions revealed that both these factors influenced growth of nestlings, particularly during the later nestling period. The interaction terms between treatment and weather showed no consistent pattern, indicating that weather affected growth in a similar way regardless of manipulation of clutches.

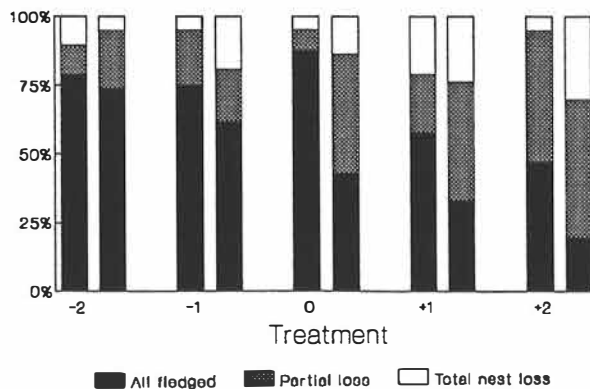


FIGURE 3 Percentage of nests with all young fledged, partial losses (i.e. brood reduction) and total nest losses in different treatments and years (left bars=1991; right bars=1992).

Enlargement of clutches increased mortality of young in both years (Fig. 3). Nestling mortality was more probable to occur when it rained a lot and among enlarged nests. Higher mortality is very likely to be caused by the difficulties of parents to find enough food for the brood.



In addition to higher demand of energy, cold and rainy weather affects the activity of prey animals of insectivorous birds (e.g. Bryant 1973, Avery & Krebs 1984). With respect to clutch size adjustment the type of food supply is a critical question (O'Connor 1978). The pied flycatcher uses food, the availability of which, largely depends on the weather (e.g. Lundberg & Alatalo 1992). Furthermore, the conditions of the forthcoming nesting season are difficult to predict at the time of egg-laying (Järvinen 1989). Consequently, brood reduction seems to be a strategy to adjust the brood size to the level that the parents are able to raise.

### **3.3.2 Blood parasites (VI)**

Because parasites use the same resources as their hosts, they may have potential to reduce the host's fitness (Anderson & May 1978, 1979, May & Anderson 1978, 1979). On the other hand, reproduction may increase the susceptibility of a host to parasite infections due to lowered resistance during breeding (Festa-Bianchet 1989, Zuk 1990, Shoop 1991, Norris et al. 1993). We studied the relationship between haematozoan parasites and breeding performance by using both nonexperimental and experimental data. The most frequent haematozoan parasites had no debilitating effects either on reproductive success or survival of pied flycatchers. It seemed that the variation in breeding effort does not influence on the susceptibility to new infections. However, there was some evidence that increased breeding effort debilitate pied flycatchers' ability to control chronic infections.

## 4 CONCLUSIONS

The results of this study give additional support for the view initially suggested by Lack as follows:

I believe that, in nidicolous species, the average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and season in question, i.e. that natural selection eliminates a disproportionately large number of young in those clutches which are higher than the average, through the inability of the parents to get enough food for their young, so that some or all of the brood die before or soon after fledging, with the result that few or no descendants are left with their parent's propensity to lay a larger clutch. (Lack 1947)

It seems that the clutch size is adaptively adjusted to correspond to the capacity of parents to rear a brood given a particular breeding condition (Perrins & Moss 1975, Högstedt 1980, 1981, I, II). The variation in clutch size thus reflects spatial and temporal differences in conditions for brood rearing. However, the low predictability of these circumstances, i.e. temporal variability, constrains the possibilities of individuals to optimize reproductive effort. This may explain why the mean clutch size of birds is frequently less than the most productive (Boyce & Perrins, 1987).

The studies of this thesis suggest that determination of clutch size is largely moulded by the amount of food available to nestlings. The availability of food and thus the feeding capacity of parents largely depends on the habitat quality, the time of season and the weather conditions. It seems that birds are able to use some kind of rule of thumb based on the territory quality and the time of season when assessing the quality of breeding option. Because the weather of the forthcoming breeding season is difficult to predict at the egg-laying time, brood size is finetuned during adverse conditions through starvation of the poorest

young. Even though the current breeding is by far the most important activity for a short-lived species like the pied flycatcher, the trade-offs between current breeding attempt and future reproduction are likely to have an additional effect on the evolution of clutch size.

I have mainly applied experimental methods in the studies of this thesis because studying these questions only with phenotypic correlations are suspect and hard to interpret (e.g. Bell & Koufopanou 1986, Lessells 1991, Lindén & Møller 1989). There may be some common uncontrolled factors that could account the observed relationship, and additionally, causality could not be detected without experiments. That is why experimental and non-experimental studies may give opposite results such as found in the study III, where clutch size was negatively correlated with the length of incubation, whereas in enlarged clutches were incubated longer than unaltered or reduced clutches.

The fact that most studies of clutch size determination have been conducted with hole-nesting birds breeding in nest-boxes, may give a reason for asking how universal these results are (Lindén & Møller 1989). For instance, predation rate is much higher on both adults and offspring in natural cavities than in nest-boxes (e.g. Lundberg & Alatalo 1992), and population densities are often higher than normal. However, the research on birds has played an important role in forming theories of life-history evolution, and hypotheses resulting from studies on birds have also been started to test in other taxonomic groups.

### *Acknowledgements*

I owe my sincerest gratitude to my supervisor Rauno Alatalo for introducing me to the fascinating world of science. Even though he gave me an opportunity to work as "a free bird", he patiently and with consideration advised me by asking: "However, it would, perhaps, be worth trying it this way, wouldn't it?". Without his help, advice and encouragement this work would have been impossible to carry out.

I am indebted to Rauno Alatalo, Matti Hovi, Janne Kilpimaa, Silja Parri and Osmo Rätti for their efforts in the field. To everyone at our department, thank you for all your contribution. Especially, my sincerest thanks are due to "downfloor ethologists": Teija Aho-Somppi, Matti Halonen, Taina Horne, Matti Hovi, Esa Koskela, Markku Kuitunen, Janne Kotiaho, Johanna Mappes, Tapio Mappes, Silja Parri, Jyrki Pusenius, Pekka Rintamäki, Osmo Rätti, Jukka Suhonen, Jussi Viitala and Hannu Ylönen. All of you deserve appreciation for creating a warm, stimulating and intensive atmosphere (sometimes even too intensive).

I would like to thank Staffan Ulfstrand for giving me an opportunity to work in the most warm, professional and inspiring environment of "Zootis" at the University of Uppsala. During my visit Ingrid Ahnesjö, Anders Berglund, Lars Gustafsson, Lars Hillström, Jacob Höglund, Juha Merilä, Anders Møller, Arne Lundberg, Karin Olsson and Staffan Ulfstrand helped me in many ways.

The Konnevesi Research Station has provided a warm and efficient working environment, for which I wish to express my warmest thanks to the staff and the other researchers working in the station. The English language of this thesis was revised by Ritva Siikamäki, whose help is warmly acknowledged. This work was financially supported by Emil Aaltonen Foundation, Nordic Council for Ecology and Nordisk Forskerutdanningsakademi.

Finally, I would like to express my deepest gratitude to Matti who made me remember that there are more important things in life than science. Many thanks for your patience, encouragement and support.

## Yhteenveto

### Kirjosiepon pesyekoon ja lisääntymismenestyksen määrättyminen

Lintujen pesyekoon tutkimus on ollut eräs elinkiertotutkimuksen ja evoluutiobiologian keskeisiä kiinnostuksen kohteita. Väitöskirjassani paneuduin pesyekoon määrätymisen ja lisääntymismenestyksen taustalla oleviin tekijöihin ja mekanismeihin pääasiassa kokeellisen tutkimuksen keinoin. Käytin tutkimuskohteenani kirjosieppoa (*Ficedula hypoleuca*), joka yleisenä pönttölintuna tarjoaa oivallisen lähtökohdan kokeellisen tutkimuksen tekemiselle.

On esitetty, että populaatioissa havaittu pesyekoon vaihtelu johtuisi siitä, että yksilöt optimoisivat munamääränsä elinympäristön laadun perusteella. Tutkin kokeellisesti, onko pesimäpaikan lähiympäristön laadulla suoraa merkitystä pesyekoon määrätymisessä. Siirsin samanaikaisesti pariutuneita, pesää rakentavia naaraita joko niiden alunperin valitseman elinympäristön sisällä tai kohti huonompaa elinympäristöä. Naaraat, jotka oli siirretty pesimään kirjosiepon kannalta huonompaan ympäristöön, havumetsään, munivat pienemmän pesyeen kuin kontrollinaaraat. Tämä vaste oli mitä todennäköisimmin sopeuma siihen, kuinka suuren poikueen emot tässä nimenomaisessa elinympäristössä kykenivät ruokkimaan.

Pesyekoon ja lisääntymismenestyksen on havaittu pienenevän pesimiskauden aikana; aikaisin pesintänsä aloittavat naaraat munivat suuremmat pesyeet ja tuottavat enemmän lentopoikasia kuin myöhemmin keväällä pesintänsä aloittavat naaraat. Tutkin kauden aikana tapahtuvan pesyekoon pienenemisen syitä kokeella, jossa viivästyttiin pesintäajankohtaa, jonka jälkeen tarjosin osalle emoista lisäravintoa. Tämä koe osoitti, että pesyekoon lasku selittyy pääosin ravintotilanteen heikkenemisellä pesimiskauden kuluessa. Toisaalta myös emojen tarve panostaa sulkasatoon oli suurempi myöhemmin kesällä, mikä osaltaan vaikuttanee pesyekoon kauden aikana tapahtuvaan laskuun. Aikuiset linnut vaihtavat koko höyhenistönsä ennen talvehtimispaikalle muuttamistaan. Emot, joilla oli suuret pesyeet joko luontaisesti tai pesyekoon manipuloinnin seurauksena, joutuivat viivästyttämään sulkasatonsa alkua. Viivästynyt sulkasato johtui todennäköisesti suuremmasta energian tarpeesta, joka kului suuremman poikueen huolehtimisessa. Tämän vuoksi emot joutuivat allokoimaan enemmän resursseja pesintään oman sulkasatonsa kustannuksella. Tämä energian allokoitongelma saattaisi olla eräs mekanismi linnuillakin todennettujen lisääntymiskustannusten taustalla.

Pesyekoon kokeellinen lisäys pidensi haudonta-aikaa ja toisaalta laski kuoriutumismenestystä. Haudonta-ajan säätila vaikutti myös suuresti haudonta-ajan pituuteen ja kuoriutumismenestykseen. Keväällä 1993 sääolosuhteet olivat erittäin huonot, mikä luultavimmin aiheutti huonon kuoriutumismenestyksen ja muutamien hautovien naaraiden menehtymisen. Nämä tulokset viittaavat siihen, että myös pesyekokoon sidonnaiset haudontakustannukset voivat olla yksi tekijä pesyekoon määräytymisessä.

Pesäpoikaset omaavien lintujen pesyekoon on yleisesti ajateltu olevan sopeutuma siihen, kuinka suuren poikueen emot kykenevät ruokkimaan. Tämä sopeuma kuitenkin edellyttää, että pesäpoikasajan ravintotilanne on ennakoitavissa muninta-aikaan. Kirjosiepon pääravintoa ovat lentävät hyönteiset ja muut selkärangattomat, joiden saatavuus vaihtelee huomattavasti säätilojen mukaan. Tämän vuoksi pesäpoikasajan ravintotilanne ei ole ennakoitavissa muninta-aikana. Tutkiakseni, kuinka emot ratkaisevat ongelman, seurasin poikueen kasvua ja poikasten kuolleisuutta suhteessa säätiloihin tilanteessa, jossa emojen lisääntymispanostusta oli muutettu. Poikasten kasvuun vaikuttivat sekä pesyekoon manipulointi että säätilat. Poikasten kasvu oli selvästi hitaampaa sateisella ja kylmällä säällä sekä keinotekoisesti suurennetuissa poikueissa. Yksittäisten poikasten nääntyminen nälkään ja koko poikueen tuhoutuminen oli myös todenäköisempää sateisella säällä ja suurennetuissa poikueissa. Poikueen pienentyminen huonokuntoisten poikasten kuoleman kautta onkin ilmeisesti tapa, jolla pesyekoko muuntuu paremmin vastaamaan emojen kykyä ruokkia poikue.

Veriloisten vaikutusta lisääntymismenestyksen eri komponentteihin tutkimme ottamalla emoista verinäytteet ja analysoimalla veressä elävien parasiittien määrät ja lajit. Emme havainneet yleisimpien veriloisten vaikuttavan mihinkään mittaamiimme lisääntymismenestyksen osa-alueisiin. Toisaalta serologiset tutkimukset ovat antaneet viitteitä siitä, että lisääntymispanostuksen lisäys vaikuttaa emojen immuunijärjestelmää heikentävästi.

Tämän väitöskirjan osatutkimukset tukevat käsitystä, jonka mukaan pesäviipyiset poikaset omaavilla linnuilla emojen ruokintakyky on yksi tärkeimmistä tekijöistä pesyekoon määräytymisen ja lisääntymispanostuksen optimoinnin taustalla. Mekanismit, jotka vaikuttavat emojen ruokintakykyyn, ovat puolestaan sidoksissa ravinnon tilalliseen ja ajalliseen vaihteluun. Toisaalta myös resurssien allokointiongelmat lisääntymisen ja emon oman elinkyvyn ylläpitämisen välillä vaikuttavat lisääntymispanostuksen optimointiin.

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