Eva Rossmanith

Breeding biology, mating system and population dynamics of the Lesser Spotted Woodpecker (*Picoides minor*): combining empirical and model investigations

Institut für Biochemie und Biologie
Arbeitsgruppe Vegetationsökologie und Naturschutz

Breeding biology, mating system and population dynamics of the Lesser Spotted Woodpecker (*Picoides minor*):

combining empirical and model investigations

Dissertation

zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin "Ökologie"

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam

von
Eva Rossmanith
aus Frankfurt am Main

Potsdam, den 06.01.2005

This thesis aims to investigate breeding biology and population dynamics of the Lesser Spotted Woodpecker (*Picoides minor*). The results presented here were obtained using a range of approaches, from the empirical investigation of a Lesser Spotted Woodpecker population, analysis of raw data and the development and analysis of a simulation model. The thesis consists of four major chapters that can be read independently, since the single chapters focus on specific aims, each one showing an autonomous contribution into ecological research. Thus, each of the chapters represents a thematic unit, in which methods and the state of research are highlighted more explicitly. Owing to the cumulative form of the thesis, some sections of the chapters, particularly concerning methods, overlap to some extent. All chapters are in only slightly different versions previewed for submission to scientific journals in cooperation with co-authors. The idea to publish every single chapter is the reason why this thesis has been written in the first person plural. Co-authors include my thesis advisor Prof. Florian Jeltsch and PD Dr. Volker Grimm, who both have been partner of discussion. Dipl. Biol. Kerstin Höntsch supported me with additional empirical raw data from two field seasons (1996 and 2000) to increase the data pool of this rare species. Beside the data I collected specifically for this thesis, I analysed here additional raw data obtained in 1998 and 1999 for my diploma-thesis.

Nontheless, all findings presented here resulted from work that has been done independently by the author of the thesis.

Table of contents

Chapter I

Abstract

The protection of species is one major focus in conservation biology. The basis for any conservation plan or management concept is the knowledge of the species' autecology. In my thesis, I studied the life-history traits and population dynamics of the endangered Lesser Spotted Woodpecker (*Picoides minor*) in Central Europe. Thereby, I combined a range of approaches, from empirical investigations of a Lesser Spotted Woodpecker population in the Taunus low mountain range in Germany, the analysis of empirical data and the development of an individual-based stochastic model simulating the population dynamics.

In the field studies, I measured reproductive success, population structure and mortality. Moreover, breeding biology and mating system were investigated in detail. Reproductive success decreased significantly with later timing of breeding, caused by deterioration in food supply. Moreover, mate fidelity was of benefit, since pairs composed of individuals that bred together the previous year started earlier with egg laying and obtained a higher reproductive success. Both sexes were involved in parental care, but care was shared equally only during incubation and the early nestling stage. In the late nestling stage, parental care strategies differed between sexes: Females considerably decreased feeding rate with number of nestlings and even completely deserted small broods. Males fed their nestlings irrespective of brood size and compensated for the female's absence. I assumed the organisation of parental care in the Lesser Spotted Woodpecker to provide the possibility for females to mate with two males with separate nests and indeed, polyandry was confirmed.

To investigate the influence of the observed flexibility in the social mating system on population persistence, I developed a stochastic individual-based model simulating the population dynamics of the Lesser Spotted Woodpecker, based on empirical results. Since pre-breeding survival rates were needed for the model parameterisation but could not obtained empirically, I introduced a pattern-oriented modelling approach to estimate missing parameters by comparing simulation results with empirical patterns of population structure and reproductive success at the population level. Using this approach, I estimated the pre-breeding survival for two Lesser Spotted Woodpecker populations to test the reliability of the results.

Finally, I used the simulation model to investigate the effect of flexibility in the mating system on the persistence of the population. With increasing rate of polyandry in the population, persistence increased and even low rates of polyandry had a strong influence. Even when presuming only a low rate of polyandry and costs of polyandry in terms of higher mortality and lower reproductive success for the secondary male, the positive effect of polyandry on population persistence was still strong.

This thesis greatly increased the knowledge of the autecology of an endangered woodpecker species. Beyond the relevance for the species, I was able to demonstrate that flexibility in mating systems is a buffer mechanism and reduces the impact of environmental and demographic noise. The study suggests that behavioural flexibility should be considered when empirical evidences are available to improve the prediction quality of population viability analyses.

General Introduction

The human population growth of the last decades is leading to global changes of the environment causing a loss of species at dramatic rates. To prevent, mitigate and reverse this loss of species, landscapes and ecosystems, the “crisis discipline” of conservation biology[1] has emerged. One major task when aiming to prevent declining or threatened species is the development and realisation of management plans. A necessary first step to develop sustainable management strategies is to understand the critical processes in the species’ population dynamics. The conservation of keystone species is particularly important, since a loss of these species can lead to cascading negative effects in many other species from different taxonomic groups. Woodpeckers, for example, excavate cavities used by a large number of avian and mammalian species. Consequently, the community of secondary cavity nesters strongly depends on the woodpeckers’ service to produce the critical resource of cavities[2]. However, several woodpecker species suffer from a decline or even a regional extinction. Six of the ten woodpecker species in Europe show an overall negative population trend[3]. One of these threatened species is the Lesser Spotted Woodpecker (*Picoides minor*); the smallest woodpecker in the Palaearctic. Its distribution ranges from Great Britain over North West Africa to Kamtschatka[4]. Its population has shown an alarmingly declining trend in several parts of its distribution range[3,5]. Census investigations showed a dramatic decrease of 4% over 15 years in Sweden[6]. In many parts of Germany, Lesser Spotted Woodpecker populations are also considered endangered[7]. Even though the species is widely distributed and conservation plans are clearly needed, many aspects of the species’ autecology are unknown. So far, most information has been obtained from a single population of the Scandinavian subspecies *Picoides minor minor* in Sweden[8,9]. Recently, the results of Höntsch[10] contributed novel knowledge of space use and habitat requirements in the subspecies *Picoides minor hortorum* in Central Europe. However, knowledge of basic demographic parameters from the whole Central European distribution range is still missing. This includes information of mortality and reproductive success that is crucial for conducting population viability analyses of this keystone species.

---

[1] Soulé, M. E. 1986. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland.

[2] Martin, K. & Eadie, J. M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115: 243-257.

[3] Mikusinski, G. & Angelstam, P. 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118: 277-283.

[4] Cramp, S. 1985. Handbook of the birds of Europe and the Middle East and North Africa. Oxford University Press.

[5] Tiainen, J. 1985. Monitoring bird populations in Finland. *Ornis Fennica* 62: 80-89.

[6] Nilsson, S. G., Olsson, O., Svensson, S. & Wiktander, U. 1992. Population trends and fluctuation in Swedish woodpeckers. *Ornis Svecica* 2: 13-21.

[7] Havelka, P. & Ruge, K. 1993. Trend der Populationsentwicklung bei Spechten (Picidae) in der Bundesrepublik Deutschland. *Beihefte zu den Veröffentlichungen für Naturschutz u. Landschaftspflege Baden-Württembergs* 67: 33-38.

[8] Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. PhD Thesis, Lund University, Sweden.

[9] Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

[10] Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Universität Frankfurt, Germany.

Therefore, the central aim of my thesis is to increase the knowledge of the Lesser Spotted Woodpecker's autecology in Central Europe as well as to gain an understanding for the crucial processes in population dynamics. Consequently, on one hand, one needs information about demographic parameters and the species' behaviour. On the other hand, one needs to understand the essential processes in the population dynamics and their influence on the persistence of the population. To reach this goal, a combination of two methodological approaches is necessary: empirical investigations and ecological modelling.

The **empirical investigations** aim at examining basic demographic parameters such as reproductive success and mortality. Furthermore, this approach gives an insight into causal relationships between different processes of the population dynamic. The empirical study was conducted in the Taunus low mountain range near Frankfurt/Main, Germany. In the field, data of reproductive success, mortality and population structure were measured. Since reproduction is one of the primary factors influencing population dynamics, one main part of the empirical investigation was an extensive examination of the reproductive success of the Lesser Spotted Woodpecker, including timing of breeding and composition of nestling diet. Recent studies found the occurrence of polyandry in the Lesser Spotted Woodpecker, the mating of one female with more than one male having separate nests each [11]. This behaviour is very rare in birds and woodpeckers especially are expected to be strictly monogamous[12]. Since the mating system is closely related to the share of parental care between partners, a further aim of my thesis is to investigate parental care behaviour and mating system in the Lesser Spotted Woodpecker in detail.

However, some parameters cannot be measured directly in the field, for example mortality rates in highly mobile dispersing juveniles. Whenever it is not possible to extensively study a system in nature, computer models can provide a powerful alternative by replacing field studies with computer simulation experiments. Subsequently, ecological modelling can help estimating missing parameters or investigating population dynamics. Therefore, I used **a modelling approach** based on the empirical results to simulate the population dynamics of the Lesser Spotted Woodpecker. Stochastic simulation models allow to include environmental and demographic noise, two key factors influencing the risk of extinction. Part of the modelling process is the sensitivity analysis testing the relative impact of certain parameters on the population dynamics in the model[13]. Thereby, the models identify the crucial processes for which further empirical investigations are necessary and, subsequently, provide a valuable feedback mechanism helping to create new field studies. However, the aim of ecological models is not to simulate reality, since ecological systems are far to complex to take all possible factors into account. They should be seen as a powerful tool to test hypotheses or to conduct simulation experiments[11]. The structure of the model is based on

---

[11] Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* 31: 447-456.

[12] Winkler, H., Christie, D. A. & Nurney, D. 1995. *Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the World*. Russel Friedman Books CC, Sussex.

[13] Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61: 261-270.

the specific questions to be answered, thus we cannot expect the model to solve all possible questions one might have for a system.

Based on the understanding of processes gained in the empirical investigations and the gathered demographic parameters, I develop a stochastic model simulating the population dynamics of the Lesser Spotted Woodpecker. The model is individual-based, since characteristics of the individual, namely the mating status, influence the reproductive success. Using this model I compare two different populations of Lesser Spotted Woodpeckers and estimate their pre-breeding survival rate. Beside the gain of knowledge of the demographic parameters of the Lesser Spotted Woodpecker's population dynamics, I introduce an alternative approach to assess a missing parameter by pattern-oriented modelling that can be applied to other species as well. Furthermore, the model helps investigating the effect of the observed mating system on the persistence of the Lesser Spotted Woodpecker. I will show that flexibility in the mating system has a strong positive effect on the persistence of populations and need to be considered in population viability analyses.

Combining these two approaches, I am able to explore a wide range of questions concerning the Lesser Spotted Woodpecker population dynamics.

Structure of the thesis

This thesis consists of four major chapters that can be read independently and are linked by short text passages. Chapter I shows parts of the empirical investigation on a Lesser Spotted Woodpecker population in Taunus, Germany. Here, timing of breeding, nestling diet and their influence on reproductive success is investigated. In Chapter II, the organisation of parental care behaviour and the mating system were examined. In Chapter III, I present empirical data of mortality and population structure as well as the structure of the simulation model. The major aim of Chapter III is to estimate pre-breeding survival rates for two Lesser Spotted Woodpecker populations, each based on empirical data from the own study population and a study conducted in Sweden. Chapter IV investigates the influence of flexibility in the mating system on the persistence of the population. Finally, the thesis includes a summary discussion and a German "Zusammenfassung". Please note also the explanation concerning the composition of this thesis on the page prior to the table of contents.

Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): the early bird gets the caterpillar

Chapter I

Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): the early bird gets the caterpillar [1]

1. Abstract

Despite the declining trend in Lesser Spotted Woodpecker (*Picoides minor*) populations, data on reproductive biology are still scarce. Since an understanding of the determinants influencing reproductive success is needed for management strategies in endangered species, the aim of this study was to investigate the influence of timing of breeding and nestling diet on the reproductive success. In five study years between 1998 and 2003, we investigated various variables of reproductive success in a Lesser Spotted Woodpecker population in the Taunus low mountain range, Germany. At the breeding holes, we observed nestling feeding to assess composition of nestling diet and its change throughout the season. Clutch size, number of fledglings as well as body mass of the nestlings declined with start of egg laying. However, local recruitment of fledglings in the following year was not predicted by timing of breeding nor by body mass. Pairs composed of individuals that had breed together in previous years started egg laying earlier than newly established pairs. Nestling diet consisted mainly of aphids, caterpillars, craneflies and wood-living larvae. The composition changed considerably within breeding season in both early and late broods. However, early broods were provided with caterpillars more frequently, whereas late broods received more often wood-living larvae. Our results suggest that Lesser Spotted Woodpeckers time their breeding in a way that highest availability of caterpillars occurs in the early nestling stage, since this is the time of highest energy demand. Moreover, food availability declines during breeding season and the decline in reproductive performance seems to be an effect of this development.

---

[1] This chapter is previewed for submission as:

Rossmanith E, Höntsch K & Jeltsch F: Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): The early bird gets the caterpillar. Journal of Avian Biology

2. Introduction

The Lesser Spotted Woodpecker *(Picoides minor)* is widely distributed over the whole Palaearctic continent (Cramp 1985; Glutz von Blotzheim & Bauer 1994). Alarmingly, a dramatic population decline was reported from Sweden and Finland (Tiainen 1985; Nilsson et al. 1992) and a similar trend is assumed for many European Countries (Mikusinski & Angelstam 1997). Reasons for his negative population development still remain unclear. Despite its wide distribution range, investigations on Lesser Spotted Woodpeckers are difficult because of their low density and their inconspicuous behaviour (Wiktander 1998). Therefore it is not surprising that many aspects of the biology and ecology in this species are still unknown. However, to gain an understanding for the critical features in the dynamic of endangered species, knowledge of demographic parameters are urgently needed. One of the most important parameters for estimating population viability is the reproductive success (Haig et al. 1993). Reproductive success can be influenced by several factors, like resource availability or weather conditions. In birds for instance, food supply during brood care period is one main determinants of reproductive success (Van Balen 1973; Perrins 1991; Brinkhof 1997; Naef-Daenzer & Keller 1999). However, information on composition of nestling diet in the Lesser Spotted Woodpecker is anecdotal or gathered at single nests (Pynnönnen 1943; Török 1990). What we do know is, that Lesser Spotted Woodpeckers are changing their foraging behaviour during breeding period from preying only on wood-living insects to additionally searching for surface living arthropods, e.g. caterpillars (Wiktander 1998; Olsson 1998). One advantage of caterpillars as nestling diet is a low degree of chitinisation, which makes them easy to digest. In addition, they contain a high amount of protein (Robel et al. 1995) and can energetically fully be recovered (Kristin 1992). These characteristics effectively promote nestling development.

Caterpillar development is strongly synchronised with the development of tree foliage in early spring (Feeny 1970). As a result of their development, caterpillars show a peak time of abundance influenced by ambient temperature in duration and timing (Perrins 1991) and consequently within a short time window, an almost endless amount of energy rich bars is available. Therefore, synchronising this period with the timing of breeding should be of benefit and was indeed found in Great Tits (*Parus major*) (Van Balen 1973; Perrins 1991; Naef-Daenzer et al. 2000) and Blue Tits (*Parus caeruleus*) (Dias & Blondel 1996).

Timing of breeding was shown to influence reproductive performance in several bird species in that the later breeding started the less reproductive success was observed (Verhulst et al. 1995; Siikamäki 1998; Naef-Daenzer et al. 2001; Arnold et al. 2004). But not only timing relative to phenology of prey organisms may be important. Also absolute timing (calendar date) can influence reproductive success, especially, when birds have to moult or migrate before winter (Murphy 1986; Perrins & McCleery 1989; Siikamäki 1998). Furthermore, timing relative to conspecifics may be important when prior occupancy plays a role in territory settlement (Wesolowski 1998; Verboven & Visser 1998).

There are two not mutually exclusive explanations for seasonal decrease in reproductive success. First, timing of breeding per se could be the causal factor, due to seasonal variation in the environment, mostly deteriorating food supply (timing hypothesis, Klomp 1970; Murphy 1986; Ens et al. 1992; Brinkhof 1997; Siikamäki 1998). Alternatively, the decrease of success within season could be caused by variation in quality of the birds, with high-quality parents breeding early on good territories and poor-quality parents later on poor territories (quality hypothesis, Price et al. 1988; Verhulst et al. 1995).

To understand how changes in environmental conditions due to habitat loss or climate change effect reproductive success, we need to gain insights into the relationships between timing of breeding and food supply of nestlings. Therefore, aim of our study was to investigate reproductive success and composition of nestling diet of a Lesser Spotted Woodpecker population in Germany. Since timing of breeding is a crucial variable, we focused on an understanding of the relationship between timing, food supply and reproductive success. Based on these findings, we will discuss whether the timing or the quality hypothesis can be supported for this species. If timing were the main cause of decrease in reproduction, we would expect the same temporal variation in food supply in pairs that breed early as in late pairs. If habitat were the ultimate cause, we would expect differences in food supply of early and late pairs independently of seasonal variations. Accordingly, we investigated the seasonal variation in nestling diet in detail.

3. Methods

3.1 Study area

The study was conducted in an area of 70 km² in a German low mountain range near Frankfurt/Main (Taunus). The study area is situated in a heterogeneous landscape with deciduous, mixed and coniferous forest, large areas of settlement and grassland as well as extensively used orchards. The area contains 12 Lesser Spotted Woodpecker territories, which were not occupied in all study years.

3.2 Reproductive parameters

To investigate reproductive performance, we collected data for six reproductive parameters: (1) laying date – defined as the date of the first egg in the clutch (2) nesting success – proportion of pairs that fledged at least one young (3) clutch size – number of eggs in the full clutch (4) fledging success –number of fledglings in successful nests (5) body mass of nestlings and (6) duration of nestling period – the time from the day the first nestling hatched to the day the young left the nest.

Laying date and size of the full clutch were determined by inspecting the breeding hole at least two times during laying, using a dentist mirror and a small lamp. The exact laying date could be calculated, assuming the females lay one egg per day (Wiktander 1998). To control for annual differences in timing, we set the annual median laying date of the population to zero and calculated the “relative laying date” for each pair by using the deviation from it. We will later refer to broods that were started before or on the median date as “early broods” and to broods that were initiated later as “late broods”.

The hatching date of nestlings was determined by expecting the nest every day from the 9th day of incubating. On the 16th nestling day, the nest chamber was opened, nestlings were counted and weighed with a pesola spring balance to the nearest 0.5 g. Nestlings were then marked with a metal ring and an individual combination of two colour rings for later identification. We decided in favour of the 16th day, since younger nestlings might be too small and lose the rings and older nestlings might try to escape their hole after been put back (own observation). The number of young present in the cavity on day 16 was defined as fledging success, if no signs of predation were found the following days. From day 20, nests were visited every afternoon to determine fledging day.

Reproductive success was investigated between 1996 and 2003, except for 1997 and 2001. We included only first broods in the analysis, i.e. secondary polyandrous nests were not considered.

3.3 Classification of birds

To identify the birds individually, adults were caught with mist nest at their roosting or breeding holes and marked with colour rings. During our observations in successive years, local recruits (i.e. bird that were marked the previous year as nestlings) were recorded and classified as yearlings. Adults that were known from previous years were defined as old birds. In 2002 and 2003 we had enough experience to classify caught birds by the moulting pattern of their greater wing coverts (following Wiktander 1998; Pasinelli 1999). Furthermore, we defined a pair to be “old” if partners had bred together the previous year and to be “new”, if at least one partner was a yearling or had been mated differently the previous year.

3.4 Observations of feeding

In 1998, 1999, 2002 and 2003, feeding of nestlings was investigated at 16 nests. The observations were made from a hidden place in 30 to 50m distances with a telescope (Optolyth 30x80) in two-hour periods for a total of 454 hours. We visited each nest on 16 different days on average (minimum 10 days). For each feeding visit, we recorded the identity of the parent, the time of arrival and leaving to the nearest minute and the food item brought to the nest. Food items were identified to its major type (i.e. spider, aphids, cranefly, larvae), with finer levels of resolution (i.e. family of insect) whenever possible. Number of food items were recorded when they could clearly be identified. Furthermore, larvae were classified by their colour in surface living larvae (brown, green or patterned) and wood living larvae (white or bright reddish). Since number and size of prey items could not be identified if parents fed very small items, (e.g. aphids or ants), we decided to calculate the relative frequency of occurrence for each type based on the number of feeding observations with identified prey type. Relative frequency of the prey type “*a*” ($F_a\%$) expresses the proportion of how many (n_a) of all feedings (n) the prey type *a* was observed.

$$F_a\% = n_a / n \times 100$$

The sum of relative frequencies of all prey types might exceed 100%, because food items in one visit sometimes belonged to more than one group. To investigate the change of food composition over the season, the period when nestlings were fed was divided into five-day units, starting at the median of egg laying every year.

We did not measure the food availability directly, but presuming that individuals always decide for the most profitable prey item, we expect that differences in composition of nestling diet reflects differences in availability of preferred food. This is supported by studies of Kristin (1992), who showed for several passerine species a strong correlation between availability of a prey type and its relative frequency in the nestlings’ food composition. Moreover, Naef-Daenzer et al. (2000) showed that changes in the diet were entirely related to the seasonal development of prey biomass, i.e. size and number of available food.

In addition, we determined feeding rates per nestling by dividing number of feeding visits per hour by number of young in the nest. We calculated feeding rate per nestling for two nestling stages: First to 12th nestling day and 13th day to fledging day (see Chapter II for details).

3.5 Statistical analysis

Statistical analyses were performed with SPSS 11.0. We used a significance level of 0.05. Unless otherwise stated, reported p-values were based on two-tailed tests. When data were not normally distributed (clutch size and laying date) we used nonparametric tests and referred to median instead of mean values. We used analysis of variance (ANOVA) and Kruskal-Wallis tests to examine between-year variation in reproductive performance.

4. Results

In the 6 study years we investigated the reproductive success of 31 first broods. From all pairs 14 were identified as new and 5 as old pairs. Within the 6 study years, reproductive performance was similar. No significant differences in fledging success between years were found, neither on the basis of all pairs (1-way ANOVA, F=0.656, p=0.660) nor when considering only successful pairs (F=1.023, p=0.439). The same was true regarding clutch size (F=0.597, p=0.708), mean body mass of nestlings (F=0.699, p=0.608) and duration of nestling period (F=0.165, p=0.952). Therefore, we pooled data from all years for analysis.

4.1 Timing of breeding

Within all years, the beginning of egg laying ranged from 14th April to 10th May. Both latest and earliest laying date was observed in one year (1999), resulting in 26 days as the maximum range of days within all pairs had started egg laying. Between years, median dates of egg laying were not significantly different (Kruskal-Wallis test, n=6, p=0.416) and varied between 24th April and 1st May.

The laying date relative to the median was not different in pairs with yearling females compared to those with older females (unpaired t-test, T= 1.774, n=17, p=0.096) and the same was found for age classes of males (T=1.329, p=0.207, n=15). In old pairs however, relative laying date was significantly earlier than in new pairs (T= 3.208, n= 19, p<0.01). Thus, long pair bond duration had a positive effect on relative laying date irrespective of individuals' age.

4.2 Reproductive success

Nesting success -Out of 31 breeding attempts, 23 pairs (74.2%) fledged at least one young. Causes of failure are listed in Table 1. The most common cause of brood loss was nest predation. From eight broods without fledglings one belonged to an old and six to a new pair, in one case pair bond duration was not known. Hence, the proportion of failure did not significantly differ in old and new pairs (Fisher's exact 1-tailed, p=0.366). Nevertheless, failure seemed to be related to the timing of egg laying, since late broods were more likely to fail than early ones (Fisher's exact 1-tailed p<0.05).

Table 1: Causes of failure to produce fledglings (n= number of breeding attempts)

n	cause of failure
1	female died before egg laying
1	male died during first nestling stage
1	eggs did not hatch
2	complete predation by Eurasian Jay *Garrulus glandarius*
3	complete predation by Great Spotted Woodpecker *Picoides major*

Clutch size – Number of eggs in the full clutch was determined in 23 broods and varied from 3 to 6 eggs, the median size was 6. The clutch size was strongly influenced by relative laying date (r^2=0.346 p<0.01, Fig. 1A). Number of eggs decreased by one egg in 11 days (clutch size = 5.36 – 0.09*day)

Fledging success - Successful nests produced on average 3.6 fledglings (s.e. ± 0.25, *n*=21). Following the same seasonal trend as clutch size, fledging success decreased with relative laying date (r^2=0.200, n=21, $p<0.05$). The slope of the decreasing number of fledglings was similar to that of clutch size (number of fledglings = 3.54 – 0.10 *day).

Nestling body mass –Body mass was measured for 60 nestlings in 17 nests on their 16th day and was on average 21.0g (range 13.0-25.0, s.e.± 0.32). Again, a negative relation to relative laying date was found for mean nestling body mass per brood (r^2=0.389, $p<0.01$, Fig.1B).

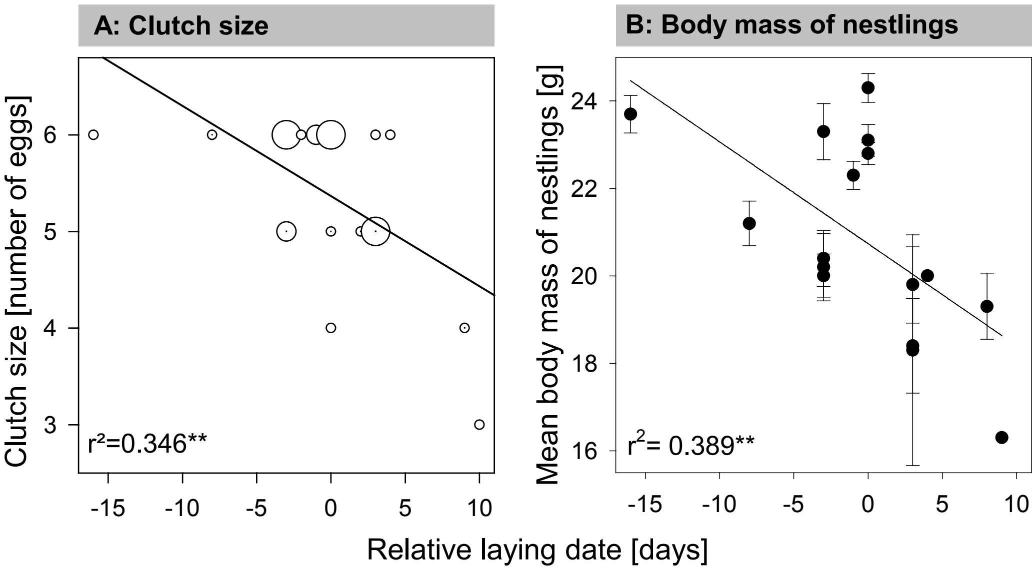

Figure 1 Influence of relative laying date on (A) Clutch size (n=23, bubble size reflects number of data points) and (B) mean body mass of nestlings per brood (± s.e.) (n=17). ** $p<0.01$.

Duration of nestling period - Nestlings fledged after 21 to 25 days (mean 23.2, s.e.± 0.29, n=17). In contrast to the other reproductive traits mentioned before, the duration of nestling period was not related to laying date (r^2=0.129, p=0.156, n=17). However, it increased with decreasing mean body mass of nestlings on their 16th day (r^2=0.314, $p<0.05$, n=16).

Local recruits – Overall, 46 nestlings had been marked in breeding seasons previous to the years we searched for local recruits. We recovered nine birds, thus the recovery rate was 19.6%. Surprisingly, there was a non-significant trend for young from late broods to be relocated more often than young from early broods (Fisher's exact 2-tailed test: p=0.054). However, body mass of nestlings did not predict the chance of being recovered, since mean body mass of recovered (21.1g ± s.e. 0.69) and non-recovered (21.1g ± s.e. 0.45) individuals was the same (Fisher's exact 2-tailed, p=0.978).

4.3 Feeding rate

In order to investigate the reason for a decreasing nestling body mass with laying date, we related the feeding rate per nestling (number of feeding visits per hour divided by number of young in the brood) of each pair to its laying date for the early (first to 12th day) and late (13th to fledging day) nestling stage. In the first stage, feeding rate per nestling showed a non-significant trend to increase with relative laying date ($r^2=0.278$, $p=0.053$), thus young in late broods were fed slightly more often than young in early broods. Whereas in the late stage, number of feeding visits per nestling was not related to the timing of egg laying ($r^2=0.173$, $p=0.157$).

4.4 Nestling diet

Overall, 4834 feeding visits were observed and food was clearly identified in 3790 cases (78.4%). Based on these cases, we found nestling diet of Lesser Spotted Woodpeckers to consist of mainly four prey types (Table 2): Aphids (Sternorrhyncha), surface-living larvae (mainly caterpillars), craneflies (Tipulidae) and wood-living larvae. Other arthropod types were fed in less than 5% of the observed feedings and are therefore pooled in the group “other items”.

Table 2 Composition of nestling diet in Lesser Spotted Woodpeckers.

Prey type	Relative frequency (%)
Sternorrhyncha (aphids)	51.6
Surface-living larvae	24.6
Tipulidae (craneflies)	14.7
Wood-living larvae	13.0
Arachnida (Spiders and harvestman)	2.9
Formicidae (ants)	0.7
Cleoptera (beetles)	0.6
Lepidoptera (butterflies)	0.6
Diptera (without tipulidae)	0.7
Other items	1.4

4.4.1 Seasonal changes

Composition of nestling diet changed remarkably over the breeding season. While relative frequency of aphids increased within season, surface-living larvae tended to decrease. Figure 2 shows that between day 11 and day 20 most feeding visits contained surface-living larvae. Interestingly, this was exactly the time when nestlings in most broods hatched. The relative frequency of surface-living larvae decreased afterwards and from day 21 after the median laying date, the most frequent prey type in the feeding visits were aphids.

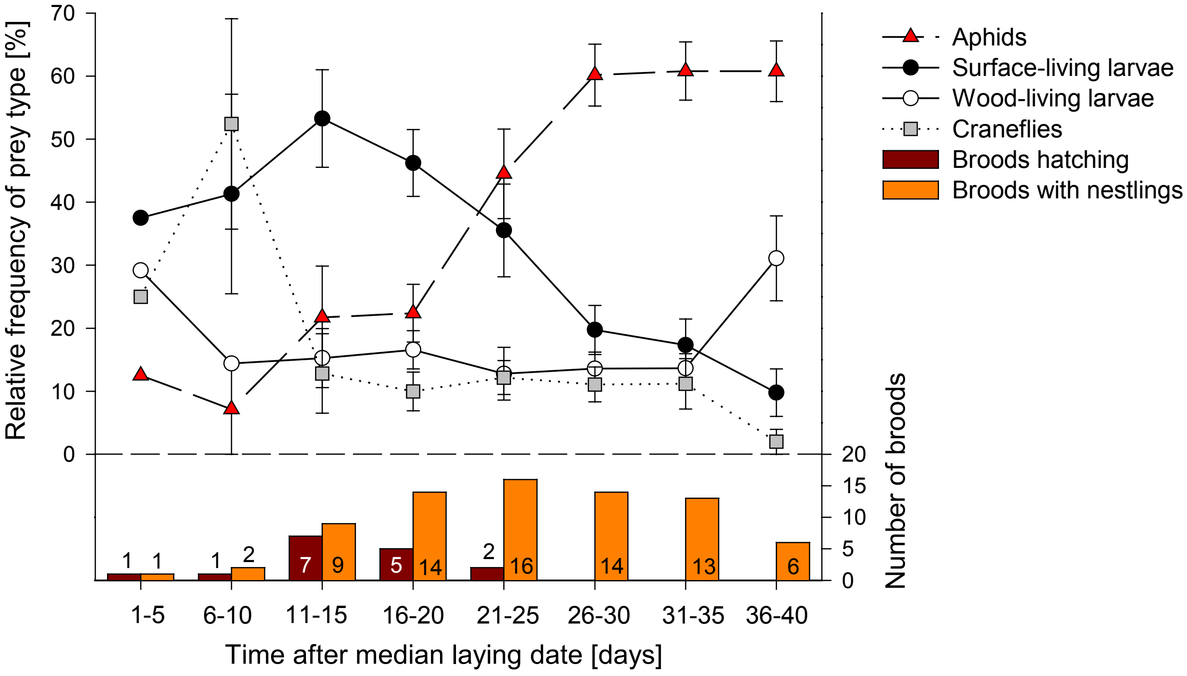

Figure 2 Seasonal change of nestling diet, all years combined. The relative frequency of occurrence in the observed feedings is shown for the four main prey types (mean ± s.e.). Since one feeding visit might include several prey types, the sum of all relative frequencies in a certain time period can exceed 100%. Feeding period is divided into five-day-units beginning at the median laying date in each year. Dark bars show the number of broods in which nestlings hatched at a certain time interval, light bars the number of broods containing nestlings.

4.4.2 Early and late broods

Seasonal variation in nestling diet was found in both early and late broods (Fig. 3). The declining trend for relative frequency in surface-living larvae was observed in both groups at the same time-units.

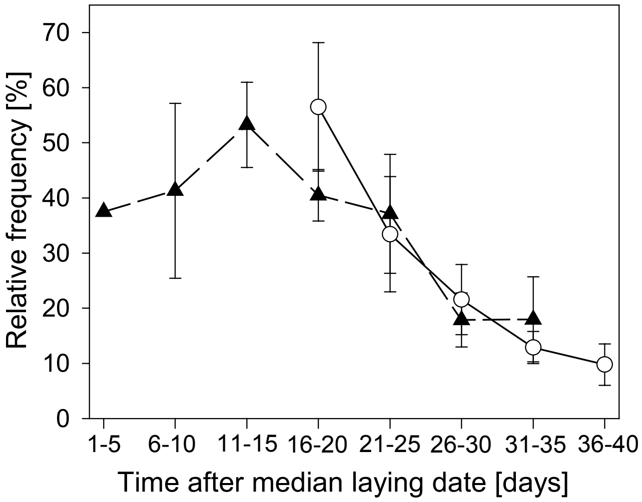

Figure 3 Seasonal changes in the frequency of caterpillars in the diet of early (triangle, n=8) and late (circle, n=6) broods.

Composition of nestling diet of early and late broods (Fig.4) differed significantly in relative frequency of surface-living (unpaired t-test: T=2.464, p<0.05) as well as wood-living larvae (T= -3.754, p<0.01). Interestingly, comparing the relative frequency of any kind of larvae in the nestling diet, we found no significant difference between the groups (T=0.386, p= 0.706). Also, relative frequency of aphids, craneflies and other items did not differ significantly (aphids: T= -0.927, p=0.372, craneflies: T= 1.087, p=0.298, other items: T=0.914, p=0.379).

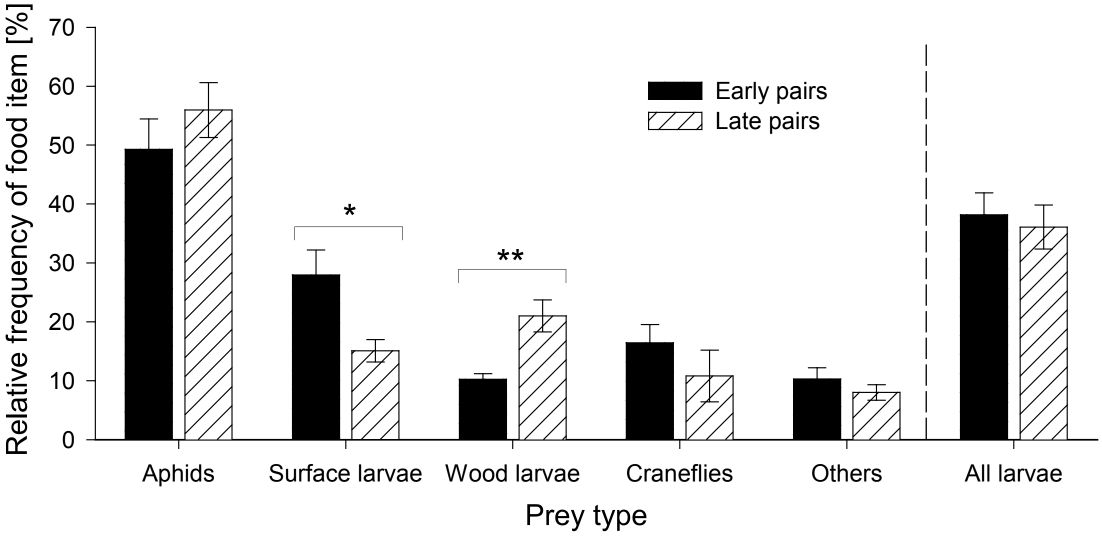

Figure 4 Food composition of early (n=8) and late (n=6) pairs. The relative frequency based on all observed feedings is shown (mean + s.e.).* p<0.05, ** p<0.01

4.5 Feeding visits with larvae

Since composition of nestling diet differed in the type of larvae between early and late broods, we compared feeding observations where surface-living larvae where fed with those where wood-living larvae were fed. We focused on the time an individual spent away from the nest before feeding larvae and the number of prey items in feeding visits where larvae were fed.

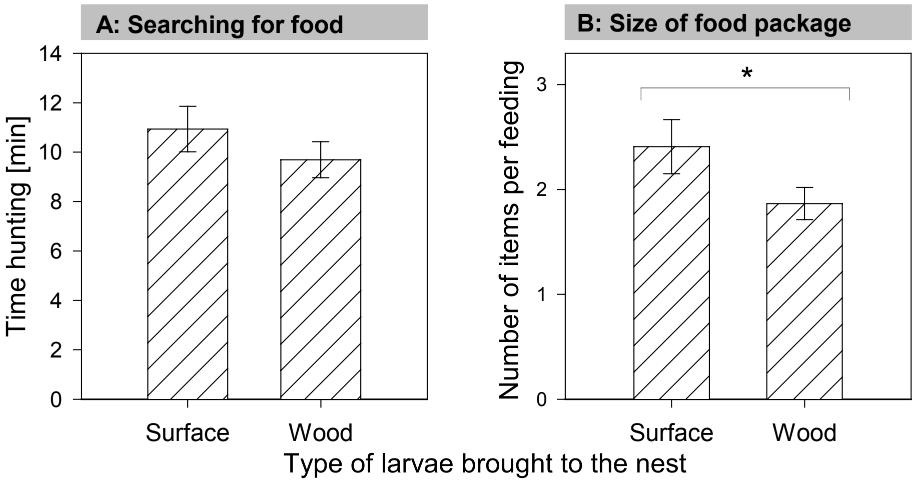

Figure 5 Comparison between feeding visits with surface-living and wood-living larvae. (A) Time spent for hunting by the parents (mean + s.e.), n=16 pairs. (B) Number of items fed in one feeding visit (mean + s.e.). n=6 pairs, 1998 and 1999 only.* p<0.05.

The time one adult spent away from the nest did not differ between feeding visits with surface-living larvae and those with wood-living larvae (paired t-test, T= - 0.283, p=0.782, n=14, Fig. 5A). Figure 5B shows that if surface-living larvae were fed, the adults brought more food items than in feedings were wood-living larvae were fed (paired t-test, T=2.689, p<0.01, n=6).

5. Discussion

In this paper, we present the first detailed study on reproductive success and nestling diet of Lesser Spotted Woodpeckers in Central Europe.

5.1 Optimal timing of breeding

In some bird species feeding their nestlings with caterpillars, an adaptation of their timing of breeding on the seasonal pattern in caterpillar abundance was found. For instance, optimal timing of breeding in the well studied Great Tits (*Parus major*) was found to be adjusted in the way that their nestlings are approximately 10-18 days old (i.e. the second half of the nestling period) when caterpillar abundance and size reaches its peak time (Perrins 1991; Wesolowski 1998; Naef-Daenzer & Keller 1999). The late nestling stage is assumed to be most energy demanding in Great Tits, since energetic needs increase with nestlings' growth (Naef-Daenzer & Keller 1999). In the Lesser Spotted Woodpecker however, we observed that caterpillars had the highest frequency in the feedings when nestlings in most broods just hatched. Thus, timing of breeding seems to be later in Lesser Spotted Woodpecker than in the Great Tit. A relative late timing of breeding in the Lesser Spotted Woodpecker compared to other non-migratory bird species including the Great Tit was found in Sweden (Wiktander et al. 2001b). But what does the Lesser Spotted Woodpecker gain from breeding later?

One advantage of starting later in the season might be the enhancement of mean daily temperatures as well as the declining probability of frost. Moderate temperature might be particularly important for woodpeckers, since they do not use insulating nesting materials other than a thin layer of woodchips on the ground of the breeding hole (own obs., Wiktander 1998) and broods are relatively small (2-6 nestlings). Consequently, heat loss can be expected to be higher in woodpecker broods than in Passerine hole-nesting species, that have usually larger broods and a thick layer of insulation material. Furthermore, woodpeckers incubate their eggs for only 10-11 days and young hatch relatively immature compared to other altricial species and need longer time to grow feathers and develop thermoregulatory abilities (Yom-Tov & Ar 1993). Therefore, the first nestling days require intensive brooding, which reduces the parents' available time for foraging and nestling feeding (see Chapter II). The early nestling stage might therefore be most demanding and should therefore coincide with the time of highest food availability. This view is further supported by Wiktander et al. (2001b) who found that most breeding failures in Lesser Spotted Woodpecker appear in the early nestling stage.

A further trait, affecting the timing of breeding in hole-nesting birds, is seen in competition for cavities (Ingold 1994; Wesolowski 1998). Pasinelli (1999) suggested that the later breeding start of Middle Spotted Woodpecker (*Picoides medius*) compared to Great Spotted Woodpecker and European Starling (*Sturnus vulgaris*) is a mechanism to reduce the probability of a cavity takeover by larger species. However, a general delay in timing caused by cavity competition with the mentioned species can be rejected for the Lesser Spotted Woodpecker in our study area. First, breeding holes are too small for European Starlings and secondly, timing of breeding was similar in Great and Lesser Spotted Woodpecker in our study area (Wölflik 2002).

5.2 Variation in timing of breeding within the population

Reproductive success of the Lesser Spotted Woodpecker decreased the later breeding started. The seasonal decline in clutch size confirms earlier findings for this species in an other climatic region (Wiktander et al. 2001b) and is similar to the pattern in many single-brooded birds (review in Klomp 1970; Wesolowski 2000). Furthermore, our results show that fledging success decreased with the same slope, indicating that clutch size is the major cause for the number of fledglings in successful nests.

But not only number of eggs and fledglings declined, also body mass of nestlings at day 16 was lower, the later a pair started breeding. Perrins (1991) stated that the body mass of nestlings provides a measure of how easily parents can find food. If body mass decreases, one might expect a deterioration of nestling provisioning.

Nestling provisioning includes the frequency a nestling gets food in a certain time as well as the amount and quality of food per feeding. Surprisingly, we did not find feeding rate per nestling to be lower in late than in early broods, in contrast it tended to be even higher. Consequently, differences in body mass between early and late broods should largely be caused by differences in quality and/or quantity of food per feeding visit. In the present study, Lesser Spotted Woodpecker nestlings in early broods were fed significantly more often with surface-living larvae (namely caterpillars) than those in late broods. In turn, feeding visits in late broods contained more often wood-living larvae (Fig.2). Presuming that individuals always decide for the most profitable prey item, we expect that differences in composition of nestling diet reflects differences in availability of preferred food (see section “methods” for details). Larvae in general are easy to digest because of their low degree of chitinisation (Kristin 1992). Additionally they have a high protein content (Robel et al. 1995), which is needed for nestling development. However, surface-living larvae like caterpillars can be collected easily, especially when highly abundant, since they are visible and relatively immobile (Kristin 1992). Wood-living larvae on the other hand are invisible and have to be pecked out of the bark. Consequently, we assume that preying on wood-living larvae requires more time and energy.

Interestingly, we found that parents did not spend more time searching for food when feeding wood-living larvae than when feeding caterpillars (Fig. 5A). Instead, they brought fewer items per feeding (Fig. 5B). Our results suggest that parents did not exceed foraging time when food availability decrease. Instead they delivered smaller packages. A similar behaviour was found in

Great Tits, where parents became less selective in prey choice when food was less available rather than decreasing feeding rate (Grieco 2002). A frequent return to the nest might be important in order to prevent predation.

5.3 Differences in time or quality?

Differences in nestling diet of early and late broods can first be causally related to the timing per se, due to a decrease of food availability with time (timing hypothesis) or secondly be caused by differences in the habitat quality of early and late breeders (quality hypothesis, see introduction). If timing were the main cause of deterioration in reproduction performance, we should see the same development of food supply within season in both groups. If habitat quality were the ultimate cause, we would anticipate differences in food supply of early and late pairs irrespective of seasonal changes.

We found, that the relative frequency of caterpillars was similar in early and late breeders at a given date in the season and decreased with time (Fig. 3). We conclude that with a late start of egg laying, food availability decreases and leads to an inferior nestling supply in later broods. This supports the timing hypothesis to be the main cause of the declining reproductive performance within season.

5.4 Fitness of fledglings

Duration of nestling period increased with the nestlings’ declining body mass. This result suggests that nestlings stayed in the nests until they reached a sufficient body condition. Similar results were found in Marsh Tits (*Parus palustris*), where the decision for a young to fledge was dependent on its body mass at day 13 (Nilsson & Svensson 1993) and in Great Tits, where duration of nestling period was negatively related to food availability (Seki & Takano 1998). Surprisingly, body mass did not predict probability of local recruitment in our study, which contradicts investigations in other species (Gaston 1997; Green & Cockburn 2001; Monrós et al. 2002).

In contrast to recent results in the Lesser Spotted Woodpecker (Wiktander et al. 2001b) and other bird species (Harris et al. 1994; Verhulst et al. 1995; Siikamäki 1998; Verboven & Visser 1998; Naef-Daenzer et al. 2001), we found that local recruitment was not higher for early than for late fledglings. This result is in accordance with Monrós et al. (2002) showing that early fledgling is not the best option every year.

In general, an early fledging date relative to conspecifics should be important when number of fledglings exceed the number of unoccupied territories. In this situation, prior occupancy is of benefit and results in higher survival and future reproduction rate. The fact that this pattern was not found in our study suggests that unoccupied territories of similar quality were available for all fledglings. Indeed, unoccupied territories were frequently found in our study area (Höntsch 2005).

Consequently, timing relative to conspecifics seems to be of only minor importance for the investigated Lesser Spotted Woodpecker population. This might also explain the lower synchronisation in our population, since Wesolowski (1998) argued that high synchronisation of breeding in Marsh Tits is caused by the intraspecific competition for fledging early. In his study, 90% of all pairs started egg laying within 10 days. In our investigation, timing of egg laying varied widely among Lesser Spotted Woodpecker pairs and in one year the earliest pair started egg laying 26 days before the latest pair.

We conclude that later pairs produce less offspring than early pairs, but with the same fitness. However, their investment in brood care seems to be higher, because food availability is lower and nestlings need more time for their development resulting in a longer nestling period.

Since clutch size determines the number of fledglings, the question arises what the ultimate cause of reduced clutch size in late broods might be. We assume that food availability during nestling time becomes suboptimal the later young hatch and might be insufficient for a large brood. However, a strategic decision by late pairs should be considered as well. Producing smaller clutches is timesaving, since for every egg the birds forego to lay, they can start incubating one day earlier and thus young hatch earlier (see Wesolowski 2000).

5.5 What is the reason for the difference in timing between individuals?

In many bird species, reproductive performance, e.g. early breeding, increases with age (Saether 1990). We did not find an age effect comparing yearlings and older birds. However, we found pairs that bred together in consecutive years to have an earlier start of egg laying, which is confirmed by observations in another region (Wiktander et al. 2001a). A positive influence of pair bond duration on reproductive performance is known for several long-living (Forslund & Larsson 1991; Pyle et al. 2001) as well as for short living birds (Perrins & McCleery 1985; McGraw & Hill 2004). Nevertheless, causes for this phenomenon remained unclear (Ens et al. 1996)

We assume that experience in the territory might lead to the observed pattern in the Lesser Spotted Woodpecker. Höntsch (2005) conducted a study investigating home ranges and found that many individuals do not have close neighbours, since population density is low and home range sizes had enormous dimensions during mating time. Therefore, newly established pairs had to shift their home range, whereas old pairs stayed in the same territories (Höntsch 2005). Since breeding experience in the same territory was shown to increase reproductive success (Pyle et al. 2001) this might explain the inferior performance found in new pairs.

5.6 Conclusion

Timing of breeding showed to be an important determinant of reproductive success in the Lesser Spotted Woodpecker. Generally, the Lesser Spotted Woodpeckers time their breeding in a way that highest availability of caterpillars occurs in the early nestling stage, since this is the time of highest energy demand. In the course of the season, food availability deteriorates and the decline in reproductive performance seems to be an effect of this development. Caterpillars play an important role in the nestling diet. Thus variation in caterpillar availability caused by environmental changes - e.g. climate change (Harrington et al. 1999) - might influence reproductive success in this species.

6. References

Arnold, J. M., Hatch, J. J. & Nisbet, I. C. T. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *Journal of Avian Biology* 35: 33-45.

Brinkhof, M. W. G. 1997. Seasonal variation in food supply and breeding success in European Coots *Fulica atra*. *Ardea* 85: 51-65.

Cramp, S. 1985. Handbook of the birds of Europe and the Middle East and North Africa. Oxford University Press, Oxford.

Dias, P. C. & Blondel, J. 1996. Breeding time, food supply and fitness components of Blue Tits *Parus caeruleus* in Mediterranean habitats. *Ibis* 138: 644-649.

Ens, B. J., Choudhury, S. & Black, J. M. 1996. Mate fidelity and divorce in monogamous birds. In: Black, J. M. (ed.) *Partnership in birds*, pp. 344-401. Oxford University Press, Oxford.

Ens, B. J., Kersten, M., Brenninkmeijer, A. & Hulscher, J. B. 1992. Territory Quality, Parental Effort and Reproductive Success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61: 703-715.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.

Forslund, P. & Larsson, K. 1991. The effect of mate change and new partner's age on reproductive success in the barnacle goose, *Branta leucopsis*. *Behavioral Ecology* 2: 116-122.

Gaston, A. J. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* 139: 673-678.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1994. Columbiformes - Piciformes. Aula-Verlag, Wiesbaden.

Green, D. J. & Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* 70: 505-514.

Grieco, F. 2002. How different provisioning strategies result in equal rates of food delivery: an experimental study of blue tits *Parus caeruleus*. *Journal of Avian Biology* 33: 331-341.

Haig, S. M., Belthoff, J. R. & Allen, D. H. 1993. Population viability analysis for a small population of Red-Cockaded Woodpeckers and an evaluation of enhancement strategies. *Conservation Biology* 7: 289-301.

Harrington, R., Woiwod, I. & Sparks, T. 1999. Climate change and trophic interactions. Trends in Ecology & Evolution 14: 146-150.

Harris, M. P., Buckland, S. T., Russell, S. M. & Wanless, S. 1994. Post Fledging Survival to Breeding Age of Shags *Phalacrocorax aristotelis* in Relation to Year, Date of Fledging and Brood Size. *Journal of Avian Biology* 25: 268-274.

Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Ingold, D. J. 1994. Influence of Nest-Site Competition between European Starlings and Woodpeckers. *Wilson Bulletin* 106: 227-241.

Klomp, H. 1970. Determination of Clutch-Size in Birds - A Review. *Ardea* 58: 1-16.

Kristin, A. 1992. Trophische Beziehungen zwischen Singvögeln und Wirbellosen im Eichen-Buchenwald zur Brutzeit. *Der Ornithologische Beobachter* 89: 157-169.

McGraw, K. J. & Hill, G. E. 2004. Mate attentiveness, seasonal timing of breeding and long-term pair bonding in the house finch (*Carpodacus mexicanus*). *Behaviour* 141: 1-13.

Mikusinski, G. & Angelstam, P. 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118: 277-283.

Monrós, J. S., Belda, E. J. & Barba, E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99: 481-488.

Murphy, M. T. 1986. Temporal Components of Reproductive Variability in Eastern Kingbirds (*Tyrannus tyrannus*). *Ecology* 67: 1483-1492.

Naef-Daenzer, B. & Keller, L. F. 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.

Naef-Daenzer, L., Naef-Daenzer, B. & Nager, R. G. 2000. Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* 31: 206-214.

Nilsson, J. A. & Svensson, M. 1993. Fledging in altricial birds - parental manipulation or sibling competition. *Animal Behaviour* 46: 379-386.

Nilsson, S. G., Olsson, O., Svensson, S. & Wiktander, U. 1992. Population trends and fluctuation in Swedish woodpeckers. *Ornis Svecica* 2: 13-21.

Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. PhD Thesis, Lund University, Sweden.

Pasinelli, G. 1999. Relations between habitat structure, space use and breeding success of the Middle Spotted Woodpecker *Dendrocopos medius*. PhD Thesis, Universität Zürich, Switzerland.

Perrins, C. M. 1991. Tits and their caterpillar food supply. *Ibis* 133: 49-54.

Perrins, C. M. & McCleery, R. H. 1985. The Effect of Age and Pair Bond on the Breeding Success of Great Tits *Parus major*. *Ibis* 127: 306-315.

Perrins, C. M. & McCleery, R. H. 1989. Laying Dates and Clutch Size in the Great Tit. *Wilson Bulletin* 101: 236-253.

Price, T., Kirkpatrick, M. & Arnold, S. J. 1988. Directional Selection and the Evolution of Breeding Date in Birds. *Science* 240: 798-799.

Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology* 70: 1088-1097.

Pynnönnen, A. 1943. Beiträge zur Kenntnis der Biologie finnischer Spechte, Teil II - Die Nahrung. *Annales Zoologici Societatis Zoologicae-Botanicae-Fennicae Vanamo* 9: 1-59.

Robel, R. J., Press, B. M., Henning, B. L., Johnson, K. W., Blocker, H. D. & Kemp, K. E. 1995. Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology* 66: 44-53.

Saether, B. E. 1990. Age-specific variation in reproductive performance of birds. In: Power, D. M. (ed.) Current Ornithology 7

Seki, S. I. & Takano, H. 1998. Caterpillar abundance in the territory affects the breeding performance of great tit *Parus major minor*. *Oecologia* 114: 514-521.

Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79: 1789-1796.

Tiainen, J. 1985. Monitoring bird populations in Finland. *Ornis Fennica* 62: 80-89.

Török, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos spp.* during breeding season. *Holarctic Ecology* 13: 257-264.

Van Balen, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-91.

Verboven, N. & Visser, M. E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81: 511-524.

Verhulst, S., Vanbalen, J. H. & Tinbergen, J. M. 1995. Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. *Ecology* 76: 2392-2403.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 265: 1867-1870.

Wesolowski, T. 1998. Timing and synchronisation of breeding in a Marsh Tit *Parus palustris* population from a primeval forest. *Ardea* 86: 89-100.

Wesolowski, T. 2000. Time-saving mechanisms in the reproduction of Marsh Tits (*Parus palustris*). *Journal für Ornithologie* 141: 309-318.

Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001a. Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). *Auk* 118: 624-635.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001b. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Ibis* 143: 72-82.

Wölflik, O. 2002. Vergleichende Untersuchungen der Bruthöhlenhabitate von Kleinspecht (*Picoides minor*) und Buntspecht (*Picoides major*). Diplomarbeit, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Yom-Tov, Y. & Ar, A. 1993. Incubation and Fledging Durations of Woodpeckers. *Condor* 95: 282-287.

Link to the proceeding Chapter

In the last Chapter I investigated nestling diet and reproductive success of the Lesser Spotted Woodpecker. My results showed significant effects of the timing of breeding on the reproductive success, since nestling diet deteriorated within the breeding season. Moreover, pairs composed of individuals that bred together the previous year started earlier with egg laying and had a higher reproductive success. When mate fidelity is of benefit, the future condition of the mate becomes important to its partner[2]. This might influence the social mating system in the species and the organisation of parental care behaviour. These two issues will be investigated in Chapter II.

---

[2] Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Sex-related parental care strategies in the Lesser Spotted Woodpecker *(Picoides minor)*: of flexible mothers and dependable fathers.

Chapter II

Sex-related parental care strategies in the Lesser Spotted Woodpecker (*Picoides minor*): of flexible mothers and dependable fathers [1]

1. Abstract

We investigated sex-specific parental care behaviour in the course of the breeding cycle in an individually marked population of Lesser Spotted Woodpeckers (*Picoides minor*) in the low mountain range Taunus, Germany. Parental care was observed at the breeding holes and included incubation of eggs, nest sanitation as well as brooding and feeding of nestlings.

In monogamous pairs, contributions of male and female to parental care changed in progress of the breeding period. During incubation as well as in the first half of the nestling period, parental care was divided equally between the partners. However, in the late nestling stage, we found different strategies for males and females: while males fed their nestlings irrespective of brood size, females considerably decreased feeding rate with the number of nestlings. This behaviour culminated in complete desertion of small broods by females shortly before fledging. The fact that even deserted nests were successful indicates that males were able to compensate for the females' absence. Interestingly, the mating of one female with two males with separate nests could be found in the population, which confirms polyandry in the Lesser Spotted Woodpecker as an unusual but frequently occurring social mating system.

We conclude that although successfully raising young requires both parents in the early nestling stage, biparental care is not essential in the later stage. From then, one parent can reduce effort and thus costs of parental care, at least in broods where the mate is able to compensate for that behaviour. This is more likely in small broods, because of their lower energy demand. For the unusual fact that reduced care and desertion appears only in females, we discuss a combination of two traits: First, females might suffer higher costs of investment in terms of mortality and secondly, male-biased sex ratio in the population lead to higher mating probabilities in females than in males. The occurrence of polyandry seems to be a result of these conditions.

---

[1] This chapter is previewed for submission as: Rossmanith, E., Höntsch, K. & Jeltsch, F. Sex-related parental care strategies in the Lesser Spotted Woodpecker (*Picoides minor*): of flexible mothers and dependable fathers. Journal of Behavioral Ecology and Sociobiology

2. Introduction

Parental care is any form of parental behaviour that appears likely to increase the fitness of a parent's offspring (Clutton-Brock 1991). The effort in parental care is a trade-off between investment in current and future reproduction, since increased reproductive expenditure may reduce parental survival and therefore parental future reproductive output (Nur 1984; Horak 2003). In species with biparental care, the optimal expenditure is furthermore influenced by the effort of the mate (Chase 1980) and can be different for the sexes. Therefore, parental care is not always shared equally between the partners. Predictions on how parental care should be divided must take into account both conflicts of interests (Trivers 1972) and co-operation between the sexes (Wiebe & Elchuk 2003). If there is a chance to gain extra-mates, one individual should make its mate work harder and reduce its own investment to increase future reproductive success. However, reduction of one's own care only pays off if the partner is able and willing to compensate for this behaviour (Lazarus 1990). Alternatively, if full expenditure of both parents is needed to successfully raise a brood, an equal share of the duties can be assumed. This is especially true in species where mating the same partner in subsequent years leads to an increased future reproductive success (e.g. Perrins & McCleery 1985; Forslund & Larsson 1991; Pyle et al. 2001; McGraw & Hill 2004). In this case, body condition of the mate is of direct importance. Additionally, share of parental duties could be influenced by value of the current brood. This can change with the number of nestlings but also with time, since older nestlings have a higher probability to reach reproductive age.

Biparental care is the norm in birds, occurring in over 90% of the more than 9,000 bird species (Lack 1968). In most monogamous bird species, females take the larger part of brood care, e.g. in most Passerines (Clutton-Brock 1991). Here, facultative multi-nest polygyny occurs frequently, where one male is mated with more than one female with separate nests (Clutton-Brock 1991; Kempenaers 1995; Lubjuhn et al. 2000). In contrast, species where males contribute highly to brood care are rare. One example are woodpeckers, where males stay with the eggs and young during the night (Winkler et al. 1995), which is an uncommon trait known otherwise only from Cuckoos among altricial birds (Ligon 1993). But only few studies have investigated parental care behaviour in woodpeckers (Hogstad & Stenberg 1997; Wiktander et al. 2000; Michalek & Winkler 2001; Wiebe & Elchuk 2003). In general, biparental care is seen to be essential for raising a brood in this family and they are regarded as being strictly monogamous (Winkler et al. 1995). Therefore, an equal division of parental care between the sexes during daytime should be predicted. Indeed, this was shown for Middle Spotted Woodpecker (*Picoides medius*) and Great Spotted Woodpecker (*Picoides major*) (Michalek & Winkler 2001). However, a recent discovery disturbs the general view: Wiktander et al. (2000) reported several cases of multi-nest polyandry in the Lesser Spotted Woodpecker (*Picoides minor*). The occurrence of this mating-system shows that gaining extra-mates is possible for females in the Lesser Spotted Woodpecker and therefore reduced care by females could be possible as well.

Polyandry was found only in about 1% of all bird species and is mostly performed in the order of Gruiformes and Charadriiformes (Emlen & Oring 1977). The occurrence of this very rare mating system in a species that was thought to be strictly monogamous, makes the Lesser Spotted Woodpecker a good model organism to study the conditions under which polyandry can occur and might evolve. An important feature in this context is share of the parental care between the partners, since this is closely related to mating-systems. However, neither was the performance of polyandry confirmed in other Lesser Spotted Woodpecker populations, nor had the parental care behaviour been explored in detail before.

Therefore, we investigated parental care behaviour and mating system of the Lesser Spotted Woodpecker in a population in Central Europe. Our main objective was to examine the share of duties between the partners. Since optimal expenditures for the sexes might not be static but change within the season or differ with value of the current brood, we furthermore focused on the effect of age and number of nestlings on the effort in parental care by both sexes.

3. Methods

3.1 Study area

The study was conducted in an area of 70 km² in a German low mountain range (Taunus) 30 km NW of Frankfurt/Main. The study area was situated in a heterogeneous landscape with deciduous, mixed and coniferous forest types, extensively used orchards as well as interspersed areas of settlement and grassland. The area contains 12 Lesser Spotted Woodpecker territories, which were not occupied in all study years.

3.2 Observations

Before egg laying started, the area was searched for breeding holes and adult birds were caught and marked with two colour rings for individual identification. To examine influence of offspring value on parental care behaviour, we determined the size of the full clutch and the number of nestlings (brood size) in the breeding holes, using a dentist mirror and a small lamp. Number of young was counted at least twice, shortly after hatching and on day 16, when the nest chamber was opened to mark the nestling and again, if signs of predation were found (e.g. pecking in the bark)

We investigated parental care in its narrowest sense, meaning the care of eggs or young when they are detached from the parent's body (Clutton-Brock 1991). This included incubation, brooding, feeding and nest sanitation (i.e. removal of faecal sacs). Observations were made in the breeding seasons of 1998 to 2003, except for 2001. Pairs were observed at their breeding holes from a hidden place at a distance of 30 to 50m with a telescope (Optolyth 30x80). We recorded identity of the visiting bird, time of arrival and leaving to the nearest minute for each visit and removal of faecal sacs. If an individual stayed for more than two minutes in the breeding hole with hatched young, we defined this behaviour as brooding.

Incubation was examined on 11 nests in 49 periods of 3 (1998) or 2 (2002 & 2003) hours and a minimum of 4 different days per nest. After hatching, we observed 19 broods in 304 periods of 2 hours and visited every nest on 16 different days on average (minimum 10 days). Observation days were distributed evenly over the whole nestling period. Observations were cancelled in heavy rain, since we found parents to decrease feeding frequency noticeably under these conditions.

3.3 Data analysis

To compare parental effort in incubating and brooding, we calculated relative percentage of time spent on this behaviour based on the total observation time at the nest. In terms of providing for the young, we calculated the feeding frequency, i.e. number of feeding visits per hour. Since individuals feeding more frequently are also more likely to remove faecal sacs, we calculated number of visits with faecal sac removal based on all feeding visits to exclude influence of feeding frequency.

Statistical analyses were performed with SPSS 11.0. We used a significance level of 0.05 and, unless otherwise stated, reported p-values are based on two-tailed tests. In cases when data were not normally distributed we used nonparametric tests and referred to median values instead of mean values.

4. Results

4.1 Clutch and brood size

The median size of a full clutch was 6 eggs and varied from 3 to 6 (n=19). Shortly after hatching, mean brood size in nests with hatched young was 4.2 (2-6 young) (n=14). Due to nest predation the mean number of nestlings on the 16th nestling day decreased to 3.6 (n=17).

4.2 Parental care within the breeding cycle

Incubation started within the last day of egg laying and the following two days. Incubation intensity did not change with time (Fig.1). Over the 11 days of incubation period, the eggs were incubated between 69% and 100% of the observation time, on average 92%. Parents with clutches smaller than the median of 6 eggs invested the same amount of time in incubation as pairs with larger clutches (U-test, U= 4.0, p=0.629, n=7)

When eggs had hatched, parents stayed in the breeding hole after feeding and nestlings were brooded. The proportion of time spent brooding decreased with the age of the nestlings from 77.6% (s.e. ±8.76) on the first day to 10.5% (s.e.±5.28) on day 12 (Fig.1). After day 13, most parents entered the hole only to feed the nestlings or to remove faecal sacs but brooding was hardly observed (Fig.1). Between day 22 and day 25, nestlings fledged.

Following this pattern, the nestling period was divided into two stages for further analysis:

- early stage: first day to day 12
- late stage: day 13 to fledging day.

Beside the strong influence of nestling age, proportion of brooding decreased also with number of nestlings and with mean daily temperature in the first nestling stage (Table 1). When the nestlings were 3 days old, parents started to remove faeces covered with woodchips to keep the breeding hole clean.

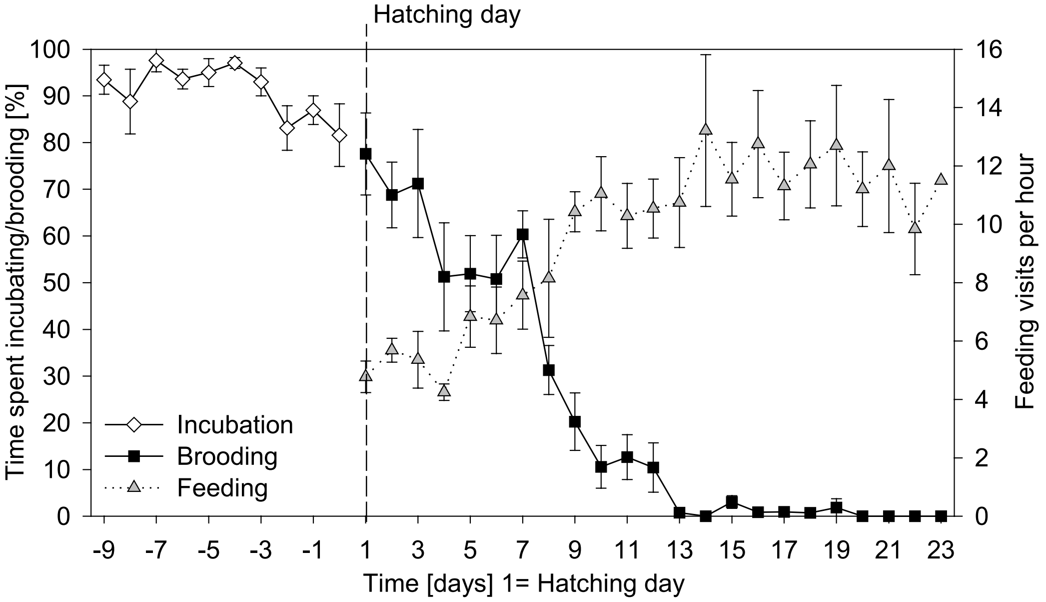

Figure 1 Change of parental duties in course of the brood cycle. Mean proportion of time parents spent incubating (diamonds) and brooding (squares) and mean feeding visits per hour (triangles) (mean ±s.e.).

Table 1 Stepwise multiple regression of variables influencing the proportion of time parents spent brooding in the first 12 nestling days. Overall model statistics: $r^2=0.727$, n=15 pairs, $p<0.001$

Variable	T	p
Age of nestlings	-14.56	<0.001
Number of nestlings	-5.68	<0.001
Mean daily temperature	-4.00	<0.001
Constant	12.28	<0.001

In the early nestling stage, parents' feeding visits per hour increased with age of nestlings from an average of 4.8 (s.e. ±0.54) on the first day to 10.5 (s.e. ±1.00) on day 12 (Fig. 1) and was positively influenced by brood size but not by mean daily temperature (Table 2). However, in the late stage, feeding rate was strongly affected by brood size but neither by age of young nor by temperature (Table 2).

Table 2 Stepwise multiple regression analysis of variables influencing the feeding frequency in the early (1st-12th day) and late (13th-fledging day) nestling stage. Overall model statistics: Early: $r^2=0.438$, $p<0.001$, n=15; Late: $r^2=0.493$, $p<0.001$, n=14

	Early stage		Late stage	
Variable	T	p	T	p
Age of nestlings	7.093	<0.001	0.553	0.582
Number of nestlings	2.865	<0.01	8.766	<0.001
Mean daily temperature	0.075	0.941	-0.134	0.894
Constant	-0.013	0.989	0.459	0.648

4.3 Share of the parental care between the partners:

Males and females shared both diurnal incubation (Wilcoxon 2-tailed: p=0.499, n=7, Fig. 2A) and brooding equally (p=0.570, n=15, Fig.2A). In terms of nest sanitation, males removed faeces in significantly more visits than females (paired t-test, T= 2.934, n=15, p<0.05, Fig.2B).

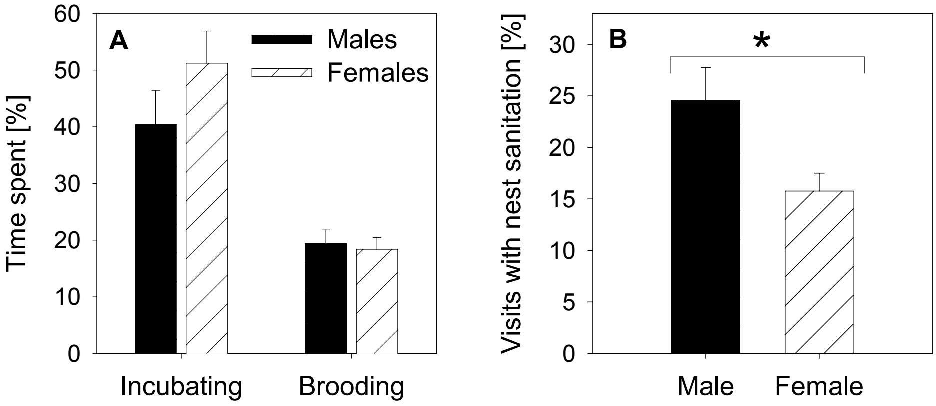

Figure 2 Share of parental duties between partners in the Lesser Spotted Woodpecker. (A) Percentage of time (mean ± s.e.) males and females spent incubating (n=7 pairs) and brooding (n=15 pairs). (B) Percentage of visits with removal of faecal sacs (mean ±s.e.) by males and females (n=15 pairs).

From the statistical point of view, the mean feeding frequencies of males and females differed neither in the early (paired t-test, t=0.499, n=15, p=0.626, Fig.3) nor in the late nestling stage (paired t-test, t=1.273, n=15, p=0.225, Fig.3). However, whereas both parents fed in the early nestling stage at all nests, almost half of the females (7 out of 15) stopped visiting their nest, most of them one or two days before the young fledged. The earliest desertion appeared on the 13th nestling day at a nest with only one young. All females were seen alive after desertion and we observed some of them feeding young after fledging. All nests where females stopped feeding were successful, i.e. at least one young fledged. Remarkably, the number of nestlings in deserted nests was significantly smaller (mean 2.5 young) than in non-deserted nests (mean 4.4 young) (unpaired t-test, t=3.980, n=12, p<0.01).

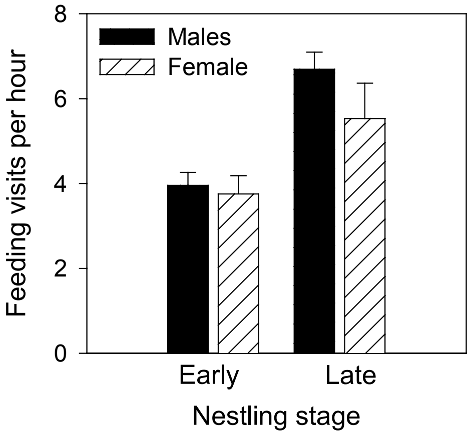

Figure 3 Feeding visits per hour (mean ± s.e.) by male and female Lesser Spotted Woodpeckers in early (n=15) and late nestling stages (n=15).

4.4 Effect of brood size on nestling provisioning

The share of brooding between the sexes was not influenced by brood size (Pearson: r =0.342, p=0.212, n=15, Fig.4).

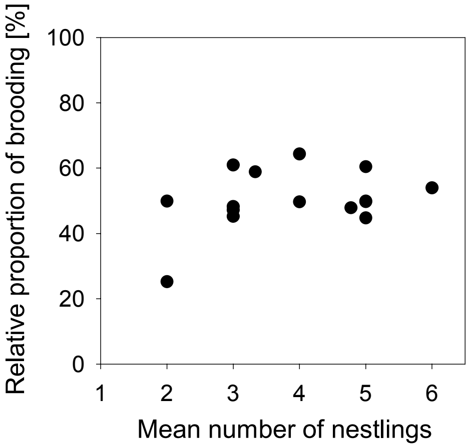

Figure 4 Relationship between females' relative proportion of total brooding and number of nestlings (n=15 pairs).

To investigate the effect of brood size on feeding frequency, we calculated the overall feeding frequency for each breeding individual. We distinguished here between early and late nestling stage and related the results to the number of young. In three pairs, number of nestlings declined within the season, since young starved to death or were killed by predators. In these cases, we calculated the mean nestling number over the observation days

In the early nestling stage (Fig. 5A), brood size also had no effect on feeding rates of females (Pearson: r=0.296, p=0.284, n=15) or males (r=0.118, p=0.675, n=15). However, in the late stage (Fig. 5B), feeding frequency of females was positively related to brood size (r =0.878, p<0.001, n=14), whereas males showed no relation between feeding frequencies and number of nestlings (r=0.310, p=0.281, n=14).

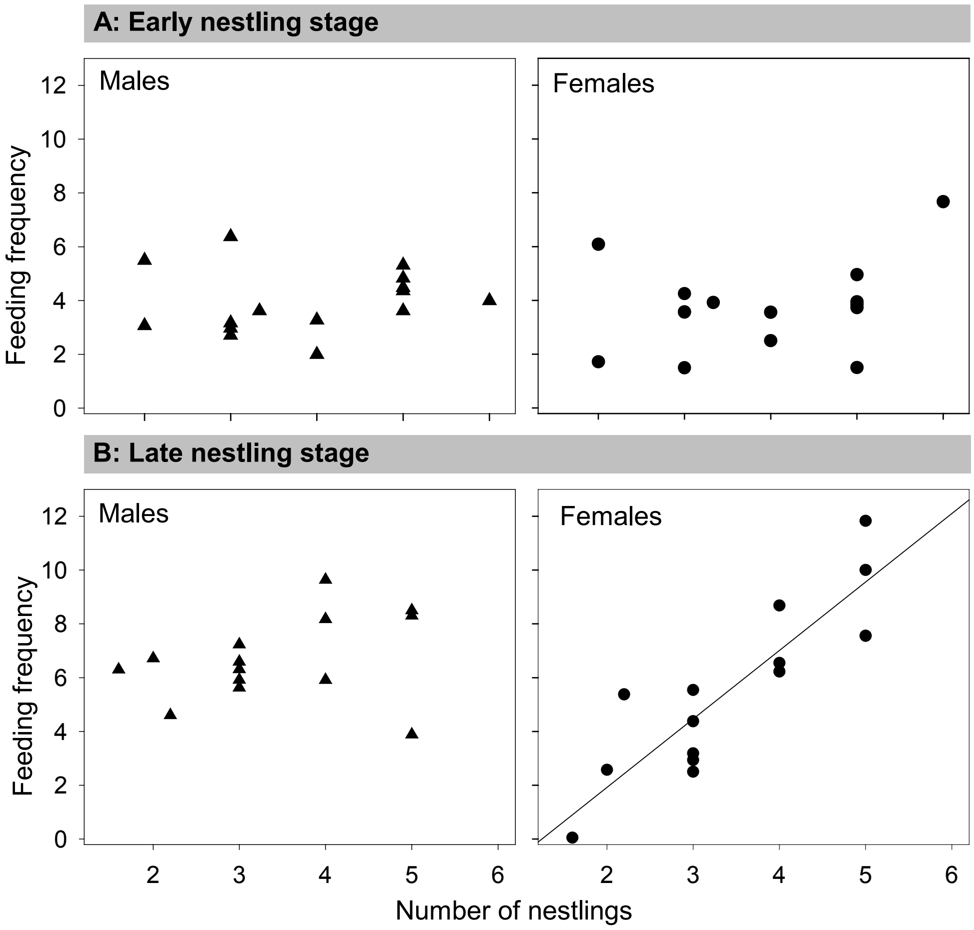

Figure 5 Feeding frequencies of males (triangles) and females (circles) in relation to the number of nestlings. (A) early stage, n=15 and (B) late stage, n=14.

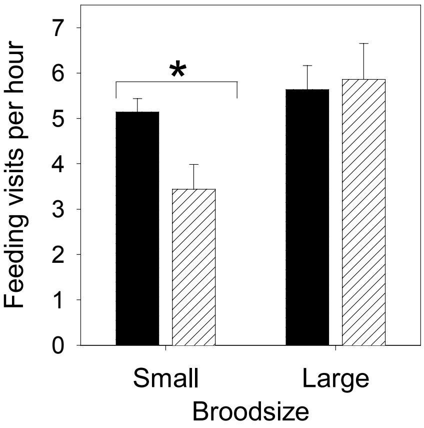

Figure 6 Feeding visits per hour (mean ± s.e.) in the late nestling stage by males (dark bars) and females (light bars) in pairs with small broods (<=3, n=8) and larger broods (>3, n=6). * p<0.05

Looking only at the late stage, males showed a significantly higher feeding frequency in relative small broods (smaller than the median of 3.5 nestlings) than females (paired t-test, T=3.8, n=8, p<0.01, Fig.6), whereas in large broods the difference in feeding rates was not significant (males: 7.4, females: 8.5, T= -0.707, n=6, p=0.511, Fig.6).

4.5 Polyandrous pairs

Out of 34 breeding attempts, 6 (17.6%) belonged to polyandrous females. The three females observed laid eggs in the nests of two males that were 0.8 – 1.2 km apart from each other (mean 1.0 km). After completing the clutch in the primary nests (5-6 eggs, mean 5.7) the females started one or two days later a second clutch with an average of 4.7 eggs (4-5). Consequently, polyandrous females laid up to 11 eggs per season. The number of fledglings in primary nests was 4 on average. In secondary nests, only one out of three nests was successful and produced two fledglings. The other two nests failed because the eggs did not hatch and the male died, respectively. Polyandrous females produced 4.7 fledglings on average, i.e. 1.2 nestlings more than monogamous females.

Parental care was observed on 4 broods belonging to two polyandrous females in 1998 and 2002. In both years, the polyandrous females invested more time and energy in the primary than in the secondary nest (Table 3). We observed incubation on secondary nests on 3 (1998) and 8 (2002) days but never observed the female care for the eggs, though we cannot finally exclude incubation to a minor extent. In 1998, the secondary male died on the third nestling day. After its death, the polyandrous female kept feeding the nestlings and roosted in the nest. For the next 6 days the female was feeding on both nests until it finally deserted the secondary nest and the young died. The results in Table 3 include only days when both parents were alive. In 2002 the polyandrous female cared for the nestlings in the secondary nest only in the first nestling stage and was last seen at the nest on the 10th nestling day.

Table 3 Parental care in primary and secondary polyandrous nests in the years 1998 and 2002.

		1998		2002	
		primary	secondary	primary	secondary
Time spent incubating [%]	male	56	68	50	67
	female	38	0	41	0
Feeding visits with nest sanitation [%]	male	21	0	15	27
	female	19	0	18	13
Feeding visits per hour early nestling stage	male	5.1	10.8	9.7	5.0
	female	4.3	3.3	7.8	4.3
Feeding visits per hour late nestling stage	male	11.5	failed	16.4	12.8
	female	5.4	failed	11.1	0

5. Discussion

5.1 Share of parental care

Lesser Spotted Woodpeckers incubated their eggs around 92% of the observation time and intensity did not change with time or with number of eggs. After hatching, nestlings were brooded intensively. In woodpeckers, brooding of young in the early nestling days is particularly important since they have a short incubation period and nestlings hatch relatively immature, compared to non-cavity nesters (Yom-Tov & Ar 1993). Furthermore the breeding holes have no insulating nesting material, resulting in heat loss, which is further increased by the relatively small size of the brood (Royama 1966). Brooding intensity increased with decreasing number of nestlings as well as with lower temperatures. This is not surprising as both parameters lead to heat loss and parents have to spend more time to keep the nestlings at optimal temperature. The influence of temperature on brooding intensity confirms earlier results (Wiktander 1998) and was also reported in other woodpecker species, e.g. Northern Flickers (*Colaptes Auratus*, (Wiebe & Elchuk 2003).

Moreover, brooding declined with the age of the young. This is a typical trait in altricial species caused by improved thermoregulatory abilities of the young (Clark 1985; Sanz & Tinbergen 1999; Chastel & Kersten 2002). With decreasing time spent on brooding, feeding frequency increased, which is necessary because of the rising energy demand throughout the nestlings growing phase (Royama 1966; Ricklefs 1984).

During incubation and early nestling stage, parental care was divided equally between partners. Brooding and feeding are both very time-consuming and we suppose that the early nestling stage is most challenging for parent Lesser Spotted Woodpeckers. This is supported by observations on their timing of breeding: Rossmanith et al. (Chapter I) found that Lesser Spotted Woodpeckers time their breeding, so that early nestling stages coincide with the time of highest food availability. Thus, we assume that successful rearing of a brood is only possible if both parents, male and female, invest highly in their parental duties during early nestling stage.

In the late nestling stage, feeding frequency stopped to increase with the age of the nestlings and brooding became obsolete. Feeding frequency was positively correlated with number of nestlings in the early as well as in the late nestling stage. This is not surprising as higher feeding frequency in larger broods is a common pattern observed in many bird species (Nur 1984; Laiolo et al. 1998) and the obvious reason is the higher energy consumption in larger broods. However, in the late nestling stage, this relationship between feeding frequency and brood size was not consistent for the sexes. In this period, only feeding frequency of females but not males was related to the number of nestlings. The decrease in females' feeding frequencies in relation to brood size culminated in the complete desertion of small broods. Almost half of the females deserted their brood a couple of days before fledging and these broods were smaller than non-deserted ones. Desertion by females was found in the Lesser Spotted Woodpecker before, although it was not related to brood size (Wiktander et al. 2000), but it has never been observed in other woodpecker species (Michalek & Winkler 2001; Wiebe & Elchuk 2003).

However, desertion of the brood by one partner will only be favoured by natural selection if the present brood requires only little additional parental investment (Lazarus 1990). Indeed, all broods deserted by their mothers fledged nestlings, indicating that care of both parents was not essential in the late nestling stage and the male was able to compensate for the missing female.

We assume two reasons for the influence of brood size on the parental effort in females: First, males might be able to compensate for the lack of female investment only in small broods due to a lower food requirement. Secondly, value of small broods and therefore benefit for the parents are lower. Indeed, Rossmanith et al. (Chapter I) argued that survival probability after fledging was the same for all young, thus the number of young in the nest reflects the value of the brood.

5.2 Why are females always the ones reducing care?

Interestingly, in species where females take the larger part of parental care, studies found the opposite pattern, in that males adapt their parental investment to the brood size or that females compensated for a decreasing feeding rate in handicapped males (*Tachycineta bicolor*, Whittingham et al. 1994; *Parus major*, Sanz et al. 2000). One reason for these differences between males and females can be seen in the lack of confidence in paternity (Slagsvold & Lifjeld 1990), since extra-pair paternity occurs frequently in these species (Dunn et al. 1994; Lubjuhn et al. 1999; Griffith et al. 2002). In woodpeckers however, a high confidence in paternity was found (Haig et al. 1994; Michalek & Winkler 2001) and can also be assumed for Lesser Spotted Woodpeckers. Therefore, value of the current brood should be the same for both females and males. Consequently, reasons for the difference in parental investment between the sexes should be found in the future reproductive value of the parents.

Since Lesser Spotted Woodpeckers are single brooded, the future reproductive value of the breeding individual is dependent on reproductive success in the following year. This includes survival to the following year and the chance to find a mate. Accordingly, to explain the observed differences in investment, either (1) chances for mating or (2) costs of parental effort in terms of lower survival rates must be different between sexes.

The chance to find a mate should be different for the sexes, since Lesser Spotted Woodpecker populations are often male biased (Chapter III; Wiktander et al. 2000). An excess of males leads to a higher competition for females and thus higher mating probabilities for females than for males. If future reproductive success is not secure, it might be more beneficial for the male to increase his own effort in the current brood and compensate for the female’s reduced care.

Moreover, Wiktander (1998) found that survival rates were lower for Lesser Spotted Woodpeckers that raised young compared to widowed birds that gave up the breeding attempt and these costs were higher for females than for males. This is supported by results in other bird species, where the effort in parental care negatively influenced the survival of females but not of males (Nur 1984; Chastel & Kersten 2002; Horak 2003). Our data about mortality are sparse, but we found evidence that surviving females had smaller broods (and were therefore likely to perform less effort in nestling feeding) than females who did not survive to the next breeding season and this was not true for males (Rossmanith unpubl.). Thus, the magnitude with which reduction of effort increases survival might be higher for females than for males. In addition, Lesser Spotted Woodpeckers have lifelong pair bonds, and reproductive success was shown to be higher in pairs that breed together in consecutive years (Wiktander et al. 2001). A higher survival rate of females is therefore increasing the likelihood for the male to mate the same partner and thus increase reproductive success. Consequently, males compensate for the lack of female effort, since survival costs might be higher for females and survival of the own mate is of benefit for the male.

In the light of these assumptions we conclude that parental care of females is adjusted to the reproductive value of their offspring, to its importance on offspring fitness and to their cost for parental expenditure. It also indicates that the optimal level of parental expenditure varies with brood size for females but not for males. Males compensate for the decreasing or lacking feeding by females, because the mates future physical condition is of direct importance for the male. The basis for this behaviour seems to be the male-biased sex ratio, which leads to a higher competition for females. An influence of the population’s sex ratio on the share of parental care was also assumed in Breitwisch et al. (1986).

5.3 Conclusion for the mating system

We confirmed social polyandry in the German Lesser Spotted Woodpecker population. Though being an exception from the general performed monogamy in this species, polyandry occurs frequently. It occurred in 17.6 % of the breeding attempts in our study, which is comparable to the rate of 16.2% found by Wiktander et al. (2000). Even though mating system in other woodpecker species was intensively studied (Glutz von Blotzheim & Bauer 1994; Michalek & Winkler 2001; Wiebe & Elchuk 2003) only one single case of polyandry was observed before (Great Spotted Woodpecker, Kotaka 1998). Despite the fact that our observations on polyandrous broods are limited, the results suggest that polyandrous females did not share their effort in parental care evenly between their two broods. They invested more time and energy in incubation, brooding and feeding at their primary brood, and males on the primary brood had a higher breeding success than males on secondary broods. A comparable but inverse pattern was found in facultative polygynous, altricial birds. Here, seconddary females often get little or no assistance from their mating partner, while primary females may get as much help as in monogamous species (Clutton-Brock 1991; Slagsvold & Lifjeld 1994; Kempenaers 1995; Searcy & Yasukawa 1996). In addition, secondary females often, but not always, have lower reproductive success than primary females (Kempenaers 1995; Searcy & Yasukawa 1996). The unequal share of effort between the two broods of polyandrous females in our study is a further support of the trade-off theory. First, food availability deteriorates with time (see Chapter I) and the secondary brood might be too late for optimal food supply. Secondly, the brood size and thus the value of the brood are lower in secondary broods, probably caused by late timing.

We conclude that the pattern of expenditure in parental care in monogamous pairs is the prerequisite for the occurrence of polyandry. If the males were not able or willing to compensate a reduced effort in parental care, it would be unlikely for females to have the opportunity to mate with additional males.

6. References

Breitwisch, R., Merritt, P. G. & Whitesides, G. H. 1986. Parental investment by the Northern Mockingbird - male and female roles in feeding nestlings. *Auk* 103: 152-159.

Chase, I. D. 1980. Cooperative and Noncooperative Behavior in Animals. *American Naturalist* 115: 827-857.

Chastel, O. & Kersten, M. 2002. Brood size and body condition in the House Sparrow *Passer domesticus*: the influence of brooding behaviour. *Ibis* 144: 284-292.

Clark, L. 1985. Consequences of homeothermic capacity of nestlings on parental care in the European Starling. *Oecologia* 65: 387-393.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton.

Dunn, P. O., Robertson, R. J., Michaud-Freeman, D. & Boag, P. T. 1994. Extra-pair paternity in Tree Swallows - Why do females mate with more than one male. *Behavioral Ecology and Sociobiology* 35: 273-281.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Forslund, P. & Larsson, K. 1991. The effect of mate change and new partner's age on reproductive success in the barnacle goose, *Branta leucopsis*. *Behavioral Ecology* 2: 116-122.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1994. Columbiformes - Piciformes. Aula-Verlag, Wiesbaden.

Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11: 2195-2212.

Haig, S. M., Walters, J. R. & Plissner, J. H. 1994. Genetic-evidence for monogamy in the cooperatively breeding Red-Cockaded Woodpecker. *Behavioral Ecology and Sociobiology* 34: 295-303.

Hogstad, O. & Stenberg, I. 1997. Breeding success, nestling diet and parental care in the White-backed Woodpecker *Dendrocopos leucotos*. *Journal für Ornithologie* 138: 25-38.

Horak, P. 2003. When to pay the cost of reproduction? A brood size manipulation experiment in Great Tits (*Parus major*). *Behavioral Ecology and Sociobiology* 54: 105-112.

Kempenaers, B. 1995. Polygyny in the Blue Tit - Intra-sexual and inter-sexual conflicts. *Animal Behaviour* 49: 1047-1064.

Kotaka, N. 1998. Classical polyandry in the Great Spotted Woodpecker *Dendrocopos major*. *Ibis* 140: 335-336.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co , London.

Laiolo, P., Bignal, E. M. & Patterson, I. J. 1998. The dynamics of parental care in Choughs (*Pyrrhocorax pyrrhocorax)*. *Journal für Ornithologie* 139: 297-305.

Lazarus, J. 1990. The logic of mate desertion. *Animal Behaviour* 39: 672-684.

Ligon, J. D. 1993. Role of Phylogenetic History. In: D.M.Power (ed.) Current Ornithology 10, 1-46. Plenum Press, New York.

Lubjuhn, T., Strohbach, S., Brun, J., Gerken, T. & Epplen, J. T. 1999. Extra-pair paternity in Great Tits (*Parus major*) - A long term study. *Behaviour* 136: 1157-1172.

Lubjuhn, T., Winkel, W., Epplen, J. T. & Brun, J. 2000. Reproductive success of monogamous and polygynous Pied Flycatchers (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology* 48: 12-17.

McGraw, K. J. & Hill, G. E. 2004. Mate attentiveness, seasonal timing of breeding and long-term pair bonding in the House Finch (*Carpodacus mexicanus*). *Behaviour* 141: 1-13.

Michalek, K. G. & Winkler, H. 2001. Parental care and parentage in monogamous Great Spotted Woodpeckers (*Picoides major*) and Middle Spotted Woodpeckers (*Picoides medius*). *Behaviour* 138: 1259-1285.

Nur, N. 1984. Feeding frequencies of nestling Blue Tits (*Parus Caeruleus*) - Costs, benefits and a model of optimal feeding frequency. *Oecologia* 65: 125-137.

Perrins, C. M. & McCleery, R. H. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major*. *Ibis* 127: 306-315.

Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's Auklets. *Journal of Animal Ecology* 70: 1088-1097.

Ricklefs, R. E. 1984. The optimization of growth-rate in altricial birds. *Ecology* 65: 1602-1616.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. *Ibis* 108: 313-347.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the Great Tit (*Parus major*).). *Journal of Animal Ecology* 69, 74-84.

Sanz, J. J. & Tinbergen, J. M. 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the Great Tit *Parus major*. *Behavioral Ecology* 10: 598-606.

Searcy, W. A. & Yasukawa, K. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in Red-winged Blackbirds. *Journal of Avian Biology* 27: 225-230.

Slagsvold, T. & Lifjeld, J. T. 1990. Influence of male and female quality on clutch size in Tits (*Parus spp*). *Ecology* 71: 1258-1266.

Slagsvold, T. & Lifjeld, J. T. 1994. Polygyny in birds - the role of competition between females for male parental care. *American Naturalist* 143: 59-94.

Trivers, R. L. 1972. Parental investment and sexual selection. In: Campbell, B. (ed.): Sexual Selection and the Descent of Man. 136-179. Aldine, Chicago.

Whittingham, L. A., Dunn, P. O. & Robertson, R. J. 1994. Female response to reduced male parental care in birds - an experiment in Tree Swallows. *Ethology* 96: 260-269.

Wiebe, K. L. & Elchuk, C. L. 2003. Correlates of parental care in Northern Flickers *Colaptes auratus*: Do the sexes contribute equally while provisioning young? *Ardea* 91: 91-101.

Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* 31: 447-456.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001. Age and reproduction in Lesser Spotted Woodpeckers (*Dendrocopos minor*). *Auk* 118: 624-635.

Winkler, H., Christie, D. A. & Nurney, D. 1995. Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the World. Russel Friedman Books CC, Sussex.

Yom-Tov, Y. & Ar, A. 1993. Incubation and fledging durations of woodpeckers. *Condor* 95: 282-287.

Link to the proceeding Chapter

In the last Chapter, I investigated parental care behaviour in the Lesser Spotted Woodpecker and found different trade-off strategies for males and females. While females decreased expenditure or even deserted the nest, males compensated for the females absence. Furthermore, the facultative occurrence of polyandry was confirmed and I discussed the organisation of parental care as a prerequisite for polyandrous mating systems in the Lesser Spotted Woodpecker.

The social mating system in a species is likely to influence its population dynamics. In the following part of the thesis, I aim to investigate the impact of social mating systems on the persistence of the Lesser Spotted Woodpecker population. The appropriate approach for this question is the use of a stochastic individual-based model simulating the population dynamics of the Lesser Spotted Woodpecker. The parameterisation of the model requires demographic data of reproduction and mortality.

In Chapter III, I will present an empirical investigation of mortality rates in the Lesser Spotted Woodpecker and the development of the simulation model. However, survival of fledged juveniles cannot be measured in the field and is missing. Therefore, I will furthermore introduce a method to estimate pre-breeding survival rates by a pattern-oriented modelling approach using empirical data of population structure. The pre-breeding survival rate will be estimated for two different populations and compared to test the prediction quality of both, the method and the model.

Tracking a missing parameter: A pattern-oriented modelling approach to estimate pre-breeding survival rates in two Lesser Spotted Woodpecker (*Picoides minor*) populations

Chapter III

Tracking a missing parameter: A pattern-oriented modelling approach to estimate pre-breeding survival rates in two Lesser Spotted Woodpecker (*Picoides minor*) populations[1]

1. Abstract

Investigating the viability of populations, researchers often face a lack of knowledge of mortality rates in animals. However, data of population structure might be easier to collect and useful to estimate missing parameters indirectly. The aim of this study was to present a method to estimate the missing parameter pre-breeding survival rate for an endangered bird species, the Lesser Spotted Woodpecker (*Picoides minor*). We developed an individual-based stochastic model simulating the population dynamics in two different scenarios, based on empirical data from long-time studies at lake Möckeln, Sweden and Taunus, Germany. Pre-breeding survival rate was varied systematically and both reproductive success and structure of the simulated populations were compared with patterns obtained from empirical investigations. For both populations, we could identify a range for pre-breeding survival where all simulated patterns corresponded best to the empirical values. The estimated pre-breeding survival rate was remarkably higher in the German than in the Swedish scenario. For a reason, a geographical variation in life-history traits was discussed, since population performance was similar in both scenarios. We conclude that the presented pattern-oriented modelling approach is a valuable method to estimate missing demographic parameters using even weak patterns from empirical investigations. However, it was demonstrated that use of multiple patterns is necessary for this purpose.

---

[1] This chapter is previewed for submission as: Rossmanith, E., Wiktander, U. & Jeltsch, F. Tracking a missing parameter: A pattern-oriented modelling approach to estimate pre-breeding survival rates in two Lesser Spotted Woodpecker (*Picoides minor*) populations. Ecological Modelling

2. Introduction

In applied ecology, stochastic simulation models are increasingly used to gain an understanding of the processes in population dynamics (Beissinger & Westphal 1998; Grimm 1999). Particularly in conservation biology, the use of modelling tools for population viability analysis (PVA) has become important in the last two decades to assess extinction probabilities in populations and to aid management decisions for endangered species (Boyce 1992; Akcakaya & Burgman 1995; Walsh et al. 1995; Beissinger & Westphal 1998; Brook et al. 2000). Evidently, reliable models of population dynamics require data on demographic parameters, like mortality or reproduction rates. However, researchers developing a PVA often face uncertainty or lack of data, especially concerning endangered and thus rare species (Beissinger & Westphal 1998; Wiegand et al. 2003). Despite the urgent need of data to make management decisions, we have to accept that rarity of species itself precludes precise measurement of some model parameters (Wiegand et al. 2003).

Facing the problem of missing information for a given population, common practice in ecological modelling is the application of data available from other species as well as other populations or sub-species (Wiegand et al. 1998; Wichmann et al. 2003). However, life-history traits can differ dramatically not only between species but also within the same species between different populations. In fact, a geographical variation in life-history traits is known, due to a gradient in environmental conditions (Murray 1985; Karr et al. 1990; Griebeler & Böhning-Gaese 2004). In birds for instance, a trend for increasing clutch size and decreasing survival from the tropics to the poles is generally assumed (reviews in Murray 1985). Ashmole (1963) explained this strong intraspecific variation with the increase of environmental variability between seasons, i.e. stronger fluctuation in food availability. Hence, mixing data from different sources might therefore be misleading, when trying to predict the viability for a certain population.

However, even in cases when demographic parameters are missing, there might be a source of information in data sets that is often not exploited thoroughly. For example, time series data of population structure or its spatial organisation integrate information of several processes in population dynamics. Grimm et al. (1996) first used the term “pattern” for a characteristic, clearly identifiable structure in nature itself or in data extracted from nature. Obvious patterns are e.g. the wave-like pattern of spread of rabies (Jeltsch et al. 1997) or the spatial distribution of plants (Tews et al. 2004). But patterns can also be less obvious structures in observations, as long as they are non-random (Grimm et al. 1996). Non-random means that certain processes or mechanisms have created this pattern and consequently, the observed pattern contains “hidden” information on these processes or mechanisms and can be used to estimate missing parameters (Grimm et al. 1996; Wiegand et al. 1998; Wiegand et al. 2003). Recent studies have used pattern-oriented modelling to identify processes in the dynamic of plants that lead to a certain pattern (Jeltsch et al. 1999), to investigate dispersal patterns (Gilbert et al. 2004) or to validate model output (Ferrer et al. 2004; Tews et al. 2004). However, although it has proved to be a promising approach, pattern-oriented modelling is still rarely used.

Mortality rates are one of the essential demographic parameters often missing. Reasons for this lack of data can be found in the long time span needed to gain reliable results for long living species as well as the elusive character of this parameter: since mortality is rarely observed directly, it is difficult to differentiate between mortality and emigration. Therefore, investigating mortality is particularly difficult in the life stage of dispersal, which is in most vertebrates the time span between independence and maturity. Hence, information about this pre-breeding survival is usually missing completely for highly mobile animal species, and it is often impossible to accurately measure this parameter in the field. But since it is assumed to be the major source of individual variation in lifetime reproduction success (Newton 1989), knowledge of pre-breeding survival rates is essential to understand population dynamics.

Owing to its importance for population dynamics, pre-breeding survival should have a distinct effect on variables on population level that might be easier to measure than survival itself. For instance, survival of juveniles affects the proportion of young individuals in the population and thus the age structure. Furthermore, this factor could have a less obvious influence, like effects on mean breeding success in the population, since young individuals often have a minor reproductive success (Curio 1983; Saether 1990; Pyle et al. 2001; Reid et al. 2003). Such variables on population level are not eye-catching pattern, but might include enough information to be used for estimating the missing parameters. Our study aims to test whether pre-breeding survival can be estimated indirectly using patterns extracted from data on population level.

Example organism is the endangered Lesser Spotted Woodpecker (*Picoides minor*), a species that was investigated in two long-time studies, conducted at lake Möckeln in Southern Sweden (see Olsson 1998; Wiktander 1998) and in a low mountain range near Frankfurt/Main, Germany (Chapter I & II; Höntsch 2005). In these studies, data about the most important demographic parameters could be collected. Only information on the fate and survival of fledged young is missing. However, data on population structure and reproductive success are available and might be useful to estimate the missing parameter. In our approach, we developed two scenarios, each based only on data from the specific study population.

Aim of this study was to present an approach to assess pre-breeding survival using data on reproductive success and structure of the population. Thereby, we combine empirical examination of adult survival and population structure on an individually marked Lesser Spotted Woodpecker population in Germany, analysis of empirical data from two long-time studies and the construction of an individual based simulation model. Since there are no obvious strong patterns, we examine whether using putative weak patterns that are easy to detect and often collected incidentally can be provide a possibility to estimate a missing parameter.

2.1 Study organism

The Lesser Spotted Woodpecker is distributed over the whole Palaearctic region, from Great Britain and Northwest Africa to Kamtschatka (Cramp 1985). The species is monogamous and territorial (Glutz von Blotzheim & Bauer 1994). This year-round resident feeds mainly on arthropods living in dead wood (Olsson 1998) but switches to surface-living arthropods during breeding time

(Chapter II; Olsson 1998). Caused by changes in food availability throughout the breeding season, timing of breeding is a crucial factor influencing reproductive success (Chapter I). Although living solitary in the non-breeding season, in general Lesser Spotted Woodpeckers form lifelong pair bonds (Glutz von Blotzheim & Bauer 1994; Wiktander et al. 2000). Mating the same partner in successive years leads to an early breeding start and therefore to higher reproductive success (Chapter I; Wiktander et al. 2001a).

Alarmingly, Lesser Spotted Woodpecker populations have suffered a decline in several countries over the last decades (Tiainen 1985; Nilsson et al. 1992; Mikusinski & Angelstam 1997). Reasons for the dramatical decline remain unclear, although loss of the preferred habitat is discussed (Nilsson et al. 1992). This development and the lack of knowledge of the species' autecology have stimulated two long time studies that provide the data basis for our model investigation.

2.2 Basis for the model scenarios: two empirical investigations

The first empirical investigation was conducted between 1989 and 1998 by Wiktander and Olsson on the subspecies *Picoides minor minor* in the boreo-nemoral region in southern Sweden (see Olsson 1998; Wiktander 1998). About half of the study area was covered by water of lake Möckeln, the land area was mostly forested, with both agricultural land and marshland areas interspersed (for details see Olsson 1998; Wiktander 1998). This long-time study provided data about all main demographic parameters needed for modelling the population dynamic, except survival rate of fledged young before their first breeding.

The second long-time study was carried out by Höntsch (in the years 1996 to 2000) and Rossmanith (years 1998-1999 and 2002-2003) in a German low mountain range (Taunus) near Frankfurt/Main, on *Picoides minor hortorum*. The study area consisted of a mosaic of different forest types, old orchards as well as grassland and settlement areas (see Chapter II). This observational study provided information on reproductive success and behaviour that are analysed in Chapter I and II. In the empirical part of this paper, we present the examination of mortality in both sexes as well as adult sex ratio in the population and brood sex ratio.

3. Empirical investigations

3.1 Empirical methods

To investigate mortality and population structure, it was necessary to identify the birds individually from a distance. Therefore, they were caught at their roosting or breeding holes and marked with two colour rings.

In the years 2002 and 2003, systematically mapping of the study area was accomplished. For this purpose, we divided the study area in 7 sub-areas of approx. 300 hectare. Each sub-area was visited at least four times between the end of February and the start of egg laying (approx. mid April), which is the time of highest acoustical activity in the Lesser Spotted Woodpecker. Starting at sunrise, we used playbacks of the species' drumming and callings to provoke a reaction. In cases of acoustical or visual encounters, birds were followed until identified by their colour rings.

Additionally, the study area was searched intensively for breeding and roosting holes to verify the presence or absence of the individuals. Between end of 1997 and 2000, intensive search for breeding and roosting holes was conducted between November and June every year and all territories in the study area were visited frequently. Thus, information on sex ratio and mortality are also available for those years.

We differentiated between survival during breeding time, which is defined as the time-span between start of egg laying (approx. mid of April) and fledging of the young (approx. mid June) and survival in the non-breeding time (mid June until mid April the following year). Assuming strong site fidelity in Lesser Spotted Woodpeckers, we followed Wiktander (1998) and defined an adult individual as dead, when it disappeared from the study area. Survival rate in the non-breeding season was defined as proportion of surviving individuals between two breeding seasons. Survival rate during breeding time was investigated by regular observations at the breeding holes during parental care, which is conducted by both sexes (Chapter II).

Adult sex ratio of the population was assessed when breeding time started. At day 16 after hatching, breeding holes were opened and nestlings were counted and marked with rings. At this age, sex of the young is already identifiable by different coloration of the forehead and brood sex ratio could be determined.

3.2 Empirical results

3.2.1 Survival rates

Survival rate during breeding time was calculated separately for males and females. In the breeding times of the 5 study years, all but one of 32 males (96.9%) and all but one of 28 females (96.4%) survived. The widowed partner left the nest in both cases and had no reproductive success.

In the non-breeding seasons mean survival rate for females over 5 years was 0.621 ($\pm$ 0.207 s.d.), but varied widely between 0.33 and 0.86. Mean survival rate for males was lower (0.582 $\pm$ 0.060 s.d., 0.5 to 0.667) but difference between sexes was not significant (paired t-test, p=0.682, T=-0.441, n=5). Survival rates for males and females were not correlated in the 5 study years (Pearson: r=0.255, p=0.679, n=5).

3.2.2 Sex ratios

Over all the years, 53.8% of all adult individuals in the population (n=78) were males. This was not significantly different from an even distribution between sexes (chi-test, p=0.497). However, operation sex ratio was male-biased in 4 of the 6 study years.

We also found slightly more male than female young in the nests (37 males, 30 females), but again difference was not significant (chi-test p=0.392).

4. Model investigations

4.1 Methods and model description

The aim of the model was the estimation of pre-breeding survival rate in two populations of Lesser Spotted Woodpeckers. To achieve this objective, we constructed an individual-based stochastic model simulating the population dynamics. Model construction was progressed in four steps. (i) First, we constructed a general framework for the model with a set of rules describing the processes within the population dynamic (e.g. survival). These processes occur with certain probabilities described by parameters. (ii) In the second step, we calculated values for all included parameters based on empirical investigations. Since we wanted to compare pre-breeding survival in two populations, we created two different scenarios, one based on the field investigations in Germany, the other on the investigations in Sweden. (iii) In the third step, independent empirical data that might be useful as pattern were selected and analysed. (iv) In the last step, simulations were run varying the value of the missing parameter systematically. That way the value was detected where model output matches best with all selected empirical pattern. These four steps are described below in detail.

4.1.1 (i) General framework and model rules

Structure of the model is individual-based, i.e. birds are followed individually between fledging and death and the population is seen as the assemblage of all individuals. All individuals have the attributes age, sex, mating status (newly paired, old paired and unpaired), breeding start (early and late) as well as an identification number. When individuals are paired, all attributes of the mate are known.

Simulations have a yearly time step, beginning in spring and including the processes of mating, reproduction and deaths (see Fig. 1). Some attributes (e.g. mating status) are set every time step, following model rules (e.g. when the partner dies, the individual becomes “unpaired”).

Based on the knowledge of the species’ autecology, we described the processes within the individual’s life cycles in rules. These processes occur with certain probabilities, which are not fixed in the model rules but described by parameters (see Table 1). Therefore, the following rules are consistent for any Lesser Spotted Woodpecker population and scenarios for particular populations can be developed by a specification of the model parameters (see (ii)). Empirical background and derived model rules are described as follows:

Model rules

Mating Male and female Lesser Spotted Woodpeckers start to breed in their first year after fledging and form usually lifelong pair bonds, although divorce might occur (Glutz von Blotzheim & Bauer 1994; Wiktander et al. 2000, own obs.). **Rule 1:** If both partners from the previous breeding season are still alive, they establish an *old pair*. With a minor probability (*pDivorce*) they split up and mating status becomes *unpaired*. Unpaired males mate with unpaired females and establish a *new pair*. If there is no unpaired partner available, the individual remains unpaired.

Non breeder*:* In the Swedish population, some Lesser Spotted Woodpecker pairs did not produce eggs, even though they occupied a territory and built a breeding hole. All those non breeders were *new pairs* (Wiktander et al. 2001b). However, this behaviour never appeared in the German population (own obs.). **Rule 2:** While *old pairs* always lay eggs, probability for a *new pair* not to breed is *pNonBreed*.

Start of egg laying: Old pairs start earlier with egg laying than new pairs, which has a positive effect on reproductive success (Chapter I; Wiktander et al. 2001a). **Rule 3:** All *old pairs* have an *early* breeding start, while *new pairs* have an *early* breeding start with the probability *pStartEarly*, otherwise their breeding start is *late*. The breeding start is an attribute that influences the number of young that fledge (see rule 7).

Failure in reproduction: Some pairs fail to reproduce, because eggs do not hatch or both parents desert the nests without obvious reason (Chapter I; Wiktander et al. 2001b). **Rule 4:** The probability to fail because eggs do not hatch or parents desert the nest after egg laying is for all pairs *pFailure*. Additionally, issues described in rule 5 and 6 can cause failure in reproduction.

Nest predation*:* Most common nest predators are Great Spotted Woodpeckers (*Picoides major*) and Eurasian jays (*Garrulus glandarius*) (Chapter I; Wiktander et al. 2001b). **Rule 5:** Nest predation occurs with the probability *pPredation* and result in the death of all nestlings.

Mortality during breeding season*:* If one partner dies during breeding season, the mate leaves the nest and the brood fails (Chapter I; Wiktander et al. 2001b). **Rule 6:** When an individual dies (probabilities to survive $pSurvBreed_{male}$ and $pSurvBreed_{female}$) its brood fails and its mate remains unpaired until the next breeding time.

Fledging*:* Pairs that start early with egg laying produce more fledglings than late broods (Chapter I; Wiktander et al. 2001b). **Rule 7:** In successful nests, i.e. when parents have survived the breeding season and no predation has occurred, nestlings fledge. The probabilities for a certain number of fledglings were calculated based on empirically observed distribution of brood sizes in the field, divided in early $p(x)Fledglings_{early\ pairs}$ and late broods $p(x)Fledglings_{late\ pairs}$ with *x* indicating the number of fledglings (Table 1). Based on the observed sex ratio of fledglings in the field, the probability for a fledgling to be male is *pYoungMale,* otherwise it is a female.

Pre-breeding survival: Empirical data about mortality after fledging are missing. **Rule 8*:*** Fledglings suffer a certain mortality rate after leaving the nest until they reach their first breeding time. The survival probability ($pSurvWinter_{juvenile}$) is unknown and is varied systematically.

Emigration: Adult Lesser Spotted Woodpeckers have a strong site fidelity and stay in the area once they have settled. Emigration appears only in immature individuals (Wiktander 1998). **Rule 9:** There is a maximum number of territories, i.e. a maximum number of individuals that can exist in the area, given in the parameter *carrying capacity*. Only if the number of birds is below the carrying capacity, fledglings can stay in the area, otherwise they emigrate. Since adult birds do not emigrate, an occupied territory only becomes available once an individual dies.

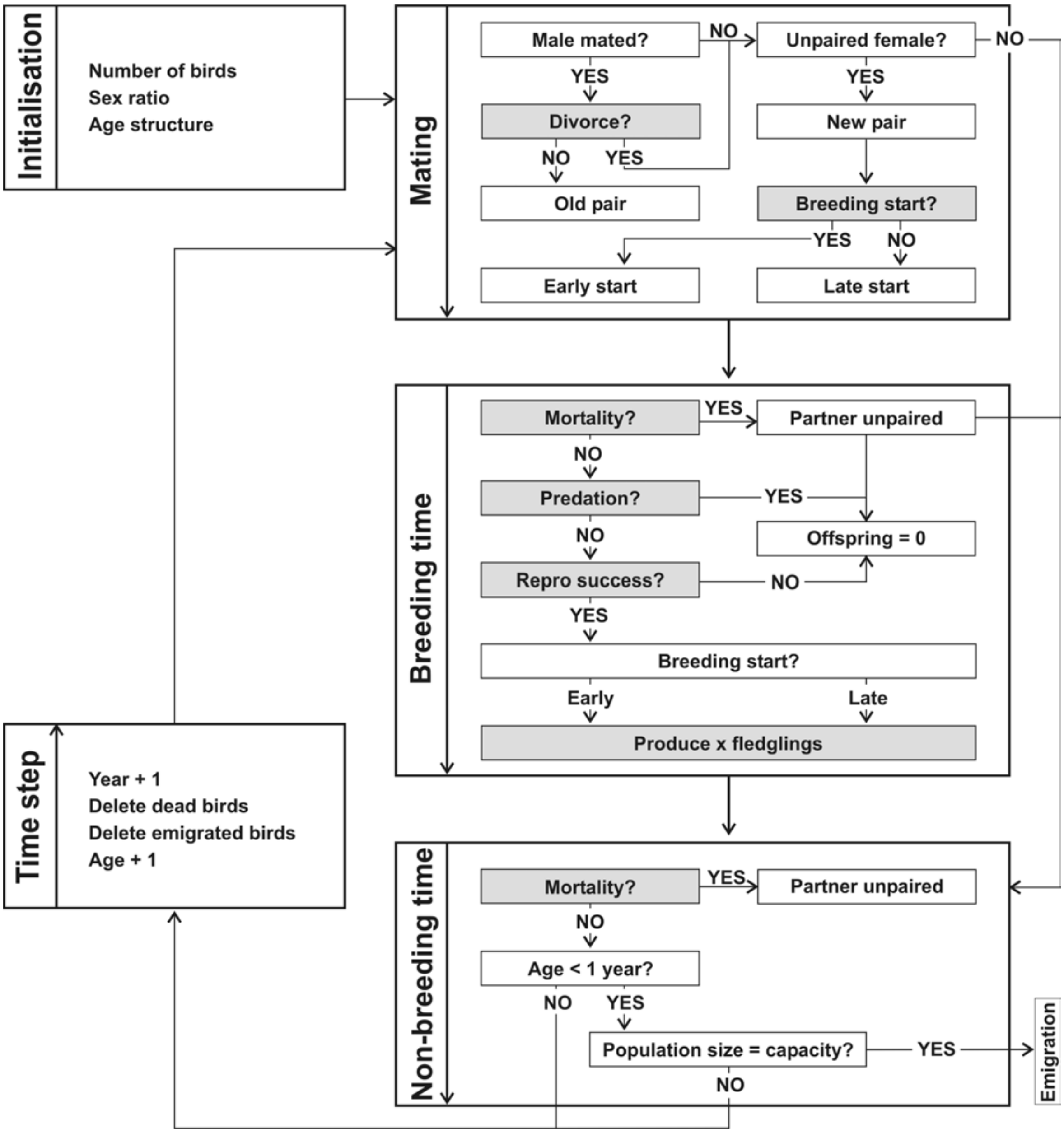

Figure 1 Simplified float chart for the Lesser Spotted Woodpecker simulation model. Grey boxes indicate stochastic processes in which the result is determined by a probability and a random number.

Adult survival in non-breeding season*:* The oldest individual Lesser Spotted Woodpecker of known age reached 10 years (Wiktander pers.comm.). **Rule 10:** If an individual exceeds maximum age (=10 years), it dies. Otherwise it has the probability of $pSurvWinter_{male}$ and $pSurvWinter_{female}$ to survive.

Ageing: **Rule 11:** At the end of the simulation year, dead individuals are removed from the population and the age of all individuals is enhanced by one year.

In the Lesser Spotted Woodpecker, density dependent effects on reproduction or survival could not been found (Wiktander et al. 2001b). Therefore, parameter values do not change with population densities in the model. However, emigration is density dependent, since fledglings emigrate when all territories are occupied.

Model rules were implemented as a computer program in C++ and simulations were conducted on a common personal computer.

Stochasticity

In natural variable environments, population dynamics are subject to demographic as well as environmental noise (May 1973). To mimic demographic noise, all parameter values shown in Table 1 are interpreted as probabilities (Wichmann et al. 2003). In processes that are supposed to be influenced by environmental changes between years (see Table 1), involved parameter values for the current year were determined at the beginning of each time step by drawing from a normal distribution cut at 0 and 1, based on mean and standard deviation of the empirical data. The drawn value is then interpreted as the probability for the process in the current year and demographic stochasticity acts additionally.

Furthermore, there are non-stochastic parameters, like maximum age, carrying capacity and population size at simulation start.

4.1.2 (ii) Analysis of parameter values

In Table 1, parameters for both scenarios (Germany and Sweden resp.) are shown. The column “quality” in Table 1 gives an estimation on the reliability of the parameter values based on sample sizes (n<=20: +, n>20: ++).

For the unknown parameter pre-breeding survival, we can only assume a realistic range based on theoretical considerations: In birds, survival of juveniles is generally lower than that of adult individuals (Newton 1989; Van der Jeugd & Larsson 1998). Therefore, in the Lesser Spotted Woodpecker we assume maximum pre-breeding survival to be lower than survival rate in adults. The minimum rate of survival in juveniles is the rate of recoveries of local recruit in the study areas.

In the Swedish population, survival rate of yearling birds was 0.63 (males) and 0.45 (females) resp. (Wiktander unpubl.). Therefore, pre-breeding survival rate is supposed to be below 0.45. The proportion of recovered fledglings as local recruits and therefore the lower limit was 6% in Sweden (Wiktander 1998). In the German population, yearling survival rate is not known, but adult survival rate is 0.58 (males) and 0.62 (females) resp. We therefore assume that pre-breeding survival in the German scenario is remarkably lower than 0.58. The lower limit for survival rate is set at 0.20, based on local recoveries (Chapter I).

There is no sex-specific behaviour before the first breeding time and body mass and thus “quality” of fledglings was not different between the sexes (Rossmanith unpubl.). Therefore, we do not distinguish between survival rates of male and female juveniles.

Table 1 Parameter set for the two scenarios. All parameter values for the German scenario are shown in the empirical part of this paper or are based on Chapter I, II, Höntsch unpublished and own observations. For the Swedish scenario, values are based on Wiktander (1998), Wiktander et al. (2000, 2001a, 2001b & 2001c) and Wiktander & Olsson unpublished.

	Germany		**Sweden**		**Description**
Stochastic parameters	**Value**	**Qual.**	**Value**	**Qual.**	**Probability...**
$pDivorce_{old\ pairs}$	0.03	+	0.034	++	for old pairs to split up
$pNonBreed_{new\ pairs}$ (± *s.d.*)	0.0± 0.0	++	0.126 ± 0.139	++	for new pairs to lay no eggs
$pStartEarly_{new\ pairs}$	0.46	+	0.49	++	for new pairs to start early
pFailure	0.03	++	0.04	++	to fail reproduction due to unhatched eggs
pPredation (± *s.d.*)	0.16 ± 0.02	++	0.056± 0.05	++	to fail due to predation
$pSurvBreed_{male}$ $pSurvBreed_{female}$	0.969 0.966	++ ++	0.936 0.936	++ ++	to survive during breeding time
$p(x)Fledglings_{early\ pairs}$	0.09 [x=2] 0.33 [x=3] 0.33 [x=4] 0.25 [x=5]	+	0.02 [x=2] 0.07 [x=3] 0.14 [x=4] 0.35 [x=5] 0.37 [x=6] 0.05 [x=7]	++	for successful pairs with early breeding start to produce x fledglings
$p(x)Fledglings_{late\ pairs}$	0.20 [x=1] 0.20 [x=2] 0.40 [x=3] 0.00 [x=4] 0.20 [x=5]	+	0.09 [x=1] 0.13 [x=2] 0.17 [x=3] 0.35 [x=4] 0.04 [x=5] 0.17 [x=6] 0.05 [x=7]	++	for successful pairs with late breeding start to produce x fledglings
pYoungMale	0.54	++	0.446	++	to become male at birth
$pSurvWinter_{male}$ (± *s.d.*) $pSurvWinter_{female}$ (± *s.d.*)	0.582 ± 0.060 0.621 ± 0.207	+ +	0.737 ± 0.230 0.618 ± 0.190	++ ++	to survive during non-breeding season
Missing parameter	**Realistic range**		**Realistic range**		**Probability...**
$pSurvWinter_{juvenile}$	0.20-0.57		0.06-0.44		to survive before first breeding

Determinate parameters (for both scenarios)		
Capacity	500	Max. number of territories
StartSize	400	Number of individuals at initialisation
MaxAge	10	Maximum age

4.1.3 (iii) Identification of pattern

As patterns to estimate pre-breeding survival, we selected variables available in the data set of empirical investigations that are influenced by several processes of the population dynamics, including pre-breeding survival. We decided to use more than one of such patterns, since the reliability of the determined value is higher, if the model is able to reproduce multiple patterns (Wiegand et al. 2003). The selected patterns and their relation to pre-breeding survival is described below:

1. **Sex ratio** – calculated by log(adult males/adult females): proportion of surviving fledglings influences population sex ratio, due to a bias in brood sex ratio (see rule 7).
2. **Pair ratio** – calculated by log(old pairs/new pairs): The more fledglings survive, the higher is the proportion of newly established pairs in relation to old pairs.
3. **Nesting success** – defined as proportion of nests that fledge at least one young: Since new pairs are more likely not to lay eggs (rule 2), nesting success is influenced by the proportion of new pairs.
4. **Breeding success** – defined as the number of fledglings per successful nest:. A proportion of new pairs have a late breeding start and thus produce fewer nestlings (rule 3).
5. **Occupancy** of territories – defined as proportion of occupied territories: Pre-breeding survival influences population size and therefore occupancy of territories directly. Data for this pattern are available only for the Swedish scenario.

For these patterns, empirical data from 9 years in the Swedish population and 5 years in the German population are available. Based on these annual values, we calculated the 95% confident interval for the mean over all years, for both scenarios separately (see Table 2). The confident interval presents the range within simulated mean values have to fit to reflect the empirical pattern from the field.

Table 2 Lower and upper limit of 95% confident intervals for five patterns based on empirical data from German (see 3.2, Chapter I&II, Höntsch unpublished, own observations) and Swedish investigations (Wiktander et al. 2000, Wiktander et al. 2001b and Wiktander & Olsson unpublished). Mean values of simulated populations have to fit within the limits to reflect the pattern.

	Germany		Sweden	
	lower	upper	lower	upper
Sex ratio [log(male/female)]	0.004	0.170	-0.017	0.130
Pair ratio [log(old/new pairs)]	-0.763	-0.171	-0.740	-0.022
Nesting success [%]	57.0	100	64.6	96.0
Breeding success [number of young]	2.84	4.72	4.31	5.02
Relative occupancy [%]	—		0.572	0.905

4.1.4 (iv) Simulation runs and output variables:

To detect a reliable value for pre-breeding survival, we run simulations varying this parameter systematically in 0.01 steps within the realistic range (see Table 1) and compared the model output for each pattern with the values obtained from the field studies (Table 2).

Before the actual model analysis started, each population was initialised with 400 individuals of random sex and age (between 1 and 6 years) and run for 15 time steps. Earlier statistical analysis on the model, which is not shown here proved that this time span is sufficient to exclude initialisation effects. Thereafter, population dynamic was simulated over 100 time steps but stopped earlier when the number of individuals reached 0. In every time step, values for all patterns were noted to calculate the mean over all simulated years, which was compared with the pattern observed in the field. To avoid extreme values, only years with at least 25 individuals (which equals an occupancy of only 0.5% of all territories) and only populations with more than 9 years above that level were included in the analysis. We defined a population to reflect the pattern when the simulated mean value for a pattern fell within the empirical 95% confident interval.

Due to the stochastic processes in the model, no single run is representative. Therefore, we started 500 populations with the identical parameter set for each simulation run and calculated the proportion of simulated populations reflecting the certain pattern. We further refer to that value as “fit” in %. For each pre-breeding survival rate in both populations, 50 replicate runs were conducted and mean as well as standard deviation of the fit for each pattern was calculated. Exemplary population structure obtained from a sample run of a single population over a time span of 100 years is given in Fig. 2.

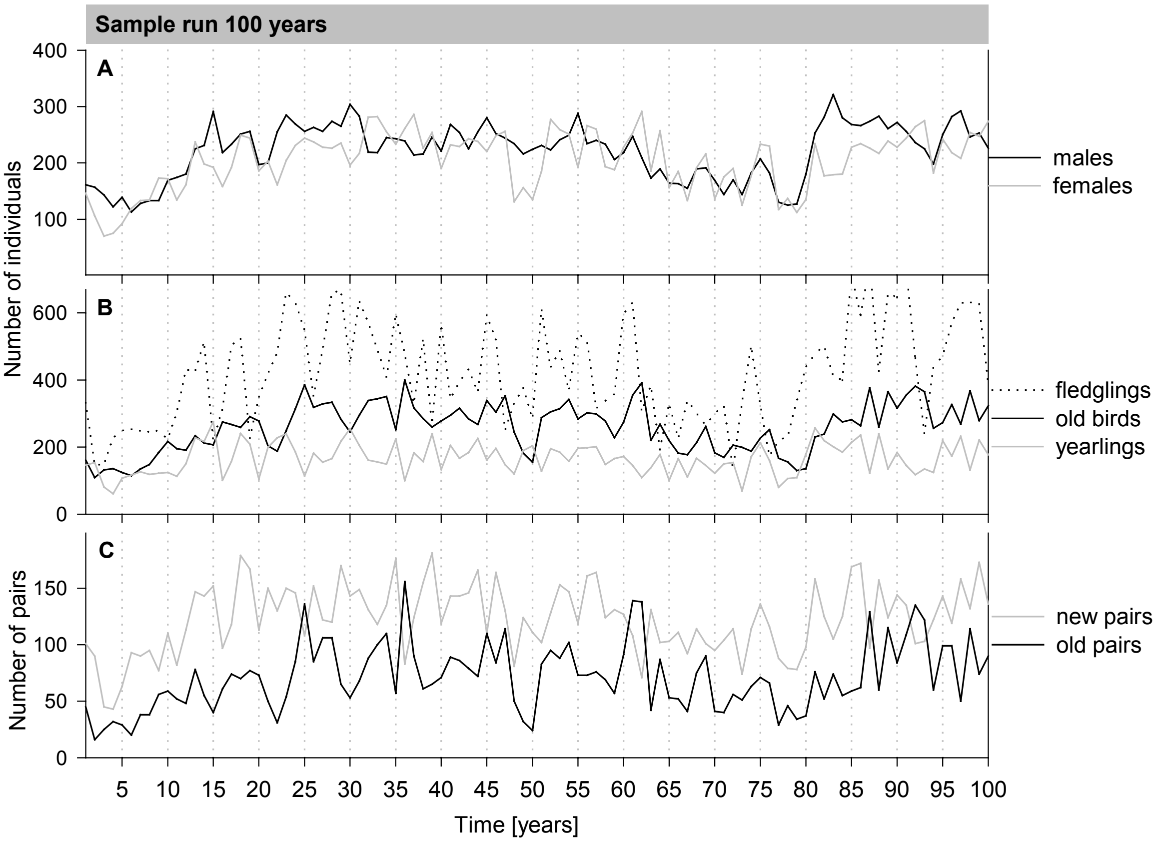

Figure 2 Sample run of a single population over 100 years. (A) number of males and females, (B) distribution of the three age classes: fledglings, yearlings and older birds,(C) old and new pairs.

4.2 Model results

4.2.1 Scenario I: German population

In scenario I, we investigated the proportion of simulated populations reflecting the pattern of nesting success, breeding success, pair ratio and sex ratio based on the empirical data of the German study population. The fit for all but one pattern changed with pre-breeding survival rate (Fig. 3). The fit with the pattern of breeding success was 100% and did not change with pre-breeding survival rate, indicating that this pattern is not adequate to estimate pre-breeding survival.

All three sensitive patterns show an increasing trend at low pre-breeding survival rates; hence increase in pair ratio is strongest. When pre-breeding survival probability exceeds 0.44, 90% of the populations reflect all three sensitive patterns simultaneously. However, when pre-breeding survival rate exceeds 0.5, there is a slight decrease of the fit with the pattern of sex ratio. Moreover, from the biological point of view, pre-breeding survival rate should be clearly below adult survival rate of 0.58 (see 4.1 for details). Therefore, we conclude that pre-breeding survival rate is around 0.50 in the German scenario.

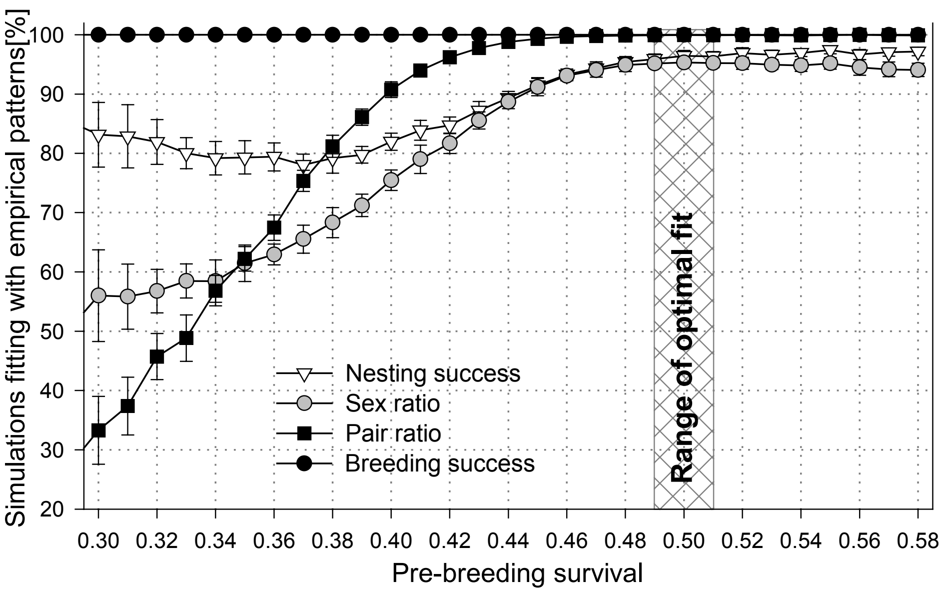

Figure 3 Scenario Germany: Proportion of simulated populations reflecting empirical patterns under various pre-breeding survival rates (mean and standard deviation of 50 simulation runs). A population reflects a pattern, if its mean value fits within the 95% confident interval of the observed values.

4.2.2 Scenario II: Swedish population

In the Swedish scenario, additionally to the four patterns used in the German scenario we included "occupancy", which reflects the observed proportion of occupied territories in the field. In this scenario, not only the fit with the pattern of breeding success but also the fit with the patterns of pair ratio and nesting success was high at all tested pre-breeding survival rates, detecting those patterns as weak (Fig.4). However, the fit with the pattern of sex ratio increased with increasing pre-breeding survival rate and exceeded 80% when pre-breeding survival was above 0.34.

Thereafter, the fit increased only slightly. Interestingly, occupancy proved to be a very clear pattern, showing an unimodal relationship with pre-breeding survival with a maximum at 0.37 (74%). Even though fit with sex ratio increased slightly at higher survival rates, the clear result in the fit with the pattern of occupancy suggests that pre-breeding survival is around 0.37.

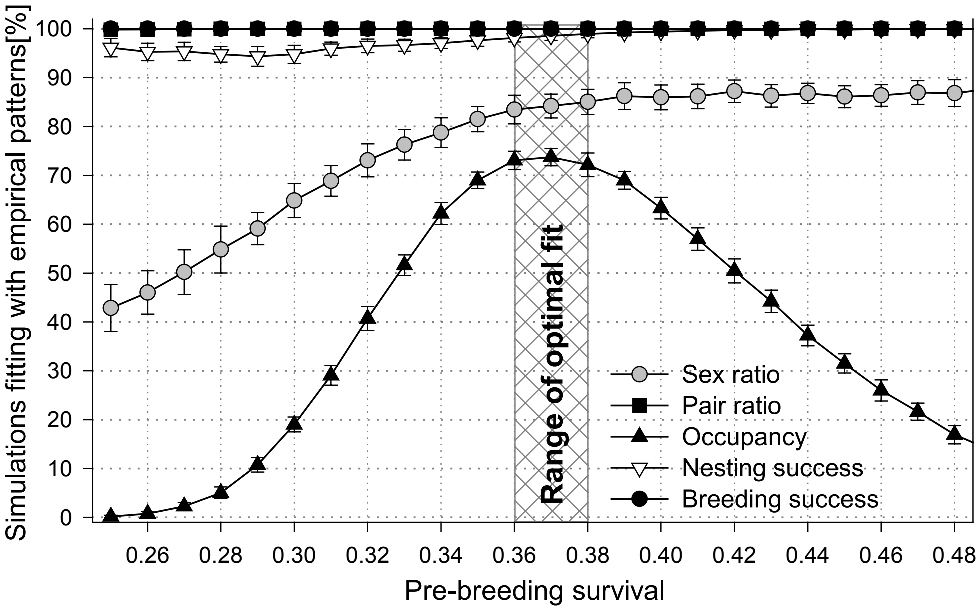

Figure 4 Scenario Sweden: Proportion of simulated populations reflecting a certain pattern observed in the field for various pre-breeding survival rates (mean and standard deviation of 50 simulation runs). A population reflects a pattern, if its mean value fits within the 95% confident interval of the observed pattern. The result of the pattern of breeding success is not visible, since fit is always 100% and the plot is covered by results of pair ratio.

4.2.3 Comparison of scenarios

Pre-breeding survival rates showed to be very different between the two investigated populations. However, based on the observations in the field, we did not expect the populations to differ dramatically in their population performance. Therefore, we simulated population performance in the two scenarios at various pre-breeding survival rates and compared the performance. Population performance is here analysed by the proportion of years in which the population is at carrying capacity and by the proportion of occupied territories. To test the impact of the different pre-breeding survival rates, we simulated 500 populations over 100 years and calculated the mean proportion of occupied territories and the proportion of years when the population reached carrying capacity (Fig. 5).

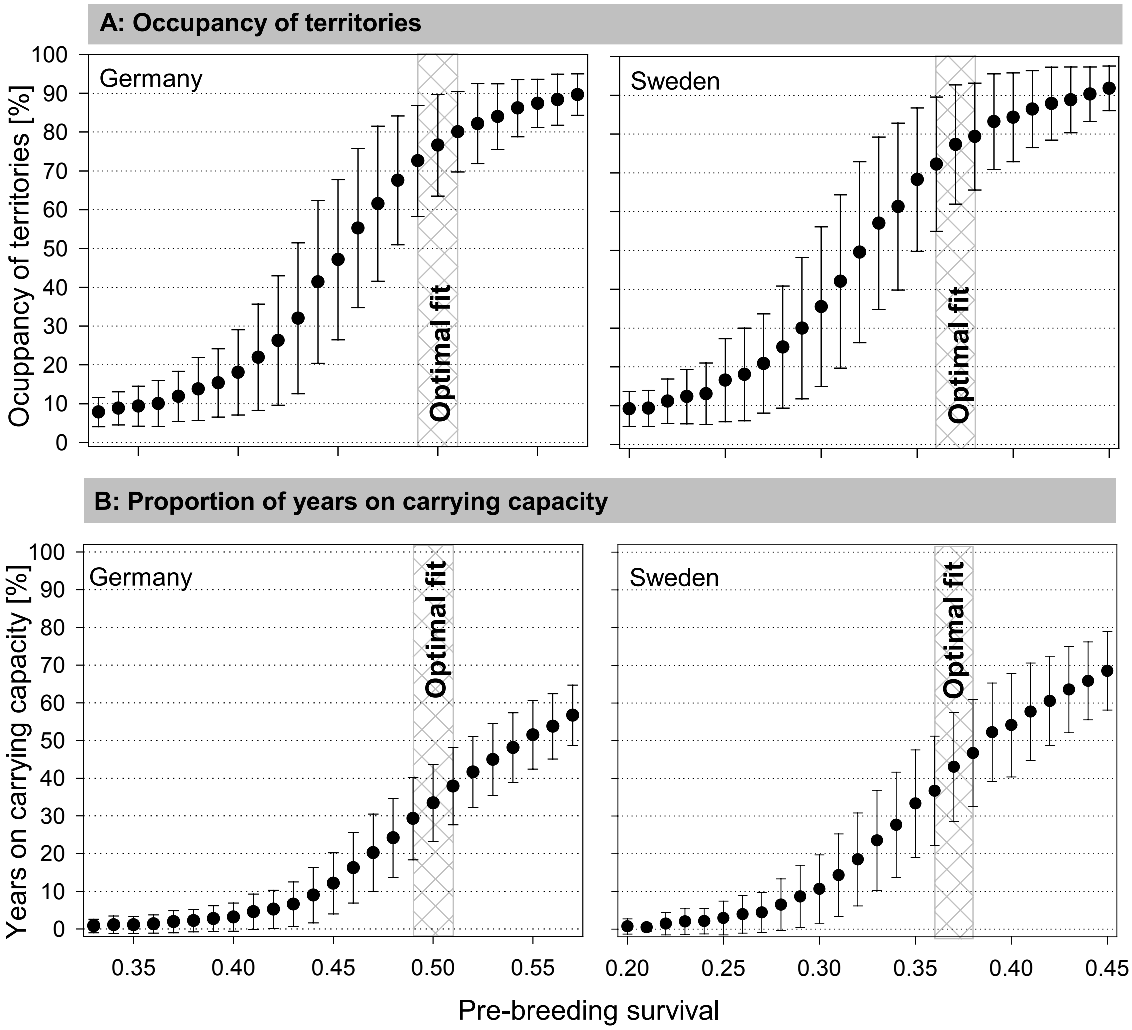

Figure 5 Simulation results: Population performance at various pre-breeding survival rates in the German and the Swedish scenario. Hatched areas indicate estimated pre-breeding survival rates. (A) Mean occupancy of territories in % (mean and s.d., n= 500 populations for each parameter value). (B) Proportion of years with population size at carrying capacity (mean and s.d., n= 500 populations for each parameter value).

In simulations with pre-breeding survival rates have the estimated values (0.50 and 0.37 resp.), we find that relative occupancy of the territories is not significantly different between the two scenarios (Fig.5A, unpaired t-test, T= -0.787, p=0.432). The almost total correspondence in occupancy is surprising, taking into account the large differences in the assumed pre-breeding survival. In Figure 5B is shown that size in both populations is in most years not at the maximum carrying capacity. At the estimated pre-breeding survival rates, the populations in the German scenario reaches carrying capacity in 33.4% of years on average, in the Swedish scenario the proportion of years is with 43.0% significantly higher (unpaired t-test: T=12.14, p<0.001).

5. Discussion

In this study, we presented a modelling approach to estimate a missing demographic parameter using patterns in empirical data on population level. Pre-breeding survival was determined for two populations of Lesser Spotted Woodpeckers at different geographical latitudes in which empirical investigations had been conduced. Pre-breeding survival was estimated by comparing the structure and the reproductive success of the simulated populations with empirically found pattern. The value was different in the two populations, being lower in the population at higher latitude. We demonstrated that the use of multiple weak patterns is able to give a reliable estimation of a previously unknown parameter.

5.1 Method of Pattern oriented modelling

We developed a relatively simple individual-based model simulating the population dynamics of the Lesser Spotted Woodpecker. The number of processes and parameters was reduced to what is absolutely necessary in order to reflect the patterns and estimate pre-breeding survival rate in order to reduce complexity. Discussions, whether models are too simple or too complex are a general issue in ecological modelling (Beissinger & Westphal 1998; Grimm 1999; Wiegand et al. 2003). Especially in conservation biology when dealing with rare species, information is often too scarce to parameterise very complex models (Reed et al. 2002). However, when creating a too simple model, important processes might be missing (Grimm et al. 2005). In their protocol for pattern-oriented modelling, Wiegand et al. (2003) stated that model construction should not only be guided by the initial question and the available knowledge but also by patterns observed in the field. Trying to reflect multiple patterns found on population level, one is forced to include all processes that are important for the system. For example, several factors can influence mortality in animals, like age (Newton 1989), sex (Breitwisch 1989), investment in reproduction, (Nur 1984; Horak 2003) or habitat quality (Pettorelli et al. 2003). However, small sample sizes in both studies of Lesser Spotted Woodpeckers did not allow for distinguishing between all factors. Since we wanted to use sex ratio as a pattern describing population structure, analysis of sex specific survival was most important and thus included.

The model framework was consistent for both investigated Lesser Spotted Woodpecker populations and can easily be used for other populations as well by entering population-specific demographic parameters. The parameterisation of both scenarios was completely based on empirical data from the specific population to take credit for habitat specific differences as well as geographical variations within the species.

Not all selected patterns were able to detect the realistic range for pre-breeding survival rate. For instance the fit in the pattern of breeding success was not affected by pre-breeding survival rate in both scenarios. The weakness of this pattern is not too surprising, since breeding success was only influenced indirectly by juvenile survival through the proportion of new and thus late laying pairs (see rule 1 and rule 3).

In the Swedish scenario, pair ratio and nesting success were also not useful for parameter estimation. The differences in the prediction quality between patterns within the same species demonstrate that multiple patterns are needed to gain reliable results. Despite the weakness of some patterns to detect the missing parameter, the high proportion of fit indicates the reliability of the selected processes and parameters simulating realistic population dynamics and can thus be seen as model validation.

Our results showed the high value of empirical data of population structure and reproductive success on population level when estimating missing demographic parameters. Although these data are not eye-catching patterns like the spatial distribution of individuals, they are qualified as “control variables”. Their benefit is that they might be already available in many data sets and are easy to collect in the field. Therefore, we suggest that our approach can easily be transferred to other species. Moreover, we demonstrated that population data which are not even statistically significant, like the bias in sex ratio of the population, can serve as valuable patterns leading to determine or at least to estimate missing parameters.

5.2 Pre-breeding survival rate

Pre-breeding survival refers to the time-span between fledging and first breeding. The duration of this time-span varies between species dependent on their age of maturity. In the Lesser Spotted Woodpecker, yearlings are already mature, thus pre-breeding survival refers to the time-span between fledging the nest and the following breeding season. This juvenile stage is usually a period of heavy mortality in birds (Breitwisch 1989). Pre-breeding survival probabilities in Lesser Spotted Woodpeckers estimated here were high, with 0.50 (German population) and 0.37 (Swedish population), compared to other short-living species. Comparative data for pre-breeding survival are rare (Monrós et al. 2002) and most studies are limited to survival of fledglings in the time span between fledging and dispersal from the parents’ territory (Soler et al. 1994; Zelenak et al. 1997). The few existing empirical investigations on short-living species estimated pre-breeding survival probabilities to be around 0.20 (e.g. 0.18 in Blue tits *Parus caeruleus* Dhondt 1989; 0.22 in Kingfisher *Alcedo atthis* Sternberg 1989).

Thereby, we have to keep in mind that our model only determines the proportion of young birds entering the population. This corresponds to pre-breeding survival only in cases when immigration does not exceed emigration. Otherwise, the high pre-breeding survival rate identified in the German scenario could also be explained by a high immigration rate. However, the exceptional high recovery rate of local recruits (20% in the German investigation, see Chapter I) supports the assumption of a high pre-breeding survival rate.

Our results reveal the remarkable difference between pre-breeding survival rates in the German and the Swedish study population. We suppose the geographical variation in demographic parameters to be the reason for this result. Geographical variation in life-history traits on a latitudinal gradient is known for many bird species (Murray 1985) including woodpeckers (Koenig 1986). Clutch size increases from tropical areas to the poles, which is explained by a geographical gradient in environmental conditions, causing a gradient in food resources (Lack 1947) or nest-predation (Skutch 1985). Ashmole (1963) interpreted this gradient with different levels of seasonality of resources in tropics versus temperate areas. Accordingly, in temperate areas, strong seasonality results in (i) low adult winter survival rates due to resource scarcity, which can (ii) be balanced by larger clutch sizes due to high food availability during breeding time. Following this idea, it is generally assumed that adult survival rates decrease from the equator to the poles, despite the lack of comparative data (Johnston et al. 1997; Ricklefs 1997; Ricklefs 2000; Griebeler & Böhning-Gaese 2004). Assuming fecundity and adult mortality to balance each other, Ricklefs (1997) concluded pre-breeding survival to be similar in different geographical regions.

However, a contradicting hypothesis was formulated by Karr et al. (1990). They disagreed with this generalization and presented a detailed comparison of adult survival rates between tropical and temperate forest birds showing very similar adult survival rates between groups. The authors assumed other factors, including pre-breeding survival, to have a latitudinal gradient, which have to be balanced by larger clutches in stable populations of temperate birds. Furthermore, Griebler & Böhning-Gaese (2004) demonstrated that Ashmole’s hypothesis is only consistent when costs for larger clutches exist. In their model, costs for juveniles in form of lower survival were more important to apply than adult survival.

The results of the two Lesser Spotted Woodpecker populations compared here confirm Karr’s Hypothesis. The northern population (Sweden) produces larger clutches (Wiktander et al. 2001b) than the German population (Chapter I) but the adult survival rates are similar (around 0.60 per year, Wiktander 1998). Consequently, higher fecundity and lower juvenile survival should balance each other. Indeed, estimated pre-breeding survival differed largely between the two populations, which showed a similar performance in terms of occupancy of the territories (Fig.5). Moreover, although pre-breeding survival rate was approx. 35% higher in the German than in the Swedish scenario, the populations in the Swedish scenario reached carrying capacity in more years (Fig. 5), indicating a slightly better population performance. This comparison between the two populations supports the reliability of our simulation results. Therefore, we are confident that our model reflects population dynamics well and that our estimation of pre-breeding survival is realistic.

5.3 Conclusion

We demonstrated here that pattern-oriented modelling exhibits a good method to estimate missing demographic parameters that are needed for population viability analyses. Furthermore, the difference in prediction quality of the used patterns between populations of the same species showed the need of multiple patterns to ensure the results. Using multiple patterns allows including weak patterns available in the data set. We suppose that there are a variety of other long-term field studies especially in birds providing data of population structure. These should be considered as patterns when trying to predict viability of the population.

6. References

Akcakaya, H. R. & Burgman, M. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 705-707.

Ashmole, N. P. 1963. The regulation of tropical oceanic birds. *Ibis* 103: 458-473.

Beissinger, S. R. & Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821-841.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics. 23: 481-506.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. In: Power, D. M. (ed.) Current Ornithology 6. Plenum Press, New York.

Brook, B. W., O'Grady, J. J., Chapman, A. P., Burgman, M. A., Akcakaya, H. R. & Frankham, R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404: 385-387.

Cramp, S. 1985. Handbook of the birds of Europe and the Middle East and North Africa. Oxford University Press, Oxford.

Curio, E. 1983. Why do young birds reproduce less well? *Ibis* 125: 400-404.

Dhondt, A. A. 1989. Blue tit. In: Newton, I. (ed.) Lifetime reproduction in birds. Academic Press Inc., London.

Ferrer, M., Otalora, F. & Garcia-Ruiz, J. M. 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. *Ecological Applications* 14: 616-624.

Gilbert, M., Gregoire, J. C., Freise, J. F. & Heitland, W. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *Journal of Animal Ecology* 73: 459-468.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1994. Handbuch der Vögel Mitteleuropas. Columbiformes - Piciformes. Aula-Verlag, Wiesbaden.

Griebeler, E. M. & Böhning-Gaese, K. 2004. Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis. *Evolutionary Ecology Research* 6: 679-694.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115: 129-148.

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J. & Wissel, C. 1996. Pattern-oriented modelling in population ecology. *Science of the Total Environment* 183: 151-166.

Grimm, V., Groeneveld, J., Kramer-Schadt, S., Schwager, M., Revilla, E., Tews, J., Wichmann, M. C. & Jeltsch, F. 2005. On the importance of buffer mechanisms for population viability analysis. *Conservation Biology* (in press).

Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Horak, P. 2003. When to pay the cost of reproduction? A brood size manipulation experiment in great tits (*Parus major*). *Behavioral Ecology and Sociobiology* 54: 105-112.

Jeltsch, F., Moloney, K. & Milton, S. J. 1999. Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. *Oikos* 85: 451-466.

Jeltsch, F., Muller, M. S., Grimm, V., Wissel, C. & Brandl, R. 1997. Pattern formation triggered by rare events: Lessons from the spread of rabies. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264: 495-503.

Johnston, J. P., Peach, W. J., Gregory, R. D. & White, S. A. 1997. Survival rates of tropical and temperate passerines: A Trinidadian perspective. *American Naturalist* 150: 771-789.

Karr, J. R., Nichols, J. D., Klimkiewicz, M. K. & Brawn, J. D. 1990. Survival Rates of Birds of Tropical and Temperate Forests - Will the Dogma Survive. *American Naturalist* 136: 277-291.

Koenig, W. D. 1986. Geographical Ecology of Clutch Size Variation in North-American Woodpeckers. *Condor* 88: 499-504.

Lack, D. 1947. The Significance of Clutch-Size. *Ibis* 89: 302-352.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton.

Mikusinski, G. & Angelstam, P. 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118: 277-283.

Monrós, J. S., Belda, E. J. & Barba, E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99: 481-488.

Murray, G. B. 1985. Evolution of clutch size in tropical species of birds. *Ornithological Monographs* 505-519.

Newton, I. 1989. Lifetime reproduction in birds. Academic Press Inc., London.

Nilsson, S. G., Olsson, O., Svensson, S. & Wiktander, U. 1992. Population trends and fluctuation in Swedish woodpeckers. *Ornis Svecica* 2: 13-21.

Nur, N. 1984. Feeding Frequencies of Nestling Blue Tits (*Parus caeruleus*) - Costs, Benefits and a Model of Optimal Feeding Frequency. *Oecologia* 65: 125-137.

Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. PhD Thesis, Lund University, Sweden.

Pettorelli, N., Gaillard, J. M., Duncan, P., Maillard, D., Van Laere, G. & Delorme, D. 2003. Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology* 84: 3307-3316.

Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology* 70: 1088-1097.

Reed, J. M., Mills, L. S., Dunning, J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M. C. & Miller, P. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16: 7-19.

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *Journal of Animal Ecology* 72: 765-776.

Ricklefs, R. E. 1997. Comparative demography of new world populations of thrushes (*Turdus spp*). *Ecological Monographs* 67: 23-43.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 102: 9-22.

Saether, B. E. 1990. Age-specific variation in reproductive performance of birds. In: Power, D. M. (ed.) Current Ornithology 7. Plenum Press, New York.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithological Monographs 36, 575-594.

Soler, M., Palomino, J. J., Martinez, J. G. & Soler, J. J. 1994. Activity, Survival, Independence and Migration of Fledgling Great-Spotted-Cuckoos. *Condor* 96: 802-805.

Sternberg, H. 1989. Pied Flycatcher. In: Newton, I. (ed.) Lifetime reproduction in birds. Academic Press Inc., London.

Tews, J., Schurr, F. & Jeltsch, F. 2004. Seed dispersal by cattle may cause shrub encroachment of Grewia flava on southern Kalahari rangelands. *Applied Vegetation Science* 7: 89-102.

Tiainen, J. 1985. Monitoring bird populations in Finland. *Ornis Fennica* 62: 80-89.

Van der Jeugd, H. P. & Larsson, K. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology* 67: 953-966.

Walsh, P. D., Akçakaya, H. R., M., B. & Harcourt, A. H. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 704-710.

Wichmann, M. C., Jeltsch, F., Dean, W. R. J., Moloney, K. A. & Wissel, C. 2003. Implication of climate change for the persistence of raptors in arid savanna. *Oikos* 102: 186-202.

Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. 2003. Using pattern-oriented modelling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos* 100: 209-222.

Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs* 68: 539-570.

Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* 31: 447-456.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001a. Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). *Auk* 118: 624-635.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001b. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Ibis* 143: 72-82.

Zelenak, J. R., Rotella, J. J. & Harmata, A. R. 1997. Survival of fledgling Ferruginous Hawks in northern Montana. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* 75: 152-156.

Link to the proceeding Chapter

In the last Chapter, I presented the development of an individual-based stochastic model simulating the population dynamics of Lesser Spotted Woodpeckers. By a pattern-oriented modelling approach I estimated the unknown value for the parameter pre-breeding survival for two different populations in Germany and in Sweden respectively. The comparison of the population performance in these two populations demonstrated the reliability of the estimated values. Only the implementation of the estimated pre-breeding survival rate into the simulation model allows now for the final investigation in Chapter IV: The impact of the observed facultative occurrence of polyandry on the persistence of a population of Lesser Spotted Woodpeckers. I will thereby test whether flexibility in the social mating system can act as a buffer mechanism against extinction of populations.

Behavioural flexibility in the mating system buffers population persistence: lessons from the Lesser Spotted Woodpecker *(Picoides minor*)

Chapter IV

Behavioural flexibility in the mating system buffers population persistence: lessons from the Lesser Spotted Woodpecker *(Picoides minor)*[1]

1. Abstract

The persistence of small populations is strongly affected by demographic and environmental noise. In most stochastic population models addressing persistence, environmental noise is included by imposing a synchronized effect of the environment on all individuals. However, many different mechanisms are likely to exist which counteract this synchronization to some degree.

We here study whether the flexibility in the mating system, which has been observed in some bird species, is a potential mechanism counteracting the synchronization of environmental fluctuations. Study organism is the Lesser Spotted Woodpecker (*Picoides minor*), a generally monogamous species. However, facultative polyandry, where one female mates with two males with separate nests, was observed in years with male-biased sex ratio.

We constructed an individual-based stochastic simulation model, which is based on observations and data of a population in Taunus, Germany. We tested the impact of three behavioural scenarios on population persistence: (i) strict monogamy, (ii) polyandry without costs and (iii) polyandry assuming costs for polyandry in terms of lower survival and reproductive success for secondary males. We assumed that polyandry occurs only in years with male-biased sex ratio and only in females with favoured breeding conditions.

With increasing polyandry, the persistence of the population increased in both polyandry scenarios and even low rates of polyandry had a strong influence. The increase in population persistence with carrying capacity was flat in the monogamous scenario, indicating strong environmental noise. In the polyandrous scenarios, the increase of persistence was stronger, indicating a buffer mechanism. In the polyandrous scenario, populations had a higher mean population size, a lower variation in number of individuals, and recovered faster after a population breakdown. Presuming a realistic polyandry rate and costs for polyandry, there was still a strong effect of polyandry on the persistence of the population.

The results show that polyandry and in general flexibility in mating systems are buffer mechanisms and reduce the impact of environmental and demographic noise. Consequently, we suggest that even behaviour that seems to be exceptional should be considered explicitly when predicting the persistence of populations.

---

[1] This chapter is previewed for submission as: Rossmanith, E., Grimm, V. & Jeltsch, F. Behavioural flexibility in the mating system buffers population persistence: lessons from the Lesser Spotted Woodpecker (*Picoides minor*). Journal of Animal Ecology

2. Introduction

Understanding mechanisms causing extinction of small populations is one of the major challenges of conservation biology (Shaffer 1987). A widely used tool for predicting extinction risk under different environmental conditions or management options is population viability analysis (PVA) (Akcakaya & Burgman 1995; Walsh et al. 1995; Brook et al. 2002). PVAs are usually based on stochastic population models, which allow including two key factors influencing the risk of extinction of small populations: demographic and environmental noise. The strong effect of environmental noise on extinction risk is due to the synchrony induced by environmental fluctuations: if in unfavourable years the survival or reproduction of all individuals is reduced to more or less the same degree, the population might become so small that extinction due to demographic noise becomes likely (Wissel et al. 1994).

In most PVA models, environmental fluctuations are included by reducing survival and/or reproduction of all individuals simultaneously, for example by reducing the survival rate of all adults by 20% in bad years. However, buffer mechanisms might exist counteracting the synchronizing effect of environmental fluctuations (Grimm et al. 2005). Examples include: safe sites (or territories, home ranges) in the habitat where individuals are less affected by environmental variation (McLaughlin et al. 2002; Greene 2003); “floaters”, i.e. non-breeding individuals in territorial species, which can rapidly occupy territories that have become vacant due to the death of a breeder (Walters et al. 2002); in general individual variability, which means that individuals differing in weight, age, social status or other correlates of fitness are not equally affected by environmental conditions (Uchmanski 1999; 2000).

A further potentially desynchronising mechanism, which so far has received little attention in PVA models, is adaptive behaviour (Sibly & Smith 1985; Houston & McNamara 1999; Railsback 2001): individuals adapt their behaviour to changing environmental conditions. Imperial Eagles (*Aquila adalberti*) for instance mature at earlier ages when population density is low (Ferrer et al. 2004). Here we explore the consequences of the flexibility of the social mating system for population persistence. In several generally monogamous bird species, the occurrence of social polygamous mating systems was described (Davies 1991). In these cases, one sex mates with two or more partners with separate nests during a single breeding season. The social mating system of species is closely related to their organisation of parental care (Clutton-Brock 1991). Members of the sex less involved in parental care can spend more time and energy for intrasexual competition for extra-mates. The occurrence of this behaviour is furthermore influenced by the operational sex ratio in the population, e.g. the ratio of fertilisable females to sexually active males (Emlen & Oring 1977).

Mathematical population models showed that persistence time is shorter for species with monogamous than with polygynous mating systems (Engen et al. 2003; Saether et al. 2004). These models are, however, based on the simplifying assumption that survival rates are not sex-specific although different survival rates for the sexes have been reported especially for polygamous species (Promislow et al. 1992; 1994). Furthermore, these models compare the two extremes of strict polygyny and strict monogamy. Whether the model results also hold for real bird species that are generally monogamous and show only a low degree of polygamous mating is uncertain. In such a mating system, we would expect costs for the unusual mating behaviour. Indeed, empirical investigations reported the secondary mate in a polygamous mating to get usually less help in parental care than the primary mate (Kempenaers 1995), which can result in lower survival rates and reproductive success (Slagsvold & Lifjeld 1994; Bensch & Hasselquist 1994; Garamszegi et al. 2004).

Our study system is the Lesser Spotted Woodpecker (*Picoides minor*), a generally monogamous species, in which the facultative occurrence of social polyandry was observed, i. e. the mating of one female with more than one male with separate nests (Chapter II; Höntsch 1996; Wiktander et al. 2000). Since individual behaviour has to be included explicitly to investigate flexibility in the social mating system, we are using an individual-based model (IBM). IBMs have been used for a wide variety of ecological problems (Bart 1995; Wiegand et al. 1998; Grimm 1999; Walters et al. 2002). The advantages of this model type over other stochastic models, which consider average individuals, is that in IBMs the behaviour of the individual is included explicitly and can be related to both their own characteristics and their environment (Ferrer et al. 2004). Our model is based on empirical data obtained from a Lesser Spotted Woodpecker population situated in a German low mountain range near Frankfurt/Main (Taunus) (see Chapters I, II & III).

We will address the question whether occurrence of polyandry in years with male-biased sex ratio has the potential to affect the persistence of the population positively, i.e. to act as a buffer mechanism. We will explore whether this effect exists (i) if the rate of polyandry is low and (ii) if we assume costs for secondary broods in terms of lower fecundity and higher adult mortality.

3. Methods

3.1 Biological background

The Lesser Spotted Woodpecker is distributed over the whole Palaearctic region, from Great Britain and Northwest Africa to Kamtschatka (Cramp 1985). This year round resident has a strong site fidelity and stays in the area where it first settled as yearling. Yet the species is highly mobile and home ranges reach several 100 hectares in size (Wiktander 1998; Höntsch 2005). The species feeds mainly on arthropods living in dead wood (Olsson 1998) but switches to surface-living arthropods during breeding time (Chapter II; Olsson 1998). Caused by changes in food availability throughout the breeding season, reproductive success decreases the later breeding starts. The timing of breeding is influenced by pair bond duration, in that pairs that bred together before have an earlier start of egg laying than newly established pairs (Chapter I; Wiktander et al. 2001). Thus, although living solitary in the non-breeding season, Lesser Spotted Woodpeckers perform in general monogamous live-long pair bonds and are single-brooding (Glutz von Blotzheim & Bauer 1994; Wiktander et al. 2000). However, social polyandry – one female is mated with two males and has two separate nests in one breeding season – was occasionally observed in two different populations (Chapter II; Höntsch 1996; Wiktander et al. 2000). The proportion of polyandrous females based on all females was 8.5% in Sweden (Wiktander et al. 2000) and 9.7% in Germany (Chapter II).

The Lesser Spotted Woodpecker study population lives in a heterogeneous landscape in the Taunus low mountain range near Frankfurt/Main, Germany. The study area consisted of deciduous and coniferous forests, old orchards as well as grassland (for details see Chapter I).

3.2 Simulation model

3.2.1 General structure

The model simulates the population dynamics of the Lesser Spotted Woodpecker in annual time steps. The simulations run until populations' extinction or for 6000 year at maximum, to limit simulation time. Each individual in the population is followed from fledging the nest to its death and is characterised by the state variables age, sex, mating status (unpaired/old paired/newly paired/polyandrous paired) as well as breeding start (early/late). Moreover, the identity of the current partner and its characteristics are known.

Each time step begins in spring and includes the processes of mating, reproduction and deaths, which are described by the following 10 rules. Parameter values are shown in Table 1. For a more detailed motivation of the rules see Chapter III[2].

Rule 1: If both partners from the previous breeding season are still alive, they establish an *old pair*. With a minor probability (*pDivorce*) they split up and mating status becomes *unpaired*. Unpaired males mate with unpaired females and establish a *new pair*. If there is no unpaired female available, the mating opportunities of the unpaired male depends on the mating system scenario (monogamy/polygamy, see 3.2.2).

Rule 2: All *old pairs* have an *early* breeding start, while *new pairs* have an *early* breeding start with the probability *pStartEarly*, otherwise their breeding start is *late*. The breeding start is an attribute that influences the number of young that fledge (see rule 6).

Rule 3: The probability to fail because eggs do not hatch is for all pairs *pFailure*. Additionally, issues described in rule 4 and 5 can cause failure in reproduction.

Rule 4: Nest predation occurs with the probability *pPredation* and results in the death of all nestlings.

Rule 5: When an individual dies (probabilities to survive $pSurvBreed_{male}$ and $pSurvBreed_{female}$) its brood fails and its mate remains unpaired until the next breeding time.

Rule 6: In successful nests, i.e. when eggs have hatched, parents have survived the breeding season and no predation has occurred, nestlings fledge. The probabilities for a certain number of fledglings were calculated based on empirically observed distribution of brood sizes in the field, divided in early $p(x)Fledglings_{earlypairs}$ and late broods $p(x)Fledglings_{latepairs}$ with *x* indicating the

---

[2] Numeration of model rules in this Chapter differs from Chapter III, since one rule - referring to the Swedish scenario only - was excluded in here.

number of fledglings (Table 1). Based on the observed sex ratio of fledglings in the field, the probability for a fledgling to be male is *pYoungMale,* otherwise it is a female.

Rule 7*:* Fledglings have a certain probability to survive ($pSurvWinter_{juvenile}$) in the time between fledging and first breeding time.

Rule 8: There is a maximum number of territories, i.e. a maximum number of individuals that can exist in the area, given in the parameter *carrying capacity*. Only if the number of birds is below the carrying capacity, fledglings can stay in the area, otherwise they emigrate. Since adult birds do not emigrate, an occupied territory only becomes available once an individual dies.

Rule 9: If an individual exceeds maximum age (=10 years), it dies. Otherwise it has the probability of $pSurvWinter_{male}$ and $pSurvWinter_{female}$ to survive.

Rule 10: At the end of the simulation year, the age of all individuals is updated.

To mimic demographic noise, all demographic parameter values (shown in Table 1) are interpreted as probabilities (Burgman et al. 1993). In processes that are supposed to be strongly influenced by environmental fluctuations between years, at the beginning of each time step parameter values were drawn from a normal distribution (cut at 0 and 1) with given mean and standard deviation (see Table 1).

Except for pre-breeding survival and its annual variation ($pSurvWinter_{juvenile} \pm s.d.$), all parameter values were derived from data collected in an empirical investigation on a Lesser Spotted Woodpecker population in Germany (Chapters I, II & III). Pre-breeding survival was estimated by pattern-oriented parameterisation using the model presented here (Chapter III).

Table 1 Default parameter set. Quality of the parameters: values based on empirical investigations with large (++) and small (+) sample sizes (see Chapters I, II and III), parameter estimation by pattern oriented modelling (+/-; Chapter III) and assumptions (-). A sensitivity analysis was conducted for the monogamous (mono) and the high costs polyandrous (poly) scenario.

Stochastic parameters	**Value**		**Quality**	**Sensitivity**		**Description: Probability...**
				mono	**poly**	
$pDivorce_{old\ pairs}$	0.03		+	<1	-1	..for old pairs to split up
$pStartEarly_{new\ pairs}$	0.46		+	3	3	..for new pairs to start early
PFailure	0.03		++	-2	-1	..to fail in reproduction
pPredation	0.16		++	-6	5	..to lose brood to predators
(± s.d.)	± 0.02		+	-4	6	
$pSurvBreed_{male}$	0.969		++	-3	-3	..to survive during breeding time
$pSurvBreed_{female}$	0.966		++	-3	<1	
$p(x)Fledg_{early\ pairs}$	0.09	[x=2]	+	57	27	.for successful pairs with early breeding start to produce x fledglings
	0.33	[x=3]				
	0.33	[x=4]				
	0.25	[x=5]				
$p(x)Fledg_{late\ pairs}$	0.20	[x=1]	+	16	14	.for successful pairs with late breeding start to produce x fledglings
	0.20	[x=2]				
	0.40	[x=3]				
	0.00	[x=4]				
	0.20	[x=5]				
pYoungMale	0.54		++	8	28	..for young to become male
$pSurvWinter_{male}$	0.582		+	-62	-97	..to survive during non-breeding season
(± s.d.)	± 0.060		+	<1	-3	
$pSurvWinter_{female}$	0.621		+	-7	-4	
(± s.d.)	± 0.207		+	-6	-6	
$pSurvWinter_{juvenile}$	0.50		+/-	-49	-54	..to survive before first breeding
(± s.d.)	± 0.03		-	<1	-1	
Parameters for polyandrous broods						
$pFailure_{sec.brood}$	0.15		-		<1	..for secondary broods to fail because eggs do not hatch
$pSurvBreed_{sec.male}$	0.845		-		-4	..for secondary males to survive during breeding time
$p(2)Fledg_{sec.brood}$	1.0		-		1	..for successful secondary males to produce x fledglings
pPolyandry			-		<1	..for unpaired male and early breeding, paired female to mate
Other parameters						
Capacity	250			6		Max. number of territories
StartSize	200			<1		No of individuals at initialisation
MaxAge	10			<1		Maximum age

3.2.2 Scenarios

In the monogamous scenario, unpaired males mate with females from the unpaired stock and form a "new pair". If no unpaired partners are available, the individual cannot reproduce within this time step.

In the polyandrous scenarios, males that remained unpaired after monogamous pair formation can mate with an already paired female. Yet, the existence of an unpaired male alone does not determine the proceeding of a polyandrous mating event. First, we assume that only females with an early breeding start can initiate an additional brood with a second male, because the breeding conditions deteriorate with time (see Chapters I and II for details). Secondly, polyandry has to be seen as an exceptional behaviour in woodpeckers and we assume that it will only be realised in some cases. In fact, unpaired males were observed in the field even though early breeding females were available (own obs.), which demonstrates that polyandrous mating events occur only with a certain probability (*pPolyandry*). Thus, if *pPolyandry* equals zero, no polyandrous mating will occur. If it equals one, all unpaired males finding an early breeding female will mate. However, at maximum one female can mate with two males and produce two broods.

In species with biparental care, polyandrous females have to share their parental care between two broods. Empirical investigations showed that especially the secondary partner suffers from reduced care of the polygamous mate, which yields in lower smaller proportions of successful broods, smaller brood sizes or lower adult survival (Kempenaers 1995; Albrecht & Johnson 2002, Garamszegi et al. 2004). An unequal share of care by polyandrous females between their two broods was also reported from the Lesser Spotted Woodpecker study population (Chapter II). Here, females invested more care in the primary than in the secondary brood and secondary males had a lower reproductive success and survival during breeding time compared to primary and monogamous broods (Chapter II). Since the exact costs are not known, we used two polyandrous scenarios to test the impact of polyandry under different assumptions of costs for the secondary male.

1. The optimistic "no cost" scenario: demographic parameters for reproductive success and mortality are the same for individuals from polyandrous as for those from monogamous broods.
2. The pessimistic "high costs" scenario. Mortality during breeding time and brood failure caused by unhatched eggs was set 5 times higher for the secondary male. The number of fledglings in successful secondary nests is reduced to 2 juveniles. The reduction of breeding survival rate reduces the annual survival rate (calculated by *SurvBreed* * *SurvWinter*) from 0.564 to 0.495.

3.2.3 Output variables and sensitivity analysis

For each parameter set, the model was run 2000 times until the population became extinct or after 6000 time steps. From the distribution of extinction times, we calculated the intrinsic mean time to extinction T_m by using the "$\ln(1-P_0)$ plot" described by Grimm & Wissel (2004). From T_m we also calculated the risk of extinction, $P_0(100)$, after 100 years. As viability for the population, we here defined a $P_0(100)$ that does not exceed 5%.

To check sensitivity of model outputs to changes in parameter values, each parameter was changed by ±10% of its default value (Table 1) while keeping all other parameters constant

(Dunning et al. 1995; Wichmann et al. 2003). Since number of fledglings per brood (*p(x)Fledg*) is a discrete value, we had to modify the value by one young. This equals a modification by 26% (early broods), 36% (late broods) and 50% (secondary polyandrous broods), respectively. Survival rates during breeding times were around 0.96. It is not possible to raise these values by 10%, since a probability cannot exceed 1. Therefore, we referred to mortality rates (1-survival rate) in the sensitivity analysis.

Sensitivity is calculated as the relative change of T_m divided by the relative change of the parameter. In Table 1, for all parameters the sum of the sensitivity towards increase and decrease in the parameter is given. Moreover, the qualities of the data underlying the parameters are indicated as follows: good data based on empirical investigations with large (++) and small (+) sample sizes, validated parameter estimation (+/-) and experts estimations (-).

4. Results

4.1 Influence of polyandry on population persistence

When the probability for a polyandrous mating event, *pPolyandry*, is 0.5, the proportion of polyandrous females was similar to the rate found in the empirical investigation (9.7%, Chapter II); when all potential polyandrous mating events are realised (*pPolyandry*=1), the mean rate of polyandrous females is 20.2% (Fig. 1A).

With increasing *pPolyandry* and consequently with an increasing proportion of polyandrous females, the mean time to extinction increased in both polyandry scenarios (Fig. 1B). The slope increased steep in the no cost scenario (linear regression: T_m= 296 + 780**pPolyandry*, r^2= 0.920, $p<0.001$), and still was more than doubled in high cost scenarios if compared to the monogamous scenario (T_m=296+327**pPolyandry*, r^2=0.560, $p>0.001$).

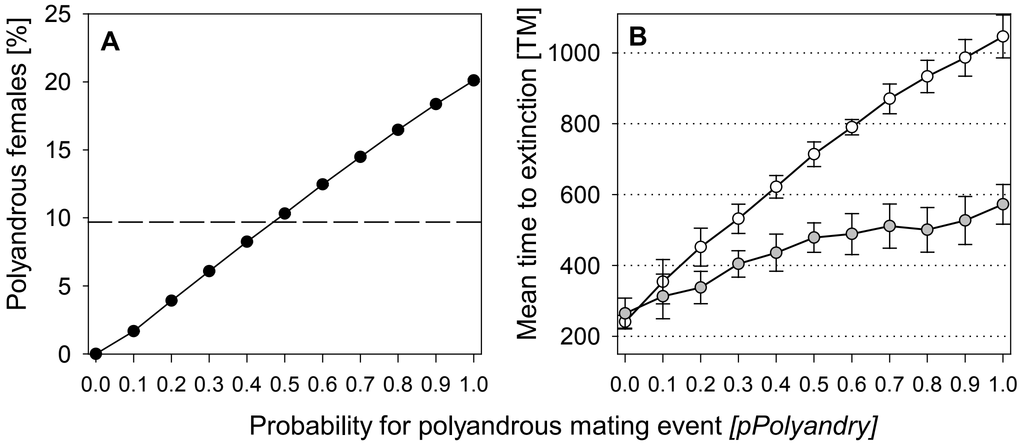

Figure 1 Effects of the probability *pPolyandry* for an unpaired male to mate an early breeding, paired female on (A) the proportion of polyandrous females in the population and (B) the population's mean time to extinction. The dashed line in (A) marks the proportion of polyandrous females found in the field. Regarding T_m, the "no-costs" scenario (white circles) and the "high–costs" scenario (grey circles) are compared. *pPolandry*=0 equals a strict monogamous mating system.

4.2 Influence of different mating systems on population persistence

Based on the results presented in Fig. 1A, we set *pPolyandry* at 0.5 in the following simulations, to receive a polyandry rate similar to the rate found in the field. To assess the relationship between polyandry and the influence of environmental fluctuations on the persistence of populations, we computed mean time to extinction (T_m) and risk of extinction in 100 years for various carrying capacities (number of territories) (Fig.2).

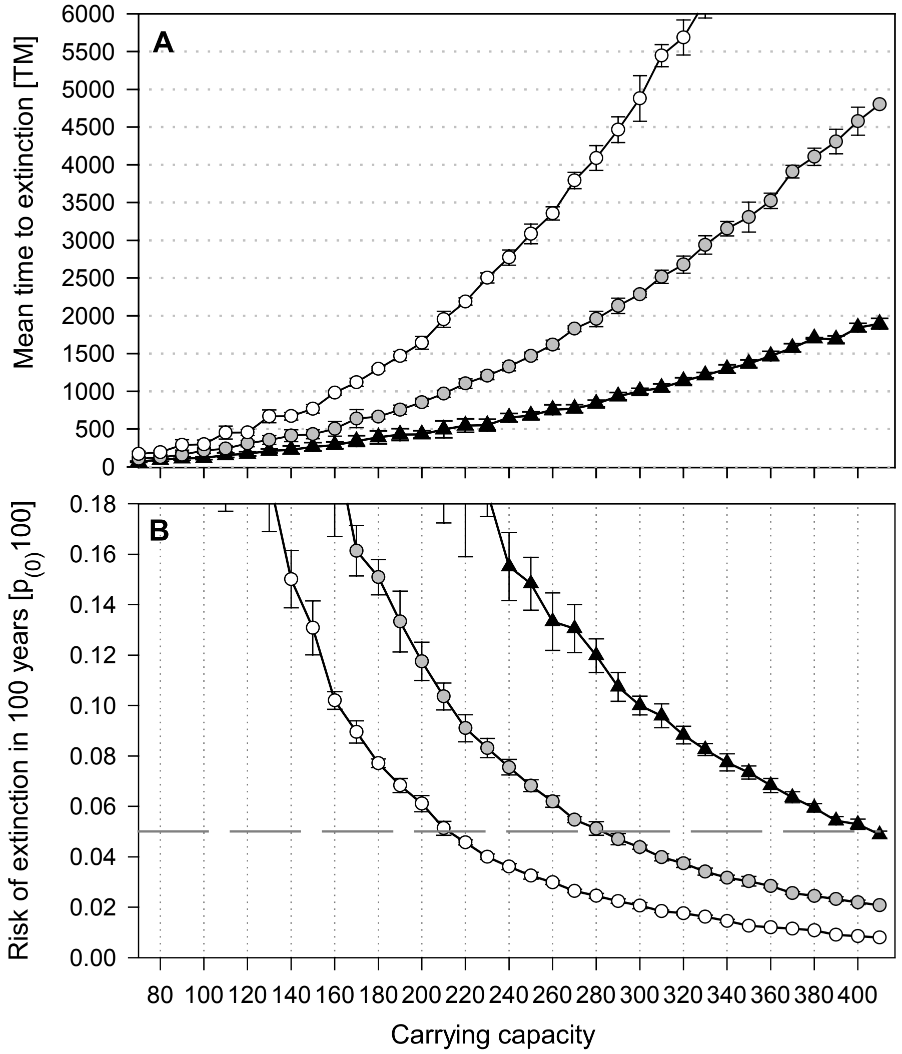

Figure 2 Persistence of the population versus carrying capacity for three different scenarios: purely monogamous (black triangles), polyandry with "high costs" (grey circles) and polyandry with "no cost" (white circles) (mean and standard deviation for 15 replicate runs). (A) Mean time to extinction (T_m) (B) Risk of extinction within 100 years, $P_0(100)$; viability, here defined as $P_0(100)<0.05$, is indicated by the dashed line.

In the monogamous scenario, the increase of T_m with carrying capacity is flat (Fig. 2A), indicating high environmental noise (i.e., environmental fluctuations cause a variation of the population's growth rate). In the "no costs" scenario, the increase of T_m is much steeper, indicating the polyandry might buffer environmental effects. The “high costs” scenario shows an intermediate result, but the buffer effect of polyandry is still considerable.

Consequently, the risk of extinction in 100 years decreased with carrying capacity in all three scenarios (Fig. 2B). Assuming strict monogamy, the minimum size for a viable population (risk of extinction smaller than 5% in 100 years) was 410 individuals. Assuming “high cost”-polyandry, the minimum size decreases to 290 and if polyandry does not include costs, the minimum size of a viable population is 220. Thus, considering different mating systems and costs, the carrying capacity for a minimum viable population differs strongly.

4.3 Effect of mating system on population dynamics

To better understand the reason for the effect of polyandry on population persistence, we investigated the dynamic of the population in the monogamous and the polyandrous scenario with costs in more detail. First, we simulated 300 populations assuming a carrying capacity of 300 individuals and compared the population performance under the scenario with monogamy and the high costs polyandrous scenario.

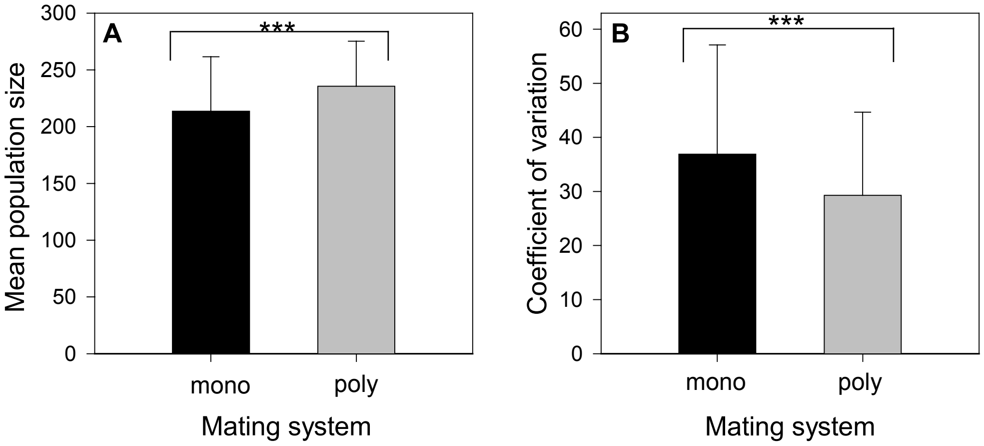

Figure 3 Differences between the population dynamics of monogamous versus “high costs” polyandrous scenario. (A) Mean population size over 100 years (mean and standard deviation). (B) Coefficient of variation of the population sizes (mean and standard deviation) ***p<0.001.

Population size was significantly higher in the polyandrous scenario than in the scenario with strict monogamy, (Fig. 3A, unpaired T-test, T= -4.680, n=300, p<0.001). Moreover, the fluctuation in the number of individuals - given as the coefficient of variation - is lower in scenarios with a flexible mating system (Fig. 3B, T= 3.875, n=300, p<0.001). Consequently, in the polyandrous scenario, the population size is fluctuating with smaller amplitude around a higher number of individuals.

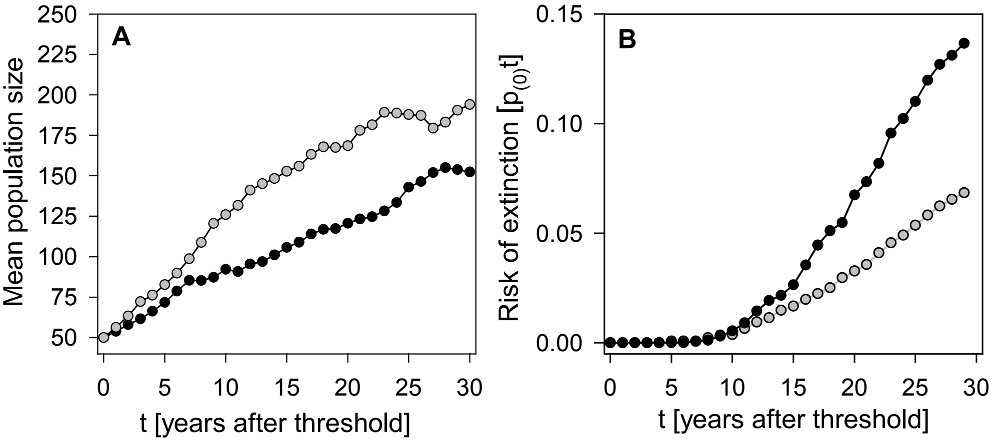

Figure 4 Population dynamics after a threshold of 50 individuals was reached. (A) Recovery of mean population size. Only populations that survived the first 30 years are included. (B) Risk of extinction by time t after the threshold. Carrying capacity is 300; monogamous scenario (black) and "high costs" polyandrous scenario (grey) are compared. For the latter a probability for polyandrous mating, *pPolyandry*, of 0.5 and high costs for the additional male were assumed.

Because small populations suffer a higher risk of extinction due to demographic stochasticity, persistence of a population can be influenced by the probability of reaching a certain threshold. This probability is higher the more the population size fluctuates. We analysed the performance of the population after falling below the threshold of only 50 individuals. Populations had a higher ability to recover after falling under a certain threshold when polyandry is permitted. The increase in population size is stronger (Fig. 4A) and the risk of extinction within the next 30 years after reaching a critical threshold (here 50 individuals) is lower (Fig. 4B) in the polyandrous scenario. These results demonstrate that the population has a higher ability for recovery when females can mate polyandrous with remaining males.

5. Discussion

We developed an individual-based population model to address the question whether occurrence of polyandry in years with male-biased sex ratio has the potential to affect the persistence of the population positively, i.e. to act as a buffer mechanism. Our study system was the Lesser Spotted Woodpecker, a generally monogamous species with facultative occurrence of social polyandry. All model parameters were based on a field study of a population in Germany (Taunus) or determined indirectly by fitting the model to observed patterns (see Chapter III).

We did not aim to present absolute values for viability or mean time to extinction, but to compare the persistence of the population under different mating system scenarios. The sensitivity analysis of the model shows that the parameters with lowest quality (all estimations for secondary males and fluctuation of juvenile survival rate) only have a low sensitivity (Table 1). The most sensitive parameters are all based on empirical investigations on the Lesser Spotted Woodpecker. Thus, we are confident that the parameter quality is sufficient for this purpose.

The comparison of the sensitivity analysis of monogamous and the polyandrous scenarios shows that male mortality and its fluctuation becomes more sensitive in the polyandrous scenario, while the mortality of females becomes less sensitive. This demonstrates that the number of males has a stronger influence on population growth rate in the polyandrous scenarios because a higher proportion of males is able to reproduce in years with male-biased sex ratio. Therefore, factors influencing the sex ratio of the population such as brood sex ratio (*pYoungMale*) and mortality in fledglings, which are mostly male-biased, become more sensitive.

Our main result is that polygamous mating systems have a positive effect on the persistence of populations. This supports results from mathematical models (Engen et al. 2003; Saether et al. 2004). In contrast to these earlier models, we assumed that the mating system is flexible and that polyandry might be linked to costs in terms of lower survival and reproductive success for the secondary male in polyandrous broods. Since in the Lesser Spotted Woodpecker polyandry is an exception from the general behaviour, we assumed that a female only mates with two males in years with male-biased sex ratio and when the female is breeding under good conditions (early breeding start).

Moreover, we varied the probability for a realized polyandrous mating event and found that the positive effect for the population was still strong even if the rate of polyandrous females was very low. For example, assuming a rate of 5% polyandry in females (*pPolyandry* =0.2), mean time to extinction increased by about 50% compared to strict monogamy (Fig. 2). This demonstrates that not only generally polygamous species persists longer compared to monogamous species, but also species that only show certain flexibility in the mating system.

Presuming a rate of polyandry, which is similar to empirical findings in the Lesser Spotted Woodpecker, we showed that polyandry has an important effect on the estimated minimum size of a viable population. In the monogamous scenario, the minimum size had to be twice as high as in the polyandrous no costs scenario to preserve a viable population. This clearly demonstrates that the mating system has to be considered when investigating population viability.

Furthermore, we assumed that in generally monogamous species polyandrous mating would involve costs. Even in the scenario with high costs for polygamous mating, the flexibility in mating system increases population persistence considerably. It reduces the minimum size for a viable population from 410 to 290 individuals. This is surprising, since the costs for polyandry include a lower survival rate in secondary males. Male survival rate proved to be the most sensitive parameter and thus a decrease should have severe effects on population persistence. However, the lower survival rates in the polyandrous high cost scenario only concern some males in the population and only in years with a surplus of males. Thus, mortality in these males affects population persistence to a minor extent and polyandry can still buffer population decline.

What are the mechanisms causing the buffer effect in the polyandrous scenarios? Polyandry occurs in years with male-biased sex ratio. In strictly monogamous systems skewed sex ratios have a negative effect, since the proportion of reproductive individuals and thus the growth rate declines. When polygamy can be performed, the proportion of reproductive individuals increases.

This mechanism buffers demographic noise, i.e. the bias in sex ratio due to the stochasticity in demographic processes.

Moreover, obviously a higher proportion of reproductive individuals increase the population's growth rate, which minimises the strength on environmental noise (Grimm et al. 2003). In theoretical population ecology, environmental noise is – somewhat misleadingly – defined as the *effect* of environmental fluctuation on the population, not as the fluctuations of the environment by itself. A measure of the strength of environmental noise is the ratio of the variance of population growth rate and the intrinsic rate of increase (Wissel et al. 1994; Grimm et al. 2003). Thus, at a higher intrinsic rate of increase, the effect of environmental fluctuations on the population is lower. This mechanism buffers environmental noise.

The buffering effect in polyandrous scenarios is visible in the plots of T_m versus capacity (Fig. 2A). Theoretical models showed that under strong environmental noise persistence time increases only slightly with carrying capacity, while it increases exponentially without environmental noise (Wissel et al. 1994). Suffering strong environmental noise, the population is fluctuating strongly and might occasionally become so small that demographic noise leads to extinction. Thus, the slight increase of persistence time with carrying capacity in the monogamous scenario indicates strong environmental noise. In contrast, in polyandrous scenarios the mean time to extinction increases steeper with capacity, proving a buffer effect reducing environmental noise.

Beside the gross buffer effect due to a higher growth rate, polygamous mating systems might act directly against negative effects caused by environmental conditions. This is the case when sex ratio is directly influenced by environmental conditions. Even though Fisher (1930) predicted a balanced brood sex ratio as long as the costs of producing males and females are equal, recent investigations showed that primary brood sex ratios might be adjusted in birds. An adjustment in the sex ratio of hatchlings was observed in response to several factors (Pike & Petrie 2003; Rosivall et al. 2004; Polo et al. 2004) including environmental conditions (Suorsa et al. 2003). Moreover, mortality rates in male and female nestlings can differ, resulting in a biased secondary brood sex ratio and theses differences might be stronger in poor environments (Oddie 2000; Szekely et al. 2004; Dyrcz et al. 2004). If primary or secondary brood sex ratio is biased towards one sex, it will depend on the performed mating system whether this affects the population persistence negatively. In these cases, flexibility in the performed mating system can buffer the effect of environmentally caused biases in the sex ratio and thus environmental noise.

5.1 Conclusions

Our analysis of the population dynamics of a monogamous species with facultative occurrence of polyandry demonstrated that flexibility in the mating system acts as a mechanism buffering demographic and environmental noise. Therefore, we suggest that PVAs should consider sex ratio by including (i) sex-specific survival rates as well as the brood sex ratio and (ii) a potential flexibility in the mating system, when empirical evidence is available. Doing so, reasonable costs for polygamous mating should be considered as well, since the costs will also influence the magnitude of the positive effects in persistence time.

The fact that even small proportions of polyandrous mating in the population had a strong effect on the population persistence further demonstrates that exceptions from the general behavioural patterns should not be ignored. Certain plasticity in the behaviour does not only occur in mating systems but should also be considered in space use (Wichmann et al. 2005) or age of maturity (Ferrer et al. 2004). Unfortunately, observations of behavioural exceptions are often not published, because they do not fit the general picture or are not “significant”. However, flexibility enables the individuals to adapt their behaviour to new or changing conditions and thus is the basis for evolution. Consequently, when investigating the performance of a population under different environmental scenarios, researchers should consider certain flexibility in behavioural traits.

6. References

Akcakaya, H. R. & Burgman, M. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 705-707.

Albrecht, D. J., Johnson, L. S. 2002. Manipulation of offspring sex ratio by second-mated female house wrens. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 461-465

Bart, J. 1995. Acceptance Criteria for Using Individual-Based Models to Make Management Decisions. *Ecological Applications* 5: 411-420.

Bensch, S. & Hasselquist, D. 1994. Higher rate of nest loss among primary than secondary females - Infanticide in the Great Reed Warbler. *Behavioral Ecology and Sociobiology* 35: 309-317.

Brook, B. W., Burgman, M. A., Akcakaya, H. R., O'Grady, J. J. & Frankham, R. 2002. Critiques of PVA ask the wrong questions: Throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16: 262-263.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton.

Cramp, S. 1985. Handbook of the birds of Europe and the Middle East and North Africa. Oxford University Press, Oxford.

Davies, N. B. 1991. Mating systems. In: Krebs, J. R. & Davies, N. B. (eds.) Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. & Stevens, E. E. 1995. Spatially explicit population-models - current forms and future uses. *Ecological Applications* 5: 3-11.

Dyrcz, A., Sauer-Gurth, H., Tkadlec, E. & Wink, M. 2004. Offspring sex ratio variation in relation to brood size and mortality in a promiscuous species: the Aquatic Warbler *Acrocephalus paludicola*. *Ibis* 146: 269-280.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Engen, S., Lande, R. & Saether, B. E. 2003. Demographic stochasticity and Allee effects in populations with two sexes. *Ecology* 84: 2378-2386.

Ferrer, M., Otalora, F. & Garcia-Ruiz, J. M. 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. *Ecological Applications* 14: 616-624.

Fischer R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.

Garamszegi, L. Z., Torok, J., Michl, G. & Moller, A. P. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia* 138: 48-56.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1994. Columbiformes - Piciformes. Aula-Verlag, Wiesbaden.

Greene, C. M. 2003. Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* 64: 1-10.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115: 129-148.

Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T. & Arnold, W. 2003. Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. *Oikos* 102: 124-136.

Grimm, V., Groeneveld, J., Kramer-Schadt, S., Schwager, M., Revilla, E., Tews, J., Wichmann, M. C. & Jeltsch, F. 2005. On the importance of buffer mechanisms for population viability analysis. *Conservation Biology* (in press).

Höntsch, K. 1996. Radiotelemetrische Untersuchungen zur Raum-Zeit-Nutzung des Kleinspechts *Picoides minor*. Diplomarbeit, Technische Hochschule Darmstadt, Germany.

Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Houston, A. I. & McNamara, J. M. 1999. Models of adaptive behavior: an approach based on state. Cambridge University Press, Cambridge.

Kempenaers, B. 1995. Polygyny in the Blue Tit - Intra-Sexual and Inter-Sexual Conflicts. *Animal Behaviour* 49: 1047-1064.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L. & Ehrlich, P. R. 2002. The route to extinction: population dynamics of a threatened butterfly. *Oecologia* 132: 538-548.

Oddie, K. R. 2000. Size matters: competition between male and female Great Tit offspring. *Journal of Animal Ecology* 69: 903-912.

Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. PhD Thesis, Lund University, Sweden.

Pike, T. W. & Petrie, M. 2003. Potential mechanisms of avian sex manipulation. *Biological Reviews* 78: 553-574.

Polo, V., Veiga, J. P., Cordero, P. J., Vinuela, J. & Monaghan, P. 2004. Female starlings adjust primary sex ratio in response to aromatic plants in the nest. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271: 1929-1933.

Promislow, D., Montgomerie, R. & Martin, T. E. 1994. Sexual Selection and Survival in North-American Waterfowl. *Evolution* 48: 2045-2050.

Promislow, D. E. L., Montgomerie, R. & Martin, T. E. 1992. Mortality Costs of Sexual Dimorphism in Birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* 250: 143-150.

Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling* 139: 47-62.

Rosivall, B., Torok, J., Hasselquist, D. & Bensch, S. 2004. Brood sex ratio adjustment in collared flycatchers (*Ficedula albicollis*): results differ between populations. *Behavioral Ecology and Sociobiology* 56: 346-351.

Saether, B. E., Engen, S., Lande, R., Moller, A. P., Bensch, S., Hasselquist, D., Beier, J. & Leisler, B. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *Journal of Animal Ecology* 73: 925-934.

Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. In: Soulé, M. E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge.

Sibly, R. M. & Smith, R. H. 1985 Behavioural ecology: ecological consequences of adaptive behaviour. 25th Symposium of the British Ecological Society pp 620. Blackwell Scientific Publications, Oxford.

Slagsvold, T. & Lifjeld, J. T. 1994. Polygyny in birds - the role of competition between females for male parental care. *American Naturalist* 143: 59-94.

Suorsa, P., Helle, H., Huhta, E., Jantti, A., Nikula, A. & Hakkarainen, H. 2003. Forest fragmentation is associated with primary brood sex ratio in the treecreeper (*Certhia familiaris*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2215-2222.

Szekely, T., Cuthill, I. C., Yezerinac, S., Griffiths, R. & Kis, J. 2004. Brood sex ratio in the Kentish plover. *Behavioral Ecology* 15: 58-62.

Uchmanski, J. 1999. What promotes persistence of a single population: an individual- based model. *Ecological Modelling* 115: 227-242.

Uchmanski, J. 2000. Individual variability and population regulation: an individual-based model. *Oikos* 90: 539-548.

Walsh, P. D., Akçakaya, H. R., M., B. & Harcourt, A. H. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 704-710.

Walters, J. R., Crowder, L. B. & Priddy, J. A. 2002. Population viability analysis for red-cockaded Woodpeckers using an individual-based model. *Ecological Applications* 12: 249-260.

Wichmann, M. C., Groenveld, J., Jeltsch, F. & Grimm, V. 2005. Mitigation of climate change impacts on raptors by behavioural adaptation: ecological buffering mechanisms. *Global and Planetary Change* 45 (in press).

Wichmann, M. C., Jeltsch, F., Dean, W. R. J., Moloney, K. A. & Wissel, C. 2003. Implication of climate change for the persistence of raptors in arid savanna. *Oikos* 102: 186-202.

Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs* 68: 539-570.

Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* 31: 447-456.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001. Age and reproduction in Lesser Spotted Woodpeckers (*Dendrocopos minor*). *Auk* 118: 624-635.

Wissel, C., Stephan, T. & Zaschke, S.-H. 1994. Modelling extinction and survival of small populations. In: Remmert, H. (ed.) Minimum animal populations. Springer-Verlag, Berlin.

General summary and outlook

In this thesis I combined empirical investigations on a Lesser Spotted Woodpecker (*Picoides minor*) population and a modelling approach simulating its population dynamics. In the field studies I measured several variables of reproductive success, population structure and mortality rates. My results showed a significant decrease of the reproductive success with later timing of breeding, caused by deterioration in food supply, mainly in caterpillars (Chapter I). The understanding of these correlations is essential for potential future investigations in the context of effects of climate change on bird species: An increase in spring temperature has been observed in the last two decades[1]. This has led to advancing tree phenology and subsequently to earlier and shorter peaks in insect abundance[2,3]. The causal relationship between timing of breeding, nestling diet and reproductive success is therefore essential to understand the impact of climate change on a certain bird species.

Moreover, my results showed mate fidelity to be of benefit, since pairs composed of individuals that bred together the previous year started earlier with egg laying and obtained a higher reproductive success (Chapter I). The advantage of mate fidelity is central for the organisation of parental care in this species: females considerably decreased feeding rate with number of nestlings and this culminated in the complete desertion of small broods by females. The males were able to compensate for the female's absence, and thus presumably can benefit from mating with the same partner, which increases next year's reproductive success. This organisation of parental care provided the prerequisite for polyandry that was observed in the field to a minor extent (Chapter II).

Mating systems are likely to influence the persistence of populations. To test the effect of flexibility in the mating system, I developed a simulation model based on the empirically gained understanding of the important factors and demographic parameters. However, one fundamental demographic parameter needed for modelling - pre-breeding survival rates - could not be obtained empirically. To close this gap, I estimated pre-breeding survival by a pattern-oriented modelling approach comparing simulation results with empirical patterns of population structure and reproductive success on population level (Chapter III). This alternative approach can help to cope with gaps in demographic data of rare animals. Especially for bird species, data bases of population structure are often available from censuses that are not used thourougly. The alternative approach introduced in this study can point out a way to use these data to improve population viability analyses.

---

[1] Huang, S. P., Pollack, H. N. & Shen, P. Y. 2000. Temperature trends over the past five centuries reconstructed from borehole temperatures. *Nature* 403: 756-758.

[2] Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society of London Series B-Biological Sciences* 265: 1867-1870.

[3] Harrington, R., Woiwod, I. & Sparks, T. 1999. Climate change and trophic interactions. *Trends in Ecology & Evolution* 14: 146-150.

Using the simulation model, I found an important impact of mating systems on population dynamics. Polyandry increased the persistence of the Lesser Spotted Woodpecker population even when presuming only the empirically found low polyandry rate and costs of polyandry in terms of higher mortality and lower reproductive success for the secondary male. Consequently, my results of the Lesser Spotted Woodpecker study suggest that flexibility in mating systems acts as a buffer mechanism against environmental and demographic noise. These results are applicable to other species and demonstrate the significance of flexibility in behavioural traits for the population performance. Especially, when investigating populations in different environments, researchers should consider certain flexibility in behavioural traits. This flexibility enables the organisms to adapt to changing environments and is subsequently basis for evolution. Empirical investigations should be challenged to report behavioural exceptions and modellers should consider flexibility, when empirical evidences are available.

This thesis demonstrates how empirical and modelling investigations can promote each other. While the empirical investigations provided the crucial basis for ecological modelling, the simulation model evaluated the present knowledge and uncovered gaps therein. Future field studies could be planned to close these gaps. Moreover, pattern-oriented modelling offered a possibility to estimate a missing parameter that was not measurable for a highly mobile species in the field. In this case an direct access to empirical raw data containing patterns for tracking a missing parameter is of great value. In this thesis the modeller investigated also the Lesser Spotted Woodpecker population in the field and was therefore “expert” herself, which helped to make assumptions when data were lacking, for example for the costs of polyandry (Chapter IV). Only by taking into account occasional field observations of behavioural flexibility in mating systems (which are often not published) allowed for the final investigation of the effects of certain behaviour on the persistence of the Lesser Spotted Woodpecker population.

However, it is important not to misinterpret results based on computer simulation models. Ecological models are neither able nor meant to reflect reality in all details. Instead of insisting on predictions of future population development, I used ecological modelling as a tool to gain a better understanding of processes in population dynamics and to test assumptions gathered in empirical studies.

This thesis improved the understanding of factors affecting reproductive success and population dynamics. In order to conduct a population viability analysis for the Lesser Spotted Woodpecker, it is now necessary to extend the model by the spatial dimension. The next step would be the explicit integration of space and habitat use into the model, since change in habitat composition is the major cause for the decline in many species, including woodpeckers[4]. The basis for this extension is provided by an extensive study of habitat use and home range sizes in the same Lesser Spotted

---

[4] Mikusinski, G. & Angelstam, P. 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118: 277-283.

Woodpecker study population[5]. With a spatially explicit population model, it will be possible to investigate habitat fragmentation and changes in habitat composition. Beyond the value of this extension for the species conservation, a spatial-explicit model of the Lesser Spotted Woodpecker population dynamic might be interesting searching for a further potential buffer mechanism: Lesser Spotted Woodpeckers use exceptional large home ranges up to 830 ha in size[5]. Consequently, space use in this species is likely to buffer habitat fragmentation and might act as a buffer mechanism against population decline as well. Furthermore, a spatially-explicit model version can take into account the probability of single individuals to find a partner within its home range. This allows for a more detailed investigation of the effects of the mating system on the persistence of a population at low population densities.

Conclusion

In this thesis, the knowledge of the autecology of the Lesser Spotted Woodpecker has been considerably improved. The gained understanding for processes influencing reproductive success and population dynamics are the crucial basis for sustainable management concepts in Central Europe.

Moreover, the possibility to use weak patterns at the population level to estimate missing demographic parameters was demonstrated and flexibility in mating system was discovered to buffer population decline. These results are important beyond the Lesser Spotted Woodpecker, since they led to new insights in mechanisms buffering demographic as well as environmental noise. One main lection of my thesis is that ecological models need to integrate behavioural flexibility in order to increase the prediction quality. This finding is especially important when investigating populations in changing environments.

---

[5] Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Zusammenfassung

Der Schutz von Arten ist eine der Hauptaufgaben des Naturschutzes. Für die Erstellung von Schutzkonzepten sind Informationen zur Autökologie der Zielart notwendige Voraussetzung. Der Kleinspecht (*Picoides minor*) ist in vielen Teilen seines Verbreitungsgebietes bestandsbedroht, das Wissen zur Biologie und Verhalten der Art ist jedoch lückenhaft. Ziel meiner Arbeit war es daher, demographische Parameter der Populationsdynamik des Kleinspechts zu erfassen, die als Grundlage für Populationsgefährdungsanalysen benötigt werden. Da Untersuchungen in Schweden eine gewisse Flexibilität im Paarungssystem des Kleinspechts zeigten, sollte darüber hinaus das Paarungssystem und sein Einfluss auf die Persistenz der Population untersucht werden.

Die Arbeit umfasste eine Reihe von methodischen Ansätzen, von empirischen Untersuchungen an einer Kleinspechtpopulation im hessischen Vordertaunus über die Aufbereitung von empirischen Daten bis hin zur Entwicklung und Auswertung eines stochastischen individuenbasierten Modells zur Simulation der Populationsdynamik.

Die Ergebnisse der empirischen Untersuchung zeigten eine Abnahme des Reproduktionserfolgs mit fortschreitendem Legebeginn. Die Zusammensetzung der Nestlingsnahrung ließ vermuten, dass dies durch eine Verschlechterung der Nahrungsversorgung begründet war. Paartreue war bei der Reproduktion von Vorteil, da Individuen, die schon im vorherigen Jahr zusammen gebrütet hatten, einen früheren Legebeginn und damit einen höheren Fortpflanzungserfolg aufwiesen als neu formierte Paare. Beide Geschlechter investierten in die Brutpflege, jedoch war die Aufteilung nur während der Bebrütung der Eier und in der ersten Hälfte der Nestlingsperiode gleichmäßig. In der späten Nestlingsperiode konnten geschlechtsspezifische Strategien im elterlichen Investment identifiziert werden: die Weibchen verringerten die Versorgungsrate in Abhängigkeit des Wertes der Brut - gemessen in der Zahl der Nestlinge - und gaben die Versorgung kleiner Bruten ganz auf. Die Männchen dagegen kompensierten dieses Verhalten, so dass auch von den Weibchen verlassene Bruten erfolgreich waren. Interessanterweise konnte mehrmals die Verpaarung von einem Weibchen mit zwei Männchen beobachtet werden. Das Auftreten dieses polyandrischen Paarungssystems wird in der Arbeit als Resultat der Aufteilung der Brutpflege diskutiert.

Die bestätigte Flexibilität im Paarungssystem könnte Einfluss auf die Persistenz der Population haben. Die Persistenz von Populationen kann jedoch nicht empirisch gemessen werden. Daher entwickelte ich ein individuen-basiertes stochastisches Modell zur Simulation der Populationsdynamik des Kleinspechts, dass auf den empirischen Daten basiert. Allerdings fehlten Überlebensraten der ausgeflogenen Jungvögel, die im Feld nicht ermittelt werden kann. Daher testete ich hier eine Methode, die durch den Vergleich von Simulationsergebnissen mit eigenen empirischen Daten zur Populationsstruktur und zum Reproduktionserfolg auf der Ebene der Gesamtpopulation die Überlebensrate der Jungvögel abschätzt. Die Überlebensraten wurde zusätzlich für eine Population des Kleinspechtes ermittelt, deren Datengrundlage aus Freilandstudien in Schweden stammten. Durch den Vergleich der Raten für die beiden

Populationen konnte die Aussagefähigkeit des Modells und die Güte der Abschätzungen untersucht werden.

Im letzten Teil meiner Arbeit nutzte ich das Modell schließlich, um die Auswirkungen des Paarungssystems auf die Überlebensfähigkeit der Population zu untersuchen. Im Modell konnte ein Weibchen polyandrisch sein, wenn es gute Brutbedingungen hatte und das Geschlechterverhältnis zum Männchen hin verschoben war. Zusätzlich variierte ich die Wahrscheinlichkeit, dass unter diesen Umständen Polyandrie auftritt. Im Model wurden 3 Szenarien getestet: (i) strenge Monogamie, (ii) gelegentliche Polyandrie und (iii) gelegentliche Polyandrie unter der Annahme von Kosten für das sekundäre Männchen in Form von höherer Mortalität und geringerem Reproduktionserfolg. Es zeigte sich, dass selbst sehr geringe Polyandrieraten und die Annahme von Kosten noch einen deutlichen positiven Einfluss auf die Persistenz der Population ausüben. Die Flexibilität im Paarungssystem dient damit als Puffermechanismus gegen demographisches Rauschen und Umweltrauschen.

Diese Arbeit trät dazu bei, die Autökologie des Kleinspechts besser zu verstehen und ist damit wichtige Grundlage für Schutzkonzepte in Mitteleuropa. Über die artspezifische Bedeutung hinaus, leistet die Arbeit einen Beitrag zur Untersuchung von Methoden zur Abschätzung fehlender demographischer Parameter sowie zur Identifizierung von Puffermechanismen. Eine wichtige Schlussfolgerung meiner Arbeit ist es, dass die Flexibilität artspezifischen Verhaltens in zukünftigen Populationsgefährdungsanalysen integriert werden sollte, um die Qualität von Prognosen zur Persistenz von Populationen zu verbessern.

References

Akcakaya, H. R. & Burgman, M. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 705-707.

Arnold, J. M., Hatch, J. J. & Nisbet, I. C. T. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *Journal of Avian Biology* 35: 33-45.

Albrecht, D. J., Johnson, L. S. 2002. Manipulation of offspring sex ratio by second-mated female house wrens. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 461-465

Ashmole, N. P. 1963. The regulation of tropical oceanic birds. *Ibis* 103: 458-473.

Bart, J. 1995. Acceptance Criteria for Using Individual-Based Models to Make Management Decisions. *Ecological Applications* 5: 411-420.

Beissinger, S. R. & Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821-841.

Bensch, S. & Hasselquist, D. 1994. Higher rate of nest loss among primary than secondary females - infanticide in the Great Reed Warbler. *Behavioral Ecology and Sociobiology* 35: 309-317.

Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics.* 23: 481-506.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. In: Power, D. M. (ed.) Current Ornithology 6. Plenum Press, New York.

Breitwisch, R., Merritt, P. G. & Whitesides, G. H. 1986. Parental investment by the Northern Mockingbird - male and female roles in feeding nestlings. *Auk* 103: 152-159.

Brinkhof, M. W. G. 1997. Seasonal variation in food supply and breeding success in European Coots *Fulica atra*. *Ardea* 85: 51-65.

Brook, B. W., Burgman, M. A., Akcakaya, H. R., O'Grady, J. J. & Frankham, R. 2002. Critiques of PVA ask the wrong questions: Throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16: 262-263.

Brook, B. W., O'Grady, J. J., Chapman, A. P., Burgman, M. A., Akcakaya, H. R. & Frankham, R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404: 385-387.

Chase, I. D. 1980. Cooperative and Noncooperative Behavior in Animals. *American Naturalist* 115: 827-857.

Chastel, O. & Kersten, M. 2002. Brood size and body condition in the House Sparrow *Passer domesticus*: the influence of brooding behaviour. *Ibis* 144: 284-292.

Clark, L. 1985. Consequences of homeothermic capacity of nestlings on parental care in the European Starling. *Oecologia* 65: 387-393.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.

Cramp, S. 1985. *Handbook of the birds of Europe and the Middle East and North Africa*. Oxford University Press, Oxford.

Curio, E. 1983. Why do young birds reproduce less well? *Ibis* 125: 400-404.

Davies, N. B. 1991. Mating systems. In: Krebs, J. R. & Davies, N. B. (eds.) *Behavioural ecology. An evolutionary approach.* Blackwell Scientific Publications, Oxford.

Dhondt, A. A. 1989. Blue tit. In: Newton, I. (ed.) *Lifetime reproduction in birds*, pp. 15-34. Academic Press Inc., London.

Dias, P. C. & Blondel, J. 1996. Breeding time, food supply and fitness components of Blue Tits *Parus caeruleus* in Mediterranean habitats. *Ibis* 138: 644-649.

Dunn, P. O., Robertson, R. J., Michaud-Freeman, D. & Boag, P. T. 1994. Extra-pair paternity in Tree Swallows - Why do females mate with more than one male. *Behavioral Ecology and Sociobiology* 35: 273-281.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. & Stevens, E. E. 1995. Spatially explicit population-models - current forms and future uses. *Ecological Applications* 5: 3-11.

Dyrcz, A., Sauer-Gurth, H., Tkadlec, E. & Wink, M. 2004. Offspring sex ratio variation in relation to brood size and mortality in a promiscuous species: the Aquatic Warbler *Acrocephalus paludicola*. *Ibis* 146: 269-280.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Engen, S., Lande, R. & Saether, B. E. 2003. Demographic stochasticity and Allee effects in populations' with two sexes. *Ecology* 84: 2378-2386.

Ens, B. J., Choudhury, S. & Black, J. M. 1996. Mate fidelity and divorce in monogamous birds. In: Black, J. M. (ed.) *Partnership in birds*, pp. 344-401. Oxford University Press, Oxford.

Ens, B. J., Kersten, M., Brenninkmeijer, A. & Hulscher, J. B. 1992. Territory Quality, Parental Effort and Reproductive Success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61: 703-715.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.

Ferrer, M., Otalora, F. & Garcia-Ruiz, J. M. 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. *Ecological Applications* 14: 616-624.

Fischer R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford.

Forslund, P. & Larsson, K. 1991. The effect of mate change and new partner's age on reproductive success in the barnacle goose, *Branta leucopsis*. *Behav. Ecol.* 2: 116-122.

Garamszegi, L. Z., Torok, J., Michl, G. & Moller, A. P. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia* 138: 48-56.

Gaston, A. J. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* 139: 673-678.

Gilbert, M., Gregoire, J. C., Freise, J. F. & Heitland, W. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *Journal of Animal Ecology* 73: 459-468.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1994. *Columbiformes - Piciformes*. Aula-Verlag, Wiesbaden.

Green, D. J. & Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* 70: 505-514.

Greene, C. M. 2003. Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* 64: 1-10.

Griebeler, E. M. & Böhning-Gaese, K. 2004. Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis. *Evolutionary Ecology Research* 6: 679-694.

Grieco, F. 2002. How different provisioning strategies result in equal rates of food delivery: an experimental study of blue tits *Parus caeruleus*. *Journal of Avian Biology* 33: 331-341.

Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11: 2195-2212.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115: 129-148.

Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T. & Arnold, W. 2003. Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. *Oikos* 102: 124-136.

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J. & Wissel, C. 1996. Pattern-oriented modelling in population ecology. *Science of the Total Environment* 183: 151-166.

Grimm, V., Groeneveld, J., Kramer-Schadt, S., Schwager, M., Revilla, E., Tews, J., Wichmann, M. C. & Jeltsch, F. 2005. On the importance of buffer mechanisms for population viability analysis. *Conservation Biology* (in press).

Haig, S. M., Belthoff, J. R. & Allen, D. H. 1993. Population viability analysis for a small population of Red-Cockaded Woodpeckers and an evaluation of enhancement strategies. *Conservation Biology* 7: 289-301.

Haig, S. M., Walters, J. R. & Plissner, J. H. 1994. Genetic-evidence for monogamy in the cooperatively breeding Red-Cockaded Woodpecker. *Behavioral Ecology and Sociobiology* 34: 295-303.

Harrington, R., Woiwod, I. & Sparks, T. 1999. Climate change and trophic interactions. *Trends in Ecology & Evolution* 14: 146-150.

Harris, M. P., Buckland, S. T., Russell, S. M. & Wanless, S. 1994. Post Fledging Survival to Breeding Age of Shags *Phalacrocorax aristotelis* in Relation to Year, Date of Fledging and Brood Size. *Journal of Avian Biology* 25: 268-274.

Havelka, P. & Ruge, K. 1993. Trend der Populationsentwicklung bei Spechten (Picidae) in der Bundesrepublik Deutschland. *Beihefte zu den Veröffentlichungen für Naturschutz u. Landschaftspflege Baden-Württembergs* 67: 33-38.

Hogstad, O. & Stenberg, I. 1997. Breeding success, nestling diet and parental care in the White- backed Woodpecker *Dendrocopos leucotos*. *Journal für Ornithologie* 138: 25-38.

Höntsch, K. 1996. Radiotelemetrische Untersuchungen zur Raum-Zeit-Nutzung des Kleinspechts *Picoides minor*. Diplomarbeit, Technische Hochschule Darmstadt, Germany.

Höntsch, K. 2005. Der Kleinspecht (*Picoides minor*) - Autökologie einer bestandsbedrohten Vogelart im hessischen Vordertaunus. PhD Thesis, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Horak, P. 2003. When to pay the cost of reproduction? A brood size manipulation experiment in Great Tits (*Parus major*). *Behavioral Ecology and Sociobiology* 54: 105-112.

Houston, A. I. & McNamara, J. M. 1999. *Models of adaptive behavior: an approach based on state*. Cambridge University Press, Cambridge.

Huang, S. P., Pollack, H. N. & Shen, P. Y. 2000. Temperature trends ever the past five centuries reconstructed from borehole temperatures. *Nature* 403: 756-758.

Ingold, D. J. 1994. Influence of Nest-Site Competition between European Starlings and Woodpeckers. *Wilson Bulletin* 106: 227-241.

Jeltsch, F., Moloney, K. & Milton, S. J. 1999. Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. *Oikos* 85: 451-466.

Jeltsch, F., Muller, M. S., Grimm, V., Wissel, C. & Brandl, R. 1997. Pattern formation triggered by rare events: Lessons from the spread of rabies. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264: 495-503.

Johnston, J. P., Peach, W. J., Gregory, R. D. & White, S. A. 1997. Survival rates of tropical and temperate passerines: A Trinidadian perspective. *American Naturalist* 150: 771-789.

Karr, J. R., Nichols, J. D., Klimkiewicz, M. K. & Brawn, J. D. 1990. Survival Rates of Birds of Tropical and Temperate Forests - Will the Dogma Survive. *American Naturalist* 136: 277-291.

Kempenaers, B. 1995. Polygyny in the Blue Tit - Intra-Sexual and Inter-Sexual Conflicts. *Animal Behaviour* 49: 1047-1064.

Klomp, H. 1970. Determination of Clutch-Size in Birds - A Review. *Ardea* 58: 1-&.

Koenig, W. D. 1986. Geographical Ecology of Clutch Size Variation in North-American Woodpeckers. *Condor* 88: 499-504.

Kotaka, N. 1998. Classical polyandry in the Great Spotted Woodpecker *Dendrocopos major*. *Ibis* 140: 335-336.

Kristin, A. 1992. Trophische Beziehungen zwischen Singvögeln und Wirbellosen im Eichen-Buchenwald zur Brutzeit. *Der Ornithologische Beobachter* 89: 157-169.

Lack, D. 1947. The Significance of Clutch-Size. *Ibis* 89: 302-352.

Lack, D. 1968. *Ecological adaptations for breeding in birds.* Methuen & Co , London.

Laiolo, P., Bignal, E. M. & Patterson, I. J. 1998. The dynamics of parental care in Choughs (*Pyrrhocorax pyrrhocorax). Journal für Ornithologie* 139: 297-305.

Lazarus, J. 1990. *The logic of mate desertion*. *Animal Behaviour* 39: 672-684.

Ligon, J. D. 1993. Role of Phylogenetic History. In: D.M.Power Current Ornithology 10. Plenum Press, New York.

Lubjuhn, T., Strohbach, S., Brun, J., Gerken, T. & Epplen, J. T. 1999. Extra-pair paternity in Great Tits (*Parus major*) - A long term study. *Behaviour* 136: 1157-1172.

Lubjuhn, T., Winkel, W., Epplen, J. T. & Brun, J. 2000. Reproductive success of monogamous and polygynous Pied Flycatchers (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology* 48: 12-17.

Martin, K. & Eadie, J. M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115: 243-257.

May, R. M. 1973. *Stability and complexity in model ecosystems.* Princeton University Press, Princeton.

McGraw, K. J. & Hill, G. E. 2004a. Mate attentiveness, seasonal timing of breeding and long-term pair bonding in the House Finch (*Carpodacus mexicanus*). *Behaviour* 141: 1-13.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L. & Ehrlich, P. R. 2002. The route to extinction: population dynamics of a threatened butterfly. *Oecologia* 132: 538-548.

Michalek, K. G. & Winkler, H. 2001. Parental care and parentage in monogamous Great Spotted Woodpeckers (*Picoides major*) and Middle Spotted Woodpeckers (*Picoides medius*). *Behaviour* 138: 1259-1285.

Mikusinski, G. & Angelstam, P. 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118: 277-283.

Monrós, J. S., Belda, E. J. & Barba, E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99: 481-488.

Murphy, M. T. 1986. Temporal Components of Reproductive Variability in Eastern Kingbirds (*Tyrannus tyrannus*). *Ecology* 67: 1483-1492.

Murray, G. B. Jr. 1985. Evolution of clutch size in tropical species of birds. *Ornithological Monographs* 505-519.

Naef-Daenzer, B. & Keller, L. F. 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.

Naef-Daenzer, L., Naef-Daenzer, B. & Nager, R. G. 2000. Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* 31: 206-214.

Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press Inc., London.

Nilsson, J. A. & Svensson, M. 1993. Fledging in altricial birds - Parental manipulation or sibling competition. *Animal Behaviour* 46: 379-386.

Nilsson, S. G., Olsson, O., Svensson, S. & Wiktander, U. 1992. Population trends and fluctuation in Swedish woodpeckers. *Ornis Svecica* 2: 13-21.

Nur, N. 1984. Feeding frequencies of nestling Blue Tits (*Parus caeruleus*) - Costs, benefits and a model of optimal feeding frequency. *Oecologia* 65: 125-137.

Oddie, K. R. 2000. Size matters: competition between male and female Great Tit offspring. *Journal of Animal Ecology* 69: 903-912.

Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. PhD Thesis, Lund University, Sweden.

Olsson, O., Wiktander, U., Holmgren, N. M. A. & Nilsson, S. G. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *Oikos* 87: 264-276.

Olsson, O., Wiktander, U., Malmqvist, A. & Nilsson, S. G. 2001. Variability of patch type preferences in relation to resource availability and breeding success in a bird. *Oecologia* 127: 435-443.

Olsson, O., Wiktander, U. & Nilsson, S. G. 2000. Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267: 1457-1461.

Pasinelli, G. 1999. Relations between habitat structure, space use and breeding success of the Middle Spotted Woodpecker *Dendrocopos medius*. PhD Thesis, Universität Zürich, Switzerland.

Perrins, C. M. 1991. Tits and their caterpillar food supply. *Ibis* 133: 49-54.

Perrins, C. M. & McCleery, R. H. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major*. *Ibis* 127: 306-315.

Perrins, C. M. & McCleery, R. H. 1989. Laying Dates and Clutch Size in the Great Tit. *Wilson Bulletin* 101: 236-253.

Pettorelli, N., Gaillard, J. M., Duncan, P., Maillard, D., Van Laere, G. & Delorme, D. 2003. Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology* 84: 3307-3316.

Pike, T. W. & Petrie, M. 2003. Potential mechanisms of avian sex manipulation. *Biological Reviews* 78: 553-574.

Polo, V., Veiga, J. P., Cordero, P. J., Vinuela, J. & Monaghan, P. 2004. Female starlings adjust primary sex ratio in response to aromatic plants in the nest. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271: 1929-1933.

Price, T., Kirkpatrick, M. & Arnold, S. J. 1988. Directional Selection and the Evolution of Breeding Date in Birds. *Science* 240: 798-799.

Promislow, D. E. L., Montgomerie, R. & Martin, T. E. 1994. Sexual Selection and Survival in North-American Waterfowl. *Evolution* 48: 2045-2050.

Promislow, D. E. L., Montgomerie, R. & Martin, T. E. 1992. Mortality Costs of Sexual Dimorphism in Birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* 250: 143-150.

Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology* 70: 1088-1097.

Pynnönnen, A. 1943. Beiträge zur Kenntnis der Biologie finnischer Spechte, Teil II - Die Nahrung. *Annales Zoologici Societatis Zoologicae-Botanicae-Fennicae Vanamo* 9: 1-59.

Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecol. Model.* 139: 47-62.

Reed, J. M., Mills, L. S., Dunning, J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M. C. & Miller, P. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16: 7-19.

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *Journal of Animal Ecology* 72: 765-776.

Ricklefs, R. E. 1984. The optimization of growth-rate in altricial birds. *Ecology* 65: 1602-1616.

Ricklefs, R. E. 1997. Comparative demography of new world populations of thrushes (*Turdus spp.*). *Ecological Monographs* 67: 23-43.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 102: 9-22.

Robel, R. J., Press, B. M., Henning, B. L., Johnson, K. W., Blocker, H. D. & Kemp, K. E. 1995. Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology* 66: 44-53.

Rosivall, B., Torok, J., Hasselquist, D. & Bensch, S. 2004. Brood sex ratio adjustment in collared flycatchers (*Ficedula albicollis*): results differ between populations. *Behavioral Ecology and Sociobiology* 56: 346-351.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. *Ibis* 108: 313-347.

Saether, B. E. 1990. Age-specific variation in reproductive performance of birds. In: Power, D. M. Current Ornithology 7. Plenum Press, New York.

Saether, B. E., Engen, S., Lande, R., Moller, A. P., Bensch, S., Hasselquist, D., Beier, J. & Leisler, B. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *Journal of Animal Ecology* 73: 925-934.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the Great Tit (*Parus major*). *Journal of Animal Ecology* 69, 74-84.

Sanz, J. J. & Tinbergen, J. M. 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the Great Tit *Parus major*. *Behavioral Ecology* 10: 598-606.

Searcy, W. A. & Yasukawa, K. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in Red-winged Blackbirds. *Journal of Avian Biology* 27: 225-230.

Seki, S. I. & Takano, H. 1998. Caterpillar abundance in the territory affects the breeding performance of great tit *Parus major minor*. *Oecologia* 114: 514-521.

Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. In: Soulé, M. E. (ed.) *Viable populations for conservation.*, pp. 69-86. Cambridge University Press, Cambridge.

Sibly, R. M. & Smith, R. H. 1985 Behavioural ecology: ecological consequences of adaptive behaviour. 25th Symposium of the British Ecological Society pp 620. Blackwell Scientific Publications, Oxford.

Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79: 1789-1796.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* 36, 575-594.

Slagsvold, T. & Lifjeld, J. T. 1990. Influence of male and female quality on clutch size in Tits (*Parus spp*). *Ecology* 71: 1258-1266.

Slagsvold, T. & Lifjeld, J. T. 1994. Polygyny in birds - the role of competition between females for male parental care. *American Naturalist* 143: 59-94.

Soler, M., Palomino, J. J., Martinez, J. G. & Soler, J. J. 1994. Activity, Survival, Independence and Migration of Fledgling Great-Spotted-Cuckoos. *Condor* 96: 802-805.

Soulé, M. E. 1986. *Conservation biology: the science of scarcity and diversity.* Sinauer, Sunderland.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61: 261-270.

Sternberg, H. 1989. Pied Flycatcher. In: Newton, I. (ed.) *Lifetime reproduction in birds*, pp. 55-74. Academic Press Inc., London.

Suorsa, P., Helle, H., Huhta, E., Jantti, A., Nikula, A. & Hakkarainen, H. 2003. Forest fragmentation is associated with primary brood sex ratio in the treecreeper (*Certhia familiaris*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2215-2222.

Szekely, T., Cuthill, I. C., Yezerinac, S., Griffiths, R. & Kis, J. 2004. Brood sex ratio in the Kentish plover. *Behav. Ecol.* 15: 58-62.

Tews, J., Schurr, F. & Jeltsch, F. 2004. Seed dispersal by cattle may cause shrub encroachment of *Grewia flava* on southern Kalahari rangelands. *Applied Vegetation Science* 7: 89-102.

Tiainen, J. 1985. Monitoring bird populations in Finland. *Ornis Fennica* 62: 80-89.

Török, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos spp*. during breeding season. *Holarctic Ecology* 13: 257-264.

Trivers, R. L. 1972. Parental investment and sexual selection. In: Campbell, B. (ed.) *Sexual Selection and the Descent of Man*, pp. 136-179. Aldine, Chicago.

Uchmanski, J. 1999. What promotes persistence of a single population: an individual- based model. *Ecological Modelling* 115: 227-242.

Uchmanski, J. 2000. Individual variability and population regulation: an individual-based model. *Oikos* 90: 539-548.

Van Balen, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-91.

Van der Jeugd, H. P. & Larsson, K. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology* 67: 953-966.

Verboven, N. & Visser, M. E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81: 511-524.

Verhulst, S., Vanbalen, J. H. & Tinbergen, J. M. 1995. Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. *Ecology* 76: 2392-2403.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 265: 1867-1870.

Walsh, P. D., Akçakaya, H. R., M., B. & Harcourt, A. H. 1995. PVA in Theory and Practice. *Conservation Biology* 9: 704-710.

Walters, J. R., Crowder, L. B. & Priddy, J. A. 2002. Population viability analysis for red-cockaded Woodpeckers using an individual-based model. *Ecological Applications* 12: 249-260.

Wesolowski, T. 1998. Timing and synchronisation of breeding in a Marsh Tit *Parus palustris* population from a primaeval forest. *Ardea* 86: 89-100.

Wesolowski, T. 2000. Time-saving mechanisms in the reproduction of Marsh Tits (*Parus palustris*). *Journal fur Ornithologie* 141: 309-318.

Whittingham, L. A., Dunn, P. O. & Robertson, R. J. 1994. Female response to reduced male parental care in birds - an experiment in Tree Swallows. *Ethology* 96: 260-269.

Wichmann, M. C., Groenveld, J., Jeltsch, F. & Grimm, V. 2005. Mitigation of climate change impacts on raptors by behavioural adaptation: ecological buffering mechanisms (in press). *Global and Planetary Change* 45.

Wichmann, M. C., Jeltsch, F., Dean, W. R. J., Moloney, K. A. & Wissel, C. 2003. Implication of climate change for the persistence of raptors in arid savanna. *Oikos* 102: 186-202.

Wiebe, K. L. & Elchuk, C. L. 2003. Correlates of parental care in Northern Flickers *Colaptes auratus*: Do the sexes contribute equally while provisioning young? *Ardea* 91: 91-101.

Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. 2003. Using pattern-oriented modelling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos* 100: 209-222.

Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs* 68: 539-570.

Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker - Effects of life history, mating system and age. PhD Thesis, Lund University, Sweden.

Wiktander, U., Nilsson, I. N., Nilsson, S. G., Olsson, O., Pettersson, B. & Stagen, A. 1992. Occurrence of the Lesser Spotted Woodpecker *Dendrocopos minor* in relation to area of deciduous forest. *Ornis Fennica* 69: 113-118.

Wiktander, U., Nilsson, S. G., Olsson, O. & Stagen, A. 1994. Breeding Success of a Lesser Spotted Woodpecker *Dendrocopos minor* Population. *Ibis* 136: 318-322.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2000. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* 31: 447-456.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001a. Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). *Auk* 118: 624-635.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001b. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Ibis* 143: 72-82.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001c. Seasonal variation in home-range size, and habitat area requirement of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in southern Sweden. *Biological Conservation* 100: 387-395.

Winkler, H., Christie, D. A. & Nurney, D. 1995. *Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the World*. Russel Friedman Books CC, Sussex.

Wissel, C., Stephan, T. & Zaschke, S.-H. 1994. Modelling extinction and survival of small populations. In: Remmert, H. (ed.) *Minimum animal populations.*, pp. 67-103. Springer-Verlag, Berlin.

Wölflik, O. Vergleichende Untersuchungen der Bruthöhlenhabitate von Kleinspecht (*Picoides minor*) und Buntspecht (*Picoides major*). Diplomarbeit, Johann Wolfgang Goethe-Universität Frankfurt, Germany.

Yom-Tov, Y. & Ar, A. 1993. Incubation and fledging durations of woodpeckers. *Condor* 95: 282-287.

Zelenak, J. R., Rotella, J. J. & Harmata, A. R. 1997. Survival of fledgling Ferruginous Hawks in northern Montana. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* 75: 152-156.

Danksagung

In meiner Zeit als Doktorandin bin ich von vielen Menschen in unterschiedlicher Richtung unterstützt worden. Ihnen gebührt mein Dank.

Besonders herzlich möchte ich mich bei Prof. Florian Jeltsch (Universität Potsdam) für die großartige Betreuung bedanken. Er hat meine Promotionsidee unterstützt, mir neue Denkanstöße gegeben und sich - auch wenn er eigentlich keine hatte – immer Zeit für mich genommen. Seine Fähigkeit sich in kürzester Zeit in jede Problemstellung einzudenken bewundere ich sehr und seine Unterstützung und Hartnäckigkeit ist es zu verdanken, dass ich die Arbeit so schnell hinter mich gebracht habe.

Ein herzliches Dankeschön auch an PD Dr. Volker Grimm (UFZ Leipzig), der mich in amüsanter Weise in die Welt der Programmierung eingeführt hat. Sein Feedback zum 4. Kapitel war sehr hilfreich für mich.

Prof. Hans Winkler (KLIVV, Wien) und Prof. Günther Fleißner (Universität Frankfurt) danke ich für die spontane Bereitschaft zur Begutachtung meiner Arbeit. Prof. Dieter Wallschläger (Universität Potsdam) danke ich für seine Ratschläge und die Hilfe beim Versuchstierabtrag, Prof. Roland Prinzinger (Universität Frankfurt) für seine Zusammenarbeit bei den Studentenpraktika.

Mit Kerstin Höntsch hatte ich großen Spaß bei der gemeinsamen Datenaufnahme. Für die Bereitstellung von Daten und die angeregten Diskussionen über „unsere Spechte“ bin ich ihr sehr dankbar.

I am grateful to Dr. Ulf Wiktander for his comments on the empirical parts of the thesis as well as for his advices and his hospitality in the Swedish study area. I want to thank him as well as Dr. Ola Olsson for the supply with their valuable data of the Swedish Lesser Spotted Woodpecker population.

Einen besonders großen Dank auch an die Feldpraktikanten, die mir selbst um 4 Uhr morgens schon beim Fang der Kleinspechte halfen und ohne die ich bei der Suche nach diesen winzigkleinen Kleinspechthöhen wohl wahnsinnig geworden wäre. Außerdem Dank an die Ornithologenwelt Kelkheims (u.a. Michael Orf, Oliver Conz) die mich beim Fangen und Finden unterstützt haben. Das schöne Titelfoto des Spechts „Lothar“ an seiner Bruthöhle wurde von Helmut Dahlem aufgenommen.

Für die finanzielle Unterstützung und die geistige Bereicherung auf den Seminaren im Rahmen meines Stipendiums bin ich der Deutschen Bundesstiftung Umwelt dankbar, hier vor allem Dank an Frau Dr. Schlegel Starmann für die nette Betreuung. Die Bekanntschaft mit vielen meiner Mitstipendiaten möchte ich nicht missen und hat mir viele Anregungen gegeben. Der Deutschen Wildtier Stiftung danke ich für ihren finanziellen Zuschuss im Rahmen des Wildtierpreises.

Meiner Bürogenossin Eva Mosner in Potsdam danke ich sehr herzlich für die aufbauenden Worte, die Durchsicht eines Manuskripts und die viele Schokolade. Dr. Matthias Wichmann danke ich für Tipps zum Programmieren und die TM-Wert-Berechnung sowie die konstruktive Kritik an Teilen meiner Arbeit. Auch der Rest der Arbeitsgruppe in Potsdam bot mir immer Bereitschaft zur Diskussion sowie eine herzliche Arbeitsatmosphäre, vor allem Monika Schwager, Aleks Popp und Birgit Seifert. Bei Ute Leonard bedanke ich mich für die professionelle sprachliche Korrektur großer Teile der Arbeit.

Meinen Eltern Jutta und Günther möchte ich für ihre liebevolle Unterstützung in jeder Richtung sehr herzlich danken. Vor allem meinem Vater Günther ist es zu verdanken, dass ich mich überhaupt getraut habe, meine wissenschaftliche Neugierde zu verwirklichen. Meiner Schwester Tanja danke ich dafür, dass sie immer für mich da ist. Meinen Freundinnen Steffi Keßler und Melle Maßlich, danke für das schöne Zusammenleben in der Wielandstrasse und ihre Rücksichtnahme auf meinen ungewöhnlichen Schlafrhythmus während der Freilandarbeit.

Der größte Dank gebührt jedoch Niels Blaum, meinem ständiger Berater, der mich nicht nur mit seiner kompetenten fachlichen Hilfe in allen Phasen der Arbeit und seiner Bereitschaft meine Manuskripte wiederholt zu lesen unterstützt hat. Er hat in den letzten Jahren die schweren Momente meines Lebens erleichtert und die frohen perfekt gemacht. Vor allem möchte ich mich bei ihm dafür bedanken, dass er mich so glücklich und mein Leben schöner macht.