“The life histories of the two tropical warblers *Sylvia boehmi* and *Sylvia lugens*”

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Contents

1 General introduction

1.1 Differences between tropical and temperate species and communities

Since centuries researchers coming from the temperate regions have been astonished by the high species richness they found in the tropics. Alexander von Humboldt (1769–1859) is the most famous early naturalist who brought knowledge of and enthusiasm for the biodiversity in tropical regions to the scientific community and public in the northern temperate regions. Since his expedition to tropical America (1799–1804), our knowledge about biodiversity in the tropics as well as in temperate regions has been growing steadily. We know today that species richness increases gradually with falling latitude, and that temperate and tropical communities differ not only in species richness. There are many other differences like, for example, the number of rare species, which is much higher in the tropics, or the dominance of common species, which we find in temperate communities. Also the species themselves show differences. Many tropical species have other diets, morphologies, or life histories than those that live in the Northern Hemisphere.

One of the biggest challenges in evolutionary biology is to identify and understand the factors, which cause these differences. Such analyses require detailed information about the communities, species' traits, their ecology, their behaviour, the biological and physical environment, and other aspects. Due to the high complexity of ecological systems, this knowledge is rarely complete. This especially applies to complex traits, which are not immediately visible or measurable, but require long lasting, intensive, and close observations, like, for example, life history traits.

1.2 Life histories

An organism's life history is its lifetime pattern of growth, differentiation, storage, and reproduction (Begon et al. 1996). It is described by traits like adult size, age at maturity, mortality rate, and age-specific fecundity rate (Roff 2002). An obvious characteristic of life histories in the living world is that they differ markedly. There is considerable variation in life histories of species from different orders and families, but differences can also be found in different populations of the same species.

The scientific field of life history analysis aims to explain these differences. It assumes that life history variation is primarily the result of natural selection and represents adaptation (Roff 2002). Therefore, it includes ecological and evolutionary perspectives and approaches. As stated above, such approaches require extensive knowledge about ecological factors and life history traits to be successful.

1.3 Life histories of temperate and tropical birds

In birds, the analysis of differences in life history traits has a long history (Rickleffs 2000a). On the one hand, this can be ascribed to the fact that knowledge about birds has always been more detailed than about many other groups of organisms, because they have always attracted special attention of many early and current naturalists. On the other hand, avian life histories around the world show a striking pattern that aroused scientific interest early. In 1944, Moreau was the first to establish scientifically that birds in the tropics lay smaller clutches than those in higher latitudes. While open nesting passerines in Central Europe usually lay clutches of four or more eggs, nests of tropical passerines consist of two or three eggs. This difference in clutch size, which exists even between phylogenetically closely related species, has been examined closely and a number of studies have confirmed its significance (e.g. Lack 1968, Yom-Tov 1994, Martin et al. 2000a). Obviously, clutch size is a very important trait in the life history of birds and must be balanced by other life history traits. However, there is only little evidence for significant differences between temperate and tropical birds concerning other life history traits like nest success, number of broods or annual fecundity (Cardillo 2002, Geffen and Yom-Tov 2000). On adult survival, only a few mark-recapture studies were conducted in the tropics, some with contradictory results (Karr et al. 1990, Peach et al. 2001). A rigorous test of the different hypotheses, stated to explain life history differences, is still hampered by a lack of knowledge, especially on tropical species (Ricklefs 2000a), and a limited comparability of results, because traits were often studied in species of varying phylogenetic relationship (Martin 1996, Cardillo 2002). As far as I know, there are only two studies, which compare life history traits of different species within a single genus (genus *Saxicola*, data of one temperate and one tropical subspecies (Gwinner et al. 1995); genus *Turdus*, data from museum material (Ricklefs 1997)). However, these studies do not contain any data on traits that require long-term studies like for example post-fledging care. In general, there are only few suitable genera with a sufficient number of species, which are distributed to temperate and tropical regions.

1.4 The genus *Sylvia* as a model system

The genus *Sylvia* is a well-suited model system for the comparison of life history traits of temperate and tropical birds within one genus. The genus is restricted to Europe, Africa and East-Asia. Recent DNA-studies have shown that it forms a monophyletic group together with the African genera *Parisoma* and *Pseudoalcippe* (Sibley and Ahlquist 1990, Blondel et al. 1996, Shirihai et al. 2001, Böhning-Gaese et al. 2003). After the merging of the three genera, *Sylvia* comprises 29 species. Among these are temperate residents, tropical residents, and long-distance migrants. Further on, many of the temperate and migrating species have been closely investigated in the past, so that the genus belongs to the best-known bird genera. However, even in this genus we have only very little information on the life history traits of the tropical species.

1.5 Aims of thesis

In this thesis I studied the life history traits of the two tropical *Sylvia* (and former *Parisoma*) warblers *Sylvia boehmi* and *Sylvia lugens* in Kenya. The aim of the thesis was to gain detailed information about the reproduction and the survival of the two tropical *Sylvia* species, in order to fully establish the genus as a model system and to allow studies about causes of life history differences in the future.

The thesis is made up of three major chapters (chapters 2–4), which can be read independently. Each chapter is structured like a journal publication. It contains an introduction, a method, results, and a discussion part and ends with a brief summary. Chapter 5 closes the thesis with general conclusions.

Chapter 2 deals mainly with the breeding biology of the two species. I report crucial life history traits like clutch size, nest success, annual fecundity, and post-fledging care. In chapters 3 and 4 I focus on traits and ecological factors that are more difficult to analyse but are considered particularly important for the evolution of life history traits: that is adult survival and seasonality of the habitat (chapter 3) and nest predation (chapter 4).

All analyses are based on almost two years of field observations, covering two breeding seasons of both species. I would like to emphasize that I entered the study, which is described in this thesis, in July 2001. The fieldwork had started one year earlier, in April 2000, and was initiated by Prof. Katrin Böhning-Gaese and Dipl. Biol. Silke Schmidt. Standardized observations of the birds began in October 2000 and were conducted by two Kenyan field assistants, George Were Eshiamwata and Fred Barasa Munyekenye. From July 2001 until its end in late 2002 I took full responsibility for the field project, visited the study areas twice, and spent six weeks in the field myself. All analyses described in this thesis have been conducted by myself. They are based on data collected during the whole study period from October 2000 to August 2002.

The discussion parts of each chapter contain interspecific comparisons of the two tropical species with each other and comparisons of the traits of the tropical species with those of their temperate congenerics. In chapter 5, I shortly summarize the most important results of my studies, draw general conclusions, and give an outlook on how the results may help to understand differences in life history traits between temperate and tropical birds in the future.

Fieldwork in Kenya was conducted under research licence MOEST 13/001/29C 178.

2 Life history of two African *Sylvia* warblers: Low annual fecundity and long post-fledging care

This chapter was published by Blackwell Publishing in Ibis 146: 427-437.
See page 2 of this thesis for details.

2.1 Introduction

The differences between temperate and tropical species and ecological communities are among the most striking patterns in community ecology (Begon et al. 1996, Brown and Lomolino 1998). In birds, temperate and tropical species differ in diet, morphology, and life history traits (Terborgh et al. 1990, Martin 1996, Cardillo 2002). With respect to life history traits tropical birds often have smaller clutches, longer developmental periods and higher adult survival than do their temperate relatives (Moreau 1944, Cody 1966, Lack 1968, Ricklefs 1980, Skutch 1985, Yom-Tov 1994, Martin 1996). Despite latitudinal differences, tropical and Southern Hemisphere species often show similar life history traits (e.g. Martin et al. 2000a, Russel 2000).

A standard approach to studying the factors causing these differences is to compare the traits of tropical and temperate species and to correlate them with environmental factors. However, this comparative approach has been hampered by a lack of information on tropical bird species (Ricklefs 2000a, b). This applies especially to data on life histories, which require detailed and extensive investigations. Furthermore, since geographical differences in life history traits might reflect different phylogenetic relationships among the species, comparisons should also consider phylogeny, and are ideally conducted within closely related species (Magrath et al. 2000, Martin et al. 2000a).

One of the best-studied bird genera in the Old World is the genus *Sylvia* (Passeriformes: Sylviidae) (Glutz von Blotzheim 1991, Cramp 1992, Shirihai et al. 2001). Recent molecular studies have revealed that the genera *Sylvia*, *Parisoma*, and *Pseudoalcippe* form a monophyletic group (Sibley and Ahlquist 1990, Blondel et al. 1996, Shirihai et al. 2001, Böhning-Gaese et al. 2003). This merging of genera added four tropical and two Southern temperate species to the former genus *Sylvia*, which now comprises 29 species: seven residents and four short distance migrants from temperate Europe and the Mediterranean, six residents from tropical and Southern Africa, and 12 long distance migrants, which breed in northern temperate regions and winter in the tropics. The high number of species and the nearly equal representation of temperate and tropical species make *Sylvia* a good taxon in which to investigate differences between temperate and tropical species. However, while many of the temperate and migrating species have been studied closely (Glutz von Blotzheim 1991, Cramp 1992, Shirihai et al. 2001), information on the tropical species (*Sylvia abyssinica, S. boehmi, S. buryi, S. lugens*) and on the South African species (*S. layardi*, *S. subcaeruleum*) is still sketchy.

The aim of my study was to provide a detailed description of the life history of two tropical *Sylvia* species: the Brown Parisoma *Sylvia lugens* and the Banded Parisoma *S. boehmi* in Kenya. Here, I present data on breeding season, proportion of breeding birds, nests, clutch sizes, developmental periods, breeding success, causes of nest failures, renesting intervals, annual fecundity, post-fledging care and fledgling survival. Subsequently, I compare the results of the two species and discuss their life history traits in relation to those of temperate *Sylvia* species.

2.2 Methods

2.2.1 *Sylvia lugens*

Study species: *Sylvia lugens* is a small (14.8 ± 0.8 g [mean ± standard deviation, if not otherwise stated], *n* = 43) warbler, endemic to East Africa, where it has a fragmented distribution in the highlands, and inhabits open woodlands. It feeds mainly on insects, small seeds, and berries, for which it forages on trees and bushes but almost never on the ground. The sexes look alike and have a plain dark grey-brown plumage. Breeding pairs are sedentary and stay together from year to year (Shirihai et al. 2001 and own observations of the authors).

Study area: The study was conducted on a 1200 hectare private farm in the Kenyan Highlands, Rift Valley Province, around 15 km northwest of Nakuru town, at 2000 m above sea level (0° 14’ S / 36° 1’ E). The two main rainfall seasons were March–May and October–November. The farm has open cultivation and pasture fields surrounded by tall hedgerows of *Acacia abyssinica* trees, interspersed with *Lantana camara* and *Rhus natalensis* shrubs planted to prevent soil erosion. Several tall isolated *A. abyssinica* and *A. lahai* trees can also be found sparsely scattered across the fields. The study was conducted over 22 months from October 2000 to July 2002. Daily rainfall recordings were provided by the farm management.

Sylvia lugens (and *S. boehmi*) breeding pairs have fixed territories, which they defend against conspecific intruders. In May 2000, before observations began, warblers were tape-lured into mist-nets at 13 different territories on the farm. On capture, the birds were measured and individually ringed with one metal and three colour rings. The ringing-sites were numbered and remained unchanged for the whole study period, even when displacement of single birds or whole pairs occurred. Additional ringing sessions were conducted in November 2000, March 2001, and December 2001.

During the non-breeding season, observations were conducted in the form of bi-monthly observation sessions (mid-month and end of month); for each session every territory was observed on three consecutive days for 30 minutes. The presence or absence of individuals and any breeding activities were recorded. During the breeding season, each pair was observed daily for 30 minutes, six days a week. The time of visits to each pair was randomized every day. Observations were conducted with binoculars from a distance of 5–10 m to avoid disturbance. Any breeding activities of the individual birds such as nest building, brooding, or feeding were noted with the time. For every breeding attempt, nesting tree and placement of nest were recorded. If possible, nest contents and reasons for nest failures were determined. The post-fledging period was observed until the fledglings disappeared from the parents' territory. The total observation time exceeded 3000 hours. Only a few clutch-sizes could be determined for the *S. lugens* study pairs, because most nests were inaccessible in high tree crowns. Additional clutch sizes were acquired from non-study breeding pairs on the farm by use of a 12V CCD-mini-finger-camera (55 x 18 mm), which was connected to a portable mini-TV (Casio LCD Color Television TV-880, with 6 cm LCD-display) and lifted to the nests at the tip of a 7-m bamboo-pole.

2.2.2 *Sylvia boehmi*

Study species: *Sylvia boehmi* weighs 13.7 ± 1.0 g ($n = 39$) and is characterized by yellow eyes, a blackish breast band, and orange undertail-coverts. It is sexually monomorphic. It is also an East African endemic with a fragmented range, but it is usually found at lower altitudes than *S. lugens*. Its favoured habitats are woodland, wooded grassland and bush land, and its diet consists of insects, small seeds, and berries, for which it usually forages in trees and bushes. As in *S. lugens*, breeding pairs are sedentary and stay together for several years (Shirihai et al. 2001 and own observations).

Study area: The study population of *S. boehmi* was located around 80 km south of Nairobi in Kajiado district, Rift Valley province, Kenya. The observation area, of approximately 10 x 3 km, was located along Magadi road close to Olorgesailie prehistoric site (1° 33’ S 36° 28’ E), at 1000 m above sea level. Rainfall in this area is highly unpredictable and long droughts can occur.

The vegetation is wooded grassland dominated by *Acacia mellifera* and *A. tortilis*. Other plant species include *Boscia angustifolia, B. coriacea, Balanites aegyptiaca* and *Maerua parvifolia*. The region is used by the local Masaai community for grazing livestock. Observations were conducted for 23 months, from October 2000 until August 2002. Daily rainfall data were recorded at the Olorgesailie prehistoric site museum.

The initial steps of establishing the observation sites and ringing the birds were the same as for *S. lugens*. The study started with 11 observed pairs in October 2000. In March 2001 this number was increased to 13 pairs. Observations during both the breeding and non-breeding periods were conducted following the same protocols as for *S. lugens* and also exceeded 3000 hours. Because the nests were easier to access, sufficient clutch size observations were confirmed without the use of the finger-camera.

2.2.3 Data analysis

To visualize the seasonal breeding activity pattern of the two species, I categorized the breeding behaviour in three classes: nest building, breeding (including incubation and feeding of nestlings), and fledglings (lasting as long as fledglings were seen in the territory of the parents). For every month of the study period, every breeding pair was assigned a specific breeding activity class. Breeding was ranked above nest building and those two were ranked above feeding fledglings, i.e. a pair that was breeding and feeding fledglings within the same month was assigned to the breeding class, a pair that was feeding fledglings and nest building was categorized as nest building. The proportion of each activity in the study population was calculated from the number of pairs in a specific class for every month of the study.

To quantify nest success, I considered only nests in which eggs were laid and incubation had started, because in both species a considerable number of nests were abandoned before eggs were laid. Nest and egg success were calculated directly from the number of started and successful breeding attempts, and also by using the Mayfield method as described by Mayfield (1975) and specified by Manolis et al. (2000). The number of exposure days was calculated by terminating exposure with the last observed active date for nests with uncertain fate and with the midpoint between last observed active and first observed inactive date for nests of known fate. To calculate the standard error and 95% confidence interval, I followed Johnson (1979). Note that different numbers of nests were used in the direct and Mayfield calculations.

To provide an overview of the causes of nest failure, I categorized them as ‘abandonment’, ‘predation’, or ‘unknown’. ‘Abandonment’ was defined as nests being deserted, leaving eggs or nestlings behind. ‘Predation’ was assumed when the nest contents (eggs or nestlings) were confirmed missing from one day to the next in the course of an ongoing breeding attempt. The cause of failure was categorized as ‘unknown’ when the attempt failed and the nest contents could not be determined.

To analyse the post-fledging period, I calculated three things: the number of days that each fledgling was observed being fed, making begging calls, and for which it was seen in its parents’ territory. The same method was used as for calculating the nest exposure days (see above). Data were analysed using the Product-Limit-Method (Kaplan-Meier) for description and the log-rank test and Wilcoxon test for comparison, as implemented in the survival analysis module of STATISTICA 5.1 (StatSoft 1997). These methods estimate and compare survival functions, when the fate of every individual is known. Furthermore, they allow the inclusion of censored data, i.e. incomplete data from fledglings that were still fed or present in the parents’ territories when the study ended. However, I had to exclude censored data, because the pattern of censoring (the distribution of incomplete data within the sample) differed strongly between the species. The values of the censored data for *S. lugens* were much lower than those for *S. boehmi*. Inclusion of the censored data would have increased the statistical significance I found. The time to independence from parental feeding was calculated as the Kaplan-Meier median of the feeding period of those fledglings that were still observed alive after parental feeding had stopped. The average time for which begging calls were heard was calculated from those fledglings that were still observed alive after begging calls had stopped. The average length of presence in the parents’ territory was also calculated from all fledglings that were observed alive after parental feeding had stopped. The daily survival rate of the fledglings until independence was calculated using the Mayfield procedure. Exposure days were calculated by summing the days over which fledglings were seen in their parents’ territory, with the median of the feeding period (time to independence) being defined as the point in time that represented the passage from fledgling to independence.

The number of breeding attempts per year, the number of successful breeding attempts per year, and the annual fecundity (number of fledglings that leave the nest per year) were calculated from the average values of the 13 observed territories for the whole study period.

2.3 Results

2.3.1 *Sylvia lugens*

The monthly rainfall in the study area showed a period of regular rain from March to November with peaks in April/May and October, and a drier period from December to February (Fig. 2.1a). The average annual rainfall during the study was 1080 mm. The study years were not particularly wet or dry and produced average crop yields on the farm. The analysis of the breeding activity of the study population was based on 116 breeding attempts. The 2001 breeding season lasted from April to December, with activity peaks in June and October, when all pairs in the study population were breeding or feeding fledglings (Fig. 2.1b). A similar pattern of breeding activity was observed in the years ore and after the 2001 breeding season. However, the breeding activity in the study population in 2000 and 2002 was lower than in 2001. While in 2001 all study pairs were breeding, in 2000 and 2002 a maximum of around 75% of the study pairs were breeding or feeding fledglings (Fig. 2.1b).

Twenty-six of the 116 *S. lugens* nests that were monitored during the study were abandoned before eggs were laid. Two nests were still in the egg and nestling stage, respectively, when the study ended. Depending on the subject, the following calculations were based either on the 90 breeding attempts in which incubation had begun, or on the 88 breeding attempts that were followed until termination. All breeding activities, i.e. nest building, incubation, brooding, feeding of nestlings and fledglings, were conducted by both parents.

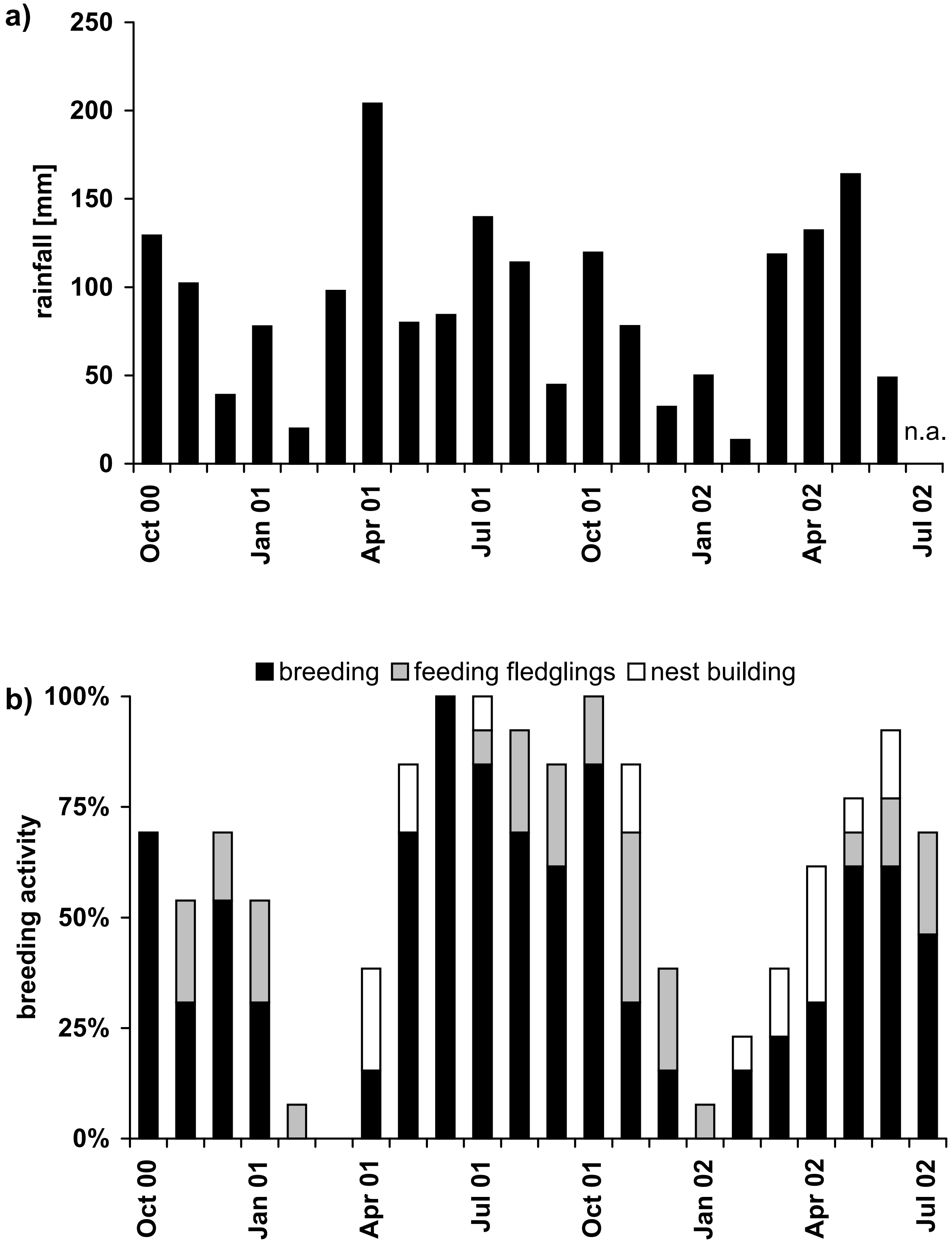

Figure 2.1 a) Monthly rainfall (mm) in *Sylvia lugens* observation area from October 2000 to July 2002. (n.a. = not available) **b)** Monthly breeding activities of the *Sylvia lugens* study population in percent (*n* = 13 territories). Black: Pairs in breeding stage (incubating or feeding nestlings); grey: Pairs feeding fledglings; white: Pairs building new nests. See text for further explanation.

Nest stage: Most nests were built in the upper canopy of the nesting trees (Table 2.1). The process of nest building from attachment of the first twigs to the beginning of incubation took between 3.5 and 16 days. Nests were open cups, robust, and built from dry grass and small twigs. Material was usually collected in the vicinity, in some cases it was taken from old nests and from the nests of other species. In three cases, the re-use of previous nests was observed.

The mean clutch size was 2.0 ± 0.0 eggs (*n* = 12). The eggs were dirty white, speckled with sayal-brown. The average egg size was 18.3 ± 0.6 mm x 13.5 ± 0.3 mm (*n* = 5). In one of the few easily accessible nests, I observed that *S. lugens* started incubating after laying the second egg. The average length of the incubation period was 14.5 ± 1.5 days (mode 14.0, min 11.5, max 19.0, *n* = 33). The nestling period lasted 16.0 ± 2.7 days (mode 16.5, min 11.0, max 21.5, *n* = 26).

Table 2.1 Data on nesting trees and nests of *S. lugens* and *S. boehmi* in Kenya. Numbers are mean ± standard deviation, if not otherwise noted.

	S. lugens	*S. boehmi*
nesting trees		
species	*Acacia abyssinica* (83%, 75/90) *A. lahai* (7%, 6/90) others[a] (9%, 8/90)	*Acacia tortilis* (38%, 35/91) *Balanites aegyptiaca* (35%, 32/91) *A. mellifera* (20%, 18/91) others[b] (5%, 5/91)
height [m] (n)	9.7 ± 2.7, min 2.5, max 18.0 (89)	4.8 ± 1.8, min 2.0, max 10.0 (90)
nests		
height ab. ground [m] (n)	8.6 ± 2.7, min 2.0, max 17.0 (89)	3.1 ± 1.7, min 1.0, max 8.0 (90)
outer diametre [mm] (n)	71 ± 18 (6)	73 ± 7 (42)
inner diametre [mm] (n)	48 ± 14 (6)	51 ± 11 (42)
height [mm] (n)	44 ± 4 (6)	43 ± 8 (42)
depth of nest cup [mm] (n)	26 ± 4 (6)	33 ± 5 (42)

[a] *Acacia mearnzii*, *Eucalyptus spec.*, *Grevillea robusta*, *Lantana camara*; one nest not located

[b] *Acacia senegalensis*, *Boscia angustifolia, B. coriacea, Grewia bicolor, Maerua parvifolia*; one nest not located

Nest success: Eighty-eight breeding attempts were observed until termination. Nestlings hatched in 61 of the 88 nests and fledglings fledged from 35 of these 61 nests. Thus, direct success rates were 69.3% for the incubation stage, 57.4% for the nestling stage and 39.8% overall. Mayfield nest success for the incubation stage was estimated from the observation of 75 nests, which yielded 824.0 exposure days. Twenty-five of these nests were lost. Thus, the daily survival rate (DSR) during incubation was 0.9697 ± 0.0060 se. For the average incubation period of 14.5 days, this yielded a nest success rate (NSR) of 64.0%. During the nestling stage, 63 nests were observed, yielding 645.5 exposure days. Twenty-six breeding attempts failed. From these data a DSR of 0.9597 ± 0.0077 (s. e.) and a NSR of 51.8% for the nestling stage were calculated. The product of the incubation success rate and the nestling success rate yielded the overall nest success rate for the whole breeding period, which was 33.2%.

On average, *S. lugens* pairs started 3.7 ± 1.0 breeding attempts per year per territory (*n* = 13 territories), 1.5 ± 0.6 of these were successful (*n* = 13). The 35 successful breeding attempts yielded 54 fledglings, i.e. 0.6 fledglings per attempt and 1.5 fledglings per successful attempt. In the 22 months of study, pairs in two territories succeeded in fledging one brood, four fledged two, four fledged three, two fledged four , and one pair fledged five broods. The annual fecundity of the study population was 2.3 ± 1.0 fledglings per year per territory (*n* = 13).

Nest failures and renesting: Twenty-seven nests failed during incubation. Due to the inaccessibility of *S. lugens*' nests, it was impossible to determine nest contents so that for 25 of these nests, the cause of failure had to be classified as 'unknown'. As for the others, in one case the eggs fell out of the nest, and in the other, one of the parents was found dead. During the nestling stage, three nests were confirmed empty and hence predation was assumed to have occurred. The other 23 failures were categorized as unknown. During the whole study period, only one predation incident was observed: a Common Fiscal Shrike *Lanius collaris humeralis* was seen preying on nestlings. This bird was very common in the study area and probably responsible for most nest failures. *Sylvia lugens* mobbed the Shrikes with alarm calls, especially when it had fledglings.

The time span between a nest failure and the beginning of the incubation of a replacement clutch depended mainly on the prevailing weather conditions. During the height of the breeding season, short renesting intervals with the start of incubation at least

7 days after the loss of eggs and 5 days after the loss of nestlings were observed. The shortest period between the day on which a brood fledged and the start of incubation of a new clutch was 31 days, at which time the fledglings were still present in the territory. However, they disappeared in the course of the new breeding attempt; fledglings from successive nests were never observed in the parents' territory at the same time.

Post-fledging stage: For the first day or two after fledging, the young birds were rather inactive and stayed in the nesting tree or very close to it. When their mobility increased they were usually observed perching in dense trees or shrubs 1–2 m from each other. When there were two fledglings, each of them was usually fed by one specific adult. Out of the 54 fledglings, 44 were monitored until they disappeared from their parents' territory. Some fledglings were lost in the first week after fledging, but most survived and stayed in the vicinity for four weeks and longer (Fig. 2.3a). The number of fledglings that were fed began to decrease strongly after 30 days. The time between fledging and independence from parental feeding (when only 50% of the fledglings were fed) was 37.5 days (Kaplan-Meier median, considering only fledglings that were observed beyond their feeding period, $n = 19$). The latest feeding event was observed on day 63 after fledging. Begging calls stopped shortly after feeding had stopped (Kaplan-Meier median 42.3 days, considering only fledglings that were observed after begging calls stopped, $n = 17$) and a few days later, the young birds usually disappeared. The time when 50% of the fledglings had disappeared was 51.5 days (considering only fledglings that were still observed after their feeding period, $n = 19$). In one case, two fledglings were observed in their parents' territory for 105 and 113 days, but this was considerably longer than usual. At the end of the study, seven fledglings (post-fledging age 4.5 to 40.5 days) were still present and being fed. The daily survival of fledglings until independence (day 37.5 after fledging) was 0.9844 ± 0.0034 (s. e.), and overall survival of fledglings over this period was 55.4%.

2.3.2 *Sylvia boehmi*

The main rainfall in Olorgesailie occured from November to January and from March to April (Fig. 2.2a). Periods of regular rainfall were interrupted by long droughts. The average annual rainfall during the study was 552 mm. According to reports of local residents, the study period was not particularly wet or dry, apart from a flooding in January 2001. The pattern of breeding activity in the course of the study is based on 132 nests and showed two clearly distinct breeding seasons, which stretched from November to June (Fig. 2.2b). During these breeding periods the proportion of pairs actually breeding was usually around 70% of the observed pairs. Only in May and June 2002 it was almost 100%.

Forty-one of 132 *S. boehmi* nests were abandoned before egg-laying. Incubation began in 91 nests. These 91 breeding attempts were observed until termination and the following calculations are all based on these 91 breeding attempts. As for *S. lugens*, all breeding activities were conducted by both parents.

Nest stage: Nests were usually built in the upper half of the nesting trees, but occasionally branches as low as 1 m above ground were used (Table 2.1). Nest construction took 4–11 days. Nests were open cups, robust, and built from dry grass. The nest material was collected in the vicinity, sometimes taken from old nests of their own or of other species. The reuse of previous nests was observed twice.

The mean clutch size was 2.0 ± 0.4 eggs ($n = 29$). Twenty-five of the clutches that were found consisted of two eggs, two of one egg, and two of three eggs. The eggs were dirty white coloured, speckled with brown and their average size was 18.8 ± 0.3 mm x 13.4 ± 0.6 mm ($n = 6$). *Sylvia boehmi* started incubating after the first egg was laid. The observed incubation period was 15.0 ± 1.4 days (mode 16.0, min 12.0, max 19.0, $n = 39$). The nestling period lasted for 12.9 ± 1.8 days (mode 14.0, min 10.0, max 15.0, $n = 16$).

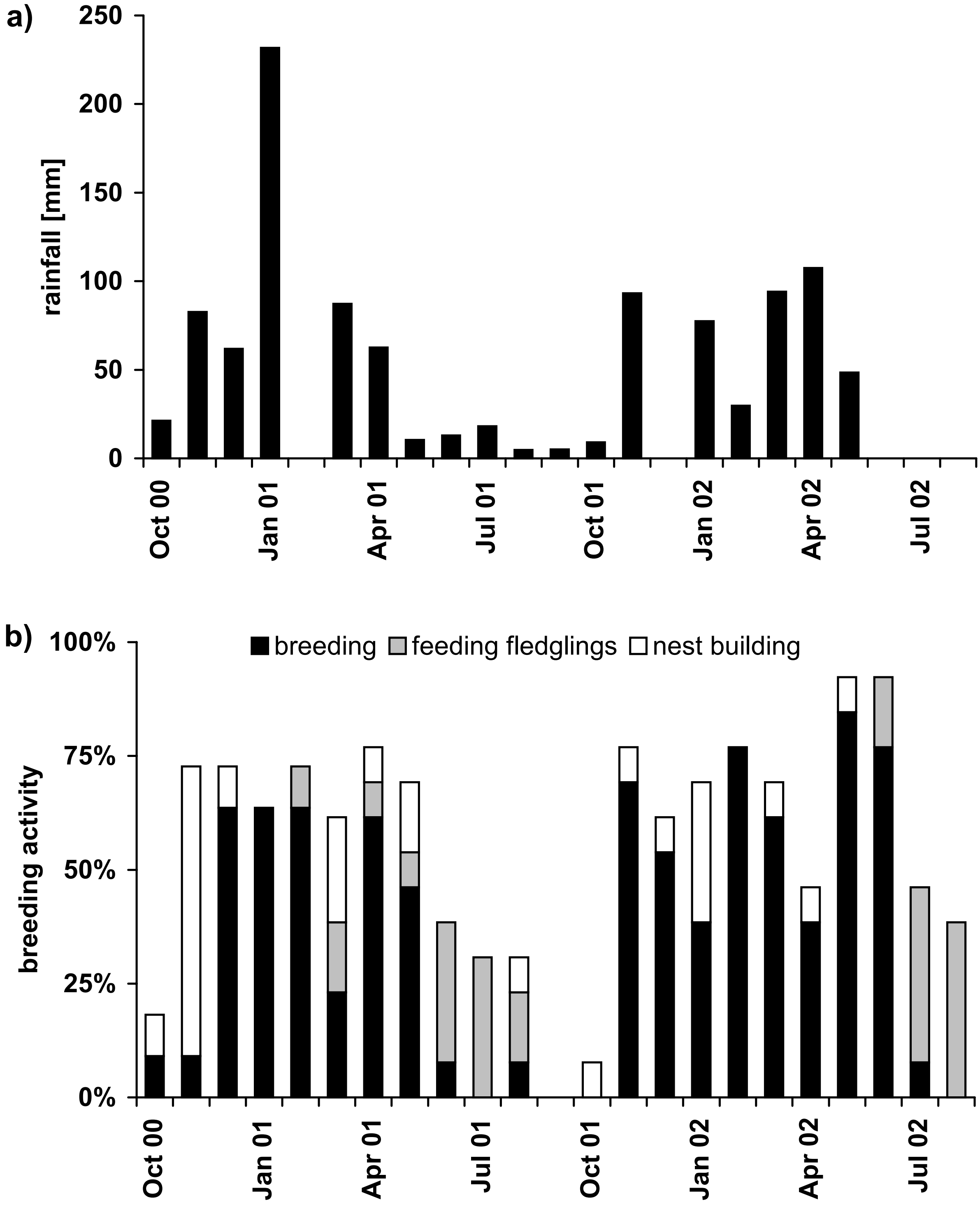

Figure 2.2 a) Monthly rainfall (mm) in *Sylvia boehmi* observation area from October 2000 to August 2002. **b)** Monthly breeding activities of the *Sylvia boehmi* study population in percent (*n* = 13 territories). Black: Pairs in breeding stage (incubating or feeding nestlings); grey: Pairs feeding fledglings; white: Pairs building new nests. See text for further explanation.

Nest success: Eggs hatched in 56 of the 91 nests and fledglings fledged from 19 of these 56 nests. Thus, direct success rates were 61.5% for the incubation stage, 33.9% for the nestling stage and 20.9% overall. The Mayfield nest success rate during the incubation stage was determined from 936 exposure days, during which 31 of 85 nests were lost. This yields a DSR of 0.9669 ± 0.0059 (s. e.). Thus, NSR during incubation was 60.3% for an average incubation period of 15.0 days. Observations during the nestling stage accumulated 440.5 exposure days. At this stage, 37 of 54 nests were not successful, translating into a DSR of 0.9160 ± 0.0132 (s. e.) and a NSR of 32.2% for the nestling stage. The resulting overall NSR for the complete breeding period of *S. boehmi* was 19.4%.

As sufficient data on clutch sizes and nestling numbers per nest were collected, the egg-based and nestling-based success rates were calculated in addition to the nest success rate. These were slightly higher than the nest based rates: NSR incubation stage: 65.2%, NSR nestling stage 33.6% and overall NSR 21.9%. Few cases of partial failures occurred. Four of 58 eggs (6.9%) were infertile, usually one egg in a clutch of two or three.

On average, *S. boehmi* pairs started 3.7 ± 1.8 breeding attempts per year (*n* = 13 territories). Only 0.8 ± 0.4 of these were successful (*n* = 13). The 19 successful breeding attempts yielded 33 fledglings, i.e. 0.4 fledglings per attempt and 1.7 fledglings per successful attempt. In the 23 months of study, one territory yielded no successful brood, pairs of six territories succeeded in fledging one brood, five fledged two broods, and one fledged three broods. The annual fecundity of the study population was 1.4 ± 0.8 fledglings per year per territory (*n* = 13).

Nest failures and renesting: From the 35 nests that failed during the egg stage 21 were categorized as predation incidences. In three nests, the eggs had been abandoned; while for the remaining 11 the cause of failure remained unknown because the nest contents could not be confirmed. During the nestling stage, predation was the cause for 36 of 37 failed nests. In one case, nestlings had fallen out of a badly constructed nest.

In nine of the 57 assumed predation events, the predators could be identified. In seven cases, Cocktail-ants of the genera *Crematogaster* and *Camponotus* infested the nests and reduced the nestlings to skeletons. In two incidences, a Gabar Goshawk *Micronisus gabar aequatorius* was observed preying upon the nestlings. Other potential predators in the study area included several raptor species, snakes, and mammals such as the Dwarf

Mongoose *Helogale parvula*. As suggested by the presence of feathers and blood, in at least one case a brood and its brooding adult became victims of a predator.

The intervals between two breeding attempts were shortest when conditions were optimal during the height of the breeding season. The start of a new incubation period was observed only 5 days after the loss of eggs or nestlings. The shortest interval after a successful brood was 24 days from fledging until the start of incubation of the next clutch. In this, and in three other cases, the parents were still feeding the fledglings of the previous brood while attending a successive brood. The feeding of the fledglings was interrupted while the new nestlings were fed in the nest. However, the older offspring did not leave the parents' territory during this time. In three cases, the parents fed the fledglings of two generations simultaneously.

Post-fledging stage: The behaviour of newly fledged birds and brood division were similar to that observed in *S. lugens*. Out of the 33 fledglings, 20 were monitored until they disappeared from their parents' territory. Several of them disappeared in the first few days after fledging (Fig. 2.3b). The number of fledglings that were fed decreased conspicuously in the weeks after day 30. The time from fledging to independence from parental feeding, i. e. the median time by which only 50% were fed was 58.5 days (considering only fledglings that survived after their feeding period, $n = 15$). The latest feeding event was observed on day 90 after fledging. Begging calls were consistently heard for many days even after the last observed feeding event (Kaplan-Meier median 74.5 days, considering only fledglings that were observed after begging calls stopped, $n = 12$), indicating that occasional feeding still occurred. The number of young birds seen in their parents' territories declined slowly and uniformly. The time from fledging to when 50% of the fledglings had disappeared was 91.5 days (considering only fledglings that were observed beyond their feeding period, $n = 12$). The longest observed time a fledgling spent with its parents was 136.5 days. At the end of the study, nine fledglings (post-fledging age 62 to 90 days) were still present at the study site. The daily survival of fledglings until independence (day 58.5 after fledging) was 0.9937 ± 0.0021 (s. e.), and overall survival of fledglings for that period was 69.2%.

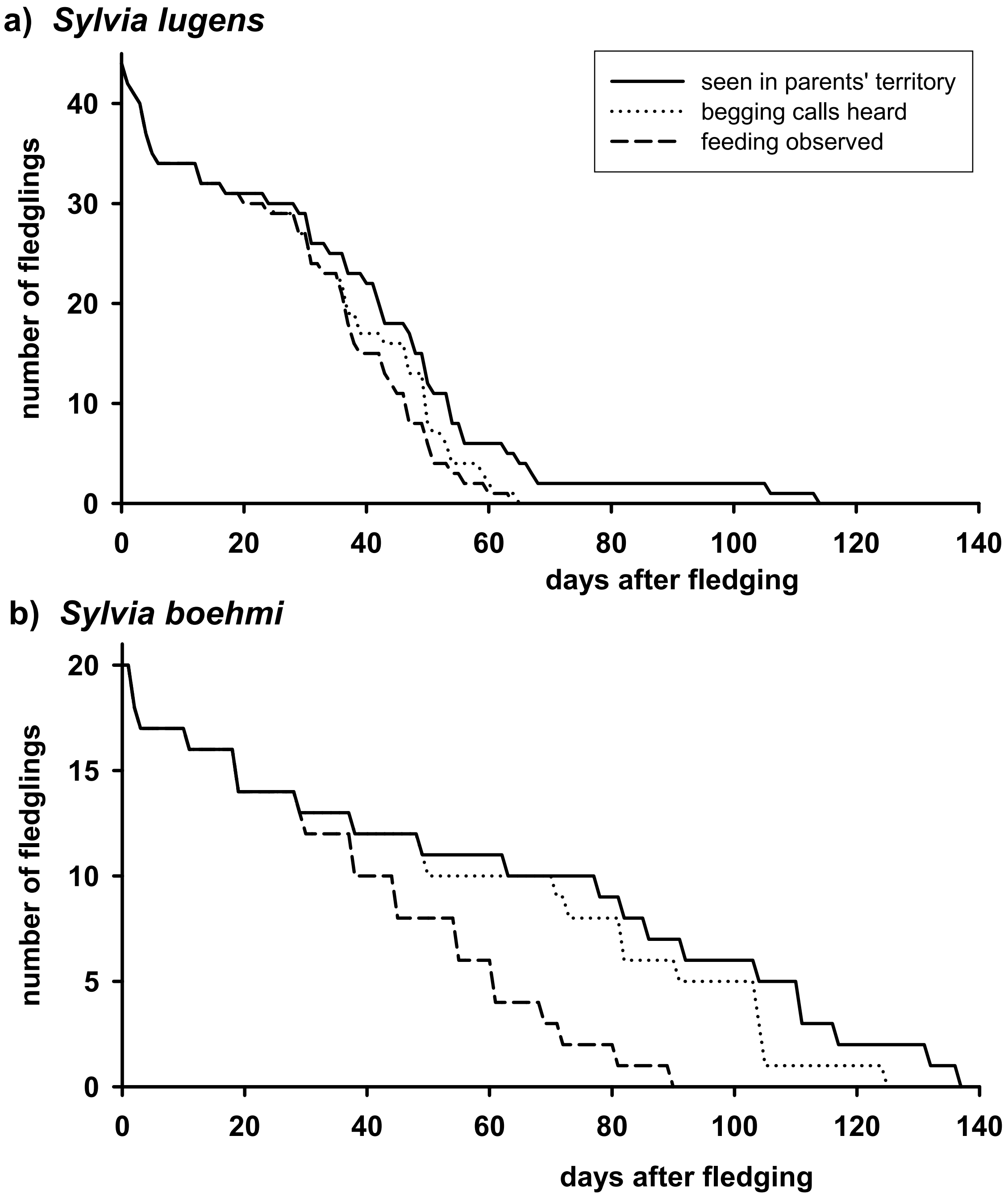

Figure 2.3 Length of three characteristics of the post-fledging period of *Sylvia lugens* (**a**) and *Sylvia boehmi* (**b**). Solid line: young birds present in their parents' territory. Dotted line: fledglings heard making begging calls. Dashed line: parental feeding. Only the fledglings that were observed until disappearance are displayed ($n_{lugens} = 44$, $n_{boehmi} = 20$).

2.3.3 Comparison of *S. lugens* and *S. boehmi*

The most important features of the life histories of *S. lugens* and *S. boehmi* showed several consistencies but also some distinct differences (Table 2.2). The two species had an identical clutch size of two eggs and laid around 3.7 clutches per year. Their incubation periods were of the same length and the daily ‘survival rates’ of nests during incubation were the same. Significant differences were detected in: the nestling period, which was shorter in *S. boehmi*; DSR during the nestling stage, which was lower in *S. boehmi*; and annual fecundity per territory, which was also lower in *S. boehmi*. Further on, the fledglings of *S. boehmi* were fed for a significantly longer period, were heard making begging calls significantly later and were seen in the parents’ territory significantly later than *S. lugens* fledglings. Finally, the DSR during the first weeks of the fledglings’ lives seems to have been higher in *S. boehmi*, although the 95% confidence intervals overlap slightly.

2.4 Discussion

2.4.1 Comparison of *S. lugens* and *S. boehmi*

The breeding biology of the two tropical warblers *S. lugens* and *S. boehmi* showed substantial similarities at the egg stage, but distinct differences in the nestling and post-fledging stages. One explanation for the shorter nestling periods in *S. boehmi* might be the difference in daily nestling survival rate, i.e. ‘nest’ predation. *Sylvia boehmi* nestlings seemed to be exposed to more numerous, or maybe more efficient, predators. These were probably attracted by parental feeding activities or nestling activities since this difference was not apparent at the incubation stage. Several studies have found that a reduction of the nestling period serves to minimize exposure to predators (Lack 1968, Bosque and Bosque 1995, Martin 1995, 2002). Although *S. boehmi* fledglings were around three days younger than *S. lugens* fledglings when leaving the nest, my observations did not provide evidence for differences between the species in the development of young fledglings. This can be explained by the findings of Remes and Martin (2002). They found that nestlings of species under high predation pressure not only leave their nests earlier and at a lighter weight, but also have higher growth rates. In spite of the shorter nestling period, high nest mortality still led to a low annual fecundity in *S. boehmi*.

Table 2.2 Life history traits of *S. lugens* and *S. boehmi* in Kenya and the results of the statistical comparison between the species.

life history trait		*S. lugens*	*S. boehmi*
clutch size	mean [eggs] (n)	2.0 (12)	2.0 (29)
incubation period	mean [days] (n)	14.5 (33)	15.0 (39)
	t-test	t=1.29, df=70, p=0.20	
	DSR[a] [95% confidence interval]	0.9577–0.9816	0.9552–0.9786
nestling period	mean [days] (n)	16.0 (26)	12.9 (16)
	t-test	t=-4.06, df=40, p=0.0002	
	DSR[a] [95% confidence interval]	0.9442–0.9752	0.8896–0.9424
number of clutches	mean [clutches territory^{-1} year^{-1}] (n)	3.7 (13)	3.7 (13)
	t-test	t=0.24, df=24, p=0.81	
annual fecundity	mean [fledglings territory^{-1} year^{-1}] (n)	2.3 (13)	1.4 (13)
	t-test	t=-2.46, df=24, p=0.02	
feeding of fledglings	Kaplan-Meier median [days] (n)	37.5 (19)	58.5 (15)
	log rank test, Wilcoxon test	p=0.0012, p=0.0014	
begging calls heard	Kaplan-Meier median [days] (n)	42.3 (17)	74.5 (12)
	log rank test, Wilcoxon test	p=0.0006, p=0.0002	
fledglings in parents' territory	Kaplan-Meier median [days] (n)	51.5 (19)	91.5 (12)
	log rank test, Wilcoxon test	p=0.0011, p=0.0006	
fledgling survival until independence	DSR[a] [95% confidence interval]	0.9776–0.9911	0.9896–0.9979

[a] daily survival rate

The characteristics of the post-fledging period are obviously associated with those of the nestling period. *S. boehmi* showed extended post-fledging care. In this species, the fledglings stayed in the parents' territory and were fed by the parents for a considerably longer period than did those of *S. lugens*. Extended parental care should increase offspring survival although, so far, only few studies give evidence for this in birds (Fodgen 1972, Skutch 1976, Russell 2000). My study cannot give clear evidence for differential offspring survival between these species, because fledglings were not colour-banded, and because the survival data are affected by dispersal. However, it is possible that the extended parental care of *S. boehmi* explains the lower fledgling mortality rate of this species during dependency and might serve as a compensation strategy for low nest success and low annual fecundity.

Yet other factors might account for the different lengths of post-fledging care in the two warblers. Parental care is assumed to be most highly developed when offspring survival is reduced by adverse environmental conditions (Clutton-Brock 1991). The habitat of *S. boehmi* in Olorgesailie was much harsher than that of *S. lugens*, with high temperatures, long droughts, and an unpredictable rainfall pattern. Survival in this environment probably demands high skill and flexibility in foraging, which might take longer to learn (Yoerg 1998). Finally, the fledglings might be forced to stay with their parents for a long time if strong territoriality is associated with high population density, so that young birds cannot establish their own territories (Langen 2000).

2.4.2 Comparison of *S. lugens* and *S. boehmi* to temperate congenerics

The peculiarities of the breeding biology of the two tropical *Sylvias* become apparent when they are compared to those of their congeneric relatives from northern and southern temperate regions (data taken from Cramp 1992 and Maclean 1993). *Sylvia lugens* and *S. boehmi* have the smallest clutches ever recorded in the entire genus. Clutch sizes of other *Sylvia* warblers vary between 2.5 (*S. subcaeruleum* in South Africa) and 5.3 (*S. curruca* in Finland). These numbers correspond to the well-known pattern of tropical and Southern Hemisphere species having significantly smaller clutches than those from the northern temperate regions (Stresemann 1927–34, Moreau 1944, Cody 1966, Lack 1968, Ricklefs 1980, Yom-Tov 1994, Martin et al. 2000a). The incubation period (14.5 and 15.0 days for *S. lugens* and *S. boehmi*, respectively) and the nestling period (16.0 and 12.9 days, respectively) fall among the highest recorded limits in *Sylvia*. Temperate *Sylvia* species incubate for 11 to 13.5 days. Only *S. leucomelaena* was reported to incubate for 15.5 days in Israel. These results seem to support those of several other authors (e.g. Skutch 1949, 1985, Ricklefs 1968, Martin 2002), indicating that developmental periods are longer in tropical and southern temperate bird species (but see also Geffen and Yom-Tov 2000).

The Mayfield success rates in the breeding process of *S. lugens* were 64.0% for the egg stage, 51.8% for the nestling stage, and 33.2% for both combined. Success rates of *S. boehmi* were even lower (60.3%, 32.2%, and 19.4%, respectively). Most studies of their congeneric relatives indicate higher success rates. Only three studies from the lower latitudes of the northern hemisphere indicate an overall nest success of around 34%, which is similar to *S. lugens* (*S. hortensis crassirostris* [TienShan], *S. leucomelaena* [Israel], and *S. nana nana* [Turkmeniya]). The low nest success of 19.4% of *S. boehmi* is unique in the genus and resulted mainly from high predation pressure.

The mean annual fecundities of the tropical *Sylvias* (2.3 and 1.4 fledglings per year per territory) are considerably lower than those of the temperate *Sylvias* (mean = 5.1 ± 1.4, min 3.0 [*S. nana deserti*], max 9.0 [*S. nana nana*], *n* = 17, calculated as average clutch size times number of successful broods per year). However, the real differences in fecundity are probably less distinct. My procedure for calculating the annual fecundity [illegible] the tropical *Sylvias* was based on territories. This results in a good estimate for the whole population because it includes pairs that were occasionally not breeding. Most breeding biology studies of temperate birds consider only breeding pairs. Thus, annual fecundities of temperate populations are probably slightly overestimated. Furthermore, I calculated temperate fecundities from the average clutch size times the number of successful broods per year. This procedure neglects partial failures and therefore results in an overestimate.

The time to independence from parental feeding was 37.5 days in *S. lugens* and 58.5 days in *S. boehmi*, while those temperate *Sylvia* species that have been studied, are usually reported to care for their young for 2–3, sometimes 4 weeks after fledging (*S. leucomelaena*). Tropical *Sylvias* seem to invest more in the survival of their offspring. They fed the young for longer periods; the young sometimes occupied parental territories for months, and *S. boehmi*, at times, fed fledglings of two generations simultaneously. These results support the studies of Geffen and Yom-Tov (2000), Langen (2000), Russell (2000), and others, who reported that the post-fledging care periods of birds from tropical and southern temperate regions are longer than those from northern temperate regions. The possible causes for extended post-fledging care are discussed above. A compensation for high nest predation and low annual fecundity seems possible because nest predation is certainly higher in the tropical *Sylvia* species (Martin 1996). However, the need for different lengths of training period for the young, caused by differences in the harshness of the habitats between arid tropical Africa and temperate regions, might also be responsible.

The crucial question, of whether this extended parental care leads to increased juvenile survival, still remains. In a preliminary analysis, Russell (2000) detected a significantly higher survival rate of Southern Hemisphere and tropical fledglings. The study of the post-fledging period is affected by the amalgamation of survival and dispersal. Nevertheless, the juvenile survival of 69% in *S. boehmi* in the first weeks of life exceeds the results of several studies in temperate passerines, which report post-fledging survival rates around 50% (e.g. Anders et al. 1997, Naef-Daenzer et al. 2001).

To conclude, the life histories of *S. lugens* and *S. boehmi* are characterized by small but numerous clutches, long developmental periods, high predation rates, low annual fecundity, long post-fledging care and high fledgling survival. It is a widely held assumption that these features are characteristic of life histories of tropical birds in general (Skutch 1985, Martin 1996, Ricklefs 2000a, b). In contrast to former studies, which often combined distantly related avian species, I showed that this pattern can be found within a single genus. Furthermore, interspecific differences between the two tropical species suggest that the post-fledging care period is especially flexible and may increase fledgling survival. However, understanding the factors that cause these differences will require further studies of life histories in temperate and tropical birds. In particular juvenile and adult survival data are required, which are rare in tropical and temperate species.

2.5 Summary

The investigation of factors that cause differences in life history traits between temperate and tropical birds is often hampered by a lack of knowledge about tropical species. Even within the well-known warblers of the genus *Sylvia*, which include resident species from temperate and tropical regions as well as migrants, there are few data from tropical species. I investigated the breeding biology of the tropical species *Sylvia lugens* and *S. boehmi* in a two-year study in Kenya. Both species had a clutch size of 2.0 and laid ca. 3.7 clutches per year. Breeding was characterized by long incubation periods (*S. lugens* 14.5 days, *S. boehmi* 15.0 days), long nestling periods (16.0 and 12.9 days, respectively), and high predation rates (Mayfield nest success *S. lugens* 33.2%, *S. boehmi* 19.4%). Annual fecundity was 2.3 fledglings in *S. lugens* and 1.4 fledglings in *S. boehmi*. After fledging, the young birds were fed for 37.5 days (*S. lugens*) and 58.5 days (*S. boehmi*) (time to independence) and they stayed in their parents' territory for days or weeks, even after feeding had stopped. Fledgling survival until independence was 55.4% in *S. lugens* and 69.2% in *S. boehmi*. In general, *S. lugens* and *S. boehmi* have smaller but more numerous clutches, longer developmental periods, higher nest predation rates, lower annual fecundity, and longer post-fledging care than their temperate congenerics.

3 Monthly survival of breeding African *Sylvia* warblers in a seasonal tropical environment

3.1 Introduction

Environmental conditions exert strong influence on life history traits of animals (Stearns 1992, Roff 2002). This is shown most evidently by geographic variation of life history traits in form of latitudinal gradients, as found for example in the clutch size of birds, which decreases from the Northern Hemisphere towards the tropics (Stresemann 1927–34, Geffen and Yom-Tov 2000, Cardillo 2002). Such latitudinal gradients present particularly challenging test-cases for understanding the relationship between environmental variables and life history traits because the crucial environmental variables and the mechanisms which produce the gradients are often unknown. Progress in understanding has been slow because the analysis has often been limited by insufficient empirical data, especially on tropical and Southern Hemisphere species (Ricklefs 2000a, b).

Seasonality and survival are suggested to be driving forces in the evolution of latitudinal life history gradients (Martin 1996). In the northern regions both food shortage and cold temperatures lead to high mortality and low population densities of birds in winter (Newton 1998). Low competition for food in spring enables the northern birds to nourish many young and selects for large clutches. Tropical and southern temperate regions are assumed to have more constant conditions. Clutch sizes are limited by constantly high food competition (Ashmole 1963, Ricklefs 1980). Another hypothesis suggests that severe periods in the northern regions reduce life expectancy of birds and therefore their residual reproductive value. Life history theory predicts that this leads to higher investment of adults in current reproduction yielding larger clutches (Murray 1985, Skutch 1985, Stearns 1992, Ghalambor and Martin 2001).

The explanation of latitudinal gradients in life history traits by the degree of seasonality of the environment assumes that northern habitats are generally more seasonal than tropical and southern temperate regions. Indeed, many data on life history traits of tropical birds were collected in the humid tropics, which have a comparably constant climate (e.g., Karr et al. 1990, Brawn et al. 1995, Johnston et al. 1997). However, not all tropical environments have a constant climate. The tropical savannahs of East Africa show pronounced seasonality, caused by distinct rainy and dry periods and accompanied by drastic changes in vegetation and insect abundance (Dingle and Khamala 1972, Sinclair 1978, Denlinger 1980, Wrege and Emlen 1991). Several studies revealed a significant impact of rainfall on breeding success, survival, or population densities of birds in arid regions (e.g., Zahavi 1971, Faaborg et al. 1984, Curry and Grant 1989, Peach et al. 1991, Baillie and Peach 1992). Thus, these seasonal tropical environments are an interesting study area to understand whether seasonality and survival are indeed the driving factors behind latitudinal gradients in life history traits.

To test whether avian survival is affected by the seasonality of rainfall I studied monthly survival of two East African *Sylvia* species (Aves: Passeriformes: Sylviidae) in a two-year mark-resighting study. The habitats of both species are characterized by rainy and dry seasons but they differ in the degree of seasonality and harshness. The following questions regarding adult survival were addressed: 1. Is monthly survival affected by dry periods? 2. Is annual adult survival lower in the species that lives in the harsher and more seasonal environment? If varying amounts of rainfall do have an effect on survival of the birds I expect a decrease in monthly survival during the dry periods and a lower annual survival rate of the birds in the region with stronger seasonality. The use of multistate (MS) models allowed to test for cost of breeding and to investigate transition probabilities between breeding states (breeding and non-breeding). In the discussion, I related the survival rates of the two species to their other life history traits such as clutch size and annual fecundity and compared the survival rates with those of their northern temperate congenerics and other tropical and northern temperate passerines.

3.2 Methods

3.2.1 Study species, sites, and data collection

Sylvia boehmi and *Sylvia lugens* are sparrow-sized warblers (weight 14 to 15g) from the family Sylviidae. They initially belonged to the genus *Parisoma*, but recent molecular studies showed that *Sylvia* and *Parisoma* form a monophyletic group. Consequently, the genus *Parisoma* was subsumed within *Sylvia* (Sibley and Ahlquist 1990, Blondel et al. 1996, Shirihai et al. 2001, Böhning-Gaese et al. 2003). Both species are endemic to East

Africa and have a fragmented distribution in savannahs and open woodlands. They mainly feed on insects, more seldom on small seeds and berries. In both species both sexes look alike. Breeding pairs are sedentary, defend their territories against conspecific intruders, and stay together from year to year (Shirihai et al. 2001, Schaefer et al. 2004).

Sylvia boehmi was investigated around 80 km south of Nairobi in Kajiado District, Rift Valley Province, Kenya. The observation area (01°34'S/36°28'E) was located along Magadi road close to Olorgesailie prehistoric site, at 1000 m above sea level. The climate in this region is characterized by strong seasonality in the form of two rainfall seasons, long droughts, and high temperatures (Fig. 3.1a, Brown and Britton 1980, Wrege and Emlen 1991). *Sylvia lugens* was observed on a private farm in the Kenyan Highlands, Rift Valley Province, around 15 km northwest of Nakuru town, at 2000 m above sea level (0°14'S/36°1'E). Climatic seasonality in this area is moderate. Annual rainfall is evenly distributed throughout the year with a drier period from December to February (Fig. 3.1b, Brown and Britton 1980, Wrege and Emlen 1991). Both study areas had meteorological facilities and daily rainfall was measured throughout the study.

Survival data were collected between October 2000 and August 2002 (*S. boehmi*) or July 2002 (*S. lugens*), respectively. For each species, the territorial pairs were tape-lured into mist-nets in 13 different territories. On capture, the birds were individually ringed with one metal and three colour rings. The ringing sites were retained during the whole study period. Birds that entered the population of breeding pairs in the course of the study, replacing ringed individuals, were ringed in two (*S. boehmi*) and three (*S. lugens*) subsequent ringing sessions (see Appendix 1 and Results for ringing occasions and number of ringed birds). Collection of resighting data was conducted at the end of each month following a fixed protocol with constant resighting effort. Individuals were searched for five minutes per territory on each of three consecutive days. If they were not detected within the five minutes, the song of a conspecific, which induced defensive behaviour, was played from a tape for two minutes. Now the birds were again searched for two minutes. If they were still not sighted, the tape was played for another two minutes at another position in the territory, followed by another two minutes of searching. The daytime of visits to each pair was randomised among days. Resighting data of the three days were pooled, i.e. if a bird was seen on at least one of the three days, it was considered alive and present in that month. Altogether, these 69 and 66 days of resighting effort yielded encounter histories of *S. boehmi* with 22 occasions and of *S. lugens* with 21 occasions.

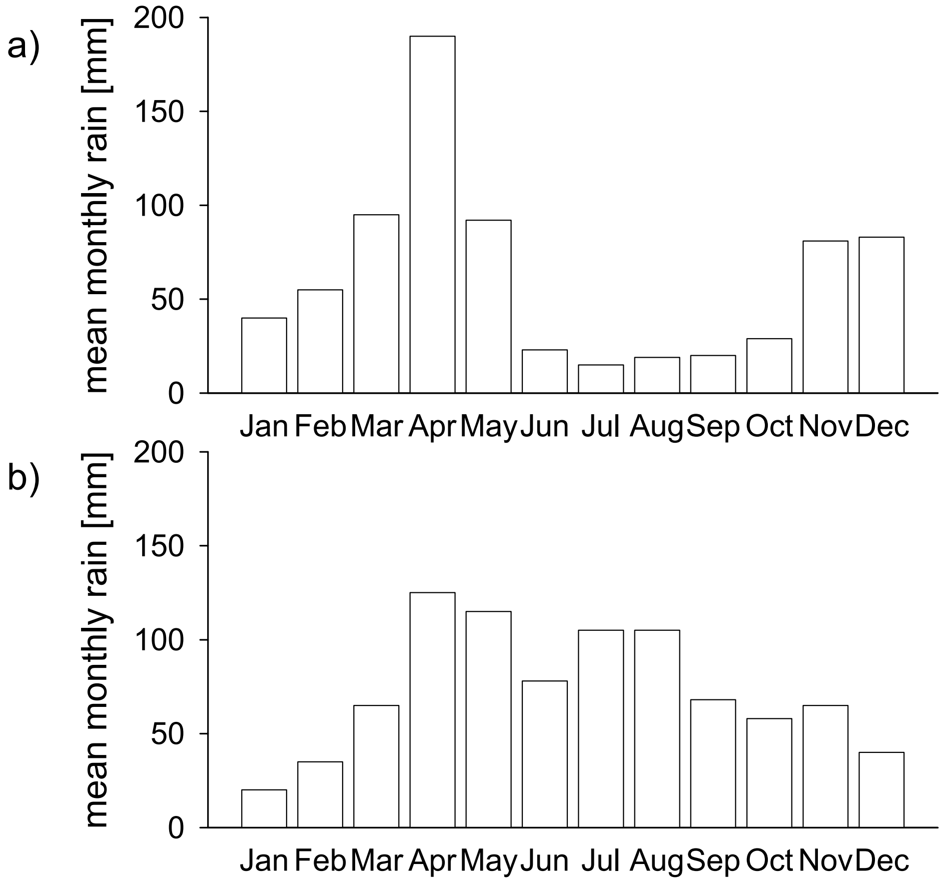

Figure 3.1 a) Average monthly rainfall from Naivasha, Magadi, Arusha, and Moshi in the vicinity of Olorgesailie, the study area of *S. boehmi*; **b)** average monthly rainfall in Nakuru in the vicinity of the study area of *S. lugens* over 56 years (Brown and Britton 1980, Wrege and Emlen 1991).

3.2.2 Survival analysis

Both species were analysed following the same procedure. Survival was estimated only for adult breeding birds, because the resighting effort focused on the territorial pairs. Individuals were included in the analysis, if they participated in at least one breeding attempt after they had been ringed. Individuals with a high emigration probability like fledglings and extra-territorial birds, which would have biased the survival data, were excluded from analysis. Fledglings stayed in their parents' territories for up to four (*S. boehmi*) and three months (*S. lugens*), but after that they usually emigrated from the study area (Schaefer et al. 2004). Adult extra-territorial birds were caught and ringed only in some rare occasions. These birds were either floaters, without an own territory, or intruders from neighbouring territories. They usually disappeared from the study area immediately after ringing and were not seen again.

It seems possible that costs of breeding affect survival of adult birds, if currently breeding pairs have an increased mortality, because they spend time and energy on the provisioning of their young, which, e.g. makes them more vulnerable to predators. This would increase mortality during the breeding season, which is also the rainy season. Consequently, any increase in mortality in the dry season, when birds are not breeding, would be more difficult to detect. In order to test for cost of breeding, individuals that were encountered on a resighting occasion were assigned to two states. If they incubated, fed nestlings, or fed fledglings on at least one day of the period between the current and the next resighting occasion they were classified to the breeding state. If they did not show any of these activities, they were classified to the non-breeding state. Information on the reproductive state of each individual for every month of the study period was entered into the encounter history matrix (Appendix 1).

The encounter histories, including information on the breeding state of resighted individuals, were analysed following the general methods of Lebreton et al. (1992), using multistate (MS) capture-recapture models. The MS models permit to test for and estimate time- and state-specific probabilities of apparent monthly survival (φ), resighting (p), and time-specific transition probabilities between breeding states (Ψ). For details see Nichols et al. (1994) and Nichols and Kendall (1995). Program MARK, Version 3.1 (White and Burnham 1999) was used for the analysis.

To assess the overall fit of my data to the Cormack-Jolly-Seber assumptions, I evaluated goodness-of-fit using the bootstrap procedure provided by MARK. The variance inflation factor, $\hat{c}$, was estimated by simulating 1000 bootstrap replications of the capture history data and dividing the observed model deviance by the mean of the simulated deviance. To avoid underestimation of $\hat{c}$ (White 2002), it was also estimated from chi-square divided by degrees of freedom as calculated by program RELEASE (as incorporated in MARK).

A model with full time dependence in survival, resighting and transition probabilities both for the breeding and the non-breeding state ($\varphi_{g,\,t}$, $p_{g,\,t}$, $\Psi_{g,\,t}$) was used as the global model. Starting from this, more general candidate models were developed and chosen prior to data analysis based on careful consideration of how rainfall and drought could affect survival, resighting, and transition between breeding states of the two *Sylvia* species, following the information-theoretic approach discussed by Burnham and Anderson (2002). First it was tested, whether there were differences in resighting and survival between breeding and non-breeding states. When the parameter estimates for survival are set the same for both states, the MS approach becomes more similar to a Cormack-Jolly-Seber analysis (Lebreton and Pradel 2002). Afterwards I looked for differences in transition probabilities between breeding states. At last, different survival models were tested. The best model supported by my data was selected using Akaike's Information Criterion, adjusted for small sample size and overdispersion ($QAIC_C$). Here, the best model is the one with the lowest $QAIC_C$. The Akaike weight w helps to better interpret the relative likelihood of a model and is considered as the weight of evidence in favour of a model being the best model in a given model set (Burnham and Anderson 2002).

To test whether seasonal changes in precipitation influence survival and transition probabilities, I developed different climate models that involve various discrete functions of rainfall (Table 3.1). Using the discrete functions allows building models, which differ in respect of extent and time lag in which dryness might influence survival and breeding activity of the birds. The pattern of rainfall in the two study areas was converted into a pattern of "severe" months, with low or no rainfall, and "average" months, with higher rainfall. Criteria, whether a month was considered to be "severe" or not, differ among models (Table 3.1), yielding different patterns of seasonality in the habitat. For example, in function 1 a month was classified to be "severe" if it was dryer than the average month. In function 6 a month was classified to be "severe" if it was at least the third consecutive month of less than 50% of the average monthly rainfall. Function 7 assumes increasing severity with every consecutive month of rainfall below average. Survival and transition parameters were modelled following the different rainfall functions, as a constant, and as a function of month, which allows the estimates to vary from month to month independently of rainfall. In my model set, all models except the global model had a constant resighting probability (p), which differed between breeding states. The resighting rate was very high and hardly varied from month to month throughout the study.

Table 3.1 List of 8 investigated climate functions with different criteria for “severe” months (see Methods). Application of the criteria results in discrete functions of rainfall, which were used to model survival and transition probabilities between breeding stages. In *S. boehmi* no. 3 and 4, and no. 5 and 6 resulted in identical functions. In *S. lugens* no. 4 and 6 resulted in constant functions and no. 8 was identical to no. 2.

no.	model criteria for a “severe” month
1	rainfall of current month below monthly average
2	rainfall of current month below 50% of monthly average
3	rainfall of current and previous month below monthly average
4	rainfall of current and previous month below 50% of monthly average
5	rainfall of current and the two previous months below monthly average
6	rainfall of current and the two previous months below 50% of monthly average
7	increasing severity after one, two, and three or more consecutive months with rainfall below monthly average
8	increasing severity after one, two, and three or more consecutive months with rainfall below

3.3 Results

3.3.1 Goodness-of-Fit

During the study, 32 breeding territorial individuals of *S. boehmi* were ringed: 14 in May 2000, 9 in March 2001, and 9 in September 2001 (Appendix 1). 23 individuals of *S. lugens* were ringed: 12 in May 2000, 2 in November 2000, 4 in March 2001, and 5 in December 2001 (Appendix 1). The bootstrap approach detected a slight overdispersion (*S. boehmi*, $\hat{c} = 1.261$; *S. lugens*, $\hat{c} = 1.630$) in the data set, which I judged to be not a serious violation of capture-recapture assumptions. Program RELEASE resulted in lower $\hat{c}$-values, but data were not sufficient for all calculations. The dataset was therefore adjusted for overdispersion using the bootstrap results.

3.3.2 *Sylvia boehmi*

Starting from the global model (Table 3.2, model 20) in *S. boehmi*, models improved if survival and resighting probability were set constant (model 12). When I looked for differences in resighting and survival between breeding states I found that setting the resighting probabilities to be the same for both breeding states made the model worse (model 13), while setting survival probabilities to be the same improved it slightly ($\Delta QAIC_C = 1.85$) (model 11). Modelling transition rates between breeding states using discrete functions of rainfall (Table 3.1) resulted in decreasing $QAIC_C$ values, especially using function 1 (Table 3.2, model 2) and 7 (Table 3.2, model 1). The best model (φ, p_g, $\Psi_{g,\ 7}$) did not improve any further when finally survival was modelled using the different rainfall functions. This model assumed constant survival between months, i.e. no effect of rainfall on survival. It also had constant resighting probability, which differed between breeding states, and a changing transition probability with increasing dryness after one, two, and three or more consecutive months with rainfall below monthly average. Although, based on AIC_C weights *w*, the best model was 2.5 times more likely than models 3 and 4, which do assume an effect of rainfall (Table 3.2), these models had approximately equal weight in the data ($\Delta QAIC_C \leq 2$; Burnham and Anderson 2002).

To detect any variation in survival caused by seasonality of rainfall, I compared monthly rainfall with the monthly survival rate estimated from model (φ_t, p_g, $\Psi_{g,\ 7}$) (Table 3.2, model 15), which is the best model of those with monthly varying survival probabilities, and from a model averaging approach. The model averaging approach accommodates model selection uncertainty in the survival estimates. The best models concerning transition probability and survival, models 1 and 3, were used to estimate the average survival rate. Estimates derived from model (φ_t, p_g, $\Psi_{g,\ 7}$) showed some variation, but no connection to rainfall (Fig. 3.2). The monthly survival rate derived from model averaging of models 1 and 3 was almost constant throughout the whole study period, ranging from 0.971 ± 0.010 (standard error, s.e.) to 0.974 ± 0.012 (s.e.). There was no decrease in survival during the dry periods, rather a slight increase for *S. boehmi*.

The average monthly survival, resighting, and transition estimates derived from the best model (φ, p_g, $\Psi_{g,\ 7}$) for *S. boehmi* were as follows: $\varphi = 0.972 \pm 0.009$ (s.e.), 95% confidence interval (CI) = [0.947, 0.986]; $p_{\text{non-breeding}} = 0.838 \pm 0.031$, CI = [0.769, 0.890], $p_{\text{breeding}} = 1.000 \pm 0.00$, CI = [1.000, 1.000]. The probability of a bird to switch from the breeding to the non-breeding state ($\Psi_{\text{b to n}}$), i.e. to stop breeding, increased with increasing number of consecutive dry months. In months with more than average rainfall $\Psi_{\text{b to n}}$ was

0.128 ± 0.039. In the first month with rainfall below average $\Psi_{\text{b to n}}$ was 0.370 ± 0.062, in the second month 0.343 ± 0.118, and in the third or more consecutive dry month 0.803 ± 0.141. Consequentially, the probability to start breeding ($\Psi_{\text{n to b}}$) decreased with increasing dryness. In wet months $\Psi_{\text{n to b}}$ was 0.545 ±0.057. In the first, second, and third or more dry month it was 0.086 ± 0.066, 0.000 ± 0.000, and 0.136 ± 0.047. Monthly survival rate raised to the power of twelve yielded an annual survival rate of 0.712 for *S. boehmi*.

Table 3.2 Multistate models to assess the effect of rainfall on apparent monthly survival (φ), resighting probability (p), and transition probability between breeding states (Ψ) for *S. boehmi.* Akaike's information criterion corrected for small sample size and overdispersion ($QAIC_C$), $QAIC_C$ differences ($\Delta QAIC_C$), $QAIC_C$ weights (*w*), number of parameters (*K*), and deviance. Subscript g indicates two breeding states, t full time dependence, number refers to climate function as described in Table 3.1.

model		$QAIC_C$	$\Delta QAIC_C$	*w*	*K*	deviance
1	φ, p_g, $\Psi_{g,7}$	559.00	0.00	0.28	11	429.1
2	φ, p_g, $\Psi_{g,1}$	560.01	1.01	0.17	7	438.5
3	φ_3, p_g, $\Psi_{g,7}$	560.94	1.94	0.11	12	428.9
4	φ_2, p_g, $\Psi_{g,7}$	560.95	1.96	0.11	12	428.9
5	φ_1, p_g, $\Psi_{g,7}$	561.04	2.05	0.10	12	429.0
6	φ_5, p_g, $\Psi_{g,7}$	561.08	2.08	0.10	12	429.1
7	φ, p_g, $\Psi_{g,8}$	562.47	3.47	0.05	11	432.6
8	φ, p_g, $\Psi_{g,2}$	562.64	3.64	0.05	7	441.2
9	φ_7, p_g, $\Psi_{g,7}$	564.59	5.59	0.02	14	428.3
10	φ_8, p_g, $\Psi_{g,7}$	564.97	5.97	0.01	14	428.7
11	φ, p_g, $\Psi_{g,t}$	566.88	7.88	0.01	45	357.5
12	φ_g, p_g, $\Psi_{g,t}$	568.73	9.73	0.00	46	356.8
13	φ_g, p, Ψ_t	583.94	24.94	0.00	45	374.6
14	φ, p_g, $\Psi_{g,3}$	584.29	25.29	0.00	7	462.8
15	φ_t, p_g, $\Psi_{g,7}$	588.11	29.12	0.00	31	413.3
16	φ, p_g, $\Psi_{g,5}$	591.88	32.88	0.00	7	470.4
17	φ_g, p_g, Ψ_g	611.54	52.54	0.00	6	492.1
18	$\varphi_{g,t}$, p_g, $\Psi_{g,t}$	660.58	101.59	0.00	86	331.2
19	$\varphi_{g,t}$, p_g, Ψ_g	678.53	119.53	0.00	46	466.6
20	$\varphi_{g,t}$, $p_{g,t}$, $\Psi_{g,t}$	795.57	236.57	0.00	126	312.3

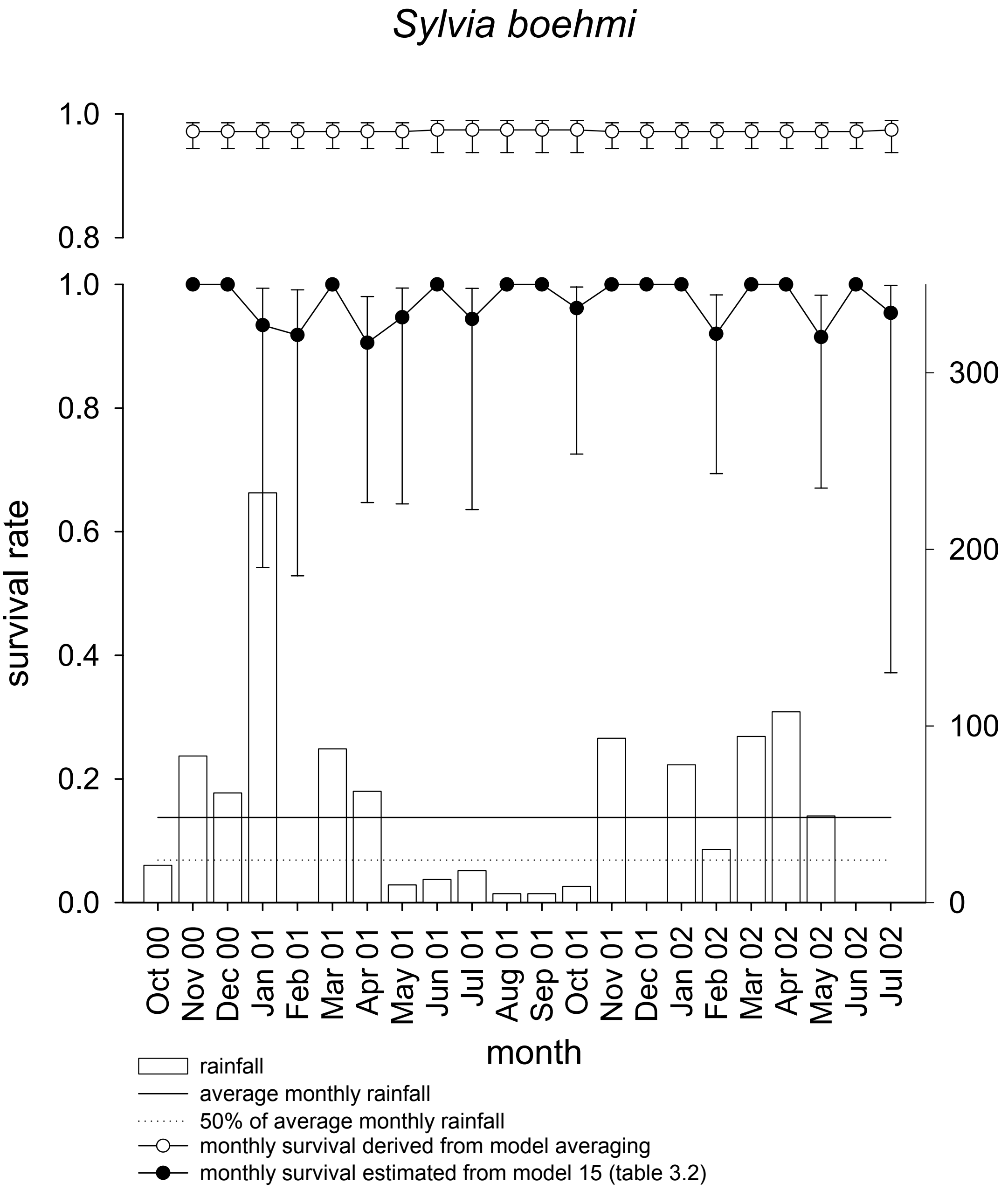

Figure 3.2 Monthly survival estimates (with 95% confidence intervals) of *S. boehmi* and monthly rainfall during the study period. Neither monthly survival estimated from the best model with monthly varying survival rate ((φ_t, p_g, $\Psi_{g,7}$), Table 3.2, model 15; lower line with black symbols), nor "averaged" survival estimates (upper line with white symbols) varied with rainfall.

3.3.3 *Sylvia lugens*

In *S. lugens* models improved when survival, resighting, and transition probability were set constant (Table 3.3, model 31). Equal resighting probabilities for both breeding states were not supported (model 33). Equal survival probabilities yielded very slight improvement ($\Delta QAIC_C = 0.07$) (model 30). To decide, whether costs of breeding are supported by model 31, I compared survival estimates of breeding and non-breeding individuals estimated from this model. Monthly survival of non-breeding birds was lower than that of breeding birds (0.97 against 0.92). Thus, reproductive costs were not detectable in the data set and modelling was therefore continued with the slightly better model 30, which assumed constant survival of both breeding states. The transition rates between breeding states were modelled best using rainfall function 3 (Table 3.1), making model (φ, p_g, $\Psi_{g,\,3}$) (Table 3.3, model 21) the best model. This model was not improved further when survival was modelled, although models 22 and 23, which incorporate rainfall functions 1 and 2, had equal weight in the data ($\Delta QAIC_C \leq 2$). As in *S. boehmi* the best model in *S. lugens* assumed no effect of rainfall on survival. It also had constant resighting rates with differences between breeding states. Transition probabilities varied with rainfall of the current and previous month. Again, two models, which do assume an effect of rainfall on survival, were of similar likelihood as the model with constant survival. Model averaging estimates of monthly survival (derived from models 21 and 22) varied slightly between 0.944 ± 0.025 (s.e.) and 0.967 ± 0.022 (s.e.) with broadly overlapping confidence intervals (Fig. 3.3). Monthly survival rate estimated from model (φ_t, p_g, $\Psi_{g,\,3}$) (Table 3.3, model 34) in comparison to monthly rainfall is shown in Figure 3.3.

For *S. lugens*, estimates from the best model (φ, p_g, $\Psi_{g,\,3}$) were $\varphi = 0.954 \pm 0.017$, CI = [0.906, 0.978]; $p_{\text{non-breeding}} = 0.898 \pm 0.039$, CI = [0.793, 0.953], $p_{\text{breeding}} = 1.000 \pm 0.00$, CI = [1.000, 1.000]. The probability of a bird to stop breeding was low when the current and the previous month had more than average rainfall ($\Psi_{\text{b to n}} = 0.172 \pm 0.048$) and higher when the two months had less than average rain ($\Psi_{\text{b to n}} = 0.400 \pm 0.125$). Conversely, $\Psi_{\text{n to b}}$ was 0.401 ± 0.079 if the current and/or previous months were wetter than average and 0.090 ± 0.055 if both months were dryer than average. Annual survival of *S. lugens* calculated from monthly φ was 0.572.

Table 3.3 Multistate models to assess the effect of rainfall on apparent monthly survival (φ), resighting probability (p), and transition probability between breeding states (Ψ) for *S. lugens.* Akaike's information criterion corrected for small sample size and overdispersion ($QAIC_C$), $QAIC_C$ differences ($\Delta QAIC_C$), $QAIC_C$ weights (*w*), number of parameters (*K*), and deviance. Subscript g indicates two breeding states, t full time dependence, number refers to climate function as described in Table 3.1.

model		$QAIC_C$	$\Delta QAIC_C$	*w*	*K*	deviance
21	$\varphi, p_g, \Psi_{g,3}$	253.09	0.00	0.28	7	195.3
22	$\varphi_1, p_g, \Psi_{g,3}$	253.22	0.14	0.26	8	193.3
23	$\varphi_2, p_g, \Psi_{g,3}$	254.22	1.13	0.16	8	194.3
24	$\varphi_3, p_g, \Psi_{g,3}$	255.21	2.13	0.10	8	195.3
25	$\varphi_5, p_g, \Psi_{g,3}$	255.22	2.14	0.10	8	195.3
26	$\varphi_7, p_g, \Psi_{g,3}$	256.53	3.44	0.05	10	192.2
27	$\varphi, p_g, \Psi_{g,2}$	257.64	4.56	0.03	7	199.9
28	$\varphi, p_g, \Psi_{g,7}$	259.37	6.28	0.01	11	192.9
29	$\varphi, p_g, \Psi_{g,5}$	260.25	7.17	0.01	7	202.5
30	φ, p_g, Ψ_g	260.78	7.69	0.01	5	207.2
31	φ_g, p_g, Ψ_g	260.85	7.76	0.01	6	205.2
32	$\varphi, p_g, \Psi_{g,1}$	262.14	9.05	0.00	7	204.3
33	φ_g, p, Ψ_g	263.03	9.95	0.00	5	209.5
34	$\varphi_t, p_g, \Psi_{g,3}$	283.37	30.28	0.00	26	181.2
35	$\varphi_g, p_g, \Psi_{g,t}$	297.67	44.58	0.00	44	145.1
36	$\varphi_{g,t}, p_g, \Psi_g$	336.05	82.96	0.00	44	183.5
37	$\varphi_{g,t}, p_g, \Psi_{g,t}$	424.17	171.08	0.00	82	124.9
38	$\varphi_{g,t}, p_{g,t}, \Psi_{g,t}$	661.71	408.62	0.00	120	114.4

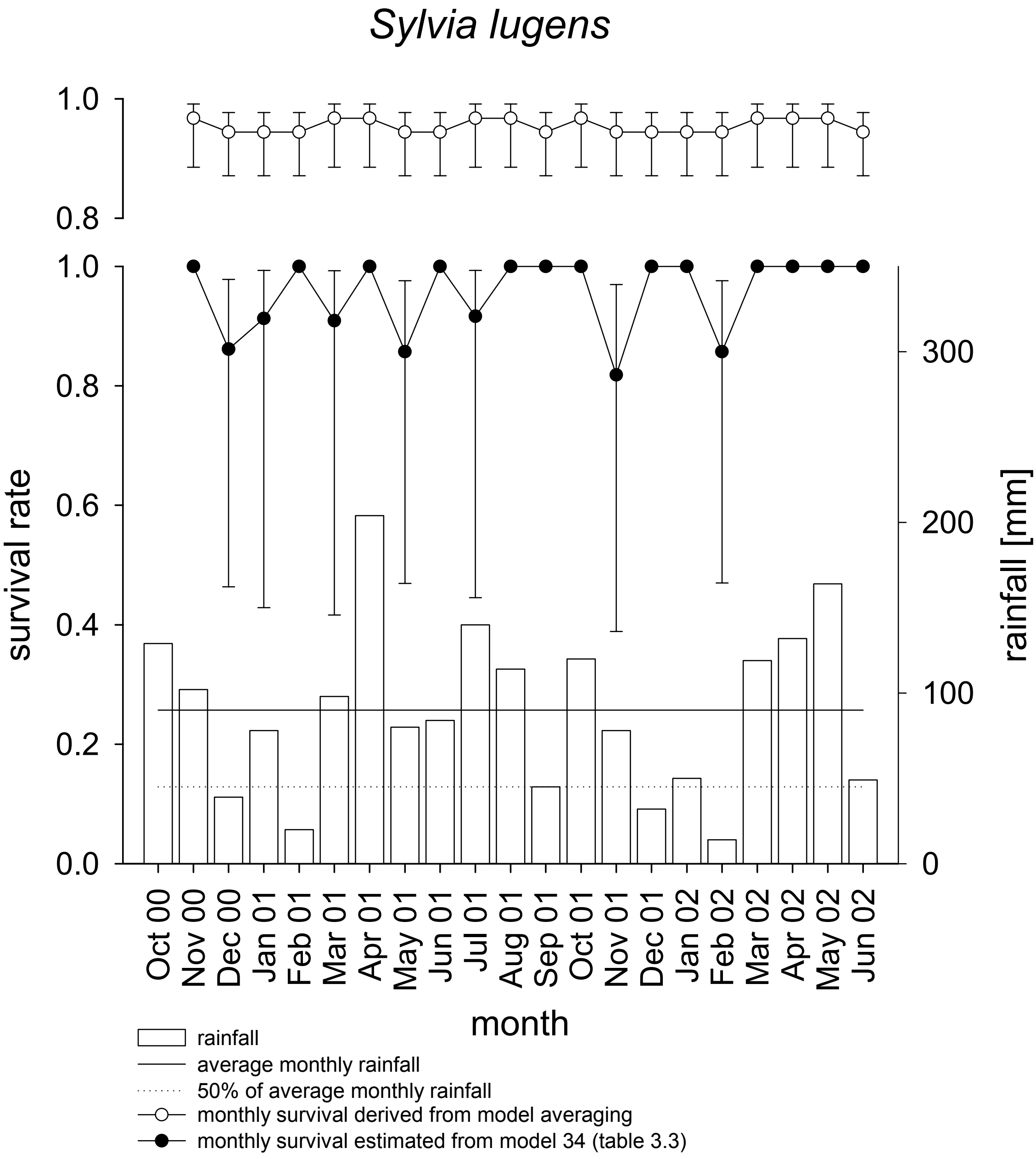

Figure 3.3 Monthly survival estimates (with 95% confidence intervals) of *S. lugens* and monthly rainfall during the study period. Monthly survival estimated from the best model with monthly varying survival rate ((φ_t, p_g, $\Psi_{g,\ 3}$), Table 3.3, model 34; lower line with black symbols) did not follow the rainfall pattern. “Averaged” survival estimates (upper line with white symbols) varied very slightly with rainfall.

3.4 Discussion

The analysis did not support my initial hypotheses. The monthly survival probability of the two African warbler species was not (*S. boehmi*) or only very slightly (*S. lugens*) affected by rainfall in their habitat. *Sylvia boehmi*, the species living in the harsher, more seasonal environment, had a clearly higher annual survival rate than *S. lugens*, living in the less seasonal environment.

3.4.1 Methodology

In my study I could not distinguish between mortality and emigration. Therefore, my survival estimates are apparent survival rates and must be considered minimum values. However, I believe that emigration was not common and usually involved the loss of the partner. In the two years of study only two emigration incidences in *S. boehmi* were observed, when an individual, which had been breeding at one site, was found breeding with a new partner in another territory.

On the other hand, my resighting study might overestimate the mean survival rate of an individual in the population because I examined only territorial, breeding birds and excluded non-territorial floaters. Such non-breeding individuals were shown to have lower resighting and survival probabilities (Nichols et al. 1994, Cam et al. 1998). I do not have direct information on the abundance of floaters in the study sites. Additional individuals were observed very rarely in the territories, but replacement of dead ringed birds by unringed birds often took only a few days, showing the omnipresence of floaters.

In this study, I also estimated annual survival of the two tropical warbler species, although the observation period lasted only for two years. This is usually considered too short to yield a reliable average annual survival rate, because variation in conditions between years can lead to pronounced variation in survival rates (e.g., Piper 2002). Nevertheless, I consider the results reliable because data for the study period were very detailed and I had high resighting probabilities. For both study sites there was no evidence that the study years were particularly wet or dry or showed any other unusual climatic conditions. Finally, the estimated survival rates fit very well to the other life history traits of the species (Schaefer et al. 2004, see below).

3.4.2 Resighting and transition probability

The high resighting efforts yielded high but different encounter rates for breeding and non-breeding birds of both species. Birds were almost certain to be found when the place of their nest was known and they did not make far trips when they had fledglings. In contrast, territories were larger and birds were less vocal in the non-breeding season, making it more difficult to find them. Transition probabilities clearly depended on rainfall. The rainfall function included in the best model indicates that *S. boehmi* reacted more sensitive to rainfall than *S. lugens*. Clear changes in transition probabilities appeared after the first wet or dry month in *S. boehmi*, while *S. lugens* waited for two rainy or dry months until breeding started or stopped, respectively.

3.4.3 Cost of breeding analysis

The multistate modelling approach showed that breeding individuals of *S. boehmi* and *S. lugens* did not have a reduced survival probability in comparison to non-breeding individuals. However, I want to emphasise that all individuals included were territorial birds that bred at some time during the study. Non-reproducing birds, like non-territorial, non-breeding floaters, were not included. Therefore, this analysis was able to detect only short-term costs of reproduction, caused by stress-related reduced attentiveness, exhaustion, or high risk-taking. Long-term effects caused by costs of repeated egg production, feeding efforts or defence of the territory could not be detected. In contrast to the assumption that breeding reduces survival, there was some evidence for lower survival of non-breeding individuals in the *S. lugens* data set. This may be caused by a lower quality of non-breeders (Cam et al. 1998, Sandercock et al. 2000).

3.4.4 Survival in dry and wet periods

In *S. boehmi*, survival hardly varied throughout the 22 months of the study, showing no decrease even after several months of drought. Further support for high survival probabilities of *S. boehmi* in dry periods comes from a pre-study: In May 2000, five months before the main study started, 18 individuals of *S. boehmi* were colour-ringed at the study site. The period from May to September 2000 was extremely dry because only 80 mm of rain had fallen in the main rainy season from January to May 2000. In 2001 and 2002 it had been 392 mm and 357 mm respectively in the same period. As a consequence, a great proportion of the cattle of the local Maasai residents starved, so that food aid programs were initiated by national and international organisations. *Sylvia boehmi* reacted to the drought by suspending its breeding season, but in October, when rain set in again and breeding began, 15 of the 18 ringed individuals were still alive and present. Annual survival rate calculated over this period and these 18 individuals (including potential fledglings, floaters or other non-breeding individuals) was 65%, indicating no effect of the severe drought on the survival of *S. boehmi*.

In *S. lugens* survival seems to vary slightly with rainfall, but pronounced seasonal variation of survival was not detected. The confidence intervals of the monthly survival estimates overlap broadly and the effect size derived from the model averaging approach, i.e. the difference between maximum survival in wet months (0.967 ± 0.022) and minimum survival in dry months (0.944 ± 0.025), of 0.023 is very small.

Consequently, and contradicting the initial hypothesis, the seasonality of the environment did not influence monthly survival of the two *Sylvia* warblers. Their survival was constant throughout the year, as one would expect for tropical birds in a climatically constant environment.

3.4.5 Survival in environments of weak and strong seasonality

Although the habitat of *S. boehmi* was harsher and more seasonal than that of *S. lugens*, the annual survival rate of *S. boehmi* was clearly higher (71.2%) than that of *S. lugens* (57.2%). This contradicts many studies, which give evidence for decreased annual adult survival in habitats with more seasonal climatic conditions (Newton 1998). Peach et al. (2001) found that in passerines, southern and tropical African insectivores have higher survival rates than European insectivores and also than African granivores. They suggest that seasonality of food availability is responsible for these differences. However, in my study annual survival is not linked to seasonality in the predicted way, again challenging my hypothesis.

While I did not find a link between seasonality and survival, there is good evidence for a link between survival and the other life history traits of the two warblers. *Sylvia boehmi* has a low annual fecundity of 1.4 fledglings per year, resulting from a clutch size of two eggs and a low nest success rate (19.4%) (Schaefer et al. 2004). Furthermore, it has long post-fledging care (time to independence of fledglings 58.5 days), supporting high fledgling survival. *Sylvia lugens* also lays two eggs but has a higher annual fecundity (2.3 fledglings per year) due to its higher nest success rate (33.2%). It also shows long post-fledging care (37.5 days), but shorter than in *S. boehmi* and with lower fledgling survival. To summarize, *S. boehmi* has a low adult mortality rate and raises a small number of well-attended fledglings, while *S. lugens* has a higher adult mortality rate and more, less well-attended young. In both species, survival and the other life history traits are linked as suggested by life history theory, strongly supporting the assumption that survival is a key-parameter in life history evolution (Murray 1985, Stearns 1992).

3.4.6 Comparison of the African *Sylvias* to other passerine species

I compared the survival rate of *S. boehmi* and *S. lugens* with those of temperate *Sylvia* species using data from Cramp (1992) and those of tropical and northern temperate passerines from several comparative studies (Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997, Peach et al. 2001). Only a qualitative comparison can be provided here, because two species are too few for a rigorous statistical analysis, especially if body size and phylogeny are taken into account.

The survival rate of *S. boehmi* lies above the 95th percentile of survival rates of its temperate congenerics and of the temperate birds from two European and one North American data set (Fig. 3.4). Compared to survival rates from Malawi, Trinidad, Panama, and Puerto Rico it lies above the median of all but below the 75th percentile of three of the four data sets. *Sylvia lugens*'s survival rate is also higher than that of the temperate *Sylvias*, but it lies between the median and the 75th percentile of two temperate data sets and below the 25th percentile of two tropical data sets. Thus, *S. boehmi*'s survival rate can be clearly assigned to the tropical birds, while *S. lugens's* survival rate lies between the northern temperate and the tropical data sets. Still, the survival rates of both species are comparatively high, especially if the small size of the tropical *Sylvias* (14 to 15g) is taken into account.

Regarding the other life history traits, the two African species share several characteristics that can be considered to be typical of tropical birds. Both have small clutches, high nest predation rates, and long post-fledging care. These traits are clearly different from average characters of temperate birds (Skutch 1985, Martin 1996, Geffen and Yom-Tov 2000, Russell 2000, Cardillo 2002). Thus, survival and the other life history traits of the two African *Sylvias* resemble rather those of tropical birds.

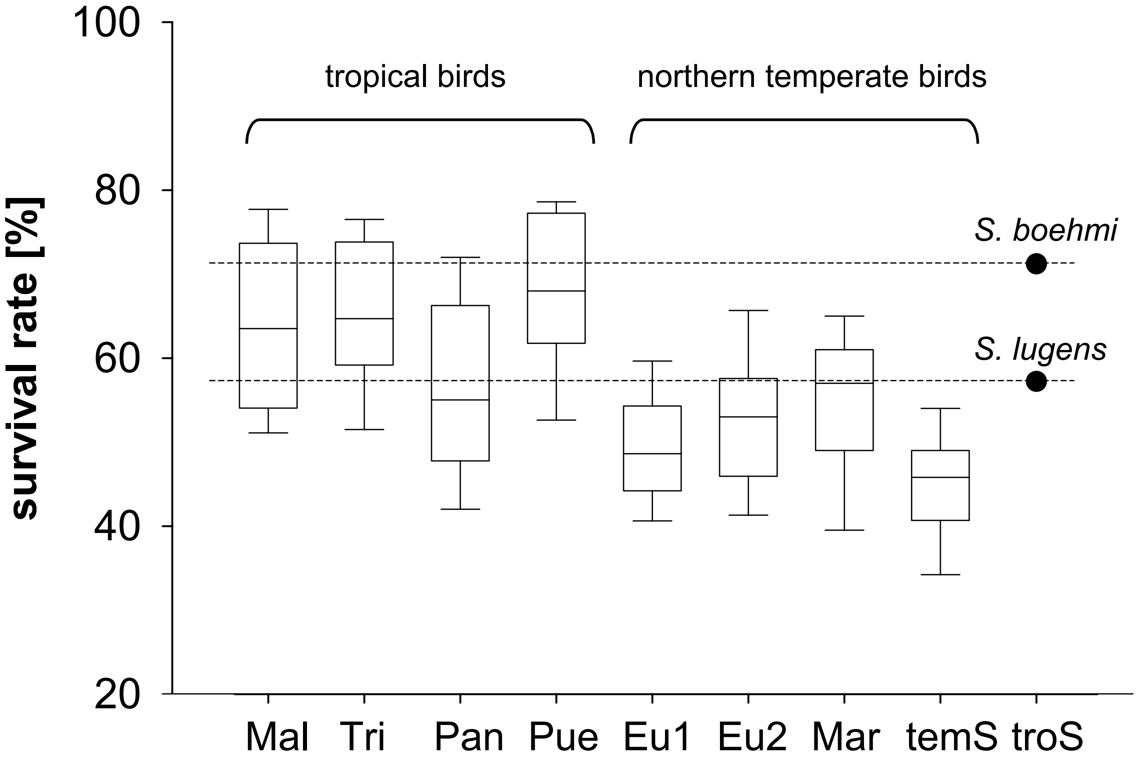

Figure 3.4 Comparison of survival rates of *S. boehmi* and *S. lugens* to those of birds from tropical and northern temperate regions. Mal: Malawian passerines (*n* = 31)[a]; Tri: Trinidadian passerines (*n* = 17)[b]; Pan: Panamanian tropical forest birds (*n* = 25)[c]; Pue: Puerto Rican birds (*n* = 9)[d]; Eu1: European passerines (*n* = 50)[a]; Eu2: European passerines (*n* = 31)[b]; Mar: temperate forest birds from Maryland (*n* = 10)[c]; temS: temperate *Sylvia* species (*n* = 7)[e]; troS: tropical *Sylvia* species from this study. Given are median value, 25th and 75th percentile, and 5th and 95th percentile. Data taken from: a) Peach et al. (2001); b) Johnston et al. (1997); c) Karr et al. (1990); d) Faaborg and Arendt (1995); e) Cramp (1992).

To conclude, the life histories of *S. boehmi* and *S. lugens*, which live in seasonal tropical environments with rainy and dry seasons, must be considered to be typically “tropical”. Rainfall had a very slight effect on the monthly survival rate and annual survival was not lower in the species that lived in the more seasonal environment. The annual survival rates and the other life history traits were more similar to those of passerine species from other tropical regions, including the humid tropics, than those of temperate species. Thus, this study shows that latitudinal gradients in life history traits of birds are very general. They apply not only to the humid tropics but also to arid, seasonal tropical regions.

How can this contradiction to my initial hypotheses be explained? First, I cannot entirely eliminate the possibility that I failed to detect time variation in seasonal survival because the sample size was small and survival estimates were high, due to short sampling intervals. However, I think that the continuously high resighting efforts, which resulted in extremely high resighting probabilities of $p = 0.84$ to 1.0 have reduced this problem. There is the possibility that the driving force behind latitudinal gradients in life history traits may not be the degree of seasonality but other factors that vary with latitude. Climatic factors like solar radiation, temperature, and potential evapotranspiration as well as ecological factors like predation pressure have also been shown to influence species traits and communities (Begon et al. 1996, Brown and Lomolino 1998). Alternatively, the East African savannahs may be less seasonal than the northern temperate regions. This may be mainly due to only little seasonal variation in temperature. However, the distinct breeding seasons of *S. boehmi* and *S. lugens* during periods of high rainfall demonstrate that the birds perceive the changes of conditions in their habitats. The fact that survival is not affected by rainfall provides evidence that the dry season might be not as harsh as often thought. Reasons may be that (1) the lower food level in the dry period is non-limiting, while there is a surplus supply in the wet periods; (2) the fluctuation of insect abundance is not as strong as some studies suppose (Morel 1973, Oatley 1982, Lack 1986); or (3) birds modify their foraging behaviours and compensate declines in abundance of one group of insects by switching to other groups or to seeds, fruits or nectar. Such modified foraging was observed by Lovette and Holmes (1995) and also in *S. boehmi* in this study. Long-term studies on survival, behaviour, and food abundance are needed to understand how the birds manage to survive long droughts and how seasonal the tropical savannahs really are.

3.5 Summary

Latitudinal gradients of life history traits in animals are thought to be shaped by environmental variables. For example, the increase of avian clutch size from the tropics towards the northern temperate regions is suggested to be caused by lower survival of adult birds in the north due to increasing seasonality of the environment. However, the tropical savannahs of East Africa show pronounced seasonality of rainfall causing distinct rainy and dry seasons. This raises the question, whether survival and other life history traits of birds living in these tropical savannahs are influenced by this seasonality, making them more similar to northern temperate species. I used two-year monthly resighting data, a multistate modelling approach, and the program MARK to test whether survival, transition probabilities between breeding states, and other life history traits of two resident Kenyan *Sylvia* species (Aves: Passeriformes: Sylviidae) are shaped by seasonality of rainfall in their environment. Contradicting my hypotheses, the two species showed only very slight influence of seasonality of rainfall on their survival. Survival in the dry months was not lower than in the rainy months. The species in the more seasonal environment (*S. boehmi*, annual survival 71.2%) survived better than the one in the more constant environment (*S. lugens*, 57.2%). Survival rates and the other life history traits of the two species were linked and resembled those of tropical passerines closer than those of temperate birds. The latitudinal gradient of life history traits in birds can therefore be considered to be very general because it holds for both, constant humid and seasonal arid tropics. This implies that either seasonality is not the driving force behind latitudinal gradients in life history traits or the East African savannahs are not as seasonal as they appear.

4 Nest predation is hardly affected by parental behaviour and nest site in two African *Sylvia* warblers

4.1 Introduction

Nest predation is an important factor for the evolution of the life histories of birds (Martin 1996). In order to reduce the risk of nest predation birds have been shown to adapt their nest size (Møller 1990), nest site (e.g. Martin and Roper 1988), and nest attendance (e.g. Rabenold 1984, Hayes and Robertson 1989). Increased predation rates are thought to lead to small clutch sizes (Doligez and Clobert 2003) through selection for multiple renesting attempts (bet-hedging strategy; Slagsvold 1982, 1984, Martin 1995, McCleery et al. 1996), or reduced parental feeding activity (Skutch 1949, 1985, Martin et al. 2000b).

Skutch (1949) argued that parents evolve low nest visitation rates when the number of predators, which use those nest visits as clues to find nests, is high. Consequently, the number of young that can be nourished is diminished. Following Skutch's hypothesis, this mechanism might cause the smaller clutches of birds in the tropics and the Southern Hemisphere in comparison to the Northern Hemisphere. In tropical habitats, where predators are more abundant than in the north, species might limit their food delivery rate in order to reduce the risk of nest predation (Martin 1996).

Skutch's hypothesis presumes that nest predation increases with parental nest visitation rate. In the past, one approach to test this relationship was to compare the predation rate in the incubation stage to that in the nestling stage (Roper and Goldstein 1997, Farnsworth and Simons 1999). It was assumed that the predation rate is higher in the nestling than in the incubation stage, because parental nest visitation rate clearly increases after hatching of the young. However, a number of studies demonstrated that the predation rate was the same in both nesting stages and the results were interpreted as contradicting Skutch's hypothesis (Roper and Goldstein 1997, Farnsworth and Simons 1999).

Martin et al. (2000b) challenged these earlier studies, revealing that a similar predation rate in the incubation and the nestling stage must not necessarily contradict a relationship between nest visitation rate and predation, but may be a consequence of nest site effects. Nest site effects occur, when predators eliminate poorly concealed nests early in the breeding process (Ricklefs 1969, Willis 1973, Gottfried and Thompson 1978, Martin et al. 2000b). This causes a high predation rate during incubation although parental activity is low. When nest site effects were separated from parental activity effects, nest predation was shown to increase with parental activity (Martin et al. 2000b).

In a different approach, Martin et al. (2000a) compared nest visitation rates of successful nests with nests that suffered predation, using data from their study sites in Arizona and Argentina. Again, they supported Skutch's hypothesis showing that birds with greater activity at the nest face greater predation risk during incubation than birds with lower activity levels.

A further factor, which is thought to influence nest predation, is nest attentiveness. Nest attentiveness is passive nest defence by sitting on the nest and serves to hide eggs or nestlings, camouflage the nest, or discourage potential predators (Montgomerie and Weatherhead 1988, Martin 1992, Weidinger 2002). Several studies gave evidence that birds can reduce predation rates through nest attendance (see references given in Martin 1992). Others showed that artificial, unattended nests suffer higher predation rates than active, attended nests (Cresswell 1997b, Wilson et al. 1998, Weidinger 2002).

Altogether, detailed studies of the relationship between parental behaviour and nest predation as underlying Skutch's hypothesis are still rare (Martin et al. 2000b). To my knowledge, no study has been published so far on Afrotropical birds, although any effects of parental behaviour on predation should be developed there. That is, because predation rates in the Afrotropis are considered to be especially high, even in comparison to other tropical regions (T. E. Martin, personal communication). An earlier study of the breeding biology of the two tropical warblers *Sylvia boehmi* and *Sylvia lugens* in Kenya revealed high predation rates and small clutches of two eggs (Schaefer et al. 2004). Here, I investigate the effects of parental behaviour on the predation rate in the two species. I test for nest site effects by looking for a decline of the nest predation rate in the course of the incubation period. I study effects of nest visits and nest attentiveness by testing 1. if daily nest predation rate is influenced by daily nest visitation rate and nest attendance; and 2. if successful and depredated nests differ in nest visitation rate and nest attendance.

4.2 Methods

4.2.1 Study species and sites

Sylvia boehmi and *Sylvia lugens* are insectivorous, sparrow-sized warblers (weight 14–15 g) from the family Sylviidae. They initially belonged to the genus *Parisoma*, which was recently subsumed within *Sylvia*, because molecular studies had shown that *Sylvia* and *Parisoma* form a monophyletic group (Sibley and Ahlquist 1990, Blondel et al. 1996, Shirihai et al. 2001, Böhning-Gaese et al. 2003). Both species are endemic to East Africa and have a fragmented distribution in savannahs and open woodlands.

The study area of *S. boehmi* was located around 80 km south of Nairobi in Rift Valley Province, Kenya (01°34'S/36°28'E), at 1000 m above sea level. It consisted of wooded grassland, dominated by different *Acacia* and *Boscia* species. The climate was harsh, with two rainfall seasons per year (552 mm p.a. during the study period), long droughts, and high temperatures. *Sylvia lugens* was observed on a private farm around 15 km northwest of Nakuru town, Rift Valley Province, at 2000 m above sea level (0°14'S/36°1'E). The farm had open cultivation and pasture fields surrounded by tall hedgerows of *Acacia abyssinica* and other *Acacia* species. Climatic seasonality in this area was moderate and annual rainfall (1080 mm p.a. during the study period) was distributed throughout the year with a drier period from December to February.

Breeding pairs of both species were sedentary. The partners shared all breeding activities, and stayed together from year to year (Shirihai et al. 2001, Schaefer et al. 2004). In the study sites, the two species built open cup nests of approximately 7 cm diameter and 4 cm height. The vast majority of nests were well hidden in dense shrubs and *Acacia* canopies. The investigation of the life history of the two species, which was conducted in the same study sites as described above, revealed the following traits: *Sylvia boehmi* had a clutch size of 2.0 eggs. Its incubation period lasted 15.0 days, the nestling period 12.9 days. The daily Mayfield nest mortality rate (DMR) in the incubation stage was 3.3%, yielding a nest success rate (NSR) of 60.3% for the incubation period. In the nestling stage DMR was 8.4% and NSR was 32.2%. The overall NSR for both stages combined was 19.4%. *Sylvia lugens'* mean clutch size was also 2.0 eggs. It incubated its eggs for 14.5 days and fed nestlings for 16.0 days. DMR in the incubation stage was 3.0%, NSR 64.0%. In the nestling stage, DMR of nests was 4.0% and NSR 51.8%. The overall nest success rate for both stages combined was 33.2% (Schaefer et al. 2004).

4.2.2 Data collection

For the present study, data on nest predation and parental activity were collected in two breeding seasons between October 2000 and August 2002 (*S. boehmi*) or July 2002 (*S. lugens*), respectively. For each species, 13 breeding pairs were individually colour ringed. During the breeding season, each pair was observed daily for 30 minutes, six days a week. In the course of the study period a total of 59 nesting attempts of *S. boehmi* were observed in the incubation stage, of which 19 failed, and 52 nesting attempts were observed in the nestling stage, of which 34 failed. In *S. lugens*, 50 nesting attempts were observed in the incubation stage, of which 14 failed, while 45 nesting attempts were observed in the nestling stage and 19 of them failed. In all breeding attempts any activities of the individual birds at their nests such as nest building, incubation, or feeding of nestlings were written down with the time. If possible, nest contents and reasons for nest failures were determined. Nest failure date was considered to be the mid-point of the period between the last visit and the visit at which the nest was found to have failed.

For the study of the predation rate, predation was defined to be ‘confirmed’ when the nest content was observed to be missing from one day to the next in an ongoing breeding attempt. Predation was ‘assumed’ if a nest was found abandoned from one day to the next in an ongoing breeding attempt, but nest contents could not be determined, for example because the nest was inaccessible. In *S. boehmi* predation was confirmed for 79% and assumed for 15% of all nest failures. Six percent of all nest failures were caused by other reasons than predation (e.g. nestlings fell out of the nest due to bad construction). Due to the bad accessibility of *S. lugens’* nests in high *Acacia* tree crowns only 6% of all nest failures were confirmed and 90% were assumed cases of predation. 4% of all nest failures were due to other reasons than predation. Information on the predator species was limited because, in order to minimize disturbance, cameras to observe nests were not installed. By chance, Cocktail-ants of the genera *Crematogaster* and *Camponotus* and the Gabar Goshawk *Micronisus gabar aequatorius* could be identified as predators on *S. boehmi* nests. However, other potential predators including several raptor species, snakes, and mammals such as the Dwarf Mongoose *Helogale parvula*, and rodents were common in the study area. In *S. lugens* the Common Fiscal Shrike *Lanius collaris humeralis* was observed preying on nestlings. This bird was very common in the study area, provoked alarm calls in *S. lugens,* and was probably responsible for most nest failures (Schaefer et al. 2004).

4.2.3 Data analysis

To test for effects of parental behaviour and nest site on predation I calculated the predation rate, the number of parental nest visits per 30 minutes, and the nest attentiveness for each day of the incubation and nestling period. The data of the two species were analysed separately. First, all observed breeding attempts of the whole study period were standardized to the average length of the incubation and nestling period of the respective species. Standardization was conducted by dividing each day by the total number of days the specific incubation or nestling stage lasted and multiplying this number by the average length of the incubation and the nestling stage. When observations were incomplete, i.e. not observed from the beginning of the specific stage, days were counted backwards from the end of the stage, i.e. hatching or fledging of the young, assuming average length of the stage. Then, all breeding attempts were pooled.

To detect nest site effects, I tested for a decrease in predation rate in the course of the incubation period using a linear regression analysis of daily predation rate against day. A decreasing predation rate is expected, if 1. the number of nest visits and nest attentiveness are constant and 2. nests are preyed upon only because of their position, so that badly concealed nests are preyed upon earlier than better-concealed nests. The nest predation rate of a specific day was calculated by dividing the number of nests that were ‘confirmed’ and ‘assumed’ depredated (see above) in the course of that day by the number of nests that were intact the previous day. Note that nest site effects were only evaluated using this indirect approach, not by classifying nests according to concealment.

To investigate effects of parental nest visitation rate and nest attentiveness, I tested, 1. whether the two factors affected the predation rate, and 2. whether successful and depredated nests differed in any of the two factors. For this, I first determined the number of times an adult bird arrived at the nest within 30 minutes of observation for every day of the breeding process. Then I calculated the daily nest visitation rate of each day from the average over all breeding attempts. Daily nest attentiveness was measured by calculating the proportion of nests, which were found occupied by a parent in the moment the observer arrived. For example, 50 breeding attempts were observed on day 5 of the incubation stage of *S. boehmi*. The average number of nest visits in 30 minutes on day 5 over all 50 breeding attempts was 0.96 and 47 of the 50 nests were occupied when the observer arrived (= 94% nest attentiveness). In *S. boehmi* mean nest visitation rate and nest attentiveness in percent for each standardized day were calculated from 1022 observation periods (30 minutes each), in *S. lugens* from 1002 observation periods (see legends of Fig.

4.2 and 4.4 for more details). Days 14, 15, and 16 of the depredated nests in the nestling stage of *S. lugens* were excluded from analysis, because there was only one observation for each of these days.

To investigate the influence of nest visitation rate and nest attentiveness on the predation rate I calculated univariate regression analyses of daily nest predation rate against daily nest visitation rate or daily nest attendance. In addition, stage was included as an additional factor using two-factor ANCOVAs to test whether stage (incubation or nestling stage) influenced predation rate per se. To test, whether successful nests and depredated nests differed in nest visitation rate or nest attentiveness, I evaluated the effect of success (successful nest or depredated nest) and day on parental activity and nest attentiveness using two-factor ANCOVAs. For this, I calculated separately the average nest visitation rate and nest attentiveness over successful and unsuccessful nests, respectively. Percent values of predation rate and nest attentiveness were arcsine-transformed prior to analysis. Interaction terms were tested in all analyses but removed from the analyses one by one, starting with the least significant, until only significant interaction terms remained. All analyses were calculated using the program JMP 4.0.4 (SAS Institute Inc. 1989–2001).

4.3 Results

4.3.1 *Sylvia boehmi*

Nest site: During the incubation stage nest visitation rate and nest attentiveness remained on an almost constant level (Fig. 4.1). Nest visitation rate was 0.9 ± 0.07 (s.d.) trips to the nest in 30 minutes (*n* = 15 days). Nest attentiveness, i. e. the number of nests that were occupied when the observer arrived, varied between 90 and 100%. Predation rate during the incubation stage varied between 0 and 10.3% per day. It did not show a significant decreasing trend that would suggest a nest site effect (Fig. 4.1; regression analysis: [predation rate] = 2.06 + 0.09 * [day], *n* = 15 days, t = 0.47, p = 0.65, R^2 = 1.7%).

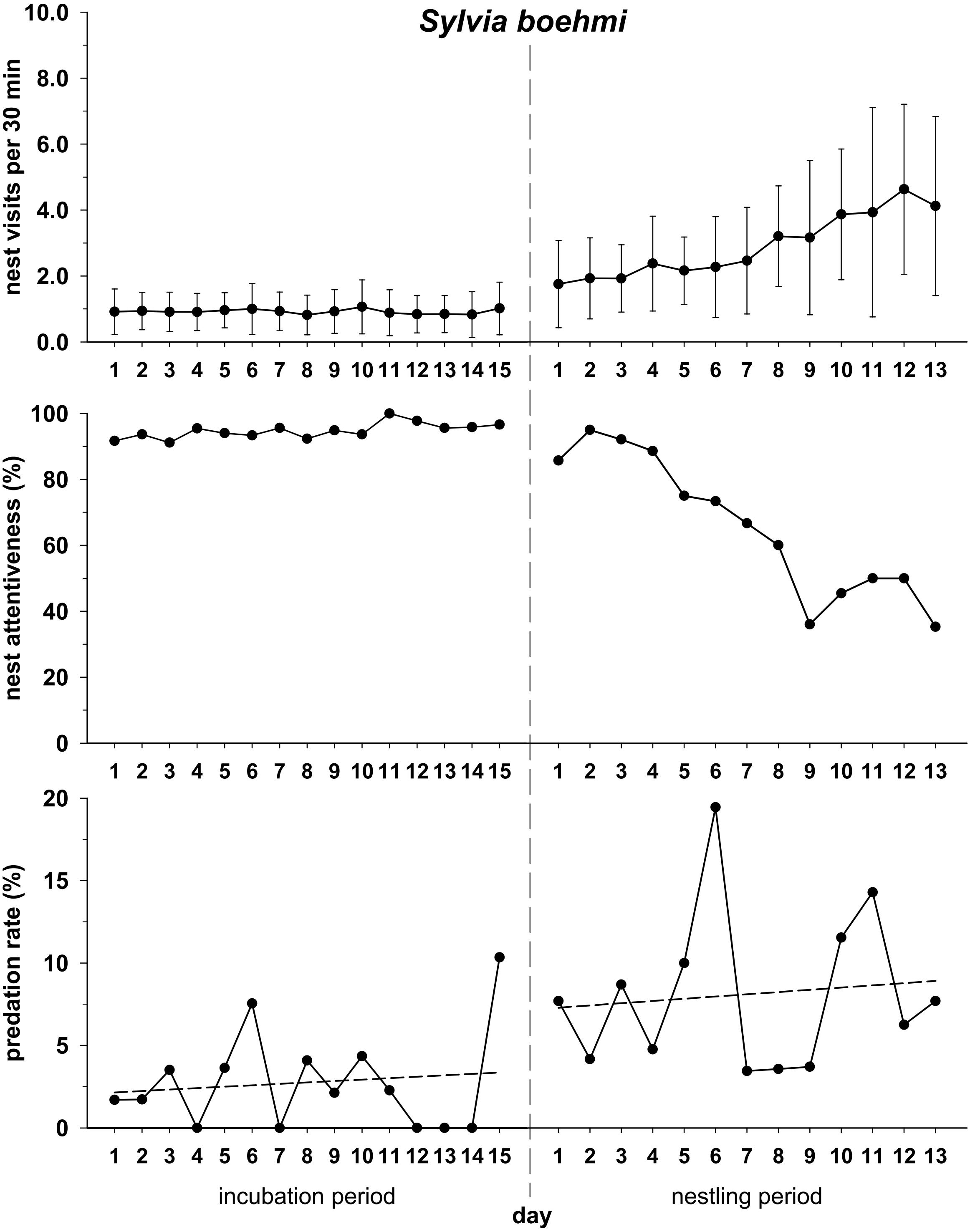

Figure 4.1 Parental nest visits in 30 minutes (mean ± 1 s.d.), nest attentiveness, and predation rate (with dashed regression line) of *S. boehmi* nests in the incubation and the nestling stage. *N* for predation rate in incubation stage: 59 nesting attempts, 19 depredated; nestling stage: 52 nesting attempts, 34 depredated. See Fig. 4.2 for details on visitation and attentiveness data.

Nest visitation rate: After being constant in the incubation stage (see above), nest visitation rate increased in the nestling stage from 1.8 trips per 30 min on day one to a maximum of 4.6 trips per 30 min on day 12 (Fig. 4.1). Predation rate also increased in the nestling stage and shifted to a significantly higher level than in the incubation stage (Table 4.1), now varying between 3.4 and 19.4% per day. However, predation rate did not change with the day within the nestling stage (univariate regression analysis of nestling stage: [predation rate] = 7.15 + 0.14 * [day], $n = 13$ days, $t = 0.4$, $p = 0.72$, $R^2 = 1.2\%$; multivariate test of both stages: see Table 4.1). The number of nest visits had a significant influence on the daily predation rate if incubation and nestling stage were analysed together, but significance was lost when stage was included as a co-variable into the analysis (Table 4.1).

Furthermore, successful and depredated nests did not differ in parental activity (Fig. 4.2, Table 4.2). The analysis showed no significant effect of ‘success’ of the breeding attempt on parental activity, neither in the incubation nor in the nestling stage, indicating that the parents visited successful nests as often as nests that were later preyed upon. The significant effect of ‘day’ in the nestling stage in Table 4.2 reflects the increase in visitation rate during the nestling stage in both groups of nests.

Nest attentiveness: Nest attentiveness was rather constant during incubation (see above). In the nestling stage, attentiveness decreased slowly in the first days and markedly after 5 days. However, even shortly before the young fledged, around 40% of the nests were found occupied (Fig. 4.1). The analysis of the influence of nest attentiveness on nest predation rate showed, that nest attentiveness affected predation rate if the analysis was conducted for both stages together, but again significance was lost when stage was included as a co-variable (Table 4.1). In the incubation stage, successful and depredated nests differed significantly in nest attentiveness and nest attentiveness increased with the days (Fig. 4.2, Table 4.2). Surprisingly, nest attentiveness was slightly higher in the depredated nests than in the successful nests. In the nestling stage, nest attentiveness decreased with ‘day’, but was similar in successful and depredated nests (Fig. 4.2, Table 4.2).

Table 4.1 Univariate regression analyses and ANCOVAs evaluating the effect of day, stage (incubation or nestling), daily nest visitation rate, and daily nest attentiveness on the daily predation rate in *S. boehmi* and *S. lugens*. Given are degrees of freedom (df), test statistics F, p, and R².

	Sylvia boehmi				*Sylvia lugens*			
	df model, error	F	p	R²	df model, error	F	p	R²
effect of day:								
whole model	2, 25	6.4	<0.01	0.34	2, 28	1.5	0.24	0.10
day	1, 25	12.8	0.57		1, 28	1.2	0.28	
stage	1, 25	0.3	<0.01		1, 28	1.9	0.18	
effect of nest visitation rate:								
univariate analysis:								
nest visits	1, 26	9.2	<0.01	0.26	1, 29	1.1	0.30	0.04
multivariate analysis:								
whole model	2, 25	6.2	<0.01	0.33	2, 28	0.9	0.43	0.06
nest visits	1, 25	0.1	0.75		1, 28	0.1	0.82	
stage	1, 25	2.7	0.11		1, 28	0.6	0.44	
effect of nest attentiveness:								
univariate analysis:								
attentiveness	1, 26	8.1	<0.01	0.24	1, 29	1.7	0.20	0.06
multivariate analysis:								
whole model	2, 25	6.3	<0.01	0.34	2, 28	0.9	0.41	0.06
attentiveness	1, 25	0.2	0.65		1, 28	0.2	0.68	
stage	1, 25	3.7	0.06		1, 28	0.2	0.67	

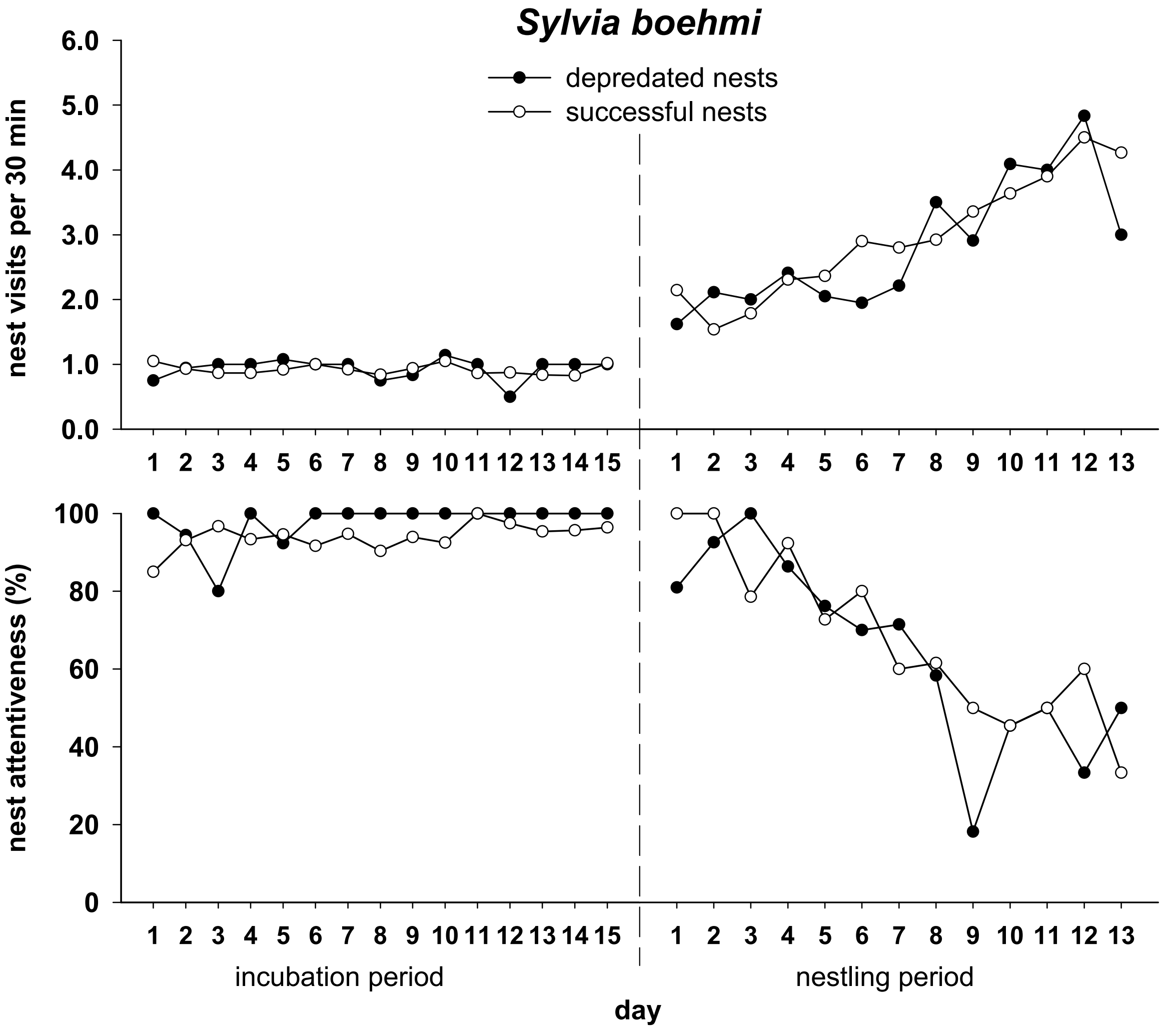

Figure 4.2 Mean parental nest visits in 30 minutes and nest attentiveness at successful nests and depredated nests of *S. boehmi* in the incubation and the nestling stage. Data from 1022 observation periods (30 minutes each) which were distributed as follows: mean number of observation periods per day during incubation stage, successful nests: *n* = 36 (range 20–55), depredated nests: *n* = 9 (range 2–18); nestling stage, successful nests: *n* = 12 (range 7–15), depredated nests: *n* = 15 (range 2–27).

Table 4.2 Multivariate ANCOVAs evaluating the effect of success of the nesting attempt (successful nest or depredated nest), and standardized day of the attempt (day 1, day 2, …) on daily nest visitation rate and daily nest attentiveness in the two *Sylvia* species. Given are degrees of freedom (df), test statistics F, p, and R².

	Sylvia boehmi				*Sylvia lugens*			
	df model, error	F	p	R²	df model, error	F	p	R²
incubation stage								
nest visitation rate								
whole model	2, 27	0.1	0.91	<0.01	3, 26	2.0	0.14	0.19
success	1, 27	0.1	0.79		1, 26	0.2	0.66	
day	1, 27	0.1	0.74		1, 26	0.4	0.55	
success*day					1, 26	5.4	0.03	
nest attentiveness								
whole model	2, 27	14.1	<0.01	0.51	2, 27	1.3	0.29	0.09
success	1, 27	19.4	<0.01		1, 27	0.6	0.44	
day	1, 27	8.7	<0.01		1, 27	2.2	0.15	
nestling stage								
nest visitation rate								
whole model	2, 23	42.2	<0.01	0.79	2, 26	21.0	<0.01	0.62
success	1, 23	0.6	0.47		1, 26	<0.1	0.96	
day	1, 23	83.9	<0.01		1, 26	40.8	<0.01	
nest attentiveness								
whole model	2, 23	30.4	<0.01	0.73	2, 26	43.3	<0.01	0.77
success	1, 23	0.8	0.39		1, 26	1.1	0.30	
day	1, 23	60.0	<0.01		1, 26	86.2	<0.01	

4.3.2 *Sylvia lugens*

Nest site: Also in *S. lugens,* no nest site effect was detected. Nest visitation rate of *S. lugens* adults during the incubation stage varied slightly around 0.9 ± 0.14 (s.d.) trips to the nest in 30 minutes (*n* = 15 days) (Fig. 4.3). Nest attentiveness at arrival of the observer was between 85 and 100%. In the same period nest predation varied between 0 and 6.7% per day. There was a slight but non-significant decreasing trend (Fig. 4.3; regression analysis: [predation rate] = 3.85 - 0.21 * [day], *n* = 15 days, t = -1.7, p = 0.11, R^2 = 18.3%).

Nest visitation rate: Nest visitation rate was constant during incubation (see above). After hatching, the average activity increased from 2.4 trips per 30 min on day 1 to 5.8 trips per 30 min on day 15 of the nestling stage (Fig. 4.3). Predation rate in the nestling stage varied between 0 and 9.1% per day. In contrast to the visitation rate, the predation rate in the nestling stage did not increase significantly, neither in comparison to the incubation stage nor within the nestling stage (univariate regression analysis of nestling stage: [predation rate] = 3.85 - 0.05 * [day], *n* = 16 days, t = -0.27, p = 0.79, R^2 = 0.5%; multivariate test of both stages: see Table 4.1). The nest visitation rate did not affect the predation rate, neither if nest visits were analysed alone, nor when stage was included in the analysis (Table 4.1).

Successful and depredated nests did not differ in parental activity (Fig. 4.4, Table 4.2). The significant effect of ‘day’ in the nestling stage reflects the increase of the visitation rate in the nestling stage in both groups of nests. The interaction term ‘success*day’ in the analysis of the incubation stage was significant, caused by successful nests having lower nest visitation rates than depredated nests at the beginning of the incubation period and successful nests having higher nest visitation rates than depredated nests at the end of the incubation period (Fig. 4.4). However, these effects were very small.

Nest attentiveness: While incubating, the birds showed high and constant nest attentiveness. In the nestling stage, attentiveness decreased fast to around 30% after 8 days and below 10% in the last third of the stage (Fig. 4.3). Nest attentiveness did not influence the predation rate (Table 4.1) and did not differ between successful and depredated nests neither in the incubation nor in the nestling stage (Fig. 4.4, Table 4.2). Nest attentiveness decreased during the nestling stage in both groups of nests, as shown by the significant effect of ‘day’ (Table 4.2).

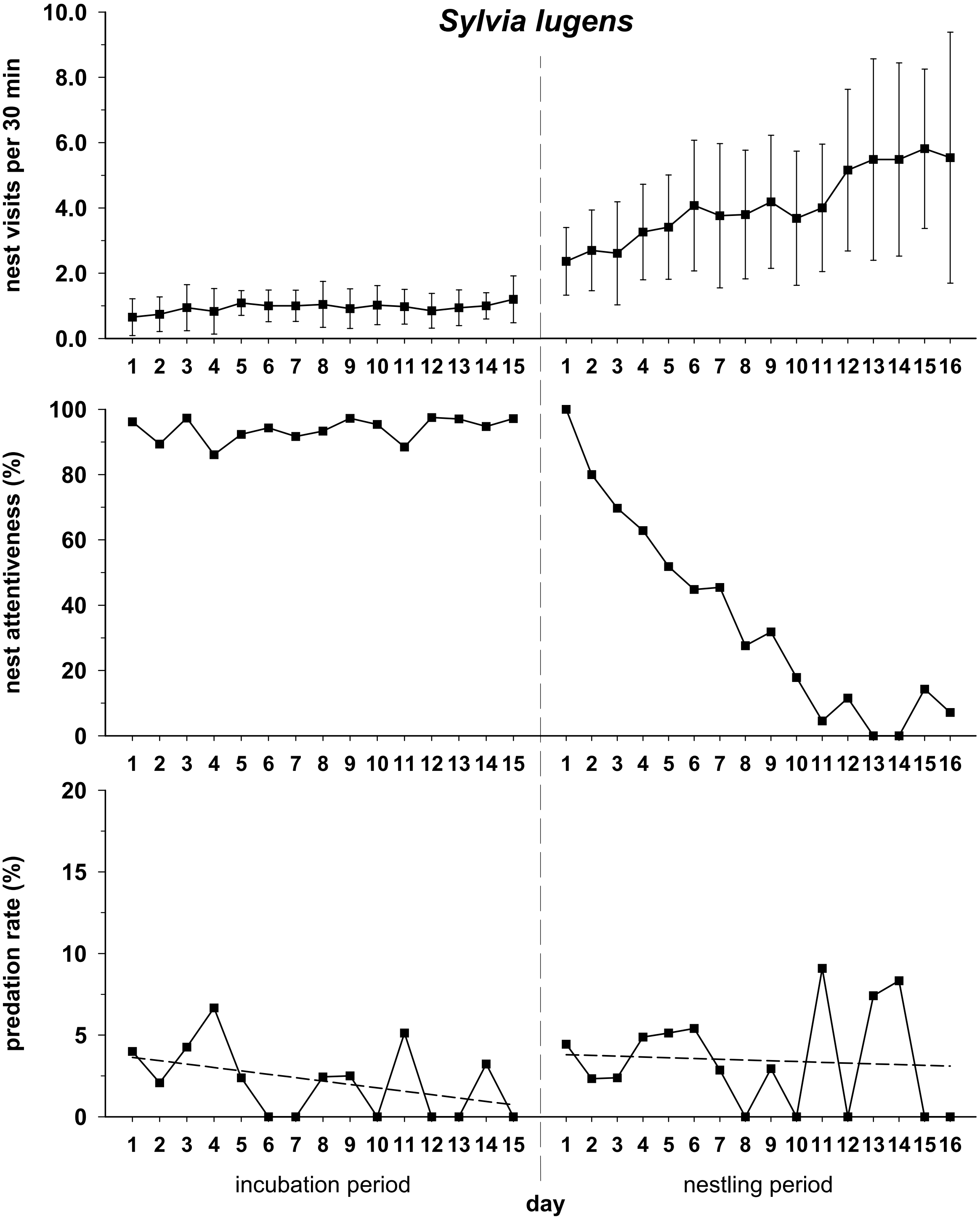

Figure 4.3 Parental nest visits in 30 minutes (mean ± 1 s.d.), nest attentiveness, and predation rate (with dashed regression line) of *S. lugens* nests in the incubation and the nestling stage. *N* for predation rate in incubation stage: 50 nesting attempts, 14 depredated; nestling stage: 45 nesting attempts, 19 depredated.

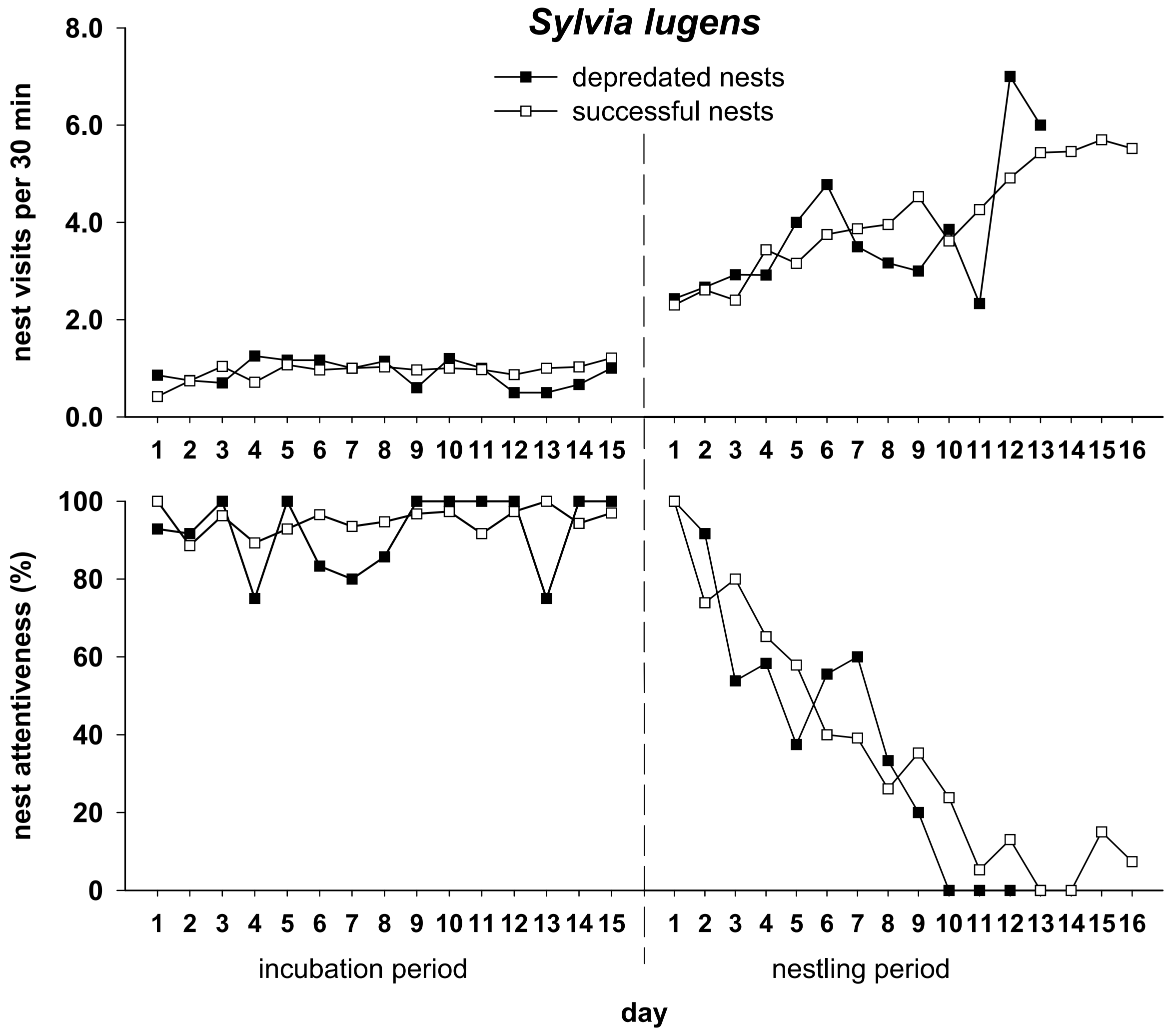

Figure 4.4 Mean parental nest visits in 30 minutes and nest attentiveness at successful nests and depredated nests of *S. lugens* in the incubation and the nestling stage. Data from 1002 observation periods were distributed as follows: mean number of observation periods per day during incubation stage, successful nests: *n* = 31 (range 12–38), depredated nests: *n* = 6 (range 2–14); nestling stage, successful nests: *n* = 21 (range 10–27), depredated nests: *n* = 8 (range 2–14). Days 14, 15, and 16 of the depredated nests in the nestling stage of *S. lugens* were excluded from analysis, because there was only one observation for each of these days.

4.4 Discussion

In both species, I did not detect a significant increase or decrease in daily predation rate within the incubation and nestling stage. The only significant change in nest predation rate was detected at the transition from incubating eggs to feeding nestlings in *S. boehmi*, when the predation rate shifted to a higher level. In *S. lugens* the predation rate was similar in both breeding stages.

Nest site effects should have been detectable in the incubation stage, when nest visitation rate and attentiveness were constant and nest site was the only factor potentially influencing the predation probability of a nest. If predators quickly remove badly concealed nests in the first days of incubation, predation should be high in these days. The remaining nests should be increasingly harder to find, causing the nest predation rate to decrease. Fig. 4.5b illustrates this connection schematically. In this study, predation rate in the incubation stage did not show a significant trend in any of the two species. Thus, nest site effects were not detected and a constant predation rate throughout the whole incubation stage as shown in Fig. 4.5a has to be assumed. The results suggest that all nests had the same probability of being found by a predator, presumably because they were all equally well (or badly) concealed. My experience in the field was that virtually all nests of both species were very well concealed in dense bushes and *Acacia* thickets. Due to their thin, translucent bottoms they were difficult to spot from the ground, at least for the human observer. Nest site effects and the fast removal of badly concealed nests were demonstrated by Gottfried and Thompson (1978), Martin et al. (2000b) and others. However, other studies showed that nest site effects might often be weak or not regularly detectable (Cresswell 1997a).

Parental activity effects, i.e. effects of nest visitation rate, should cause the predation rate to be high when the nest visitation rate is high, because with increasing numbers of parental nest visits, predators should have a higher chance of finding nests. Parental activity effects should therefore be detectable through 1. an increasing predation rate in the course of the nestling stage because the number of nest visits increased from day to day; 2. a higher predation rate in the nestling stage than in the incubation stage, because nests were visited more often when nestlings were fed; and 3. a higher visitation rate of depredated nests prior to predation in comparison to successful nests. Martin et al. (2000b) demonstrated that nest site effects and parental activity effects influence the predation rate in opposite ways. Parental activity effects might be undetectable when they are offset by nest site effects (Fig. 4.5d). In this study, nest site effects were not apparent. If nest visitation rate influences nest predation rate, one should, therefore, expect to find an increasing predation rate corresponding to an increasing visitation rate in the nestling stage (Fig. 4.5c). However, predation rate did not increase during feeding of nestlings, although nest visitation rate rose to more than the fivefold in *S. boehmi* and to more than the sixfold in *S. lugens*. In spite of the high feeding frequency, nest predation in *S. lugens* did not increase significantly at the transition from the incubation to the nestling stage. Successful and depredated nests did not differ in parental activity. The only evidence for parental activity effects comes from the fact that predation in the nestling stage of *S. boehmi* was clearly higher than in the incubation stage (Fig. 4.1). This shift may be due to an increased visitation rate, but also due to a different behaviour of the parents and/or the presence of nestlings. For example, nests have been shown to become more conspicuous in the nestling stage due to movements and begging calls of the young (Redondo and Castro 1992, Leech and Leonard 1997).

High nest attentiveness should lead to a reduced predation rate. Successful nests should therefore be characterized by a higher attentiveness than depredated nests. However, a relationship between nest attentiveness and nest predation was not supported by this study, because nest attentiveness did not affect daily predation rate at all or not in the expected way. The higher attentiveness in depredated than successful *S. boehmi* nests in the incubation stage might be a random effect caused by the relatively small sample size in the group of depredated nests and by the simplified measure I used to quantify attentiveness.

The weak effects of nest attendance showed that the ability of the two species to deter predators from their brood was limited. This probably holds for most passerine bird species, as indicated by high nest predation rates. Especially, nest defence by small birds like the two study species is unlikely against larger predators like raptors or snakes because parents would become victims themselves. Successful nest defence seems feasible against smaller predators like rodents, which might be discouraged if the parents sit on the eggs or nestlings. This is supported by some studies, which found that survival in the incubation stage was higher in active nests than in artificial nests (Cresswell 1997b, Wilson et al. 1998, Weidinger 2002). In this study, the predation rate was hardly influenced by nest attentiveness. The higher nest attentiveness of *S. boehmi* as compared to *S. lugens* was probably caused by the harsh climate in Olorgesailie, where temperatures were often very high. In this case, nest attentiveness might have served to protect the young against the sun and heat rather than against predators.

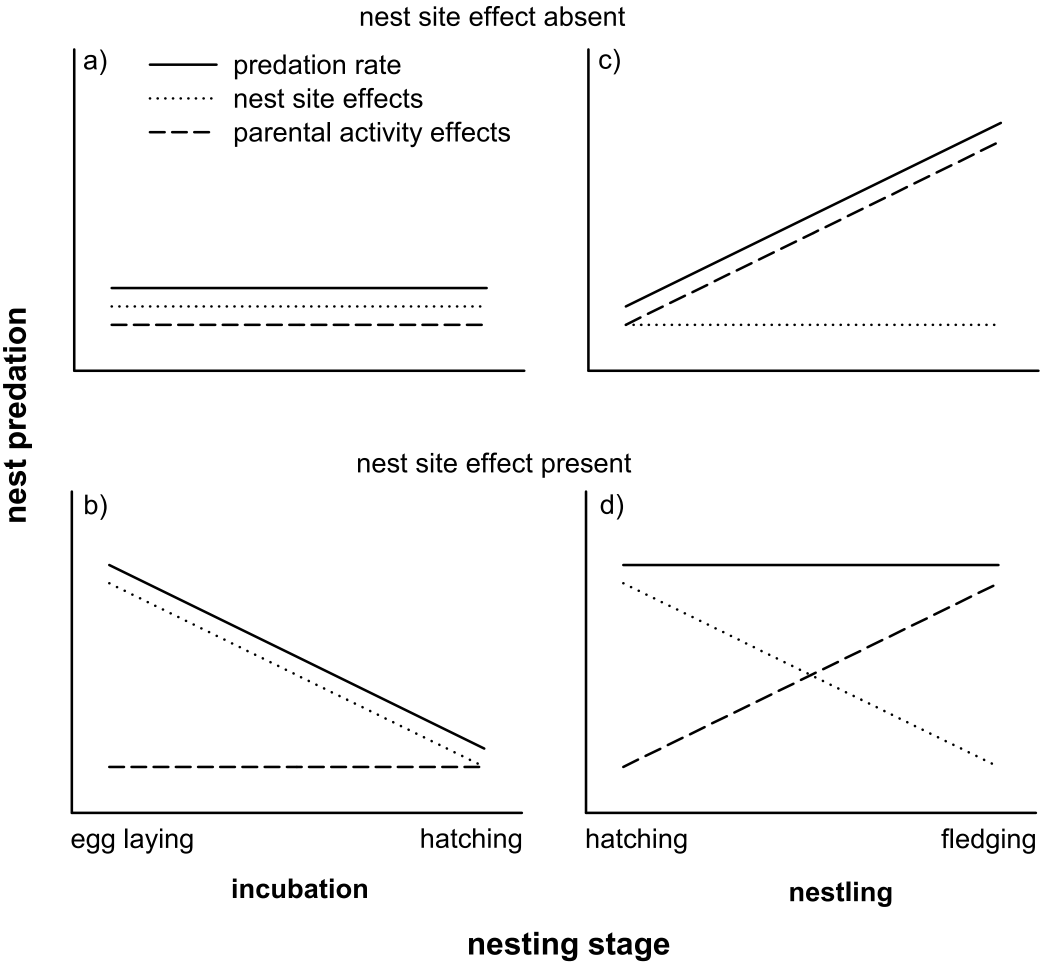

Figure 4.5 Potential effects of nest site and parental activity (= nest visits) on nest predation rate in the incubation and nestling stage of breeding birds. In all graphs, parental activity is assumed to affect predation. a) Incubation, no nest site effects. Predation rate remains constant throughout incubation because of constant parental activity. b) Incubation, nest site effect. Predation rate decreases, because parental activity is constant and nest site effects cause poorly concealed nests to be quickly removed. c) Nestling stage, no separate nest site effects. Predation rate increases, because parental activity increases with rising food demand of nestlings. d) Nestling stage, nest site effects. Predation rate is constant, because antagonistic effects of nest sites and parental activity offset each other. (Following Martin et al. (2000b), modified.)

In conclusion, I found only weak evidence for effects of nest site, nest visitation rate, and nest attentiveness on the predation rate in the study species. It seems that nests were preyed upon at random. Consequently, this study cannot support Skutch's hypothesis and the studies of Martin et al. (2000a, b). The proposed mechanism that increased nest visitation rates result in increased predation rates seems not to presently act in the study populations, although predation rate was high.

Nevertheless, several observations suggest that some life history traits of both species are influenced by predation. The shorter nestling stage of *S. boehmi* (12.9 days) in comparison to *S. lugens* (16.0 days) may have evolved due to higher predator exposure of *S. boehmi* nests and might serve to reduce nestling exposure to predators (Lack 1968, Bosque and Bosque 1995, Martin 1995, Martin 2002). A comparison of the two tropical with the temperate *Sylvia* species, which are thought to be less exposed to nest predation (Schaefer et al. 2004), revealed that the feeding rates of the tropical species are less than 50% of those of temperate *Sylvia* species. For example, Bibby (1979) reported a maximum feeding rate of 193 feeding visits in 8 hours (i.e. ca. 12.1 visits in 30 minutes) in *S. undata* in Britain. Begging calls of the nestlings of the two tropical species were very soft, the clutch sizes of two eggs of the tropical species were the smallest in the genus, and post-fledging care in the tropical Sylvias lasted much longer than in the temperate species.

Three scenarios can explain these contrasting findings. First, the mechanism proposed by Skutch was active in the past but is not active now. Abundance and diversity of predator species in an ecosystem may fluctuate. If the study period fell into a period of low predation pressure, the life history traits and behaviour of the *Sylvia* warblers we observe today may be a "ghost of their predation past". Second, I might have failed to detect differences between successful and depredated nests, because they may be very small. High predation pressure may have reduced feeding rates to a limit, showing very little variation. Third, predation is not an important factor in the evolution of parental behaviour and life history traits of the African Sylvias. The small clutches in tropical and Southern Hemisphere passerines might also be caused by weak seasonal changes in resource levels and high adult survival (Martin 1996). Then, low feeding rates may be a consequence of low food demands of only two young.

4.5 Summary

Parental behaviour and nest site are supposed to affect nest predation in birds. Few nest visits and high nest attentiveness are assumed to lead to low predation rates. Nests at poor sites are thought to be more likely to be preyed upon than nests at good sites. Studies on the relationship between parental behaviour, nest site, and nest predation are rare and none have, so far, been conducted in the Afrotropis where predation is considered to be especially high. I studied the effect of nest site, nest visitation rate, and nest attentiveness on the nest predation rate of the two tropical warblers *Sylvia boehmi* and *Sylvia lugens* in Kenya. Parental behaviour and predation on nests of 13 breeding pairs of both species were observed daily in two subsequent breeding seasons. In both species, parental activity at the nest was low (0.9 trips to the nest in 30 min during incubation, maximum 4.6 (*S. boehmi*) and 5.8 (*S. lugens*) trips to the nest in the nestling stage). Predation rates in both species were high (Mayfield nest success 19.4 and 33.2%). My analysis revealed only weak evidence for an effect of nest site, nest visitation rate, and nest attentiveness on the predation rate. It is suggested that smaller clutches of tropical in comparison to northern temperate birds result from lower feeding rates in tropical ecosystems with high predation rates (Skutch's hypothesis). This mechanism could not be proved to presently act in the study system.

5 General conclusions

Temperate and tropical bird species show distinct differences in their life history traits. For example, tropical birds have considerably smaller clutches than temperate species. The test of hypotheses that claim to explain these differences is difficult, because knowledge about tropical species is rare and phylogenetic effects hamper analyses. In this thesis, I studied a number of life history traits of the tropical warbler species *Sylvia lugens* and *S. boehmi* in order to establish the genus *Sylvia* as a model system to investigate factors that cause life history differences. Field data were collected in a two-year field study in Kenya.

In a first approach, I focussed on the breeding biology of the two *Sylvia* species. The study revealed that both species have small clutches of two eggs, long incubation and nestling periods, and high nest predation rates, which can be considered typical tropical life history traits. The post-fledging period was characterized by long time to independence and relatively high survival rates of the young. An interspecific comparison of the two tropical species showed that *S. boehmi* might compensate low nest success by extended post-fledging care. In comparison to their temperate congenerics, *S. lugens* and *S. boehmi* have smaller but more numerous clutches, longer developmental periods, higher nest predation rates, lower annual fecundity, and longer post-fledging care.

In a second study, I analysed the survival of the breeding adults of both species, using a multistate modelling approach. I especially addressed the question, whether seasonality of rainfall in the habitat affected the monthly survival rate. Survival rates of the two species were relatively high, resembling those of tropical passerines closer than those of temperate birds. Survival rates were plausibly linked to other life history traits, in a way that the species with lower annual fecundity had the higher survival rate. Contradicting my hypotheses, the monthly survival of the two species was hardly affected by seasonality. Monthly survival in the dry months was as high as in the wet months.

Finally, I analysed nest predation in detail and looked for any link between nest predation and parental feeding rates, nest attentiveness, or nest site. Predation rates in both species were high, although parental activity at the nest was low. I could not detect a clear effect of feeding rate, nest attentiveness, and nest site on predation.

In this thesis, I publish a number of important life history traits of two tropical *Sylvia* species. I analysed the influence of several environmental and behavioural factors like rainfall and parental feeding activity on some of these traits. My results reveal detailed information about two rather inconspicuous and small African passerines. Such species are rarely studied and it is significant to increase knowledge about them. Our knowledge about the two tropical birds is now more detailed than that we have on many European *Sylvia* species. Such information can be helpful when measures for species conservation should become necessary, e.g. in case of increasing habitat loss. Most notably, the data on the tropical species ideally complement the existing data on life history traits of the genus *Sylvia*, which can be found in literature. Until now, life history data on tropical *Sylvia* species were broadly missing. If we combine the life history data from literature together with the results of this thesis, we get a data set of life history traits of almost 20 *Sylvia* species, among which are temperate and tropical residents as well as short- and long-distance migrants. In particular, this data set contains characteristics like post-fledging care, whose investigation afford detailed long-term studies. The data set is, therefore, one of the very few, which, in the future, will allow the empirical test of hypotheses about the causes of the differences in life history traits between tropical and temperate birds. The most important factors potentially causing the differences are 1. nest predation (Skutch's hypothesis), 2. food limitation (Ashmole's hypothesis), 3. adult mortality, and 4. phylogeny. Most of these factors were briefly discussed in this thesis. The role of nest predation was considered in chapter 4. Clutch size should decrease and developmental periods should shorten when predation rates get higher. Food limitation and adult mortality are directly linked to seasonality of the environment of the birds. This was investigated in chapter 3. A correlation between seasonality of the environment and life history traits may reveal the impact of seasonality on these traits. The role of phylogeny can be expected to be weak, because all species are closely related, of comparable size, and have similar ecological niches. However, as DNA sequences of most species exist, this aspect can be studied as well. The *Sylvia* data set will be especially interesting, because in contrast to other data sets, which were used to address these questions, the tropical species suffer high nest predation rates and live in seasonal tropical habitats.

However, empirical studies and correlations between life history traits and environmental gradients will not suffice to explain the differences. This is, on the one hand, because many of the life history traits are linked in complex circles or triangles. A change in one trait entails a change in another trait, because limited resources have to be allocated differently. Consequently, the different hypotheses are sometimes difficult to distinguish. Furthermore, empirical studies can show correlations, but they cannot verify causal connections. In the future, the study of factors, which cause the differences in life history traits between temperate and tropical bird species, would ideally be complemented by a modelling approach. This should allow testing the hypotheses separately and rigorously, possibly bringing us a deeper understanding of the plethora of forms and strategies in the living world around us.

6 Abstract of the thesis of Hans-Christian Schaefer

The life histories of the two tropical warblers *Sylvia boehmi* and *Sylvia lugens*

Temperate and tropical bird species show distinct differences in their life history traits. For example, tropical birds have considerably smaller clutches than temperate species. The test of hypotheses that claim to explain these differences is difficult, especially because knowledge about tropical species is rare and phylogenetic effects hamper analyses. The aim of this thesis was to quantify a number of life history traits of the tropical warbler species *Sylvia lugens* and *S. boehmi* (Aves: Sylviidae). These data complement the existing data on life history traits of the genus *Sylvia*, which can be found in literature, and establish the genus *Sylvia* as a model system to investigate factors that cause life history differences. For the thesis, field data were collected in a two-year field study in Kenya from 2000–2002, covering two breeding seasons. 13 breeding pairs of both species were individually colour-ringed and observed for 30 minutes a day, six days a week during the breeding season. In the non-breeding season the pairs were observed on three consecutive days every fortnight. Multivariate statistics and an information theoretic modelling approach were used to analyse the data.

In comparison to their temperate congenerics the life histories of the two tropical *Sylvia* species is characterised by small clutches of two eggs, long incubation periods (*S. boehmi* (*b.*) 15.0 days, *S. lugens* (*l.*) 14.5 days), long nestling periods (*b.* 12.9 days, *l.* 16.0 days), and low nest success rates (*b.* 19.4%, *l.* 33.2%). The post-fledging period showed long time to independence (*b.* 58.5 days, *l.* 37.5 days) and relatively high survival rates of the young until independence (*b.* 69.2%, *l.* 55.4%). The annual survival rates of the breeding adults were 71.2% in *S. boehmi* and 57.2% in *S. lugens*, which is higher than the one of temperate *Sylvia*-species. Seasonality of rainfall in the habitat did not affect the monthly survival rate. Although nest predation rates in both species were high, there was no clear effect of parental feeding rate, nest attentiveness, and nest site on nest predation.

7 References

Anders, A.D., Dearborn, D.C., Faaborg, J., and Thompson, F.R. 1997. Juvenile survival in a population of Neotropical migrant birds. Conserv. Biol. 11: 698–707.

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

Baillie, S.R. and Peach, W.J. 1992. Population limitation in Palearctic-African migrant passerines. Ibis 134: 120–132.

Begon, M., Harper, J.L., and Townsend, C.R. 1996. Ecology. Blackwell Science Ltd, Oxford.

Bibby, C.J. 1979. Breeding biology of the Dartford Warbler *Sylvia undata* in England. Ibis 121: 41–52.

Blondel, J., Catzeflis, F., and Perret, P. 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). J. Evol. Biol. 9: 871–891.

Böhning-Gaese, K., Schuda, M.D., and Helbig, A.J. 2003. Weak phylogenetic effects on ecological niches of *Sylvia* warblers. J. Evol. Biol. 16: 956–965.

Bosque, C. and Bosque, M.T. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. Am. Nat. 145: 234–260.

Brawn, J.D., Karr, J.R., and Nichols, J.D. 1995. Demography of birds in a Neotropical forest: Effects of allometry, taxonomy, and ecology. Ecology 76: 41–51.

Brown, J.H. and Lomolino, M.V. 1998. Biogeography. Sinauer Associates, Sunderland.

Brown, L.H. and Britton, P.L. 1980. The breeding season of East African birds. East Africa Natural History Society, Nairobi.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference - A practical information-theoretic approach. Springer-Verlag, New York.

Cam, E., Hines, J.E., Monnat, J.Y., Nichols, J.D., and Danchin, E. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. Ecology 79: 2917–2930.

Cardillo, M. 2002. The life history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? J. Anim. Ecol. 71: 79–87.

Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton University Press, Princeton.

Cody, M.L. 1966. A general theory of clutch size. Evolution 20: 174–184.

Cramp, S. (ed.) 1992. Handbook of the birds of Europe, the Middle East and North Africa. Oxford University Press, Oxford.

Cresswell, W. 1997a. Nest predation rates and detectability in different stages of breeding in Blackbirds *Turdus merula*. J. Avian Biol. 28: 296–302.

Cresswell, W. 1997b. Nest predation: The relative effects of nest characteristics, clutch size and parental behaviour. Anim. Behav. 53: 93–103.

Curry, R.L. and Grant, P.R. 1989. Demography of the cooperatively breeding Galapagos Mockingbird, *Nesomimus parvulus*, in a climatically variable environment. J. Anim. Ecol. 58: 441–463.

Denlinger, D.L. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. Biotropica 12: 100–106.

Dingle, H. and Khamala, C.P.M. 1972. Seasonal changes in insect abundance and biomass in an East African grassland with reference to breeding and migration in birds. Ardea 59: 216–221.

Doligez, B. and Clobert, J. 2003. Clutch size reduction as a response to increased nest predation rate in the Collared Flycatcher. Ecology 84: 2582–2588.

Faaborg, J. and Arendt, W.J. 1995. Survival rates of Puerto Rican birds: Are islands really that different? Auk 112: 503–507.

Faaborg, J., Arendt, W.J., and Kaiser, M.S. 1984. Rainfall correlates of bird population fluctuation in a Puerto Rican dry forest: A nine year study. Wilson Bulletin 96: 575–593.

Farnsworth, G.L. and Simons, T.R. 1999. Factors affecting nesting success of wood thrushes in Great Smoky Mountains National Park. Auk 116: 1075–1082.

Fodgen, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307–343.

Geffen, E. and Yom-Tov, Y. 2000. Are incubation and fledging periods longer in the tropics? J. Anim. Ecol. 69: 59–73.

Ghalambor, C.K. and Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292: 494–497.

Glutz von Blotzheim, U.N. 1991. Handbuch der Vögel Mitteleuropas, Band 12/II, Passeriformes (3.Teil), Sylviidae. AULA-Verlag, Wiesbaden.

Gottfried, B.M. and Thompson, C.F. 1978. Experimental analysis of nest predation in an old-field habitat. Auk 95: 304–312.

Gwinner, E., König, S., and Haley, C.S. 1995. Genetic and environmental factors influencing clutch size in equatorial and temperate zone stonechats (*Saxicola torquata axillaris* and *S. t. rubicola*): An experimental study. Auk 112: 748-755.

Hayes, P.A. and Robertson, R.J. 1989. The impact of male parental care on female Eastern Kingbird reproductive success. Wilson Bulletin 101: 462–467.

Johnson, D.H. 1979. Estimating nesting success: the Mayfield method and an alternative. Auk 96: 651–661.

Johnston, J.P., Peach, W.J., Gregory, R.D., and White, S.A. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. Am. Nat. 150: 771–789.

Karr, J.R., Nichols, J.D., Klimkiewicz, M.K., and Brawn, J.D. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? Am. Nat. 136: 277–291.

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

Lack, P.C. 1986. Diurnal and seasonal variation in biomass of arthropods in Tsavo East National Park, Kenya. Afr. J. Ecol. 24: 47–51.

Langen, T.K. 2000. Prolonged offspring dependence and cooperative breeding in birds. Behav. Ecol. 11: 367–377.

Lebreton, J.D. and Pradel, R. 2002. Multistate recapture models: modelling incomplete individual histories. J. Appl. Stat. 29: 353–369.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62: 67–118.

Leech, S.M. and Leonard, M.L. 1997. Begging and the risk of predation in nestling birds. Behav. Ecol. 8: 644–646.

Lovette, I.J. and Holmes, R.T. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats - Implications for relative food availability. Condor 97: 782–791.

Maclean, G.L. 1993. Roberts' birds of Southern Africa. New Holland Publishers, London.

Magrath, R.D., Leedman, A.W., Gardner, J.L., Giannasca, A., Nathan, A.C., Yezerinac, S.M., and Nicholls, J.A. 2000. Life in the slow lane: Reproductive life history of the White-browed Scrubwren, an Australian endemic. Auk 117: 479–489.

Manolis, J.C., Andersen, D.E., and Cuthbert, F.J. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117: 615–626.

Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Curr. Ornithol. 9: 163–197.

Martin, T.E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. Ecol. Monogr. 65: 101–127.

Martin, T.E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? J. Avian Biol. 27: 263–272.

Martin, T.E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proc. R. Soc. Lond. B 269: 309–316.

Martin, T.E. and Roper, J.J. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J., and Fontaine, J.J. 2000a. Parental care and clutch sizes in North and South American birds. Science 287: 1482–1485.

Martin, T.E., Scott, J., and Menge, C. 2000b. Nest predation increases with parental activity: separating nest site and parental activity effects. Proc. R. Soc. Lond. B 267: 2287–2293.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456–466.

McCleery, R.H., Clobert, J., Julliard, R., and Perrins, C.M. 1996. Nest predation and delayed cost of reproduction in the great tit. J. Anim. Ecol. 65: 96–104.

Møller, A.P. 1990. Nest predation selects for small nest size in the blackbird. Oikos 57: 237–240.

Montgomerie, R.D. and Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. Quarterly Review of Biol. 63: 167–187.

Moreau, R.E. 1944. Clutch size: a comparative study, with reference to African birds. Ibis 86: 286–347.

Morel, G. 1973. The Sahel zone as an environment for Palearctic migrants. Ibis 115: 413–417.

Murray, B.G. 1985. Evolution of clutch size in tropical species of birds. Ornithol. Monogr. 36: 505–519.

Naef-Daenzer, B., Widmer, F., and Nuber, M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. J. Anim. Ecol. 70: 730–738.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego.

Nichols, J.D. and Kendall, W.L. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. J. Appl. Stat. 22: 835–846.

Nichols, J.D., Hines, J.E., Pollock, K.H., Hinz, R.L., and Link, W.A. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. Ecology 75: 2052–2065.

Oatley, T.B. 1982. The Starred Robin in Natal, Part 2: Annual cycles and feeding ecology. Ostrich 53: 193–205.

Peach, W.J., Baillie, S.R., and Underhill, L. 1991. Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. Ibis 133: 300–305.

Peach, W.J., Hanmer, D.B., and Oatley, T.B. 2001. Do southern African songbirds live longer than their European counterparts? Oikos 93: 235–249.

Piper, S.E. 2002. Survival of adult, territorial Longtailed Wagtails *Motacilla clara*: the effects of environmental factors and individual covariates. J. Appl. Stat. 29: 107–124.

Rabenold, K.N. 1984. Cooperative enhancement of reproductive success in tropical wren societies. Ecology 65: 871–885.

Redondo, T. and Castro, F. 1992. The increase in risk of predation with begging activity in broods of Magpies *Pica pica*. Ibis 134: 180–187.

Remes, V. and Martin, T.E. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56: 2505–2518.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110: 419–451.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9: 1–48.

Ricklefs, R.E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38–49.

Ricklefs, R.E. 1997. Comparative demography of new world populations of Thrushes (*Turdus* spp.). Ecological Monographs 67: 22–43.

Ricklefs, R.E. 2000a. Lack, Skutch, and Moreau: The early development of life history thinking. Condor 102: 3–8.

Ricklefs, R.E. 2000b. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102: 9–23.

Roff, D.A. 2002. Life history evolution. Sinauer Associates, Sunderland.

Roper, J.J. and Goldstein, R.R. 1997. A test of the Skutch hypothesis: Does activity at nests increase nest predation risk? J. Avian Biol. 28: 111–116.

Russell, E.M. 2000. Avian life histories: Is extended parental care the southern secret? Emu 100: 377–399.

Sandercock, B.K., Beissinger, S.R., Stoleson, S.H., Melland, R.R., and Hughes, C.R. 2000. Survival rates of a neotropical parrot: Implications for latitudinal comparisons of avian demography. Ecology 81: 1351–1370.

Schaefer, H.-C., Eshiamwata, G.W., Munyekenye, F.B., and Böhning-Gaese, K. 2004. Life history of two African *Sylvia* warblers: Low annual fecundity and long post-fledging care. Ibis 146: 427–437.

Shirihai, H., Gargallo, G., and Helbig, A.J. 2001. *Sylvia* warblers - Identification, taxonomy and phylogeny of the genus *Sylvia*. Christopher Helm, A and C Black, London.

Sibley, C.G. and Ahlquist, J.E. 1990. Phylogeny and classification of birds: A study in molecular evolution. Yale University Press, New Haven.

Sinclair, A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. Ibis 120: 480–497.

Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430–455.

Skutch, A.F. 1976. Parent birds and their young. University of Texas Press, Austin.

Skutch, A.F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36: 575–594.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54: 159–169.

Slagsvold, T. 1984. Clutch size variation in birds in relation to nest predation: on the cost of reproduction. J. Anim. Ecol. 53: 945–953.

StatSoft, Inc. 1997. STATISTCA for Windows, Version 5.1. Tulsa, OK, USA.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York.

Stresemann, E. (1927–34). Aves. In: Handbuch der Zoologie: Eine Naturgeschichte der Stämme des Tierreiches, VII(2) (ed. W.G. Kükenthal). de Gruyter, Berlin.

Terborgh, J., Robinson, S.K., Parker III, T.A., Munn, C.A., and Pierpont, N. 1990. Structure and organisation of an Amazonian forest bird community. Ecol. Monogr. 60: 213–238.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. J. Anim. Ecol. 71: 424–437.

White, G.C. 2002. Discussant: the use of auxiliary variables in capture-recapture modelling. An overview. J. Appl. Stat. 29: 103–106.

White, G.C. and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–139.

Willis, E.O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 90: 263–267.

Wilson, G.R., Brittingham, M.C., and Goodrich, L.J. 1998. How well do artificial nests estimate success of real nests? Condor 100: 357–364.

Wrege, P.H. and Emlen, S.T. 1991. Breeding seasonality and reproductive success of White-fronted Bee-eaters in Kenya. Auk 108: 673–687.

Yoerg, S.I. 1998. Foraging behavior predicts age at independence in juvenile Eurasian dippers (*Cinclus cinclus*). Behav. Ecol. 9: 471–477.

Yom-Tov, Y. 1994. Clutch size of passerines at mid-latitudes: the possible effect of competition with migrants. Ibis 136: 161–165.

Zahavi, A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. Ibis 113: 203–211.

8 Appendix

Appendix 1: Encounter history matrices with information on the breeding state of *S. boehmi* and *S. lugens*. *Sylvia boehmi*: 32 individuals, 22 occasions; *S. lugens*: 23 individuals, 21 occasions. Code: first letter: species, second to fifth letter: ring colours (metal, blue, green, red, orange, yellow, white). Encounter history: 0 = not resighted, b = resighted and breeding, n = resighted and not breeding.

Sylvia boehmi		*Sylvia lugens*	
code	encounter history	code	encounter history
bmbgr	nn0bbbbbn0n0nbnnnn0nbn	lwmbb	00000000000000n00000b
bmogy	00000bb000000000000000	lwmgb	00000000000000nnbbbbb
bomog	00000000000nnbnnnn0n0n	lwmby	00000000000000nnbbbbb
bmbbw	n00nnnnnnnnn0bbbbbbbbb	lwmbr	00000000000000nnnnbnn
bmorg	00000nn0nnnn0bbbbbbbbb	lwmbo	00000000000000nnnnnbb
bmbyw	nbnbbbbbbbnnnbbbnnbbnn	lbmyy	00000nb00000000000000
bmbyy	nbnbbbbbbbnnnbbb000000	lbmbb	00000nnbbbbbb00000000
bmbby	nbn0000000000000000000	lbmgr	00000nbbbbbbnnnn00000
bomrr	00000000000nbbnbbbbbb0	lbmyg	00000nbbbbbbnnnnnnbbb
bmbbr	nbn0bbnnnnnnbbbbbbbbbb	lbmbo	0bbnnnn00000000000000
bmbbb	nbbbbbnnnnnnbbbbbbbbb0	lbmbr	0bnnnn0bbbbbbbnnbbbbb
bmbrw	nbbb000000000000000000	lmbyb	b0n000000000000000000
bomgg	00000000000nnbnbnnnb0n	lmbrb	bn0000000000000000000
bomrg	00000000000nnbnb000000	lmbww	bn0000000000000000000
bmbww	n0nnnbbbbnnnnnnbbnbbnn	lmbbw	bb0n0nbbbbbbbbnnnbbbb
bmbry	nbbbbbbbnbnnbbnbbbbbbn	lmbwr	bbbn0nnbbbbbbnnn00000
bmoog	00000bbbnbnnbbnbbbbbbn	lmbwb	bbbnn0000000000000000
bmbyr	nbbbbbbnnnnnbbnb0nbbbb	lmbyr	bnnnnnnbbbbbb00000000
bmoro	00000bbnnnnnbbnbbn0bbb	lmbby	nnnnnnnbn000000000000
bomgo	00000000000nnnnnnnbbnn	lmbwy	nbbbnnnbbbbbbnnbbnnbb
bomgy	00000000000nnn0nn0bbnn	lmbrr	bbnnnnbbbbnbbnnnnnbbb
bmbbo	nbbbbbbbbnnn0000000000	lmbrw	nbbnnnbbbnbbbbbbnbbbb
bmrry	00000bbbb0000000000000	lmbbb	bbbnnnbbbbbbbnnnnnnnn
bomgr	00000000000nnnnbbbbbnn		
bomoy	00000000000nnnnbbbbbnn		
bmbrb	00000n0000nnnbn0n0n000		
bmbwr	nbbbnbbbbnnnnbnbbnbbbb		
bmbwy	nbbbnbbbbnnnnbnbbnbbbb		
bomoo	00000000000n0n0bbn0bnn		
bmbgg	00000bnnnnnnnbn0n0n000		
bmroo	00000b0000000000000000		
bmryy	00000b0000000000000000		