

Documentation for the Great and Blue Tit database at University of Antwerp

Excerpt for Boshhoek (1994-present)

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This document is an excerpt from the full documentation for analysis and interpretation of the long-term population and behavioural data collected in nestbox studies on Great Tits *Parus major* and Blue Tits *Cyanistes caeruleus* at the University of Antwerp. The document contains generic sections across all study areas in the project, and a section specific to the Boshhoek study population.

The main aim of this document is to advise future users of the data on the nature of the study systems and data collection, the strengths and limitations of the data, and important caveats such as missing or incomplete information, or data that may be affected by experimental procedures. Key points for data users to consider are given below in general terms, and again with each of the main study areas.

The document contains full descriptions of all study areas and study periods, any changes that occurred in the study plots such as changes in nestbox setup, the basic data collection protocol, and descriptions of additional datasets that are available such as environmental data, behavioural tests, or parasite data. It also contains an overview of experiments conducted during the study with comments on the extent to which these experiments may have affected the data.

1. General introduction to the database

General key points for using the database

The database contains data from **multiple study areas, most of these having a complex history**, covering different time periods and most often subdivided in multiple plots that also may differ in study period. Also, nestbox numbers and/or types have changed over time in many plots, sometimes as part of an experimental design, sometimes for more practical reasons.

Before analyzing the data, **users should verify that the selection of plots and time periods fits their purpose and research questions**. For construction of pedigrees or assessment of bird origins all data may be used, but for most analyses care will have to be taken to select plots and time periods with systematic monitoring. Of particular importance are the (changes in) nestbox densities, but also the combination of nestboxes with large and/or small entrances (LE or SE throughout the document). For any analysis, keep in mind that **nestbox density has often been high** in comparison with other studies (often around 10 boxes per ha, sometimes up to 15 per ha) and that the main study areas have through most of their history had a mixture of large and small entrances.

In general, **the most useful study areas and plots for long-term analyses are plot B in the Peerdsbos study area, most of the Boshoek study area, and plot HP in the Ghent study area** (see further comments in the respective sections; note that plots B and HP have often been referred to as “Peerdsbos” or “Ghent” in general). However, for particular investigations focusing on for example urbanization or density effects, the other plots studied for shorter time periods may also be particularly interesting. **The Boshoek study area is particularly interesting for analyses on natural selection, population structure and quantitative genetics** because of the high recapture rates and local recruitment resulting in deeper pedigrees and more accurate fitness estimates than other study areas.

The dataset is fully annotated with codes for additional manipulations or experiments at bird or nest level (such as cross-fostering, personality tests...). These are fully documented, and can be used to evaluate the inclusion of specific records in analyses. This document also provides full information on additional data available (such as vegetation, budburst, personality data, parasites...).

Note that while most of the baseline breeding and ringing data are available in standardized format through SPI-Birds, many of these additional data are not and should be requested directly from the data owner(s).

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1.1. General introduction

This document gives an overview of the nestbox study areas and data collected on Great and Blue Tits under supervision of André Dhondt and Erik Matthysen at the University of Antwerp, since 1979.

The document deals with all data collected on birds (including behavioural data, samples...), as well as other data collected in the framework of the bird research, such as vegetation data or parasites. The document only refers to Great Tit *Parus major* and Blue Tit *Cyanistes caeruleus* which make up more than 95% of all breeding records; the only other regular breeding species is the Nuthatch *Sitta europaea*, and even though these nests and captures are recorded in the database, the nests have not been monitored to the same level of detail, and presumably less than half of the breeding pairs use the nestboxes.

Section 2 describes all study areas with particular reference to (changes in) study plot extent, nestbox setup, or detail of data collection that may have important implications for the use of the data. **Overall the document makes a distinction between “study areas” and “plots” that are smaller-scale entities within a study area.** Study areas are to some extent distinct geographic entities, but they may also reflect the history and organization of the research over the decades; thus there is a wide diversity in the size of study areas, number of plots per study area, distances between plots etc. In some cases there are large differences between plot characteristics in the same study area as well as in the period and level of detail of data collection. **For that reason, information is typically provided at plot level rather than at study area level.** Importantly, study areas cannot be simply treated as “populations” and plots within study areas as “subpopulations”, given the large variation in plot sizes and distances among plots, as well as the sometimes arbitrary subdivision of plots.

For each study area we give a brief overview in Section 2 on major **additional datasets** that have been collected at plot level (e.g. vegetation data, tree budburst) or at individual bird or nest level (e.g. radiotracking data, personality scores, parasites, etc.). Additional data are only mentioned insofar as the data themselves are still available, or at least the individuals or nests that were involved can be identified. Also, additional data are included only if they cannot be directly derived from the capture and breeding data (examples are divorce rates or dispersal distances).

Note that throughout the document, if not explicitly stated otherwise, “year” always refers to the breeding season. For instance, when it is stated “boxes were added in year N” this means that boxes were added sometime between breeding seasons of years N-1 and N (often in the autumn or early winter).

1.2. Brief historical overview

The study on Great and Blue Tit populations originated with the first nestbox research project in Ghent under the direction of Jan Hublé, which was later taken over by his student André Dhondt. **The main data collection in Ghent was from 1959 to 1987**, including many different plots in and around the city of Ghent. One study area (Hutsepot - HP)) continues to this day through volunteer efforts of Jenny De Laet. The focus of this research was initially on territorial behaviour and population regulation, and later on mechanisms of intra- and interspecific competition (Dhondt and Hublé 1968, Dhondt 1977).

The main data collection in Antwerp started in 1979 under the direction of André Dhondt in the Peerdsbos area with a particular focus on intra- and interspecific competition. The main study lasted for 15 years until 1993. Similar to Ghent, **one plot (Boswachter (B)) continues to this day.** A particular feature of the study on competition in both Antwerp and Ghent was to install plots with different combinations of boxes with large and small entrance sizes, the small ones only accessible to Blue Tits. As a consequence, the mix of boxes with large and small entrances was also applied in other study areas even though these were not initiated with a particular focus on competition. Many behavioural studies were initiated in the Antwerp plots

including territoriality, singing behaviour and mating strategies (Dhondt and Schillemans 1983, Lambrechts and Dhondt 1988, Kempenaers et al. 1992). Overviews of the competition experiments in both Ghent and Antwerp can be found in (Dhondt and Adriaensen 1999, Dhondt 2010, 2012, 2023).

Starting in 1994 the main focus of the project shifted to a new study area “Boshoek” under the supervision of Erik Matthysen. This area consists of many small plots separated by open space, mostly agricultural land. The initial focus was to study forest fragmentation and dispersal (Nour et al. 1998, Matthysen, Adriaensen and Dhondt 2001, Korsten et al. 2013, Vardakis et al. 2015), while in later years a lot of research was done on parasites and infections (Heylen et al. 2013a, Teyssier et al. 2018). Over the years many studies involved some degree of experimental manipulation of individuals or nests (radiotracking, feeders, cross-fostering, parasitism). Starting in 2016 multiple changes have been made to nestbox types (entrance) and numbers, potentially compromising the value for particular long-term analyses.

In all areas, data were collected largely through the same protocol (see below for a brief summary), and were entered into a single database with an extensive series of data quality checks developed by André Dhondt and Frank Adriaensen. **In particular, the protocols in Peerdsbos and Boshoek have remained highly standardized throughout the study period. Throughout the project data collection was highly similar for Great Tits and Blue Tits**, even though the former species has been more often used for additional data collection.

Starting in the 1990s, data from the long-term study plots have been increasingly used as part of multi-population studies on climate change, spatial population synchrony, and other topics. These were mostly data from plots B and HP, in publications often referred as “Peerdsbos” and “Ghent” respectively, but more recently also data from Boshoek.

1.3. Nestboxes

From the onset of the study in 1959 boxes have had standard dimensions (initially referred to as “the Wageningen type”) which have remained virtually unchanged through the project. All boxes are made of wood of ca 15mm thickness, with inner dimensions: 235mm (top to bottom), 9mm (width) and 115mm (front to back wall) (Figure 1). A circular opening of ca 32mm diameter is situated about 35mm below the top of the front wall. Boxes are covered with a wooden top lid reinforced with metal that extends 15 to 25mm beyond the outside of the box (except at the back). Boxes are attached to a narrow wooden board at the back (ca 400x20x50mm) which is fixed to the tree with nylon rope.



Figure 1. Different views of a standard nestbox. This particular box was installed at the onset of the Peerdsbos study in 1979 and survived more than 30 years in the field. Note however that while initial boxes were painted red, after a few years we switched to green for the remainder of the study.

Boxes were almost always attached to large trees except in the Speedy study area where they were sometimes attached to walls. Boxes were placed either low (ca 1m to 1,5m) in areas with low visitor pressure, or high (ca 2,5m) in areas where disturbance or damage was judged to be more of a risk.

In a number of cases, boxes had to be moved to a different tree if the initial one fell down or was removed. This became a particular problem in plot B because of severe tree mortality in the decades after 2000. Therefore, nest records of the same nestbox may have different coordinates in different years.

While all boxes had a 32mm opening, often a metal plate with a 26mm opening was slid over the entrance, such that the box was (with very rare exceptions) only accessible to Blue Tits. **Boxes with and without metal plates are referred to as large entrances (LE) and small entrances (SE).** Most areas either had only LE or a 2:1 mixture of LE and SE, only two plots had only (or mostly) SE. In case of a 2:1 mixture, SE were regularly spaced throughout the plot.

1.4. Summary of data collection protocol

This description is based on the standard practice of data collection in the Peerdsbos and Boshoek study areas from 1979 to present. This protocol is largely identical to the one used in the Ghent study started in 1959. “Researcher” here refers to anyone participating in nestbox checks and ringing. A fairly detailed methodology for breeding data collection was published in (Matthysen, Adriaensen and Dhondt 2011). Full details on all recorded data and coding are available in the internal PARUS.DOC document.

1.4.1. Breeding season

Basic organization: Throughout the breeding season, all researchers have access to a working database with daily updated information on all nestboxes in the study. Formerly this database was kept on paper, since 2014 the database is maintained and accessed through the Parus App, a dedicated software application for data entry developed for the nestbox project. Typically, the database is consulted on a daily basis to allocate nestbox checks and ringing tasks to individual researchers (except the HP plot in Ghent where fieldwork is organized separately and data are submitted to the database after the season). Data are entered as nest visits which are after the breeding season compiled on nest cards (paper cards until 2013, digital cards since 2014 except for the HP plot). Summary data from these nest cards are then entered into

the final database. Thus, derived data such as laying date or brood type (first, second, replacement...) are only assigned after the end of the breeding season.

General nest check schedule: Nestboxes are controlled weekly from the time the first egg can be expected in the latter half of March. When a nest is found with hatched young, the age is recorded and extrapolated to the time when parents need to be caught and ringed (at nestling day 8) or nestlings are ringed (day 15). When the first nests reach day 8 of nestling age, the weekly control schedule changes to a nestbox-based schedule whereby boxes are visited based on what needs to be done. Intermittently, nests where young have not yet hatched are visited to update their status. Importantly, the date of ringing parents and nestlings is based on developmental age (i.e. stage of plumage development of nestlings) rather than exact age (see below). Approximately 4 weeks after the last full nestbox check, usually when the majority of first brood parents have been ringed, all boxes are checked again to identify any second broods which are then similarly entered in the temporary database. At the end of the season, all boxes are checked once more. In autumn or winter the main study areas are usually checked for maintenance or replacement of nestboxes.

Checking nests: Basic data recorded at every visit include the presence of nest material, stage of nest building, number of eggs and incubation status, identity of parents when caught or observed on the nest, number and (estimated) age of young, number of unhatched eggs and dead young, and the date of removal of nest material (after nests fledged or failed). When a female is found on the eggs, the bird is gently prodded with a twig or pencil to facilitate inspection of the legs for colour rings, and if possible checking for recently hatched young. At any sign of anxiety the female is left alone to avoid her leaving the nest. Females are never taken from eggs in routine controls, except when the hatching of eggs is long overdue and the brood is considered as lost.

Scoring nestling age: This is based on plumage development. Importantly, the day of hatching is counted as day 0 and not day 1. Thus, day 8 corresponds to eight days after the young hatched. Since the exact date of hatching is unknown, and since plumage development shows some variation among nests, the estimated age is recorded at every nestbox visit and if necessary updated in the temporary database. Thus in a slow-developing brood the time of ringing parents and nestlings would be postponed, usually by no more than 1 or 2 days at most. Similarly, ringing dates would be advanced in broods that develop more rapidly than expected, or where nestling age was underestimated on the first check.

General ringing procedure: In principle, birds in the main study populations receive an individual metal ring issued by the Belgian Ringing Scheme, and three (sometimes two) colour rings. Nestlings are usually only given a metal ring. Upon first capture as fullgrown bird, birds receive a metal ring (if not yet ringed as nestling) and colour-rings. At this time a sample of body feathers is also routinely taken as source of DNA (since 1998). Colour-ring combinations are unique within a study area; in Great Tits they are unique within each sex, in Blue Tits they are unique within the species. Standard data taken at most captures in the main study areas are: sex, age, wing length, tarsus length and body mass, as well as location (with spatial coordinates), capture method, observer, date and time (more information in PARUS.DOC). Section 4.1 gives additional information on measurements that were not part of the standard procedure (such as bill length and depth, tarsus asymmetry). Note that in 2000 the project switched to a new method of measuring tarsus length; from 2000 to 2015 old and new methods were combined, and after 2015 only the new method was used.

Trapping and ringing parents: In principle, parents are trapped on the nest when nestlings are 8 days old. Occasionally parents are already trapped on day 7 but only when nestlings appear in good condition and weather is favourable, or trapping is postponed because of constraints in the fieldwork schedule. Simple metal wire traps are placed on the inside of the nestbox front, often allowing to trap both male and female within an hour. If one or both parents are not trapped, new attempts are made on the following day(s). Note that these failed attempts are not explicitly recorded in the database, thus there is no record of trapping effort. Standard ringing and measuring apply as above. After capture birds are released

immediately near the nestbox or in the general vicinity of their territory. Very occasionally, birds that were present but very reluctant to enter the nestbox with a trap, have been caught with a mistnet in front of the nestbox (this is not recorded in the database as different from the use of traps). Also occasionally, females that were not caught in the daytime have been captured when roosting with the nestlings in the evening. Again this is not recorded in the database as such, but would be evident from the time of capture. In some cases parents that were not caught but present near the nestbox, were identified by their colour rings. This information is included in the database but not recorded as a capture.

Ringling and measuring nestlings: Nestlings are in principle ringed on day 15, but regularly also on day 14 depending on the fieldwork schedule, given that nestling mass tends to level off after 13-14 days of age (Barba, Gil-Delgado and Monros 1993). If due to unforeseen circumstances ringing happens on day 16, extra care is taken to avoid premature fledging by blocking the nest entrance until young have calmed down. In some years and study areas standard individual measures were taken (Table 1). In other cases only the total brood mass has been recorded. Brood age (days after hatching) is recorded in all cases, based on plumage development, and individual nestlings deviating in development age are also recorded.

Removing nest material: When ringing young at day 15, the nest is inspected for any unhatched eggs and dead young; these are recorded and removed from the nest. At the first nest inspection after the young fledged, nest material is removed, and any additional unhatched eggs or young are also recorded.

Table 1. Overview of years when nestlings were individually measured at day 15 in most or all nests. In Boshoek, smaller numbers of nests were individually measured in several additional years for Great Tits, and a few years for Blue Tit. Note that for the Ghent data prior to 2001, some individual measurements may exist but are not yet digitally available.

Study area	Plot	Species	Years with individual measurements
Boshoek	All	Great tit	1996-1998; 2000-2002; 2006-2008; 2012-2014
Ghent	HP	Great tit, Blue Tit	2001-2020
Peerdsbos	B	Great tit, Blue Tit	1979-1994; 1996
Peerdsbos	C	Great tit, Blue Tit	1979-1993
Peerdsbos	L	Great tit, Blue Tit	1980-1988
Peerdsbos	T	Great tit, Blue Tit	1979-1993
Speedy	All	Great tit, Blue Tit	2014-2015

1.4.2. Roosting checks

Depending on the study area and time period, routine nestbox checks have been carried out after dusk in autumn and winter. In the early Peerdsbos study period and in some years of Boshoek, controls were done every winter month (4-5 times per year). Since 2001 this was at most twice per winter, and since 2015 only in plot B (Table 2. Overview of standard night controls in the main study areas: number of roost controls per winter period, and months. Note that occasionally controls were canceled because of weather conditions. Start years refer to Nov/Dec, end years refer to Jan/Feb/March.). Usually all nestboxes in a study plot were checked on the same evening (or multiple successive evenings). All birds were identified, (if needed) ringed and measured (tarsus length, wing length, weight) in the field and immediately returned to their nestbox. On rare occasions, birds were transported to the laboratory for additional data collection or personality tests, and returned to the field the following morning.

Table 2. Overview of standard night controls in the main study areas: number of roost controls per winter period, and months. Note that occasionally controls were canceled because of weather conditions. Start years refer to Nov/Dec, end years refer to Jan/Feb/March.

Study area	Plot	Period	Number	Months
Peerdsbos	T	1979-1993	5	Nov, Dec, Jan, Feb, Mar
Peerdsbos	L	1980-1988	5	Nov, Dec, Jan, Feb, Mar
Peerdsbos	K	1997-2015	2	Nov/Dec, Jan/Feb
Peerdsbos	C	1980-1989	2	Nov/Dec, Jan/Feb/Mar
Peerdsbos	C	1989-1993	4	Nov, Dec, Jan, Feb
Peerdsbos	C	1993-1996	2	Nov/Dec, Jan/Feb
Peerdsbos	B	1979-1994	5	Nov, Dec, Jan, Feb, Mar
Peerdsbos	B	199-2025	2	Nov/Dec, Jan/Feb
Boshoek	All	1993-1996	2	Nov/Dec, Jan/Feb
Boshoek	All	1996-2001	4	Nov, Dec, Jan, Feb
Boshoek	All	2001-2015	2	Nov/Dec, Jan/Feb

1.4.3. Other capture data

At no time has there been a standardized capture effort outside the breeding season in any of the study areas. Captures outside the breeding season have always been done in the framework of specific projects. Most of these captures were done with mistnets at temporary feeding stations that were operated for week or perhaps months. At all times, Great and Blue Tits caught outside the breeding season inside the study area were ringed, colour-ringed, and measured (at least tarsus, wing, weight).

2. The Boshoek study area

Key points for using the Boshoek data

The Boshoek dataset, consisting of a large set of separate woodlots, is particularly useful for studying spatial population processes (dispersal, inbreeding, fragmentation effects) and for studies requiring high numbers of local recruits (selection, heritability, inbreeding).

For any analysis, **careful selection of plots and study years is essential, since plots differ in their characteristics (size, vegetation) but also in the duration of study and depth of data collection.** For pedigree construction the full dataset can always be used, but for most other analyses a selection will have to be made depending on the question. **The most standardized data are available from 13 core plots that were continuously monitored with (largely) the same nestbox setup and protocol from 1996 to 2015.**

Several processed behavioural datasets are available, in particular personality scores and postfledging family home ranges.

Throughout the study many behavioural or ecological **experiments** have been conducted involving manipulation of nests, nestlings or parents; all this information is referenced with codes in the breeding and capture dataset.

2.1. General overview and history

The Boshoek study area is a collection of 20 small forest plots with nestboxes, with plot sizes between 1 and 12 ha in a roughly 3 by 4 km area (Figure 2). **They comprise a “core” set of 13 plots that were mostly continuously monitored from 1993 to 2019**, and additional plots that were monitored less intensely. The study area lies in a fairly well preserved traditional agricultural landscape close to the city of Antwerp. **Most of the forest plots are mature, largely even-aged stands of common oak with similar understory vegetation.** One major plot (TU) differs from the others by having a combination of oak, beech, larch and a few other tree species. Nestbox plots are separated by open areas with arable land or pasture, scattered houses and gardens, and a few stands of other forest of lower quality for breeding Great and Blue Tits, mostly poplar trees. **At least the larger forest plots have been in existence in more or less the same location since at least the late 18th century** (“Ferraris map”) although the type of forest management has most likely changed substantially over next centuries. The soil is mostly sandy loam, except one of the larger plots that is on clay. Key references to this study plot are (Matthysen 2002, Van de Castele et al. 2003, Korsten et al. 2013).

The study started in 1994 with standardized nestboxes installed in late 1993, at a uniform density (except for plot TU) of ca 9 boxes per hectare, of which 2/3 LE and 1/3 SE. Prior to 1994 most of the plots already had nestboxes managed by a local ringing group; these boxes were not standardized in size or shape and their positions did not correspond to later locations. This volunteer group only ringed nestlings but no other details, not even locations, therefore the only available data are lists of nestlings per plot. Nevertheless, some breeding data were collected by researchers affiliated to our project in the years preceding 1994. In plot TU the local ringing group continued in 1994 and 1995, after which standard nestboxes and standard protocol were implemented in this plot as well. **Over the years there were many changes in the use of study plots**, mostly in the periphery of the area and/or in plots of suboptimal habitat dominated by poplar trees (**Fout! Verwijzingsbron niet gevonden.**). A set of 12 core plots (DN, HM, HN, KB, KL, LO, LW, TU, VS, ZN, ZW, ZZ) was monitored continuously from 1996 to 2015, and in 2001 BW was added to this set.

In general, capture rates of breeding birds were very high around 85% (Appendix 1). Because of the large but also fragmented study area, **local recruitment rates are high** (Matthysen, Adriaensen and Dhondt 2001) which is ideal for analyses on fitness/selection and on pedigrees.

From 2016 onwards all nestboxes were changed to large entrances to maximize the availability of Great Tits for specific experiments and data collection. In the years following this, several changes happened in the monitoring of the core plots, driven by the need to reduce the workload. The most drastic change was the two-year closure of plot KB in breeding seasons of 2020 and 2021 (see next section for more details). By 2025 all of the smaller plots were closed leaving only the four largest plots KB, LO, TU and ZZ.

While we presume that by far most of the breeding population of the area was breeding in the nestboxes, some breeding opportunities for Great and Blue Tits are known to have been present in the matrix in between the study plots, such as nestboxes in gardens, or natural cavities in small wooded patches or treerows. In some of the early years, specific efforts were done to check many of these nests; data on these nests (allocated to the virtual TF plot in the database) may give a minimal estimate of the breeding pairs in the matrix.

2.2. Study plots in Boshoek

Ten of the thirteen “core” plots in Boshoek are highly similar forest plots dominated by mature oak stands, but varying in size from 0.4 to 11 ha (**Fout! Verwijzingsbron niet gevonden.**). The management history of these oak stands is unknown, but the larger oak trees could easily be 150 years old, in some cases even 200 years or older¹. The plots dominated by oak typically have 85% or more oak trees with very few other tree species. Only plot HN has considerable admixture of red oak (37%). In addition there are two plots with mixed vegetation (TU: beech, oak, larch; BW: beech, oak, poplar) and a small plot consisting of a lane with rows of large oak trees (DN). Detailed data are available on tree species composition both at plot level and at nestbox level. Plot ZN is a special case since it had 16 boxes (in the first few years 18) in a patch of mature oak-dominated forest, but in addition 10 boxes were added in an adjacent stand of young secondary forest, the latter boxes labelled ‘ZNTF’.

While many of these plots are clearly separated from each other by unwooded area or at most treerows, some are connected by small forested areas but without nestboxes, typically poplar stands and/or younger tree plantations. In some cases distances between nearby plots were actually very small. On this basis, plots have been grouped for particular analyses as follows (e.g. (Korsten et al. 2013, Vardakis et al. 2015):

- Plots LO and LW are part of the same forest but separated by other vegetation. Together with plot KL that is less than 100m distant from LO, they have been grouped as “plot LX”
- Plots ZN, ZW and ZZ were historically part of the same forest but in the 19th century (prior to the study) bisected by a railroad. At the time the study started, ZN and ZW were separated by a very young tree plantation but three decades later they are continuous forest. The three plots have been grouped as “plot ZX”
- Plots HM and HN were likewise at the time of the study onset separated by a small clearcut area which was subsequently replanted with young forest, and have been grouped as “plot HX”
- Plots BW and DN are on both sides of a farm and a small estate, and nearly connected by a stand of younger trees, they have been grouped as “plot BX”.

In addition, plot KB is connected by wooded vegetation (poplar and young tree stands) to plots HM and HN.

¹ Frank Adriaensen in email 9/3/2010

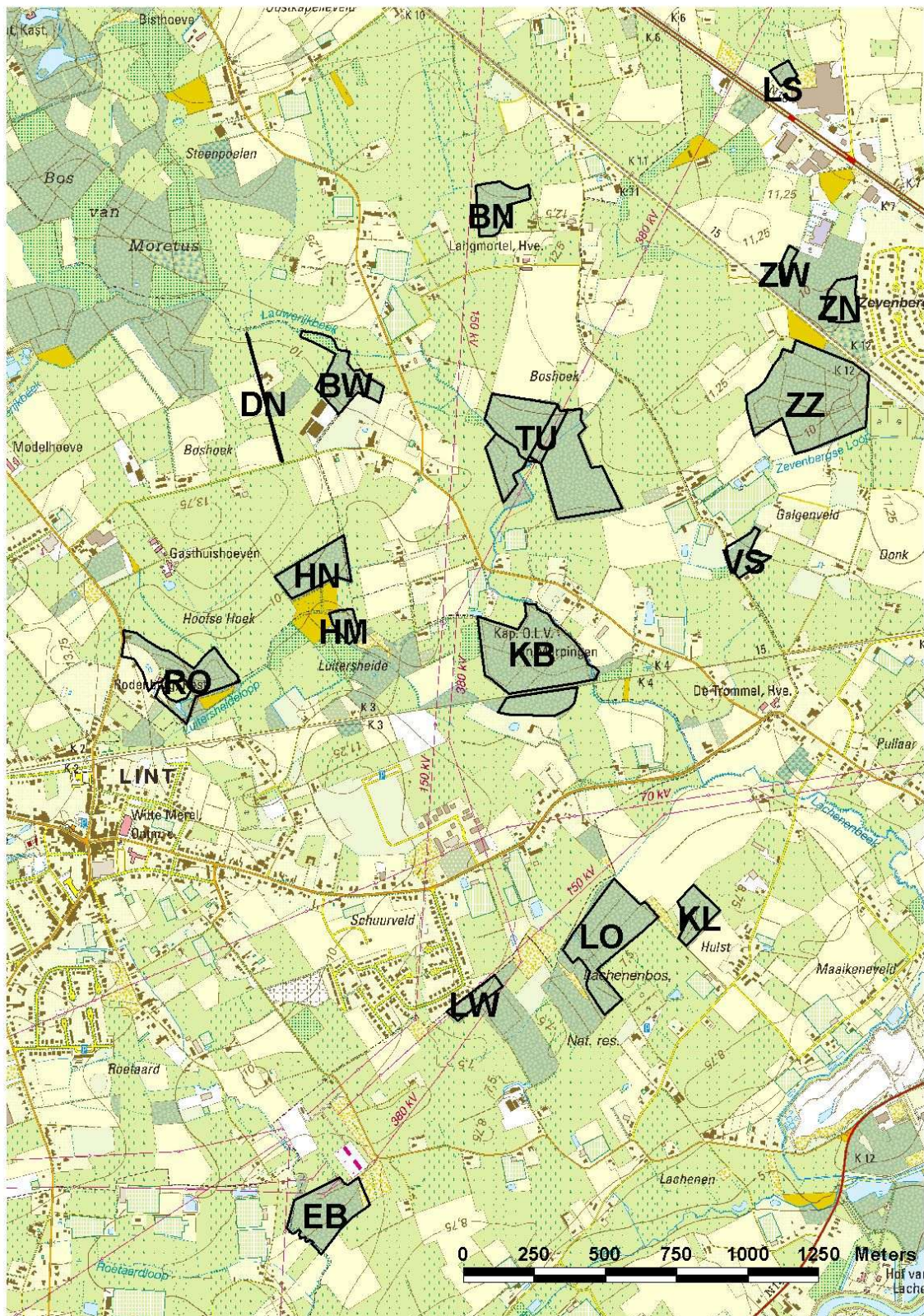


Figure 2. Main study plots in Boshhoek. Not shown are temporary plots LC (between LW and LO), LH (between HM and KB) and BOSHBP (in the centre of Lint, on the left border of the map, southwest of RO).

In addition to the core plots, some “**peripheral**” plots have been monitored but in varying degrees of detail and for different time periods (Table 3). These were mostly used as an additional source of information on ringed birds. Plot RO contained nestboxes managed by a different ringing group but ringing data of nestlings were provided to the database, while parents were only caught in a few years. Some **temporary plots** were used for only a short span of years, two of these (LC and LH) were intentionally set up to represent low

quality habitat, i.e. poplar stands, together with plot EB. The plot TF is not a proper study plot, but a code used for any nestboxes (typically in private gardens) situated in the landscape outside the actual nestbox plots.

Overall the study area landscape has not changed drastically since 1994, except that some very young plantations adjacent to the plots have matured substantially (as mentioned above), likely providing improved connectivity and foraging habitat. One important landscape change is the development of a small enterprises zone to the southwest of KB, in the second half of the 1990s. In 2014 a bike route was constructed along the railway that bisects the southern part of KB, thereby substantially increasing human disturbance in the edge zones of this plot.

Table 3. Overview of plots in the Boshoek study area. Most plots are also shown in Figure 2. “Core plots” were monitored routinely throughout most of the study period. “Peripheral plots” are plots that were not monitored fully and served mostly to monitor incoming or outgoing dispersers, and not included in most analyses. “Temporary plots” were only monitored for few years. TF is not a regular plot but refers to any nests situated outside the other plots.

Plot	Name	Size (ha)	Description	Type of plot	Years	Comments
BW	Boshoek West	2,99	Mixed plot (beech, oak, poplar...)	Core	2001-2021	
DN	Dreef Notaris	0,25	Lane with large oak trees	Core	1994-2018	
HM	Luitersheide Midden	0,79	Small oak plot	Core	1994-2021	
HN	Luitersheide Noord	2,83	Small oak plot	Core	1996-2024	37% red oak
KB	Kapellekensbos	10,08	Oak plot	Core	1994-	Closed in 2020 and 2021
KL	Klein Lachenen	1,57	Small oak plot	Core	1994-2024	
LO	Lachenen Oost	6,18	Large oak plot	Core	1996-	
LW	Lachenen West	1,02	Small oak plot	Core	1994-2024	
TU	Turk	11,91	Mixed plot (beech, oak, larch...)	Core	1996-	Lower nestbox densities; split in TU and TV for some analyses
VS	Vinkenstraat	1,28	Small oak plot	Core	1994-2024	
ZN	Zevenbergen Noord	1,53	Small oak plot	Core	1994-2024	In addition, 10 boxes ‘ZNTF’ in adjacent young forest
ZW	Zevenbergen West	0,41	Small oak plot	Core	1994-2015	
ZZ	Zevenbergen Zuid	11,13	Large oak plot	Core	1996-	
BOSHBP	Park Lint	n/a	Public park	Peripheral	2015-2019	All nestlings ringed, some adults

EB	Electrabel	4,27	Mixed plot (mostly poplar)	Peripheral	2000-2019	Typically all nestlings ringed, some adults
RO	Rodenburg	4,84	Private park	Peripheral	1994-2019	Typically most nestlings ringed, few adults
BN	Boshoek Noord	2,20	Small oak plot	Temporary	2001-2005	
LC	Lachenen Centraal		Poplar area between LO and LW	Temporary	2000-2005	
LH	Luitersheide		Mixed area between KB and HM/HN	Temporary	2000-2005	
LS	Liersesteenweg	0,49	Small oak fragmetn	Temporary	1994-2006	
TF	Tussen Fragmenten		Dispersed boxes in the matrix	Virtual	n/a	Nestlings ringed ad hoc, adults very few

Below is a chronological overview of changes in the Boshoek study area in terms of plots, numbers and types of nestboxes, with some overlap with information already provided earlier in the text (years always refer to breeding season, unless otherwise mentioned):

- At the start in 1994 plot TU was not included yet because of the very different habitat. It was added in 1996 but with a lower density of nestboxes than the other plots
- In 1996 a few boxes were removed from some of the smallest plots when the plot sizes were re-evaluated (LS: 8 to 5, ZW: 6 to 4, ZN: 18 to 16)
- From 1998 to 2002 additional efforts were done to capture breeding birds in RO, while in other years nestlings were ringed only
- In 2000 a few (putative) low-quality plots were added with mostly poplar trees, as part of the EU-METABIRD project (LC, LH and EB). After 2005 LC and LH were abandoned.
- In 2001 plots BN and BW were added on the northern edge to increase the range for dispersal data. Of these, BN only lasted until 2005 but BW was continued until 2021.
- In 2000-2001 and 2003-2004 **low- and high-density areas were created** within plot KL and LO in a split-plot design (see further under experiments)
- In 2007 the very small plot LS was abandoned because it became too degraded, and was also rather remote from the other plots.
- In July 2009 many trees in plot KB were damaged by a severe storm, this led to extraction of a large number of old trees in spring 2010
- In the course of 2014 a bike route was constructed along the railway crossing the south part of KB; no trees were removed but human disturbance increased
- **In 2016 all box entrances were changed to large openings**
- In 2019 plot DN was closed, in 2022 plots BW and HM
- In 2020 and 2021 **plot KB was closed; it was opened again in 2022** but without the boxes in the southernmost part (i.e. 76 to 90).
- In 2021 six non-standard boxes were added by a third party to VS, but were included in the monitoring
- In 2025 plots HN and ZN were closed; VS was abandoned as regular plot but only some boxes were removed

Original nestbox maps are provided in Appendix 2.

2.3. Additional data collected in Boshoek

Environmental data

Tree and vegetation data: in the early 1990s, DBH was measured (based on trunk circumference) from a random selection of common oak trees in most of the core plots, in the framework of a study on Nuthatches in the same plots. In 2005-2010 several datasets were collected on vegetation around most or all nestboxes whereby dominant tree species, shrub and herb cover, and canopy cover were noted. In september 2009 microclimate was recorded in most nestboxes. In 2024 and 2025, tree composition and tree density were recorded around all nestboxes. A summary of tree composition per plot is given in Appendix 3.

Budburst data: in 2024 and 2025, budburst date was monitored for a selection of nestboxes in the core plots. Prior to the fieldwork, clusters of nestboxes were identified as either early, average or late based on laying dates throughout the entire study. For every nestbox, five oak trees were scored for budburst by repeated visits. In 2026, a smaller set of trees were again scored for budburst.

Beech crop data: starting in 2000 beech crop estimates were made underneath a few beech trees in plots TU and BW.

Behavioural data

Feeder visits: During three years (2012-2013 to 2014-2015), **47 feeders with RFID (PIT-tag) registration** were distributed through the area, both within and outside nestbox plots. Each feeder contained peanuts in one out of three weeks from July to February with a fixed rotation schedule (Appendix 4). In these years, both nestlings and breeding birds were equipped with RFID tags. A processed dataset with individual visits to feeders is available.

Radiotracking data: from 2003 to 2013, individual Great Tits were radiotracked manually for short periods during summer, autumn or winter. Numbers were relatively small, with a total of about 110 individuals. These include birds tracked for three unpublished MSc theses with a sample size of 20-26 male Great Tits per year in autumn and winter; a set of 38 birds tracked as part of a feeder manipulation experiment (van Overveld and Matthysen 2010); and a few individuals tracked in winter for pilot studies. This does not include parents radiotracked to study postfledging movements.

Postfledging movements: From 1996 to 2002 (with one year interruption) postfledging family movements were studied in Boshoek by **observations of colour-ringed** parents and offspring (Van de Castele and Matthysen 2006, Matthysen et al. 2010). In total, observations are available for 387 different families. From 2006-2009 and in 2012-13, family movements were studied by **radiotracking** one (or two) of the parents, usually the male (van Overveld et al. 2017). In total, data were collected for 122 Great Tit and 12 Blue Tit families. Summary data per family and full method descriptions are available.

Personality tests: from 2006 onwards, standard two-minute exploration tests have been conducted, most intensively in the years 2006-9, 2012-14, and 2017. Birds were caught in the field (daytime or evening) and brought to the lab, tested the following morning and released by noon. An integrated and fully standardized dataset is available. In total, close to 2000 tests were conducted on Great Tits, mostly from October to February, but also some in the summer months (Figure 3. Annual (left) and monthly (right) number of standard exploration tests. Only valid tests from the Boshoek study area are included.. In addition, about 180 tests were done on Blue Tits in a single year; a pilot study was done on “social exploration” with two Great Tits exploring the room simultaneously (59 tests); and 183 Great Tits were tested for exploration in a much larger “arena”. The latter was published in (Arvidsson et al. 2017).

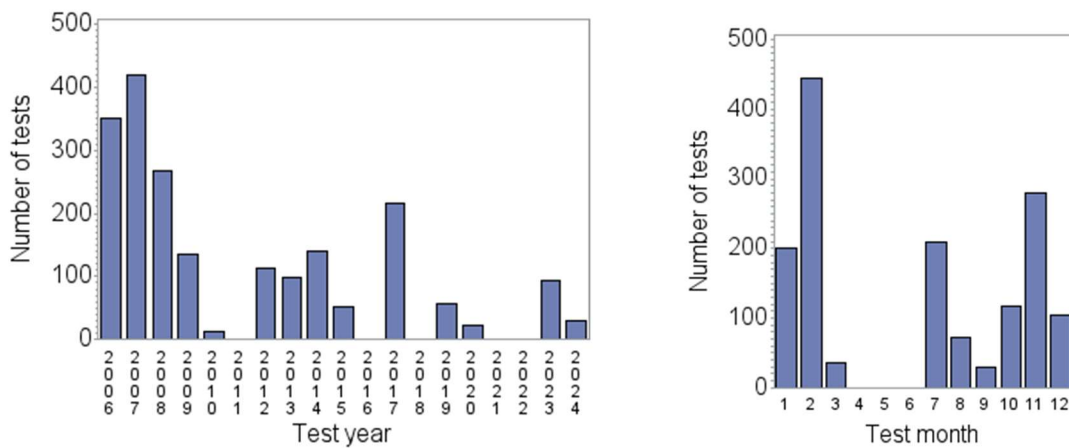


Figure 3. Annual (left) and monthly (right) number of standard exploration tests. Only valid tests from the Boshoek study area are included.

Food provisioning: in 1994 and 1995, food provisioning was recorded at 110 nests (Blue and Great Tits combined). Results were published (Nour et al. 1998), but data are no longer available.

Additional measurements

Nestling growth: additional data on body size of nestlings at various ages (i.e. before day 14-15) were collected for specific projects, usually for only one or two years and on relatively small numbers. This includes several unpublished datasets from the 1990s, a nestling stress experiment (Talloen et al. 2010), a cross-fostering experiment (Teyssier et al. 2018) and several experiments involving infestation with ticks (see further). Data are generally available but not included in the overall capture database.

Bill length and depth: these were only recorded in 1994 and (to a lesser extent) 1995, mostly on breeding birds.

Ticks and other parasites

Ticks: many studies on ticks (mostly *Ixodes ricinus* and *Ixodes arboricola*, with few findings of *Ixodes frontalis*) were performed in Boshoek in the period 2007 to 2024. Captured birds were routinely screened for the number of ticks on the head (Heylen et al. 2013a, Heylen et al. 2014) and a subset of ticks were screened for bacterial infections, notably with multiple *Borrelia* genospecies (Heylen et al. 2013b). Experimental studies whereby ticks were added to birds or nestboxes, and sometimes to birds brought for a short period into captivity, are briefly described in the next section. From October 2008 to March 2009, nestboxes in most plots were regularly checked for presence of the tree-hole tick *Ixodes arboricola*. Questing ticks of the *Ixodes ricinus* species were collected by dragging in a few smaller plots in 2006, and in some of the larger plots in 2023 and again in 2025.

Nest parasites: nest parasites and other arthropods were extracted from ca 160 Great Tit nests from Boshoek over the period 2006 to 2016. This includes ca 40 nests from 2016 where extraction was done in different nest stages (Baardsen and Matthysen 2021). All other nests were collected after fledging. In 2025, 15 nests of Great and Blue Tit each were sent to Freya Coursey (Univ Bergen) for similar extractions.

Gut microbiota: in 2016 cloacal samples were collected and gut microbiota analyzed from 26 Great Tit nests in combination with a cross-fostering experiment (Teyssier et al. 2018).

Blood parasites: As part of an international collaboration, blood smears were sent from Great Tits for the years 1997-1998, 2010 and again 2021. These were screened for blood parasites. Results were published in (Moller et al. 2013).

2.4. Major experiments

Experiments at plot or subplot level

Split-plot experiment: in 2000-2001 and again in 2003-2004, plots KB and LO were divided into a low and high nestbox density area (east vs west) by removing boxes from one half of the plot and moving them to the other half. In 2003-2004 the treatment was reversed between plot halves, with one year in between (2002) with the original nestbox placement. Boxes added to the high-density parts in 2000-2001 were labelled 'A', those added in 2003-4 were labelled 'B'. Experiments were successful in creating markedly different breeding densities between the subplots, but densities remained more or less within the range in other years in the same subplots. More information is given in Appendix 5.

Closure of plot KB: for lack of manpower it was decided to close the most central plot KB in 2020 and 2021. It was reopened afterwards but for practical reasons, the southern and least accessible part was not used again. Boxes were closed in January 2020. In november/december 2020 boxes were reopened for a few weeks, in order to do a night check for roosting birds. Many birds of KB were tested for personality score preceding the plot closure, with the aim of testing whether scores differed between birds that did or did not leave the plot after nestbox closure. However, very few birds were found outside KB.

Experiments at the level of individual nests or birds

For the far majority of these experiments, a code identifying the experiment is included in the capture and/or breeding records of the birds or nests involved. Note that the list below does not include manipulations for the purpose of collecting movement data (radiotracking, RFID tagging) or personality data. However, these manipulations are similarly annotated in the data. Experiments are not listed in a particular order.

Cross-fostering of nestlings was carried out in two periods in Boshoek: (1) in the period 1994-1999 Great and (very few) Blue Tit nestlings were exchanged with other Boshoek nests, but there were also ca 10 exchanges between Boshoek and Peerdsbos nests. Unfortunately, details are no longer fully clear (and not published), with an approximate 41 nests involved in total; (2) in 2016 nestlings of 18 broods were cross-fostered (and returned before fledging) in a study on gut microbiota (Teyssier et al. 2018)

Brood size manipulation: in 2024 a total of 26 nests were included in a brood size manipulation experiment in the context of a study on *Borrelia* infections, whereby two eggs were removed or added (Zarka, in prep).

Stress experiment on individual nestlings: In 2003 and 2004 a total of 92 Great Tit nests in Boshoek were subjected to a short-term stress "challenge". In each nest, half of the nestlings were temporarily isolated and deprived from food on days 5 and 6 ("early" treatment) or on day 10 and 11 ("late"). Body temperature and weight were taken before and after the challenge, and weight and both left and right tarsus measured at day 15. Results were published in (Talloon et al. 2010).

Immunological assay: In two winter periods (2000-2001 and 2001-2002) immune responsiveness was studied in Great Tits by injecting roosting birds with sheep red blood cells (SRBC) and taking a blood sample six days later. Only data from the second winter were published (Snoeijs et al. 2004, Snoeijs et al. 2008). In total about 100 birds per winter were injected, and about 70% of these recaptured and blood sampled; 40 additional blood samples were taken in the second winter from birds injected in the first winter only.

Nest parasite manipulation: In 2016 nest parasites were manipulated in plots KB, KL and LO by removing the nest material (and replacing with a sterile nest), sterilizing the box, addition of fleas, or combinations thereof. In total, 51 nests were affected. Data on nest parasites removed at different stages were published (Baardsen and Matthysen 2021) but not the impact of sterilizing versus flea addition.

Experiments involving ticks

Addition of ticks to breeding females: In 2007 in plot ZZ, ticks were added to individual parents when feeding 8-day old chicks. 27 broods were divided into four treatments: either male, female, both, or neither parents were infested. Parents were infested on day 8 and recaptured when young were 12 days old, and a blood sample was taken. Nestlings were weighted individually at day 3, 8, 12 and 15; blood samples were taken from three nestlings per nest on day 12. Results were published in (Heylen et al. 2009).

Adding ticks to individual nestlings: In 2008 in Boshhoek, 8-day old nestlings were infested with larvae, nymphs or adults of either *Ixodes ricinus* (IXR) or *Ixodes arboricola* (IXA). In each nest, 2 nestlings received IXA, 2 received IXR, and two were controls. In total, 33 nests were used, each with 3 or 6 infested nestlings. Starting two days after infestation, nestlings were checked daily for attached ticks. A blood sample was taken 3 to 5 days after infestation. For details and outcomes, see (Heylen and Matthysen 2011a).

In another experiment, in each of 19 nests in Boshhoek in 2009, two pairs of 8-day nestlings were subjected to a host choice experiment by ticks. Pairs of nestlings were exposed to *Ixodes arboricola* nymphs together for one hour, and immediately screened for attached ticks which were removed. After 48h the nestlings were inspected again, and after 72h a blood sample was taken. For details and outcomes, see (Heylen and Matthysen 2011b) where it is included as “experiment 2”.

In 2018 and 2019, adult female *Ixodes arboricola* ticks were added to individual nestlings, as part of a study on tick biology. Two nestlings per nest received three adult ticks at day 10 or 11, and blood samples were taken (also of uninfested control young). Details on methods and outcomes were published in (Fracasso et al. 2022, Fracasso, Matthysen and Heylen 2022). In 2017 and 2020, adult female ticks were added to nests rather than individual nestlings, and no blood samples were taken.

Temporary captivity for tick infestation: From October 2017 to February 2020, Great Tits were caught in Boshhoek and brought into captivity for 10 days for the purpose of feeding larvae (Oct-Dec) or nymphs (Jan-Feb) of *Ixodes arboricola*. In total 342 infestations were done, including some birds used more than once. Details on methods and outcomes were published in (Fracasso et al. 2022, Fracasso, Matthysen and Heylen 2022).

Xenodiagnosis of *Borrelia* infections: From the breeding season of 2022 until the summer of 2024, more than 400 Great Tits in Boshhoek were captured and infested with pathogen-free larval ticks, with the purpose of examining transmission of the pathogen *Borrelia garinii* from the bird to the ticks. In the breeding seasons (2022-2024) birds were caught when nestlings were 8-9 days old, infested with ticks, and recaptured after two or three days. In summer and early autumn (2022-2024), birds were caught with mistnets, infested, brought into captivity and released two days later. In winter (2022-23 and 2023-24), birds were captured at night when roosting in nestboxes, infested, and put back in the nestbox; birds were then recaptured approximately 60h later before sunrise. In all cases, blood samples were taken after tick removal and before release in the field. Note that in the breeding season of 2024 xenodiagnosis was combined with a small-scale brood size manipulation experiment (see above). The full methodology is described in (Zarka et al. 2024).

Adding ticks to nests: In various experiments in the years 2009-2011, ticks (of two different species) were added to nests rather than to individual birds. In most of these experiments, additional inspections of nestlings were performed which may have had more impact than the parasites themselves. Due to the complex history the experiments are not listed here individually. Outcomes were published in multiple papers (Heylen et al. 2012)

Tick infestation in combination with roost checks: in 2009-2010, great tits were subjected to an exploration test, and subsequently daily monitored for roosting in nestboxes. In addition, birds were subjected to infestation with ticks, either in situ (Oct-Nov 2009) or in the lab (Feb 2010). Results were not published.

3. Relation with SPI Birds datasets

All data for Boshoek are contained in a single SPI Birds dataset. With very few exceptions no birds have been recaptured from, or were recaptured in, any of the other study areas.

A general recommendation is to only use data from the “core” plots (Table 3). Also, depending on the question, care should be taken to select an appropriate set of years.

A few more specific recommendations:

Pedigree analysis: including all plots and years will maximize the pedigree links, but will also introduce many nest locations with few data. A safe choice is to only include the core plots.

Long-term trends: for a maximal span of years, plots LO and ZZ have the longest run (1994-present), together with KB (1994-present but two years missing) and TU (1996-present). For an optimal combination of study length and sample sizes, use the core plots from 1996 to 2019.

Habitat: to maximize habitat variation, data outside the core plots can be added (Table 3), but these are often small with a short span of years. If habitat variation is a nuisance, you can focus on the oak plot, or even the large oak plots (KB, LO, ZZ, possibly HN).

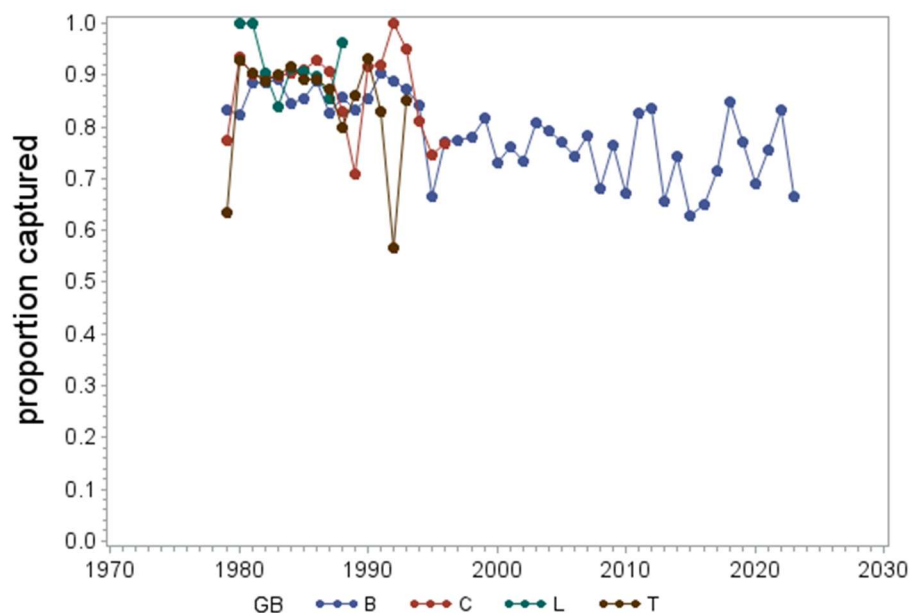
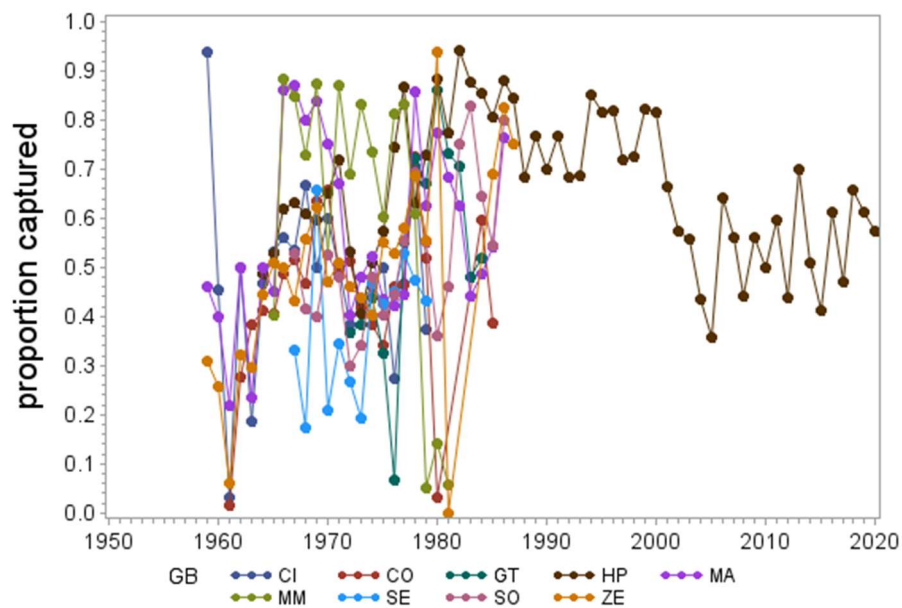
Spatial analyses: for any spatial analysis, be careful to select a set of plots and years with continuous coverage. However for specific questions (e.g. habitat choice) the additional plots may have some value.

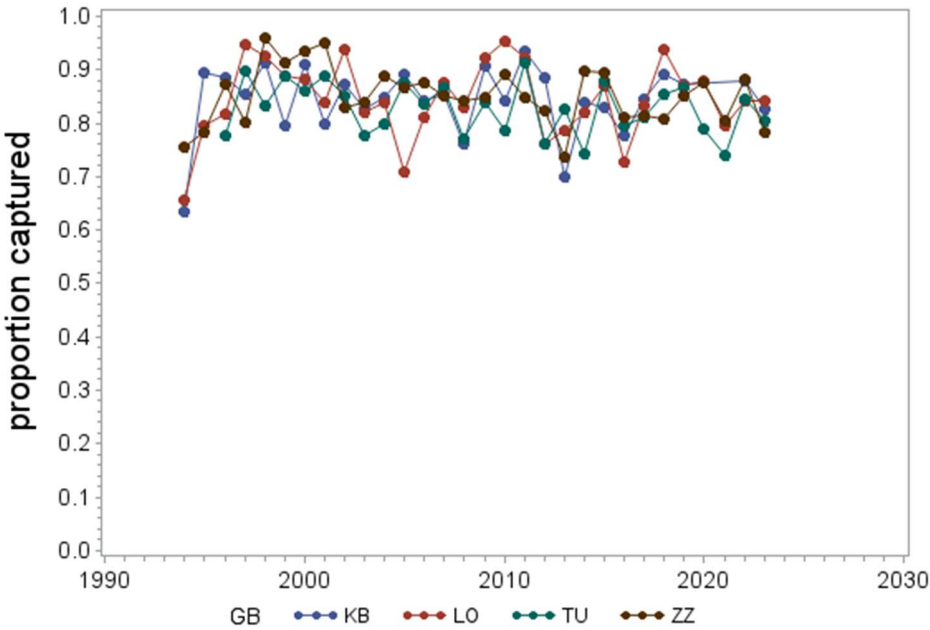
Individual nestbox level: for any study focusing on the nestbox level, keep in mind that from the 1994 to 2015 breeding seasons, one of three boxes was accessible to Blue Tits only. Thus occupancy of individual boxes will be highly unbalanced between the two species.

4. Appendices

Appendix 1. Capture rates of breeding birds in the main study areas

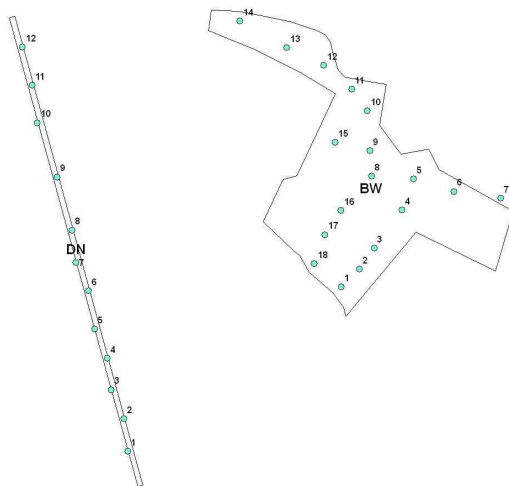
Capture rates are combined for both sexes and species per year, only in the main study periods per plot, for broods of type 1 and 9. For Boshoek only the four largest plots are shown. Note that these are capture rates over all initiated first broods, including early failed nests, thus capture rates of parents actually feeding young are much higher.



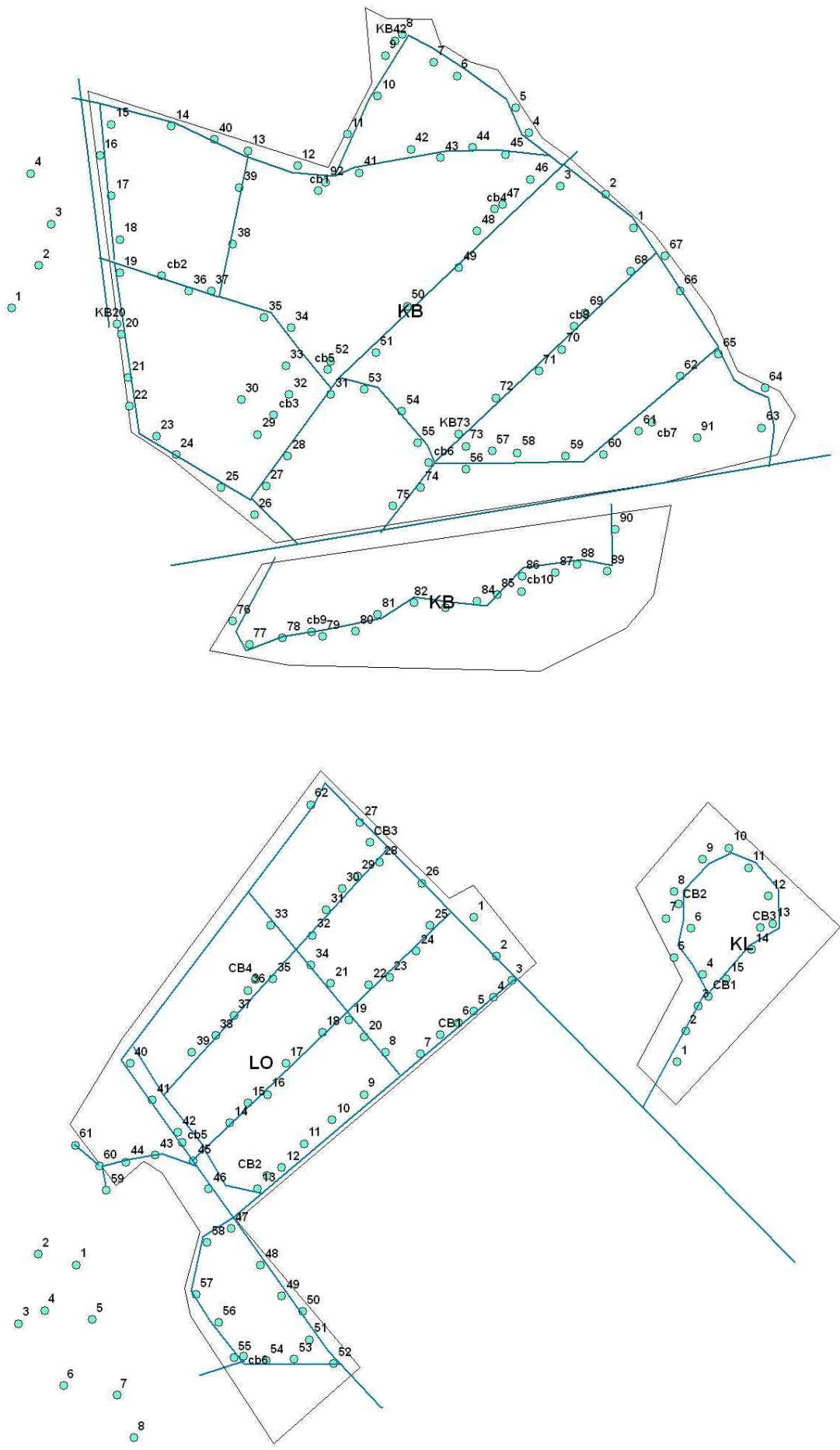


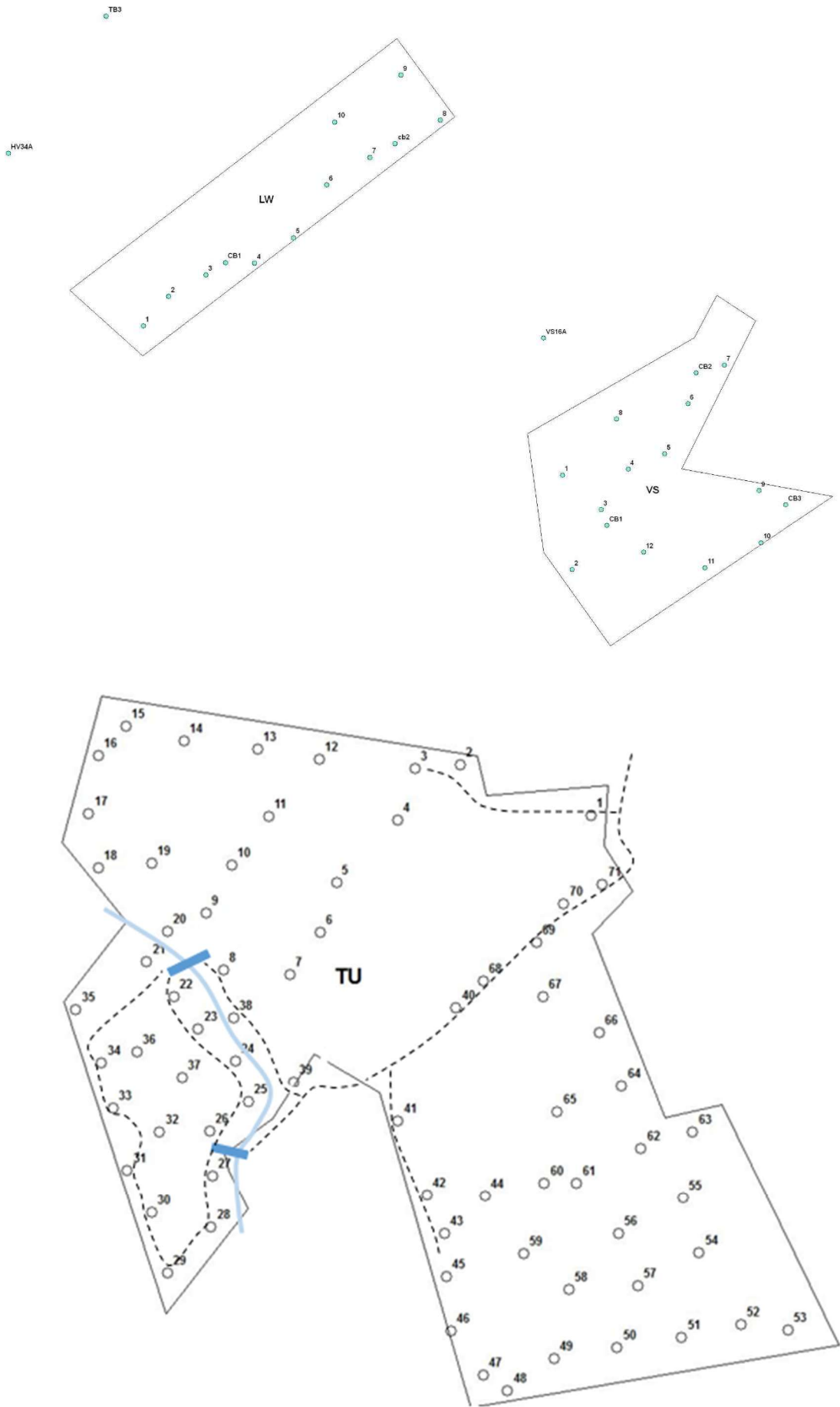
Appendix 2. Nestbox maps of Boshoek

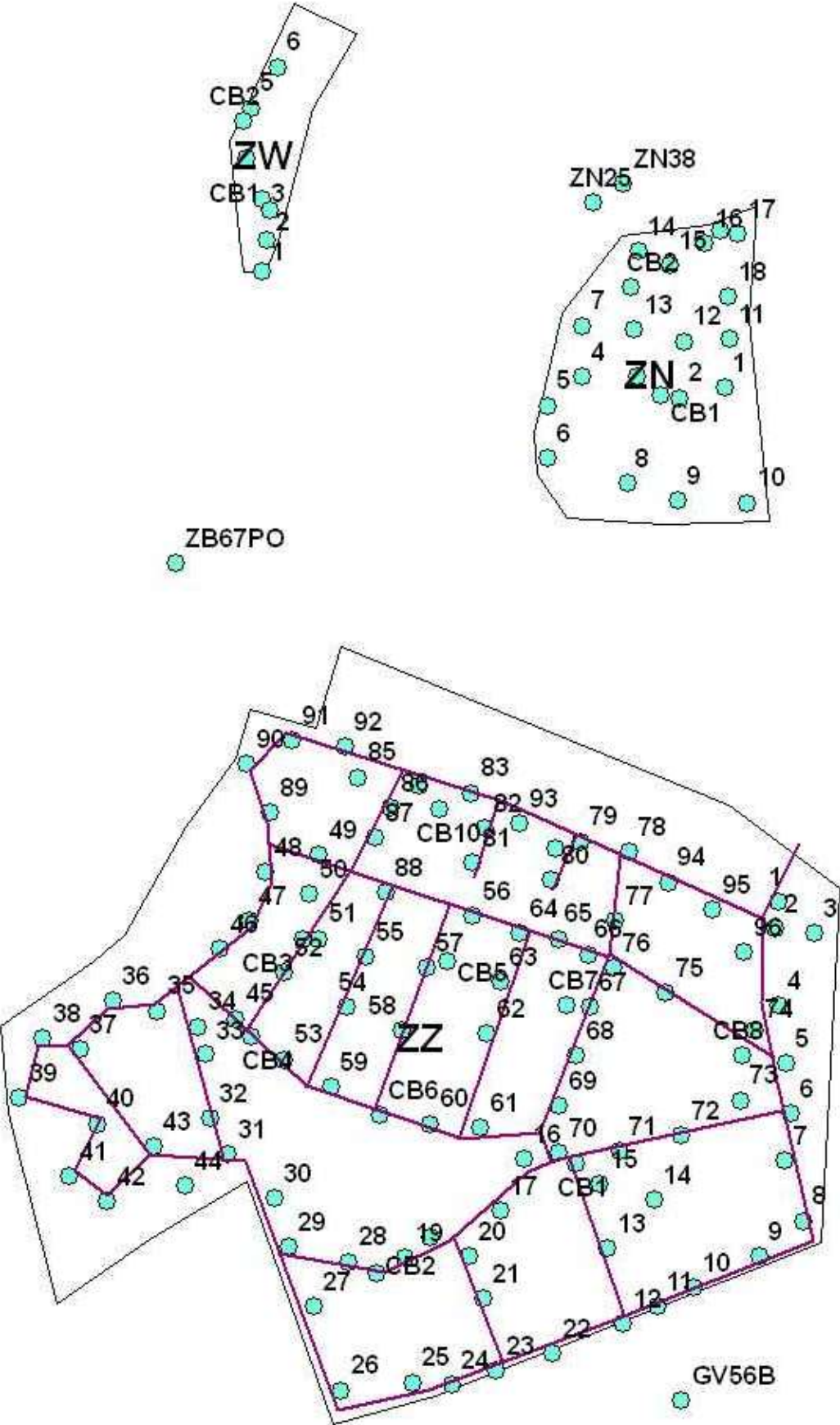
Maps are not to scale!

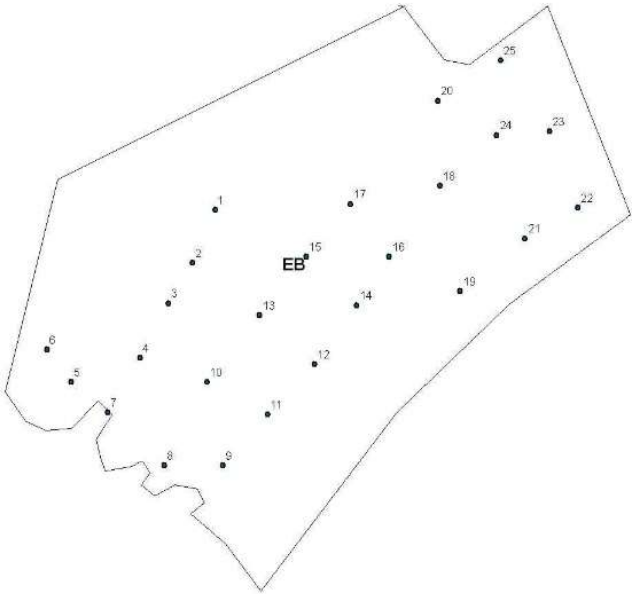












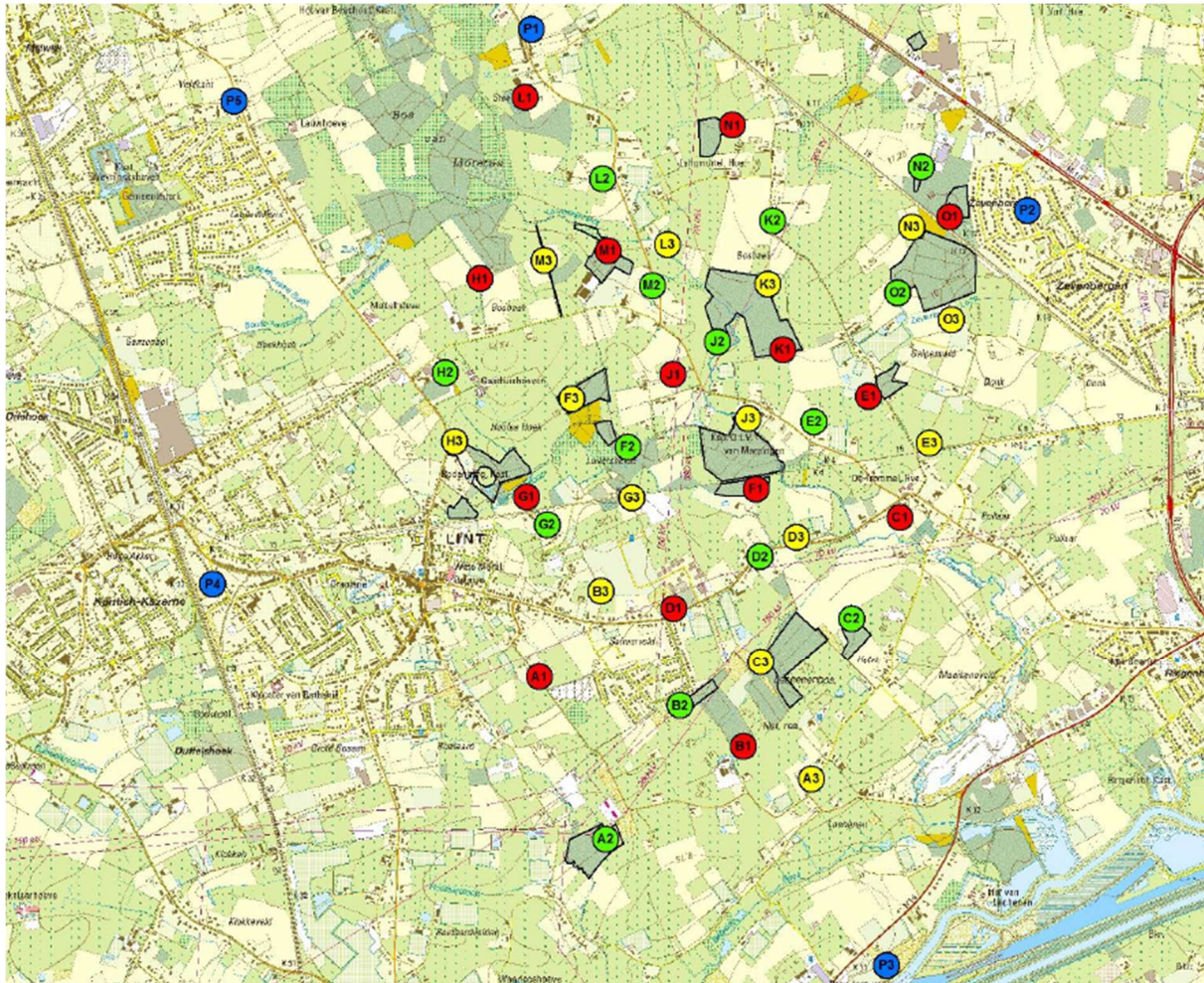
Appendix 3. Tree species for core plots in Boshoek

Percentages of tree species based on all nestbox trees and the five nearest trees for each forest plot in Boshoek (N = number of trees surveyed in 2024-2025). Note that the survey data in KB excluded boxes 79 to 90, and therefore covered only 87% of the study plot as it was before 2020. Most if not all of the trees around these boxes were probably common oak.

	Oak	Beech	Red oak	Birch	Ash	Maple	N
BW	6,7	45	0	46,7	0	1,7	60
HM	86,1	11,1	0	2,8	0	0	36
HN	60,1	0	37	1,4	0	1,4	138
KB	85,8	6,8	0	4,1	1,4	0,9	444
KL	91,1	0	0	5,6	0	2,2	90
LO	76	0,5	0,5	0,3	8,5	9,3	366
LW	83,3	0	0	15	0	0	60
TU	100	0	0	0	0	0	651
VS	84,3	0	0	13	0	0	108
ZN	74,1	18,5	4,6	0	0,9	0	108
ZZ	88,5	0	0,5	1,6	4	0,2	576

Appendix 4. Map of RFID feeders in Boshoek

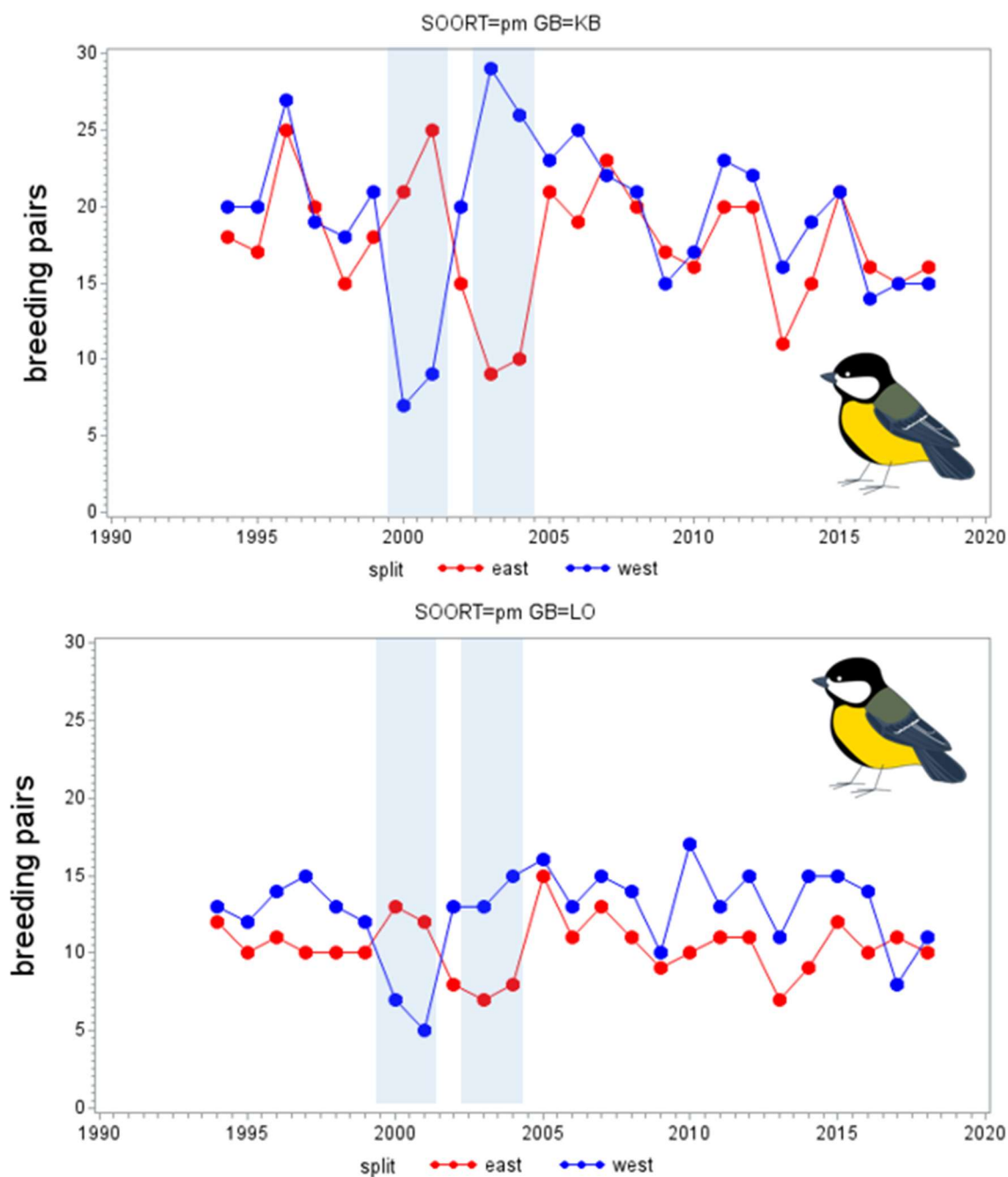
Map of feeder positions in Boshoek deployed in three years from summer to late winter (2012-2015). Letters refer to triads that were included in the same rotation; numbers and colours refer to groups of feeders that were open or closed at the same time. P (blue) = permanent feeders.

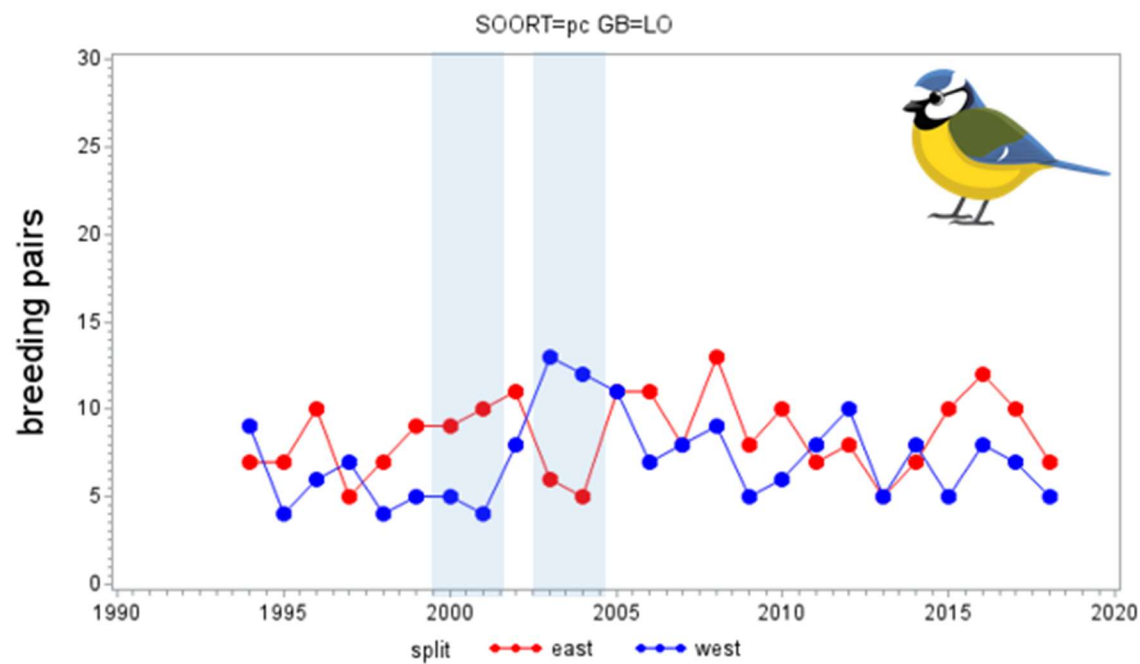
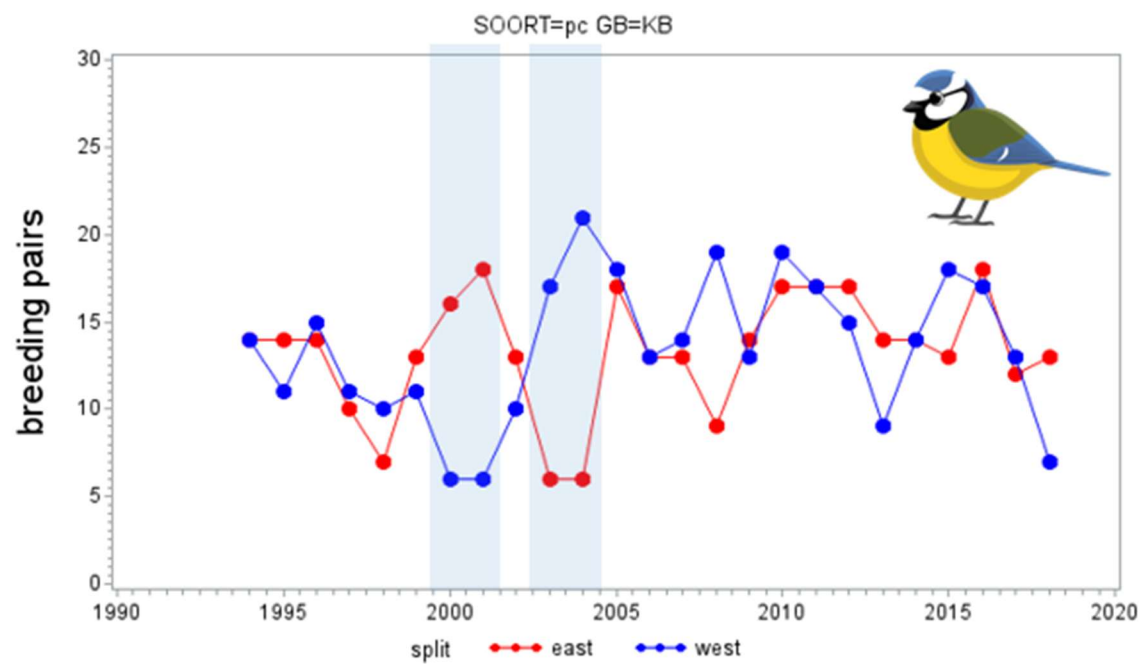


Appendix 5. Population density variation in the split-plot experiment

The figures below show Great and Blue Tit numbers in the high- and low-density treatments created by adding and removing 50% of nestboxes from half of the plots KB and LO.

Code used: splitplot.sas





5. References

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