

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

Excerpt for Peerdsbos historical data (1979-1993; plots C, K, L and T)

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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 for the historical plots (1979-1993) in the Peerdsbos study area, notably plots C, L and T with some comments on plot K. The document also refers to historical data for plot B, but there is a separate document on the long-term study in plot B continuing after 1994.

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 Boshhoek 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 Boshhoek 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.). **These are further detailed in Sections 3 and 4.** 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). The document also gives an overview of **experimental manipulations** at the level of plots, nests or individual birds.

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 “Boshoeke” 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. 2013, 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 1.5 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 Boshoeke have remained highly standardized** throughout the study period. In Ghent data were registered and processed somewhat differently, and in Speedy and some other study sites data collection was less detailed (e.g. few parents caught at the nest, or second broods not entirely followed up). **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 to as “Peerdsbos” and “Ghent”, but more recently also data from Boshoeke.

Note that during a few years, **a part of Peerdsbos was used by another research group led by Wendt Müller**, mainly for the study of parental behaviour including behavioural experiments (e.g. Griffioen, Müller and Iserbyt 2019).

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 Peerdsbos, boxes were high in publicly accessible plots T, K and B; they were low in private plots (at the time of study) C and L.

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.

- Peerdsbos: in the first 15 years, plots had different combinations of LE and SE entrances, changing per five-year period (details in 2.1.2). The long-term plot B always had a 2:1 ratio of LE and SE
- Ghent: starting in 1976, a number of plots also received different treatments in terms of 32 and 26 entrances (details in 2.3.3)
- Boshhoek: a 2:1 ratio of LE and SE was applied until 2015; starting in 2016 all changed to LE
- Zwin nestboxes: 2:1 ratio of LE and SE
- Speedy nestboxes: all boxes had LE

While the main study areas all had the standardized nestboxes, a few areas and/or plots have deviated from this:

- SPEEDY study area: here some plots utilized boxes that were already present, and also the boxes added for the project were of different sizes and shapes
- Plot TF in Boshhoek: these were private-owned boxes of different kinds
- Plot RO in Boshhoek: these were concrete boxes not installed by the project, where data on nestlings were provided by a local ringer

- Plot TU in Boshhoek: in 1994 and 1995 non-standard wooden nestboxes were present and nestlings ringed by a local ringer, but box coordinates were not recorded. These were replaced with standard boxes in 1996
- Plot T and L in Peerdsbos: in the early 1980s a small number of enlarged boxes were present
- In plot VS, a few nonstandard boxes were added in the late 2010s

Due to increasing nest predation in plot B by pine martens in the 2020s, boxes were adjusted several times by a wooden or metal extension to the entrance (see further).

1.4. Summary of data collection protocol

This description is based on the standard practice of data collection in the Peerdsbos and Boshhoek 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 (details in PARUS.DOC).

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 (for details see PARUS.DOC).

Ringing 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 Boshhoek, 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	2001-2025
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). 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

Additional (non-routine) roosting checks have been done for specific projects. In Peerdsbos this was mostly limited to plot B and T, and to the period 1979-1992. In Boshoek, many additional roost controls were done in particular years, among others for capturing birds for personality tests (e.g. 2005-2007, 2012-2014) or for xenodiagnoses (2022-2023) (Figure 2). In addition, in some years and in particular in 2013 and 2014, large numbers of roosting birds were registered by recording PIT tags from outside the nestbox, without manipulating the bird (see 4.6). Note that captures done during routine versus non-routine roost controls, have a different coding for capture type (see PARUS.DOC).

Note that periods with intensive roost controls may potentially have had some impact at population level, in particular on patterns of nestbox occupation in winter, but also on individual nestbox choices in the next breeding season.

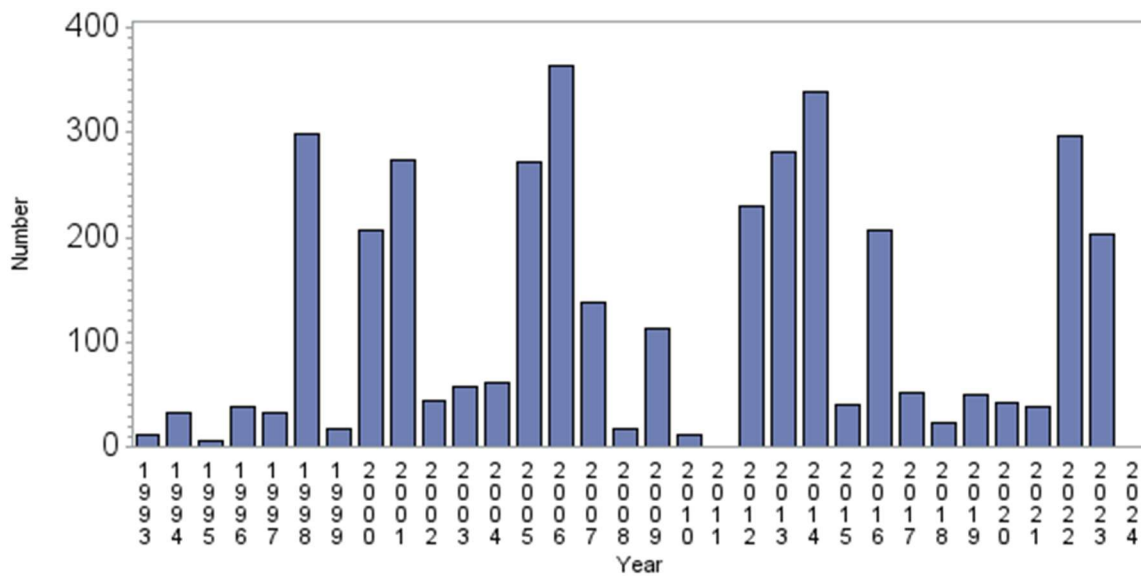


Figure 2. Number of non-routine roost checks per winter year in Boshhoek (1993 = winter 1993-94, etc).

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 Peerdsbos study area

Key points for using the Peerdsbos study area

The only true long-term plot is Plot B (“Boswachter”) which has been monitored consistently from 1979 to present, but with a major reduction in nestboxes from 1996 to 1997. Highly detailed data on tree species composition are available from the 2000s, as well as some data on lower vegetation and on tree budburst. In the years 2025-2026 many nests suffered predation by pine marten which may render some of the data less useful.

In the period 1979-1993, plots B, C and T were also monitored consistently but with different combinations of large and small entrance nestboxes. In plot T these were changed over three five-year periods. Plot L was used as an additional comparison plot but only until 1988. Due to the nestbox setup, plot C has few data on Great Tits but mostly on Blue Tits.

Other than nestbox manipulations at plot level, few experiments have been conducted that would affect individual-level data.

Since plot sizes are relatively small and plots (except C) are part of a larger forest, and despite the high capture rates of breeders, local recruitment is relatively low and pedigrees are not very deep.

2.1. General overview and history

The Peerdsbos study area in Brasschaat-Schoten contains several small plots (7 to 12 ha), some of them directly adjacent, within the larger Peerdsbos forest, plus one isolated plot (C) that lies to the south of this forest (Figure 3, Figure 4). The Peerdsbos forest is a 150-ha mixed forest dominated by common oak (*Quercus robur*, referred to as “oak” throughout this document) and beech *Fagus sylvatica* with some small conifer stands, and is adjacent to the municipal park of Brasschaat which contains similar forest stands. The total forested contiguous area is about 300ha. The plots are mostly on sandy soil (sand or loamy sand), with a smaller part on clay. The natural forest type would probably be best classified as T1E acidophilous oak-birch woodland under the EUNIS classification, but most stands originated as plantations.

The Peerdsbos study started in 1979 as part of a **large-scale experiment on interspecific competition**, in combination with a number of plots in the Ghent study area undergoing similar treatments. Four plots were included with different nestbox treatments (combinations of LE and SE¹), whereby in one plot (T) the treatments were changed every five years. **After a 15-year period, only plot B remained for standardized data collection.** Two plots (T and B) were inside the actual Peerdsbos forest, separated from each other by ca 550m of forest. Plot L was part of the same wooded area but belonged to a private estate directly adjacent to plot T to the south. Plot C was situated outside the Peerdsbos forest, in a private estate mostly surrounded by residential areas a little over 2km to the south of the other plots. In between plots T and B an additional plot (K) was installed that contained varying numbers of nestboxes over the years, and was never considered part of the standardized long-term data collection. In addition, the Peerdsbos study area has contained additional small plots with nestboxes for only a short span of years and for specific projects only (TS, MP) (Figure 4). Overall, study plots and their surrounding land use have remained very similar during their respective study periods.

¹ Large entrance and small entrance

Since plots are relatively small and (except C) not physically isolated from other forest where both tit species breed in natural cavities, **local recruitment at plot level and even for the area as a whole is relatively low** (Matthysen, Adriaensen and Dhondt 2001) and therefore pedigrees will be relatively shallow, especially compared to Boshoeck.

Table 3 gives an overview of the different plots. Population sizes are shown for all plots in Appendix 1. Capture rates of breeding birds were generally high for both species, especially in the initial 15 years (around 85% for both species and sexes combined) but dropped somewhat in the later period (Appendix 2).

Table 3. Overview of the main plots in the Peerdsbos study area. Years refer to breeding seasons.

Name	Size (ha)	Nest boxes	Years	General description	Nestbox entrances	Nestbox height
List (L)	7,5	53	1980-1988	Wooded part of private estate	All LE	Low
Tennis (T)	12,5	80-180	1979-1993	Mixed deciduous	Different treatments	High
Boswachter (B)	11,7	118-177	1979-	Mixed deciduous	LE and SE	High
Kontrole (K)	12,7	18-97	1980-	Mixed deciduous	LE and SE	High
Calixberg (C)	17	90-150	1979-1999	Partly wooded private estate	Mostly SE only	Low
Tuinen Schoten (TS)	n/a	24	2000-2004	Mixed deciduous	LE and SE	High
Melkerij Parking (MP)	n/a	24	2000-2015	Mixed deciduous	LE and SE	High

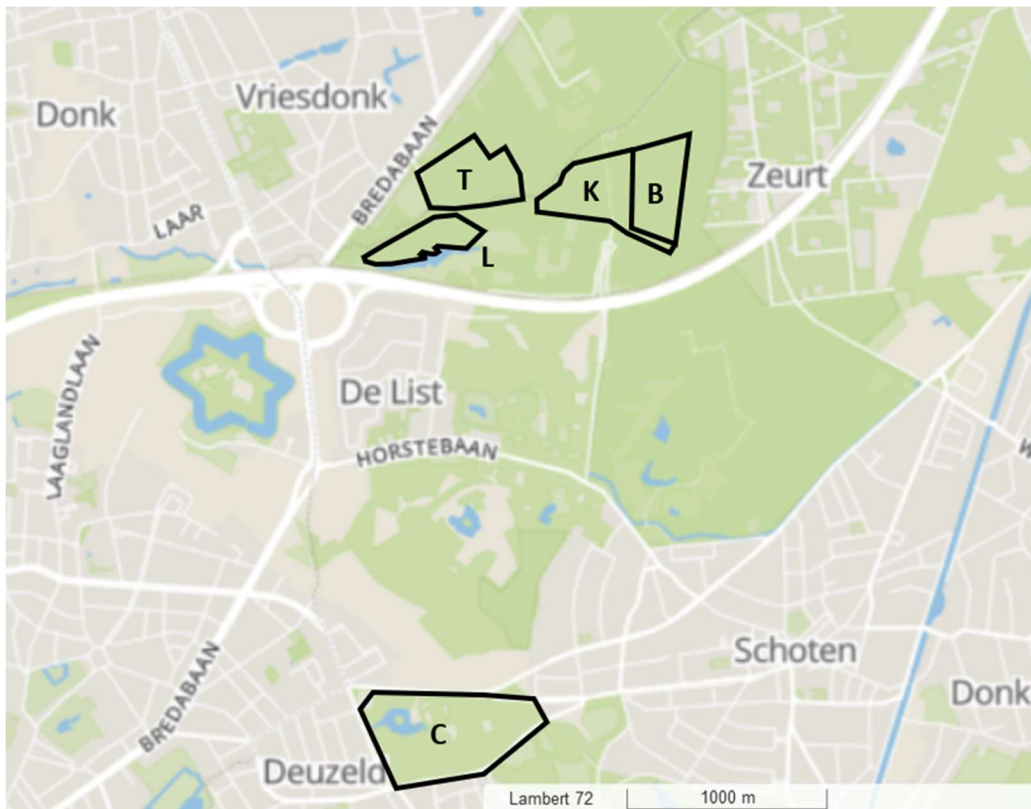


Figure 3. Overview of “Peerdsbos” plots, including plot C which lies outside the actual Peerdsbos forest. See Fig D for a more detailed overview of plots L, T, K and B.

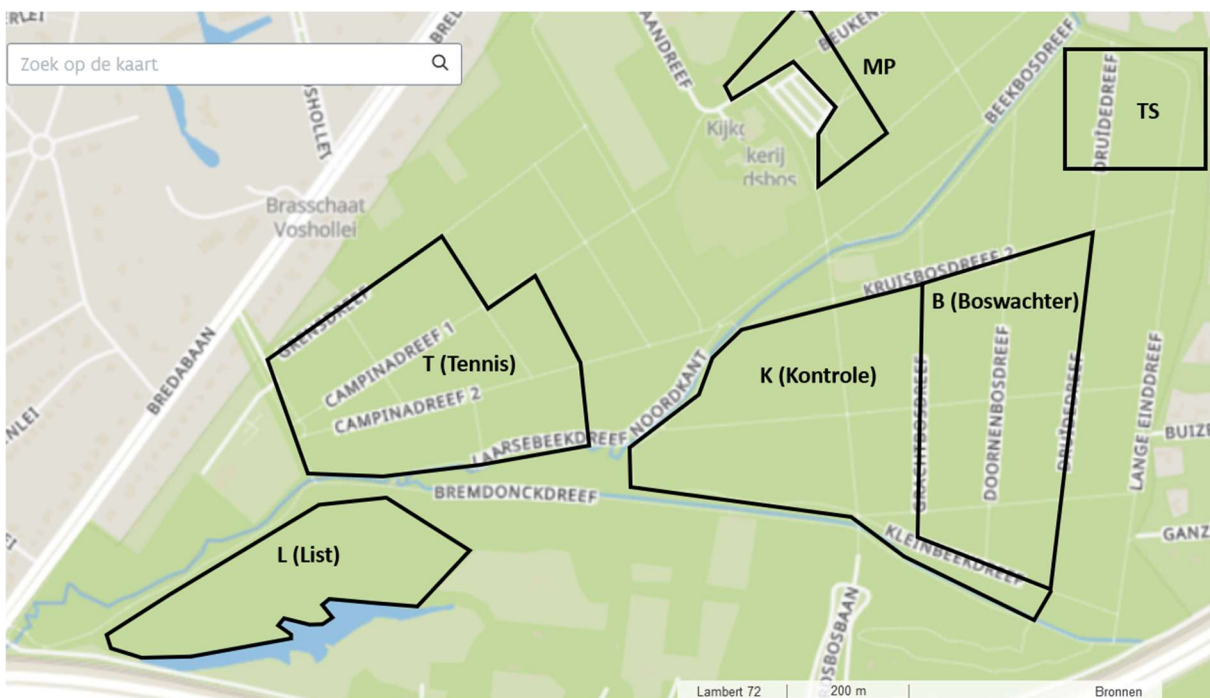


Figure 4. Detailed overview of Peerdsbos plots, including plots MP and TS. The outline of TS is only an approximation.

2.2. Study plots in Peerdsbos

The original nestbox maps of all plots are included in Appendix 4. An overview of all nestboxes is also given in Appendix 5.

Plot B (“Boswachter”) is a 11,7 ha plot dominated by old oak and beech trees and crossed by oak lanes. It is bordered by similar forest on all sides except pine stands to the north. It started in december 1978 with 118 nestboxes equally divided over large (LE) and small (SE) entrances². In january 1980, 59 additional LE boxes labelled “A” were added, thus effectively creating a 2:1 ratio of LE and SE boxes. **Starting with 1997 the nestbox density was reduced again** to the original 118 by removing the “A” boxes (Table 4). The 2:1 ratio of LE and SE was maintained however, by changing the entrance size of some of the boxes³. The rationale was to make this plot comparable to the then recently installed Boshhoek area with a similar nestbox density of 9 boxes per hectare.

Since plot B was always considered a long-term reference plot, no major experiments were conducted here. In recent decades there has been substantial mortality of oak trees, not only reducing the dominance of living oak versus beech trees but also creating gaps in the original closed-canopy stand (see 3.1.1 on available data). Due to increasing pine marten predation in the 2020s, wooden blocks were attached to the front of all nestboxes in plot B (and in the adjoining plot K) in early 2023, extending the entrance tunnel by 4cm. In the winter of 2025-26 after another season with high predation rates, tunnels were extended with another 4cm in half of the boxes, but predation continued. Thus, in late 2026 all boxes are equipped with a metal “marten protection basket”. Key references to this study plot are (Dhondt 1987a, Matthysen, Adriaensen and Dhondt 2011, Matthysen et al. 2021).

Plot T (“Tennis”). This 12,5 ha plot⁴ consists of different stands of oak, beech and other deciduous trees separated by oak lanes. It borders to large gardens in the north, sports fields to the west, and similar forest to the south (including plot L) and the east, with some pine stands directly east of the plot. While it is mostly on sandy soil, the southeastern part is on clay, more humid and with different trees (**Fout! Verwijzingsbron niet gevonden.**). **Plot T was a key plot in the 1979-1993 competition experiments and received different nestbox treatments in three 5-year periods** (Table 4). Initially 80 LE boxes were installed in january 1979, with 40 more LE boxes (labelled “A”) added after the breeding season of 1980⁵. From 1984 to 1988 all of these boxes were changed to SE (initiated in september 1983). From 1989 to 1993 the setup was changed again to 120 LE and 60 SE boxes. All of the SE boxes were labelled “B”. In december 1983 fifteen large-holed nestboxes with larger dimensions (designed for Nuthatches, labelled “S”) were also installed, but removed again in november 1984⁶. From 1994 the plot was not in use until 2000 when a small part was reinstated as part of the METABIRD project until 2004 (see also 5.3). In the late 2010s, the area was used again by Wendt Müller as part of a larger area “Peerdsbos West” (see below). Key references to this study plot are (Dhondt, Schillemans and De Laet 1982, Matthysen 1990).

Plot C (“Calixberg”) is a 31 ha private estate, of which 17 ha is wooded. It is surrounded to a large extent by dense residential areas, but to the north there is a broad corridor of partly wooded areas leading towards the other Peerdsbos plots (though interrupted by a highway and railway). **The plot was designed to have high densities of Blue Tit and low densities of Great Tits** with 90 SE boxes and 10 LE boxes until 1993⁷. The

² LE were initially the odd numbers from 1-61, the even numbers from 64-78, and the odd numbers 79-117; SE were even numbers 2-62, odd numbers 63-77, and even numbers 80-118

³ SE were from 1997 onwards: boxes 3, 6, 9, 12, 15, 20, 22, 24, 28, 30, 32, 37, 39, 41, 44, 46, 50, 53, 57, 59, 61, 63, 66, 70, 73, 75, 78, 84, 86, 88, 91, 94, 96, 99, 102, 104, 107, 109, 116, 118

⁴ Mentioned as only 11ha in (Dhondt, Schillemans and De Laet 1982)

⁵ (Dhondt and Adriaensen 1999) erroneously mentions 120 boxes starting from 1980

⁶ Referred to only in (Dhondt 2010) mentioning that “a limited number of LE boxes were available”

⁷ Many publications do not mention this small number of LE boxes, e.g. (Dhondt et al. 1990)

10 LE boxes had small entrances in most of the year, but were switched to to large entrances each year in April from 1979 to at least 1987. In the final years of the study period (1990 to 1993) data on Great Tits are partly missing. From 1994 to 1996 the area was changed to 100 LE and 50 SE boxes; the 50 SE boxes were all labelled 'A'. In 1997 the number of boxes was again reduced. The exact nature of the reduction is not clear, but apparently a few years later the number of boxes was limited to 50, with 17 of them SE⁸. Over the years the maintenance and replacement of nestboxes in this area was not a priority, hence the data from 1997 onwards should not be trusted for breeding population size or density. Aside from its role in the multi-plot competition experiment, **this plot was the focus of detailed investigations on Blue Tit ecology and behaviour**. Key references to this study plot are (Dhondt et al. 1990, Kempenaers 1995).

Plot L ("List") is 7,5 in size and had 53 LE boxes from 1979 to 1988. It was a wooded part of a private estate (with a small clearing in the middle) with a highly diverse mixture of tree species. It was inaccessible to the public, therefore boxes were at low height. This plot was used in some analyses on interspecific competition, but otherwise mostly used for research on Great Tit song and on territorial behaviour in Nuthatches. In december 1983 17 extra large nestboxes were installed for Nuthatches. A key reference is (Matthysen 1990).

Plot K ("Kontrole") is similar in vegetation to plots T and especially B and surrounded by the Peerdsbos forest on all sides. It had different sizes and nestbox configurations over the years, but was never considered one of the regular study plots, but rather as a source of additional ringed birds and/or an area that could be used for experimental manipulations. From 1980 to 1987 18 nestboxes were available in the centre of the plot (labelled B) but these were not open in winter (Dhondt 1987b). In november 1987 and march 1988, 10 and 19 LE boxes (labelled C and D, respectively) were added, and another 19 LE boxes (labelled E) in march 1989 (though no broods were recorded in the database in these boxes). The D and E boxes were removed in november 1989. From 1994 to 1996 no boxes were monitored. From 1997 onwards the entire plot was covered with 123 nestboxes. In 2001, boxes 92 to 117 were closed as part of the METABIRD project (see 5.3). In addition the western part has been used from 2015 to 2019 by a different project (see below "Peerdsbos West"). Briefly, the only part of the K dataset that would be suitable for any analysis are the boxes 1-49 in the period since 1997, since these were not used for experiments and nests were monitored at least for ringing young, although capture rate of parents has been variable.

Table 4. Overview of nestbox treatments per year in the main plots of the Peerdsbos area. LE and SE refer to large- and small-entrance boxes. Years always refer to breeding seasons when the boxes were in use. Note that plot T contained 15 additional LE boxes for Nuthatches in 1984 only. Also note that the 17 ha for plot C only refer to the wooded part (total is 31 ha).

Code	Plot name	Size (ha)	LE	SE	Total	Start	end
B	Boswachter	11,95	59	59	118	1979	1979
B	Boswachter	11,95	118	59	177	1980	1996
B	Boswachter	11,95	79	39	118	1997	
C	Calixberg	17	10	90	100	1979	1993
C	Calixberg	17	100	50	150	1994	1996
C	Calixberg	17	34	17	100	1997	1999
L	List	7,5	53 ⁹	0	53	1980	1988
T	Tennis	12,74	80	0	80	1979	1980
T	Tennis	12,74	120	0	120	1981	1983
T	Tennis	12,74	0	120	120	1984	1988

⁸ Box numbers with SE: 1, 7, 13, 18, 22, 27, 34, 40, 51, 65, 69, 73, 80, 84, 94, 98, A24

⁹⁹ Apparently erroneously as 50 in (Dhondt and Adriaensen 1999)

T	Tennis	12,74	120	60	180	1989	1993
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Additional notes on Peerdsbos study pots:

- From 2000 to 2004, two small plots (MP and TS) each with 24 nestboxes were installed to the north and northeast of plot B for the METABIRD project (in addition to a part of plot T; see further). Of these, plot MP was continued until 2015, mostly as a plot for some pilot experiments.
- From 2015 to 2019 the former plot T and a large part of plot K were part of “**Peerdsbos West**”, a study area monitored by a team led by Wendt Müller, focusing particularly on Blue Tits . These data are not in the overall Peerdsbos database, and can be obtained separately from Müller (see Appendix 5).
- From July 1982 to June 1987, plot L and an extended version of plot T were used for an intensive **study on Nuthatches** (for an overview see (Matthysen 1998) which had some implications for the Great and Blue Tit research. First, throughout this period and in all seasons except April-June, small feeders with sunflower seeds were used to attract and trap Nuthatches. As a consequence many tits were caught as bycatch. Second, 40 large nestboxes with a 32mm opening were provided in plots L and T in autumn 1983 (labelled ‘S’) with the aim of attracting Nuthatches, but with low success. These boxes were removed again after the breeding seasons of 1984 (plot T) and 1985 (plot L) to not interfere with the ongoing competition experiments. Some boxes remained in the vicinity of plot T for a few years and were attributed to **plot ME** which otherwise did not have any nestboxes.

2.3. Additional data collected

Vegetation in plot B: In 1986, vegetation surveys were conducted around all 177 nestboxes in plot B (tree species and sizes within 10m, herb and shrub coverage). In 2010 and again in 2017, all trees in plot B (including the lanes with oak trees surrounding the plot) were mapped, measured and their live/dead status recorded. All information and tree maps are available in (Matthysen et al. 2021).

Vegetation in plot T and L: in the 1980s a detailed tree cover map was made for plots T and L in the course of the Nuthatch project (Matthysen 1990) (Appendix 3).

Beech crop data: only collected in 1983-1986 in plots L and/or T.

Roosting birds: Regular roost controls have been conducted every winter from the autumn of 1979 to early 2025. In the first half of the study period until 1996, nestboxes in all plots (except K) were checked once each month from November to February for roosting birds. Note that these regular roost checks are coded specifically in the capture database to distinguish them from ad hoc captures of roosting birds.

Food provisioning: in 1994 and 1995, food provisioning was recorded at 61 nests in plots B and C (blue and Great Tits combined). Results were published (Nour et al. 1998), but the data are no longer available.

Moult data: in the early 1980s flight feather moult of adult birds was regularly scored in summer, mostly on Great Tits. From 2021 to 2023, targeted mistnet captures were done to obtain moult scores in July and August in plots B and K.

2.4. Experimental manipulations

Experiments at plot or subplot level

Nestbox setup: experiments involving combinations of LE and SE nestboxes are described in detail in 2.1.1 and 2.1.2. Briefly, from 1979 to 1993 plot C was set up to have high densities of Blue Tit and very low of Great Tit; plot B was set up to have high densities of both species (high density of both SE and LE); while

plot T had varying treatments over the five year periods. Plot L only had LE boxes and was sometimes used as an additional reference site, but not for the entire period (see 2.1.2).

Experiments at bird or nest level

Crossfostering: in spring 1979 and 1980, eggs were exchanged between most Blue Tit nests in plot C for the purpose of studying heritability in morphology (Dhondt 1982); nestlings were not returned to the nest of origin.

3. Relation with SPI Birds datasets

The data described here can be found in two SPI Birds datasets: the “Peerdsbos historical” dataset which contains plots C, L and T for the 1979-1993 period; and the “Peerdsbos plot B” long-term dataset which includes the same 15 years of data. Thus, for any (re-)analyses on the full data of the 15-year competition experiments with high and low great and blue tit densities, the two datasets need to be combined.

The data for the other Peerdsbos plots (K, MP, TS) are currently not included in any dataset. The data from plot K from the 1979-1993 period might provide a few additional data on movements of birds from the other plots, but this is probably negligible. Plots MP and TS fall outside this period.

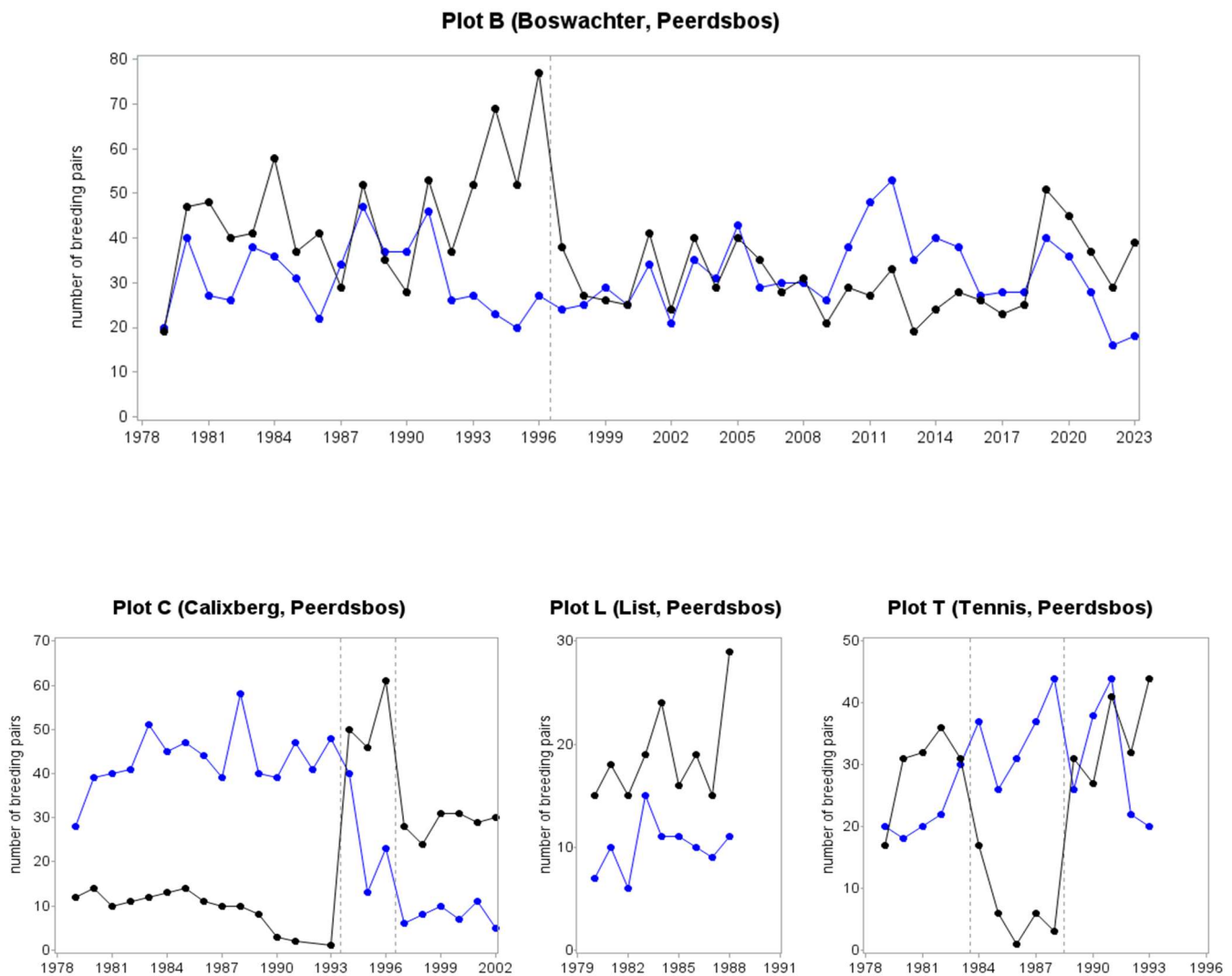
The data collected after 1993 in these plots are also not included in the Spi Birds dataset, since data are no longer comparable to the 1979-1993 time series.

All additional data are available only upon specific request.

4. Appendices

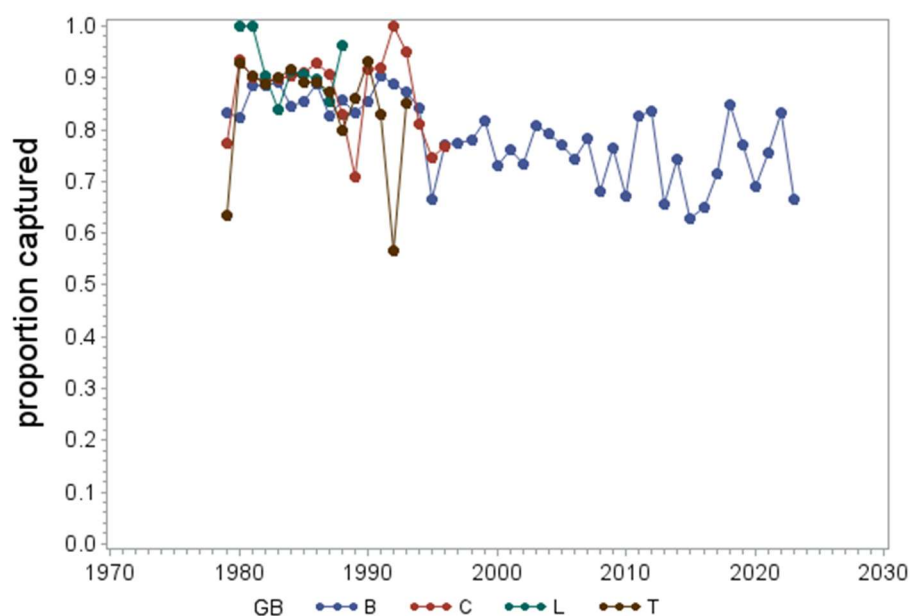
Appendix 1. Population sizes in the main Peerdsbos plots

Black and blue data points correspond to Great and Blue Tits, respectively. Note that breeding pair numbers include late broods of so-called intruder pairs (coded in the database as brood type 9) (Dhondt and Schillemans 1983). Dashed lines represent changes in nestbox setup (see Table C) (generated by SAS procedure **popsizes.sas**).



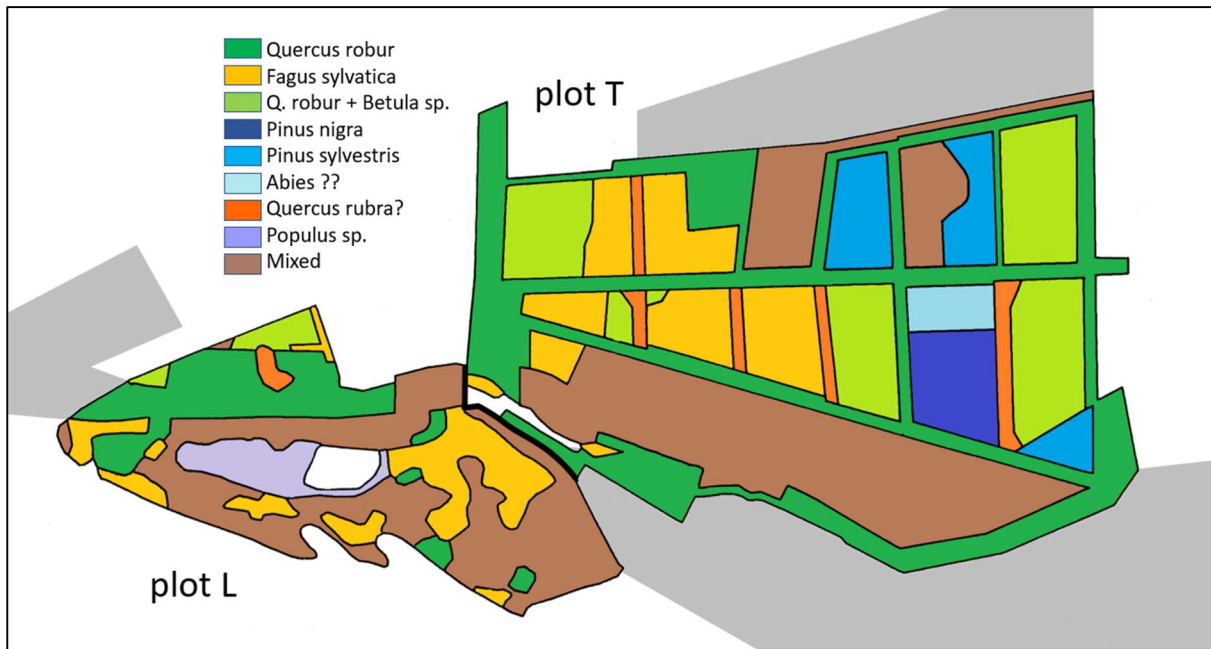
Appendix 2. Capture rates of breeding birds in Peerdsbos plots

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. 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.



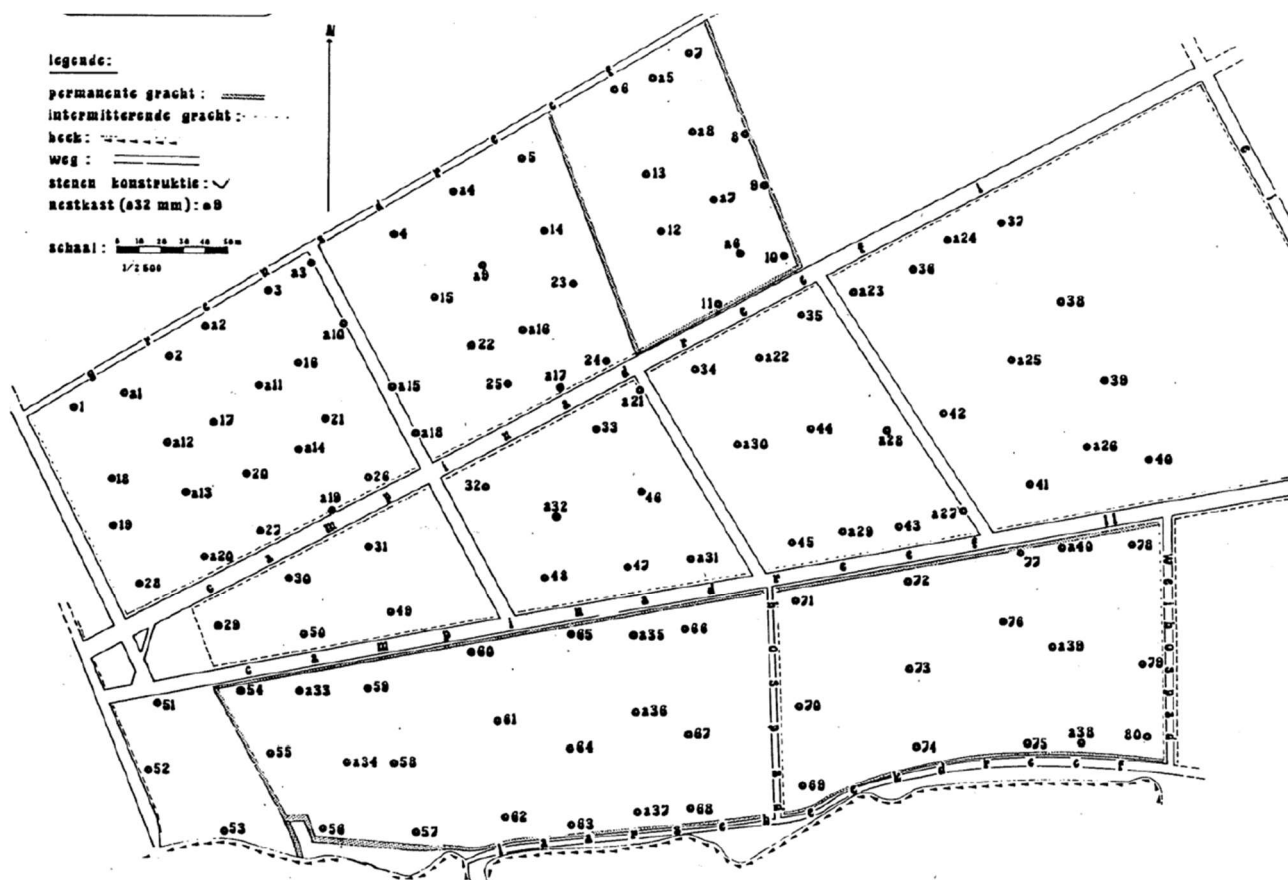
Appendix 3. Vegetation map of plots T and L

Tree species composition in plots T and L. Grey areas indicate where wooded vegetation extends beyond the borders of the study area. White areas have no or only sparse tree cover and are considered unsuitable habitat. Note the difference in structure between plot T and plot L, whereby plot T consists of discrete forest stands separated by lanes bordered with *Quercus robur* or *Q. rubra*, while plot L is more heterogeneous (redrawn from (Matthysen 1990)).



Appendix 4. Original nestbox maps of Peerdsbos

Plot T: initial 120 boxes



Plot T: with 60 boxes added

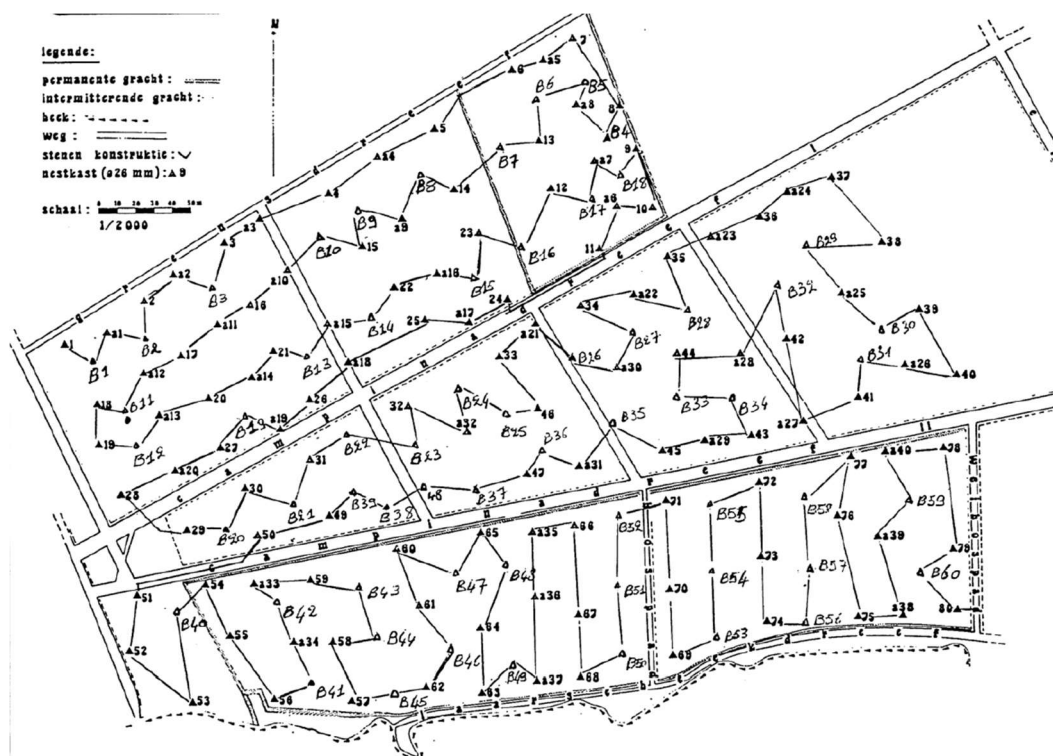
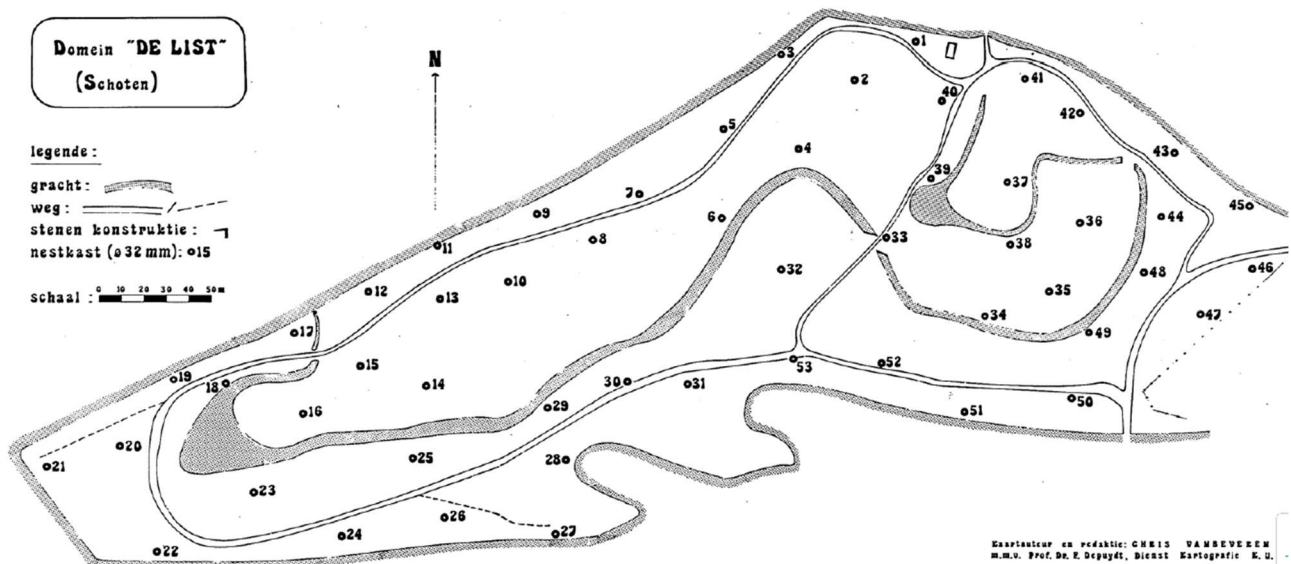


Figure below: boxes used from 2000 to 2004 as part of the METABIRD project (not the boxes labelled B). This is the minimal area as it is not clear if boxes 53, 56 or 57 were included or not (no breeding records). In 2003 the boxes remained closed as part of the experiment. Boxes 17, 19, 27, 29, 52, 59, A1 and A34 had small entrances.

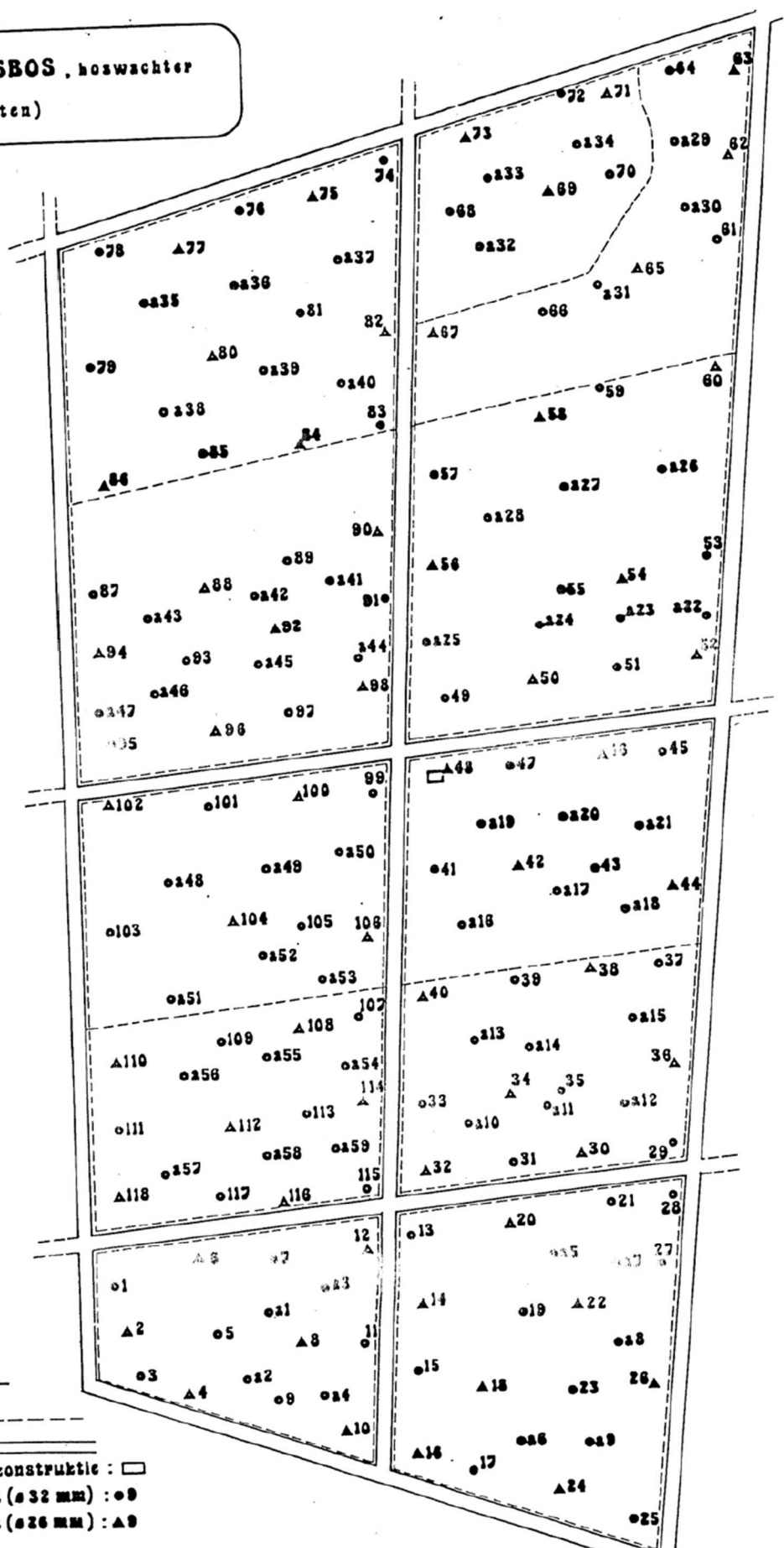


Plot L



Plot B:

PEERDSBOS . boswachter
(Schoten)

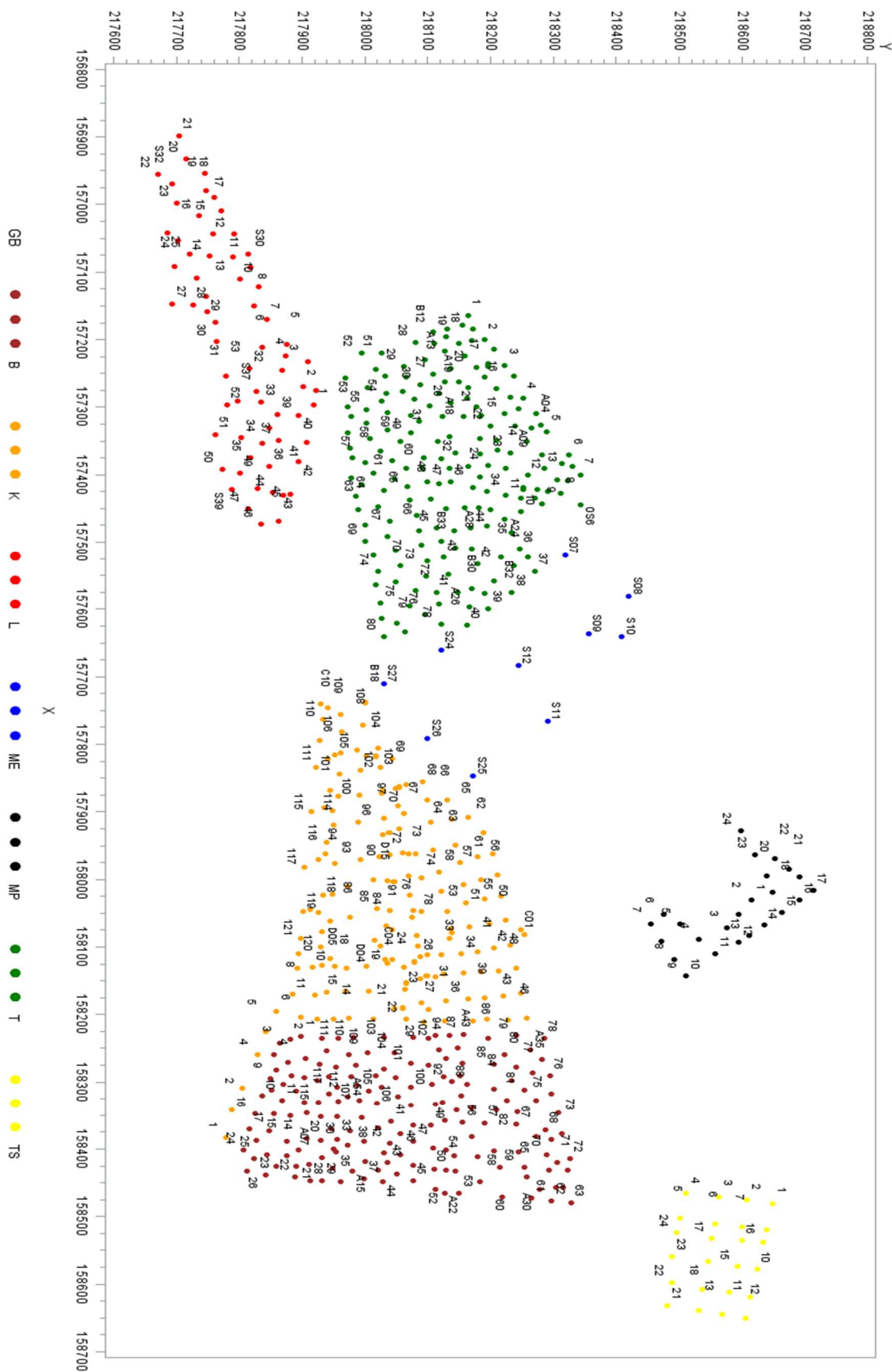


Plot K in 1988:



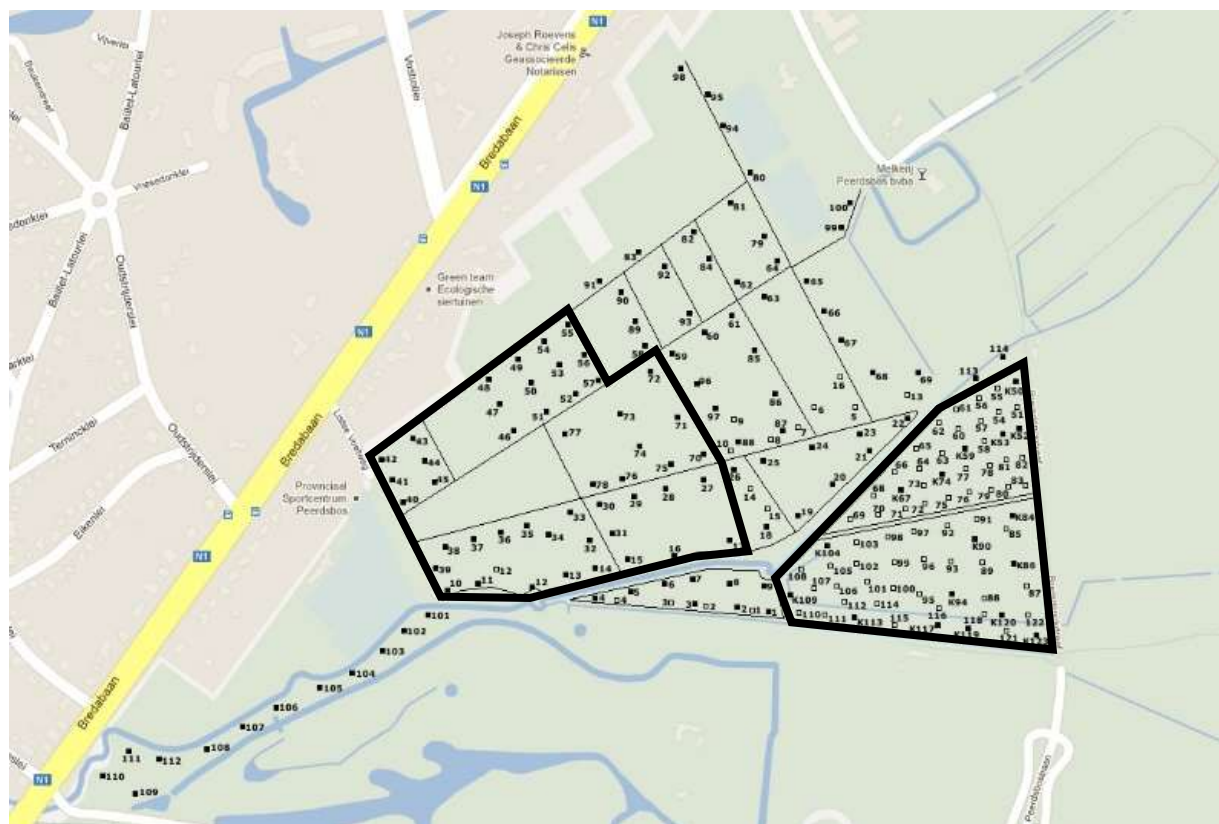
Appendix 5. Map of all nestboxes in Peerdsbos

Based on coordinates in the database. Note that nestboxes shown here have not necessarily been present at the same time. X and Y axes are in meters.



Appendix 6. Map of “Peerdsbos West”

Map of nestboxes in “Peerdsbos West” area (directed by Wendt Müller 2015-2019). Heavy lines indicate plot T (left) and part of plot K (right).



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