Colony formation and breeding success in the rapidly declining Black-headed Gull

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Title: Colony formation and breeding success in the rapidly declining Black-headed Gull

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Abstract

Black-headed Gulls are in rapid decline in Norway and is categorized as VU (Vulnerable) on the national Red List. The Norwegian population has decreased from 30 000 pairs around 1990 to just 7000 pairs in 2011. In the study area, the inner Oslo Fjord, the total breeding population counted about 3000 pairs in 2018. This study aims to explain variations in nest and chick survival both within and between colonies, with respect to date of individual nest settlement or colonies establishment, as well as stress elements and colony defence. Multiple colonies were monitored with a combination of nest cameras and drone footage throughout the breeding cycle. From this, data regarding formation, as well as nest and chick survival, were analysed.

Of 3050 Black-headed Gull nests monitored in this thesis, one in five produced chicks. Pairs settling early in the breeding season had a much higher nest survival probability than those that settled later. This was true both within and between colonies. Larger colonies had higher nest survival than smaller colonies. The most observable reason for nest and colony failures were predation from Crows, large Gulls, Red Foxes and Badgers. Colonies that failed completely were likely to have a weaker colony defence due to behavioural changes, which made the colony more accessible for predators. Low food availability and a combination of other stress factors are presumed to have made many pairs in the colonies invest less energy in current reproduction and rather focus on own survival and future breeding attempts. From a population perspective, this strategy is sustainable for a few years, but if breeding seasons with low reproduction success are too frequent, the species decline will continue, possible until extinction in Norway.

Acknowledgement

The list of people to thank for the completion of this thesis has grown unrealistically long. First of all, thanks to my supervisors, Morten, Anna and Torbjørn, for an immense degree of engagement throughout the project. Especially thanks to Morten for psychological support when the study birds slowly died during the season, Anna for extra help in the writing process, and Torbjørn for helping with the statistics. At the same time, you have all actively asked for drafts, when most other supervisors were nowhere to be found and returned them within an astonishingly short time! Thanks to Morten Lie, Anders Herland, Morten Helberg and my dad for all the help I got during the fieldwork, including transporting and carrying equipment. Thanks to Morten and Lome for letting me freely use their boat (that almost always worked) throughout the fieldwork, regardless of what state the propeller was returned in the year before. Vemund for the company in the field, and for all the help looking for/at dead chicks in the colonies, as well as not wrangling the book away from the professor, and to Vivian and Arild in Bergen who found it in the end. Also, thanks to Arild for sourcing the final cable on short notice.

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1 Introduction

Many bird species are in rapid decline throughout the world (IUCN, 2019). Anthropogenic changes, such as destruction of wetlands, intensified agriculture and climate change are responsible for many of these declines (Díaz et al., 2019). Since 1700, 83% of all wetlands in the world have been destroyed, while human food production has increased by 300% since 1970 (Díaz et al., 2019). Wetlands are highly cultivable and have often been drained in the process of creating suitable agricultural land (Holland et al., 1995). This has resulted in a decline in many wetland species due to displacement to smaller and increasingly fragmented landscapes (Guadagnin & Maltchik, 2007; PECBMS, 2018). Even though the total agricultural area is increasing, many farmland species are also in decline due to increasingly intense farming, which changes food availability and often the habitat itself (Francesiaz et al., 2017; Heldbjerg et al., 2017; PECBMS, 2018). One likely reason behind the change in food availability for farmland birds is the recent decline in insect abundance (Hallmann et al., 2017; Hambler & A. Henderson, 2019). This shows how many systems are closely connected with each other, and how important it is to preserve a multitude of ecosystems.

Black-headed Gulls inhabits both wetlands, agricultural land and coastal habitats, and might be affected by changes in multiple ecosystems. The species breeds in colonies, both on saltwater islands, in wetlands, and at, often eutrophic, inland lakes (Cramp, 1983). Some Black-headed Gull colonies might be dependent on agricultural resources, e.g. Earthworms (Lumbricina), while other colonies rely mostly on resources found near the shoreline (Cramp, 1983). The food choice is likely to vary depending on colony placement, and the abundance and availability of food sources nearby (Catry et al., 2013). The Black-headed Gull is, therefore, a particularly interesting species, as its population decline might indicate challenges in multiple ecosystems.

Black-headed Gulls have a wide distribution, from eastern Russia, through Europe, to Greenland and the north-eastern parts of America (Blotzheim, 1982; Cramp, 1983). During the 1800s, the world population started to increase, with a pronounced surge during the 1900s (Cramp, 1983). Later, the growth has stopped in most areas and Black-headed Gull populations are reported to have a moderate decline in Europe since the 1990s (Gregory et al., 2015).

In Norway, the first Black-headed Gulls started to bread in 1867 (Haftorn, 1971). The population slowly increased, with a peak around 1980-1990. The population has subsequently declined from about 30000 pairs around 1990 to only about 7000 pairs in 2011, a 77% decrease (Breistøl & Helberg, 2012). This has resulted in Black-headed Gull being classified as VU (Vulnerable) on the Norwegian Red List for Species (Henriksen & Hilmo, 2015). The same dramatic reduction is observed in Denmark and Sweden (Green et al., 2017; Ottosson et al., 2012). Today the highest density of Black-headed Gulls in Norway is in the area around Oslo, with the largest colony at the lake Østensjøvannet. This colony counted just above 1000 pairs in 2017 (pers. obs.). In addition, there are small colonies throughout the area, both in freshwater lakes and on islands in the Oslo Fjord (Andersen & Bergan, 2017). Many of these small colonies are fragile and fail to produce chicks most years, which might be part of the explanation for the continued decline in the population. The mechanisms behind these failures are poorly understood (Leito et al., 2016), however, it might be of great importance for conserving this and other colonial species.

There are multiple possible explanations to why some Black-headed Gull colonies fail. Many colonies suffer losses due to high predation from other species (Craik, 1995; Frank, 1979; Kruuk, 1964). Often, this might be predation from invasive species that the colonies do not have good defences against, e.g. as observed in invasive rat and cat predation on Cory's Shearwater (*Calonectris borealis*) colonies on the Macaronesian islands in the Atlantic (Hervías et al., 2013). Likewise, high predation pressure can be exerted from native predators (Kruuk, 1964). Predator and prey are naturally in an arms race for the best attack and defence strategies (Dawkins et al., 1979), and bird colonies are known to attract several different predators which can have devastating effects on breeding success (Ataei et al., 2014; Becker, 1995; Brunton, 1997). Both native predators as Red Fox (*Vulpes vulpes*), Crows (*Corvus* spp.), large Gulls (*Larus* spp.) and Hedgehogs (*Erinaceus* spp.), as well as invasive species such as American Mink (*Neovison vison*), are known to predate Black-headed Gull chicks to a varying degree (Kruuk, 1964). Especially Red Fox and European Mink are known to be able to eradicate whole bird colonies (Craik, 1995; Kruuk, 1964). Nevertheless, a high degree of colony defence will usually make predation difficult (Beer, 1963, 1965; Kazama & Watanuki, 2010).

If the predation pressure becomes too high, or some additional stress elements appear, birds in the colony might invest less in colony defence and thus make the colony more vulnerable for predation (Ashbrook et al., 2010; Stearns, 1992). These individual trade-offs are important for explaining survival in bird colonies, as they might not be as apparent for the observer as the predation itself. Factors such as food availability and disturbance to a colony are likely to make the individual birds invest less in the current breeding attempt, and save resources towards future breeding seasons or own survival (Anholt & Werner, 1998; Heaney & Monaghan, 1996; Stearns, 1992). Low food availability will also force adult birds to stay away from the colony in search for food for longer periods of time, further reducing the colony defence as fewer birds are present (Anderson, 1990; Ashbrook et al., 2010).

All breeding pairs within a colony do not settle at the same time. Usually, a few birds, called pioneers, settle their nests first, before the colony grows (Buck et al., 2005; Forbes & Kaiser, 1994). Two theories explaining this formation process in bird colonies are central-periphery and central-satellite theory (Hamilton, 1971; Velando & Freire, 2001; Vine, 1971). In both theories, high-quality pairs are defined as the ones producing fledged chicks. In central-periphery theory, high-quality pairs settle first in what will become the centre of the colony (Hamilton, 1971; Vine, 1971). From there, the colony grows outwards with progressively lower quality pairs toward the colony edges. The outermost low-quality pairs then have the highest predation risk. This has been observed both in Black-headed Gull colonies and in other species that seek protection within the colony boundaries (Cramp, 1983; Liordos & Lauder, 2015). The central-satellite theory also includes birds of higher quality, but they are distributed randomly throughout the colony (Velando & Freire, 2001). The next pairs to settle then establishes around these high-quality satellites throughout the colony. The details of the formation process, however, is rarely studied in gulls or other similar species.

1.1 Aim

The aim of this study is to examine the breeding success of the Black-headed Gull colonies in the inner Oslo Fjord in Norway. Breeding success is likely to vary both within and between colonies. To describe and explain this variation in breeding success, weekly drone surveys recording the occupancy state of each nest location and high frequency camera surveillance of individual nests from multiple colonies in the study area were conducted. Four hypotheses were formulated. (1) Early settlers have higher survival than late settlers, (2) large colonies have a higher degree of nest defence, and thereby higher survival, (3) colonies follow central-periphery theory, and thus, nests in the middle of the colony have higher survival, and (4) disturbance adds additional stress to the colony and reduces its survival.

2 Methods

2.1 Study locations

The fieldwork was conducted in the marine archipelago of the inner Oslo Fjord in Norway (59.8N, 10.6E), as well as in two neighbouring freshwater lakes. In the area around Oslo, there has been a colour-ringing project on urban Gulls, including Black-headed Gulls, for a few years prior to 2018. The colour-rings used for Black-headed Gulls in Oslo are white or green plastic rings with a unique alphanumeric combination attached to the birds' leg. This meant that the study population used in this thesis was easier to follow and made it possible to distinguish different individuals throughout the fieldwork. During the summer of 2018 (April-July), there were a total of 3400 ring readings in the study area, which consisted of 894 different individuals. Of these, 858 readings of 169 different individuals were registered in association with the study colonies (unpublished data, based on Norwegian colour-ringing database).

Six Black-headed Gull colonies were chosen as main study colonies (Geitungsholmen, Killingen north, Killingen south, Sognsvann, Søndre Langåra and Østensjøvannet). All these colonies had been occupied for several years in a row, except Geitungsholmen which was occupied for the first time since 2007 (Andersen & Bergan, 2007, 2013). In these colonies, seven nests were monitored with cameras during the incubation. At Østensjøvannet, the sub-colony in the south-west (SW) was chosen for the nest cameras (Figure C1). In addition, most colonies in the inner Oslo Fjord were photographed from above with a drone weekly during the entire breeding cycle (Figure 1).

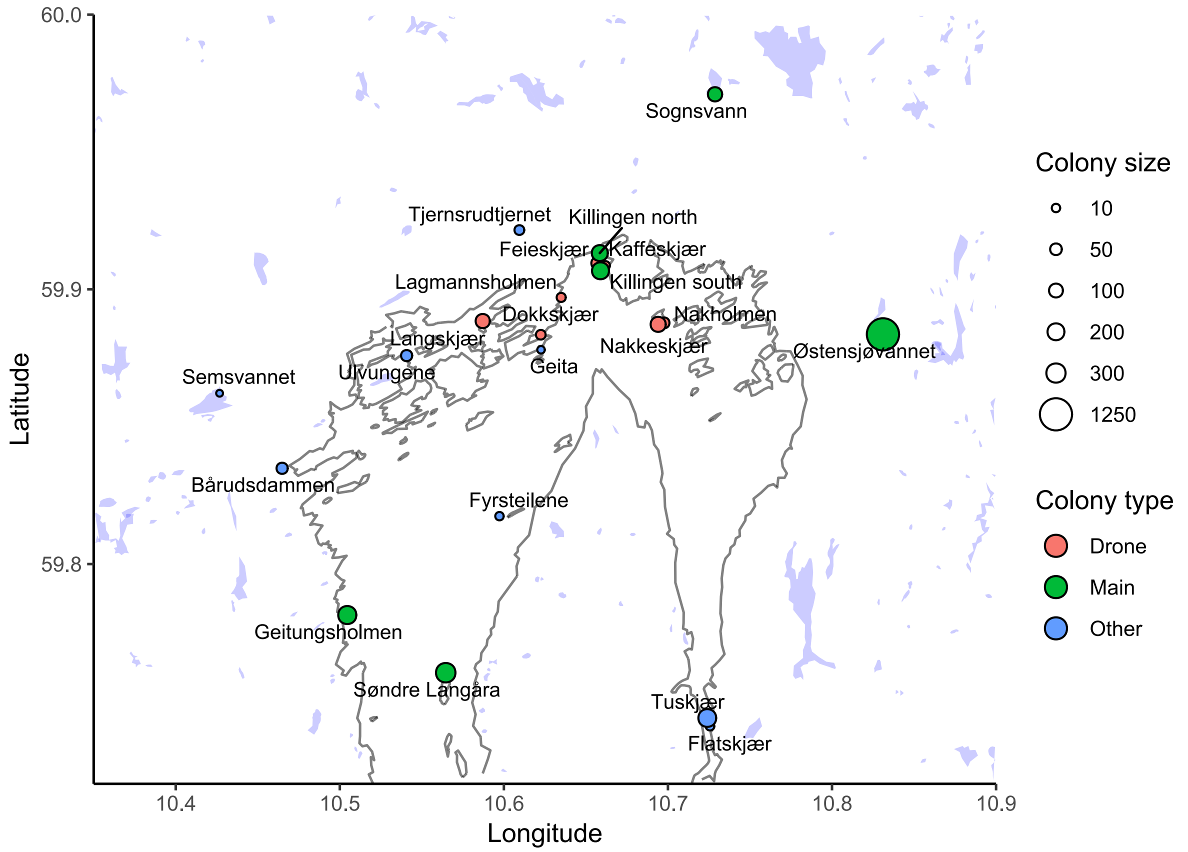

Figure 1. Map over locations included in this thesis. "Main" colonies had nest camera monitoring in addition to drone surveys, while "drone" colonies only had weekly drone surveys. "Other" colonies are either observed by me or reported on Artsobservasjoner (GBIF.org, 2019), and were surveyed for a maximum of one time. The symbol sizes are determined by the colony size, which is given as the maximum number of active nests at the same time in each colony. ©Kartverket

2.2 Fieldwork

2.2.1 Individual nest monitoring

To monitor individual nests and gather data on when the parents were present and when the nests were empty, cameras were installed on a sample of nests in the six main study colonies. Each setup consisted of seven cameras placed at seven individual nests. The cameras were connected through a USB hub and a 15- or 20-meter-long USB extension cable to a laptop. The laptop continuously ran a simple bash script to capture photos from the seven cameras sequentially (Script B1). To power the laptop and the cameras, a 120Ah car battery connected to a 150W solar panel was used. Further details on the setup can be found in Appendix A.

2.2.2 Colony monitoring by drone

Approximately once per week (Figure E1), all main and drone colonies in the study area were photographed from above using a small consumer drone, a DJI Mavic Pro. The drone was flown between 15 and 20 meters above the colony and at slow speed, not exceeding 1 m/s to avoid disturbing the birds. When doing transport routes and between parts of the colonies the speed and altitude were usually both increased.

The drone was always flown manually over the colonies, with photographs taken straight down so that there was at least 50% overlap between photos. The flight pattern did not match exactly in different flights at the same colony, but all parts of the colony were photographed every time.

Before the breeding season, there were concerns as to whether there would be negative responses from the colonies towards the drone. In this case, a negative response is defined as visual changes in the bird's behaviour, e.g. birds leaving their nests or a non-incubating bird attacking the drone. When the drone was flown slowly, there were rarely any responses from the colonies at all, and most survey flights were completed without any observed reaction. There were, however, multiple occasions when the flights had to be aborted due to negative responses. None of these was initiated by the Black-headed Gulls themselves, but rather by Oystercatchers (*Haematopus ostralegus*) or Lesser Black-backed Gulls (*Larus fuscus*). The whole colony would in most cases flush immediately if any other bird near the colony started to alarm call or do fly-bys of the drone. There were large variations in how individual birds reacted to the drone. In one colony, Ulvungene, one Oystercatcher was very alarmed during its chick phase, resulting in all but the first flight being aborted, and the colony being downgraded to an “other” colony in this thesis.

2.3 Data analysis

All finished datasets used in this thesis were analysed in RStudio, running R 3.5.0 (R Core Team, 2017).

2.3.1 Individual nest monitoring

In total, more than 16 million photos were taken, whereof 6 million were of active nests with no obstruction in front of the camera. To make it easier to determine which parent was present at the nest at any given time, only nests where at least one parent was colour-ringed were used.

As there were too many photos to handle manually, a Python3 script was written to compare two consecutive photos (Script B2). The goal was to identify the motion events in the photo sequence and only look at these. The script was based on OpenCV's "subtract" function. This function returns the differences per pixel of two photos, split into the red, green and blue colour channels. All individual pixels' and colour channels' difference values were then averaged. This resulted in a similarity index between 0 (all pixels completely identical) and 255 (maximum difference). To find the ideal similarity threshold, a few days of the full set of photos from a single nest was looked through manually. It was noted when the nest was empty or if the male or female were incubating at the nest, in addition to whether the other bird was present in the colony. In the end, every photo was given a state, consisting of who, if any, was incubating and if the other parent was present in the photo. Examples of possible states would be "MF" (male incubating, female standing next to it), "F0" (female incubating, male not present), and "00" (no bird at the nest). The state changes were then plotted against the similarity index values to be able to fine-tune the threshold. A similarity threshold of 8, with 5 photos included on each side of the motion, was found to give the highest detection of the real state changes (e.g. incubation shift swap). When running the script with these threshold values on the entire set of photos, there were some large time gaps above 30 minutes where motion was not detected. To be able to judge if these time gaps were only due to poor sensitivity in the script or whether there were real periods with no motion at the nest, an additional single photo was included every 40 photos in the final selected set of photos. In most cases, this corresponds to a photo about every five minutes.

State changes were then noted manually in the final selected set of photos, which consisted of 1 506 010 photos. Egg laying and hatching were also noted when it was possible to determine. In this thesis, the dataset resulting from this process is only used to measure disturbance in the colony, in addition to being one of the sources for known predators in the colonies.

2.3.1.1 Disturbance

To measure disturbance in the colonies, the different nests from each colony were compared. If all nests were empty at the same time, it is likely that there was a disturbance to the colony on that occasion. As the photos from the different cameras were not taken at the exact same time, the dataset was sampled every whole minute. The state from the previous photo was used, meaning that for instance 19:35:54 became 19:36:00.

Only timeframes where there were data from more or equal to 3 nests in the same colony were included. With data from fewer nests than this, it is likely that the nests can be empty at the same time without there being a common disturbance in the colony. To determine a threshold for the number of nests that needed to be empty at the same time for the data point to be regarded as a disturbance, the frequency of empty nests was plotted for each colony (Figure 2). Based on the approximate minimum frequencies of these plots, events where more than 60% of the nests were empty at the same time were regarded as a colony disturbance event. Every data point higher than this threshold is likely to be a disturbance event because multiple nests are disturbed at the same time. The data points with less than 60% empty nests are most likely parents taking short breaks collecting nest material or chasing neighbouring Black-headed Gulls. Later, this threshold is referred to as a threshold of 0.60. The start time, end time and duration of each separate disturbance event was then noted. Disturbances separated by seven or fewer minutes were regarded as the same disturbance event.

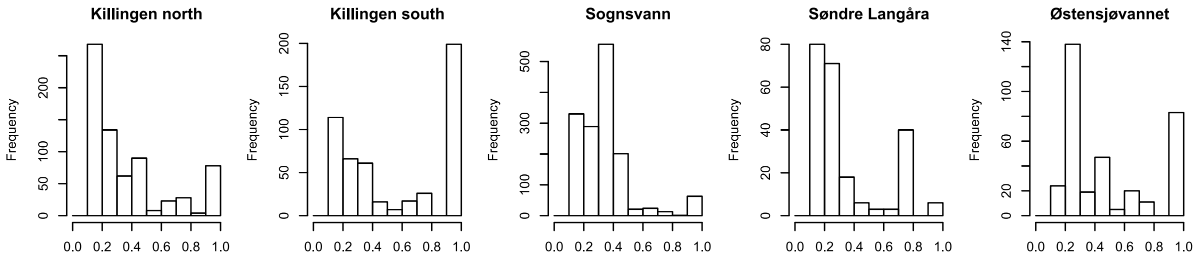

Figure 2. Histograms showing the proportion of nest cameras registered as empty for each colony per minute. All data points where all nests in the colony had an incubated bird are removed.

2.3.2 Colony monitoring by drone

The drone photos were stitched together using Photoshop CS6's "Merge" function, with "blending" turned off. If the merge worked perfectly, each nest location was in the same spot in the resulting layer stack. In many colonies, some manual alignment was done directly in the Photoshop files afterwards to adjust misaligned layers. All nests in the colony were then given a nest number, and a data matrix with the status for each nest (active/inactive/ unknown) for every week was created manually.

The coordinates of each nest within the Photoshop file was exported using a Photoshop script. To convert the pixel coordinates into meters, so that distances could be measured between nests, the distance between two structures in the colony were measured in meters on Norgeskart (https://www.norgeskart.no, accessed 2019-01-21) and in pixels in Photoshop. Using the ratio between these measurements, the pixel coordinates were scaled to meter coordinates and combined with the nest status data matrix.

The resulting data matrix was used in two analysis. The first was plotting the colony every week to visualize where nests with different statuses were located within the colony. The nest status depended on whether the nest was active or not for two consecutive drone flights. The second analysis was a survival analysis, done with the package "survival" version 2.38 (Therneau, 2015) in R. The survival analysis was used to model the time until the nests got predated or otherwise destroyed. The laying date was used as origin (time zero) and the date interval between two consecutive drone flights where the nest failed was used as endpoint. The laying date was an interval between two drone flights, but as the analysis can only process one date for this variable the midpoint between the two drone flights was used. For pairs already settled in the colony at the first flight, the midpoint between the first possible establishment date for the colony itself and the first drone flight was used. The establishment date for the colonies was defined as the first laying date in the colony and was usually also known with about a week of uncertainty. The interval between two consecutive drone flights was held as close to one week as possible (Figure E1). Nests that were still active at the last flight, or got covered with vegetation, were right-censored in the analysis. This meant that the analysis threated the status of these nests as an unknown from the last date with certain data. There were also quite a few nests with internal zeros, meaning that the nest was first registered as active, then registered as inactive, and then active again later. For these nests, it is impossible to know if it is the same pair that was active all along, but undetected one week, or if the old pair has failed and a new pair have settled at the same location. As a cautious approach, these nests were right censored from the last active date before an internal zero.

Kaplan-Meier survival curves were estimated using the “survfit” function, and the curves for different colonies compared. From the resulting “survfit” object the confidence intervals (using the default method) for the predicted survival to 25 and 50 days after egg laying at each colony were gathered. Expected hatching is around 25 days after egg laying, meaning the confidence interval represents survival until incubation. Survival until day 50 was used as a measure of chick survival. In addition, survival to day 50 given survival until day 25 was calculated to be directly comparable with survival during the chick phase (S25).

In addition to computing Kaplan-Meier curves for each colony, curves were also compared with respect to two grouping variables, the settlement date for each nest and density of neighbours around the nest. Settlement date was calculated as described above for origin in the model and was then grouped into five intervals, “Before 1.5”, “1.5 - 9.5”, “10.5 - 19.5”, “20.5 - 29.5” and “After 29.5”. The number of neighbouring nests within five meters of each nest was calculated and used as a measure of density. The resulting continuous variable was then grouped into five categories, 0-4, 5-9, 10-19, 20-49 and above 50 nests within five meters.

3 Results

3.1 Individual nest monitoring

3.1.1 General statistics

In total, 55 nests were camera monitored, which resulted in data from 33 nests. Each of these 33 nests was monitored continuously for an average of 12.05 days (sd = 5.85 days). The amount of time the parents spent at the nests are summarized in Figure D2 and Table D2.

The nest camera data was evaluated by two different people, which resulted in small differences in state frequencies. First, there seems to be a difference in the notation of empty nests, where one observer noted the nest as empty more frequently than the other. The observer that noted empty nest less frequent, also recorded significantly longer shift lengths (N = 2604 shifts with known start and end, mean observer 1 = 78.0 minutes, mean observer 2 = 110.4 minutes, p=2.941e-12).

The distributions of shift lengths are heavily skewed towards shorter shifts. 48% of shifts are less than 1 hour, 76% of shifts less than 2 hours and 94% less than 4 hours (N = 2604 shifts with known start and endpoint). This indicates that most of the food is gathered close to the colony during incubation. Longer trips are possible but are likely to be rare as long shifts do not necessarily mean long trips to gather food.

3.1.2 Disturbance

Using 0.6 as the threshold value to classify colony disturbance events, there is no obvious pattern in the timing of the disturbance events through the incubation period (Figure 3, left column). There is however a clearer diurnal pattern in the timing of the disturbance events (Figure 3, right column). Disturbances during the night are longer for Killingen north, Killingen south and Sognsvann, and Østensjøvannet only has disturbances during the night. Søndre Langåra is different from the rest of the colonies having both few and short disturbances only in the afternoon, and none during the night.

Disturbances during the night were rather common in most colonies and were caused by mammalian predators in those cases where the disturber was detected by the nest cameras. In this study, the mammalian predators detected on nest cameras were Badger (Killingen north and south) and Red Fox (Østensjøvannet). At Sognsvann there is no proof that there were any predators in the colony. Two colonies, Killingen south and Sognsvann, also had several short disturbances during the day.

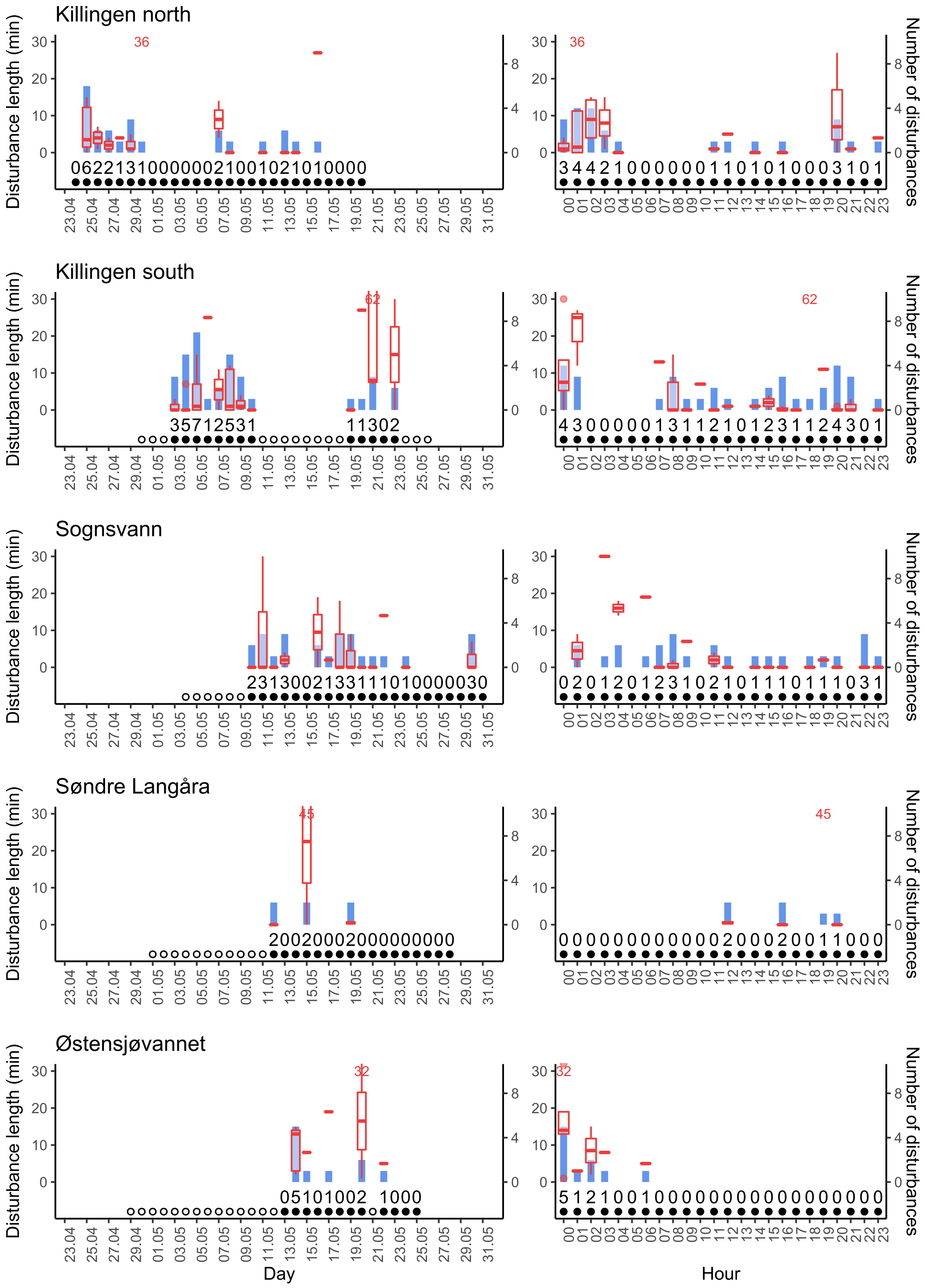

Figure 3. Length (red boxplots, left axis) and number (blue bars, right axis) of separate disturbance events per day (left column) and per hour (right column). The number below each boxplot shows the number of disturbances and is the height of the blue bars. Date and hour of disturbance-start are used for disturbances spanning over multiple days/hours. Circles under each date or hour indicate that the colony is incubating, while the filled circles show where there is disturbance data from the colony (simultaneous data from 3 or more nests). The left y-axis (disturbance length) is limited at 30 minutes, hiding a few outlier data points. The lengths of these outlier disturbances are displayed with a red number above each box. N nests>=3 and threshold=0.60.

3.2 Colony monitoring by drone

3.2.1 Formation plots

Nest locations within the colony were plotted for each week. The nests were then colour-coded depending on each nest's status in the last period. The status depends on the presence or absence of birds at each nest for two consecutive flights. This resulted in a series of plots that showed how the nests within the colony settle and fail (Figure 4 and Figure 5, in addition to Figure F1-15).

The colony at Søndre Langåra had in total 438 nests during the breeding cycle, and the sub-colony illustrated in Figure 4 includes 272 of them. We can see both from Figure 4, and from many other colonies (Figure F1-F15), that the first pioneer birds settle in the centre of the coming colony. The next settlers increase the spatial boundaries of the colony, in addition to filling out the free space in the middle. At Søndre Langåra, the predation starts around the edge, but quickly infiltrates the whole colonies. The colony collapsed completely during the chick phase, with most nest failed by the 16th of June, and being completely empty by the 23rd of June.

In most other colonies, predation seems to be randomly distributed throughout the colony. One clear exception is Killingen south (Figure 5), where eggs were preyed upon by a resident Badger. This was never seen in the field but is captured on the nest cameras many times. The Badger moves through the colony predating eggs every week, starting with the most accessible part (bottom left in the individual plots in Figure 5), and moving towards the centre of the colony. It did not reach the core of the colony before the eggs hatched, so the colony produced some chicks. There is, however, some predation in the core after hatching at Killingen south. The same is seen in most other colonies (Figure F1-15).

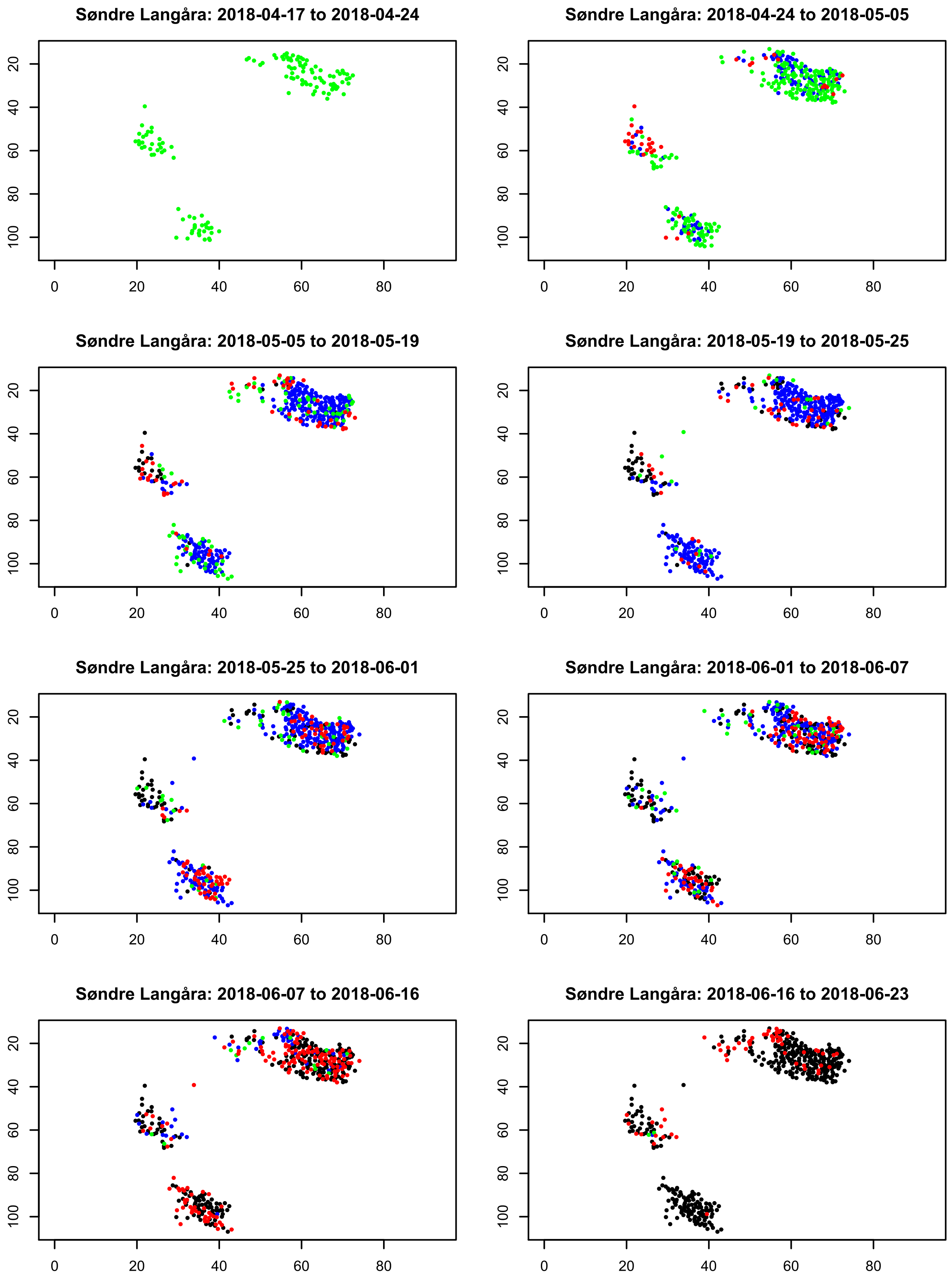

Figure 4. Formation plot for a subpart of Søndre Langåra based on drone photos. The axes are in meters from the origin of the merged image. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

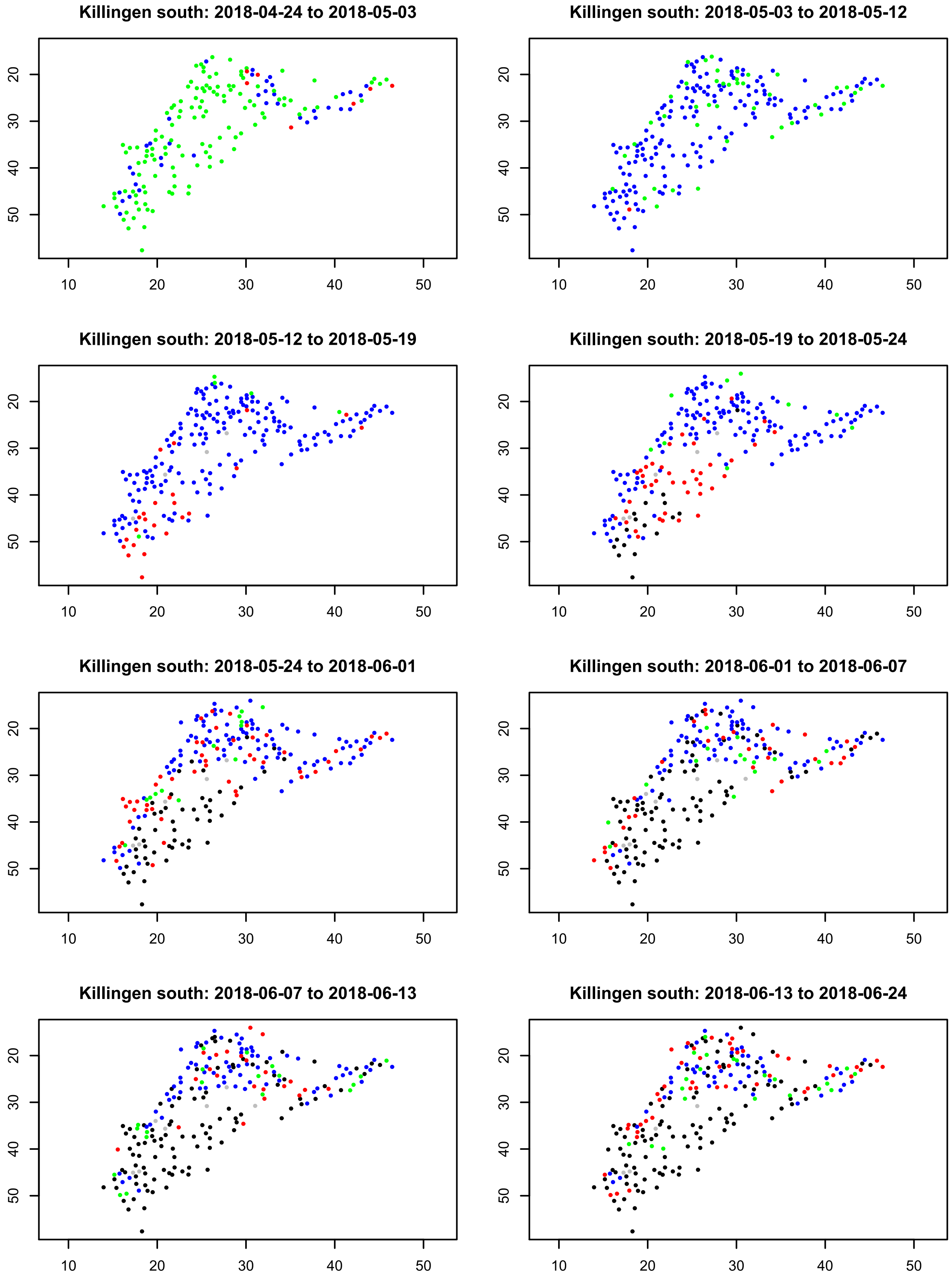

Figure 5. Formation plots for Killingen south based on drone photos. The axes are in meters from the origin of the merged image. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

3.2.2 Nest survival analysis

3.2.2.1 Differences between colonies

The nest survival varied but was generally low in all colonies (Table 1). Some colonies collapsed completely, and no nests produced chicks. The survival of nests is much higher the first 25 days after egg laying (until hatching) than during the chick phase (Figure 6 and Table 1). For most colonies the survival until hatching was high (mean = 0.63, sd = 0.28), but this starts to drop rapidly afterwards to a mean survival probability of 0.18 (sd = 0.17) at day 50. The colony with the highest fledging survival was Østensjøvannet, where around 54% of the nests fledged chicks according to the survival analysis.

Table 1. Estimated nest survival probability per colony first 25 days (expected hatching) and at day 50 (approximate fledging) from Figure 6, as well as estimated survival to day 50 given survival until 25 days, which can be directly compared with the estimate at 25 days. 95% confidence interval is shown in parenthesis. All colonies that have an estimated survival less than 0.10 at 50 days in this analysis is known to not produce any fledged chicks. The table also includes the number of breeding attempts (N), approximate date of establishment of the colony (Est.) and the average number of nests within 5 meters of each nest (<5m).

Colony	***Number of nest attempts***	***Establishment***	***N nests < 5m***	***Nest survival probability until day 25***	***Nest survival probability until day 50***	***Survival until 50 days, given survival 25 days***
Dokkskjær	27	24/4	11.5	0.89 (0.77-1.00)	0.23 (0.11-0.49)	0.26
Feieskjær	71	23/4	38.3	0.72 (0.62-0.84)	0.30 (0.20-0.45)	0.41
Geitungsholmen	290	27/4	22.1	0.83 (0.79-0.88)	0.27 (0.21-0.35)	0.33
Kaffeskjær	16	28/5	3.1	0	0	NA
Killingen north	193	24/4	26.5	0.74 (0.67-0.81)	0.22 (0.16-0.30)	0.30
Killingen south	222	23/4	26.5	0.78 (0.72-0.84)	0.35 (0.28-0.44)	0.45
Lagmannsholmen	24	19/5	5.0	0.56 (0.36-0.87)	0	0
Langskjær	135	19/5	26.2	0.26 (0.20-0.35)	0.09 (0.05-0.16)	0.35
Nakholmen	53	27/4	14.4	0.36 (0.25-0.52)	0	0
Nakkeskjær	166	27/4	30.8	0.81 (0.76-0.88)	0.08 (0.04-0.15)	0.10
Søndre Langåra	438	27/4	36.6	0.71 (0.67-0.76)	0.08 (0.06-0.12)	0.12
Østensjøvannet	1415	2/5	39.3	0.85 (0.83-0.87)	0.54 (0.49-0.60)	0.64
Mean	**254**	**3/5**	**23.4**	**0.63**	**0.18**	**0.27**
Std. dev.	**386**	**12.2**	**12.4**	**0.28**	**0.17**	**0.20**

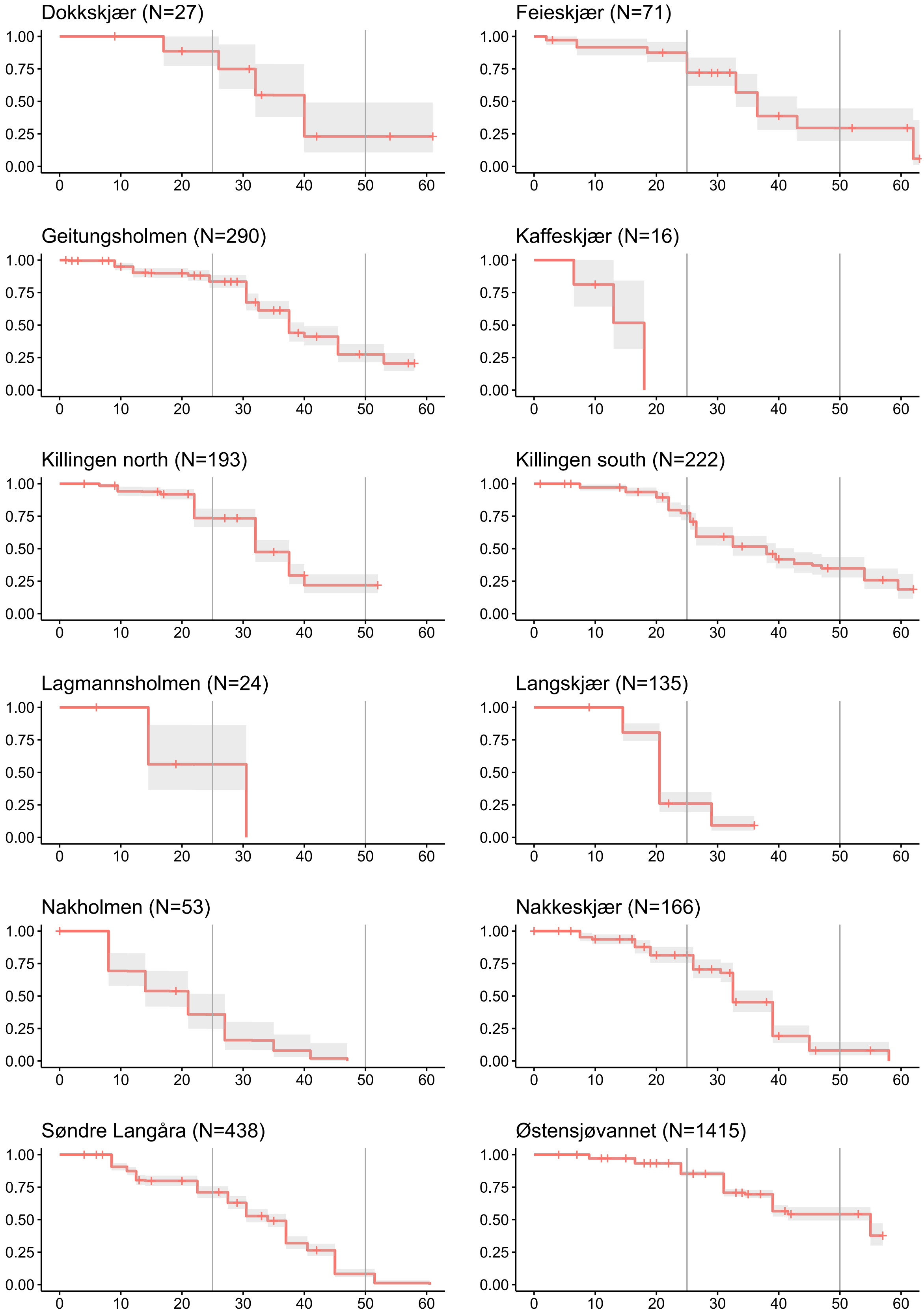

Figure 6. Kaplan-Meier survival curves based on data from each individual colony. N is the number of nests established in total in the colony through the season. The 95% confidence interval is shown in grey. Censoring times are indicated by "+" symbols.

To check whether some of the colony level explanatory variables were correlated with nest survival at each colony, a correlation plot of Table 1 was created (Figure 7). We see that all three variables (mean number of nests within 5 meters, establishment date of the colony and number of nest attempts in the colony) correlate to a varying degree with the survival rates. Many of the correlations are strong, but some are also driven up mostly by Østensjøvannet. The same plot, but with Østensjøvannet divided into its six sub-colonies can be found in Figure G1, where most of the correlations weaken considerably. Still, the correlation plots indicate that variation between colonies explains some of the variations in survival.

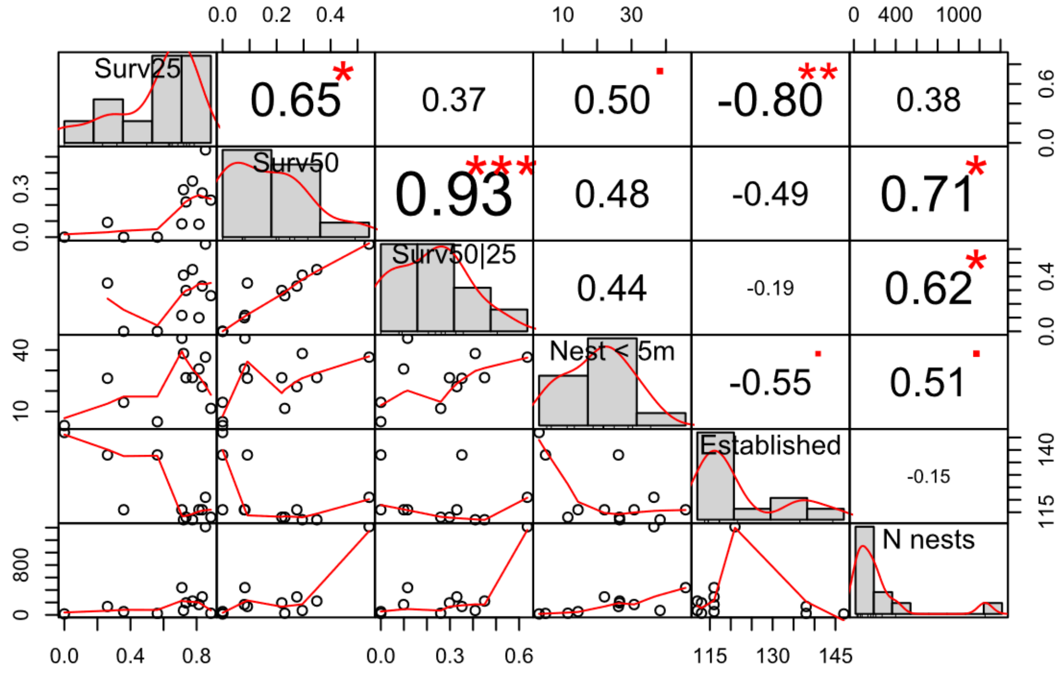

Figure 7. Correlation plot based on Table 1. Established is displayed as the number of days since 01.01.2018. An established value of 115 equals 26.04.2018, while 140 equals 21.05.2018.

When grouping the survival plots into strata depending on the number of neighbours within 5 meters (Figure 8), there is a small, but substantial, difference between the groups. The confidence intervals overlap to a higher degree, but the difference between the lowest density group (0-4 neighbours) and the highest density group (50+ neighbours) is statistically significant. The confidence interval for survival after 25 days is 0.28-0.53 for 0-4 neighbours, versus 0.82-0.88 for 50+ neighbours.

The same plots for each individual colony were created (Table G1). On these plots the groups do not seem to differ within each individual colony, indicating that the difference in survival depending on the number of neighbours seen in Figure 8, is purely an effect between colonies.

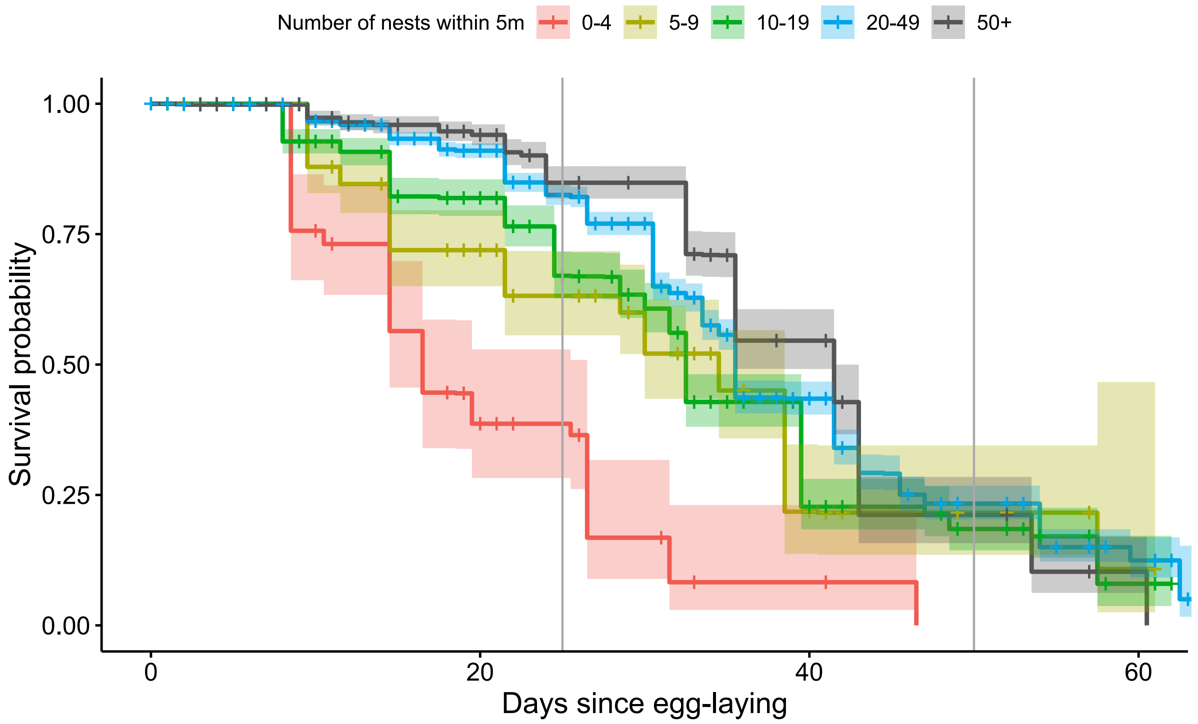

Figure 8. Survival plot based on data from all colonies divided into strata depending on how many neighbouring nests that were located within 5 meters. The number of nests for each stratum (left to right) is 78, 173, 517, 1704, and 578. Values for confidence intervals can be seen in Table G1.

3.2.2.2 Differences within colonies

When grouping the survival plots into strata depending on the date of egg-laying, nests that settled later in the season have a higher mortality rate than those that settled earlier (Figure 9). The confidence interval for each group is mostly not overlapping with others, which shows that the differences are statistically significant. Nests in the two groups settling before 9th of May have partly overlapping confidence intervals and are likely to have similar survivals. Furthermore, pairs that settle late in the colonies mostly do not reach hatching, and the difference between the two most extreme settlement groups is substantial. The confidence interval for survival at 25 days is 0.77-0.83 for “before 1.5” versus 0.21-0.43 for “after 29.5”).

For the same plots for each individual colony, we can see the same pattern, with the different egg-laying groups placing themselves in the same order, in most colonies (Table G2). The confidence intervals are overlapping to a higher degree, which is probably only due to smaller sample size in each individual colony. All of this indicates that the effect of the settlement date is not only an effect between colonies (as seen in Figure 7) but also an effect that is present within colonies.

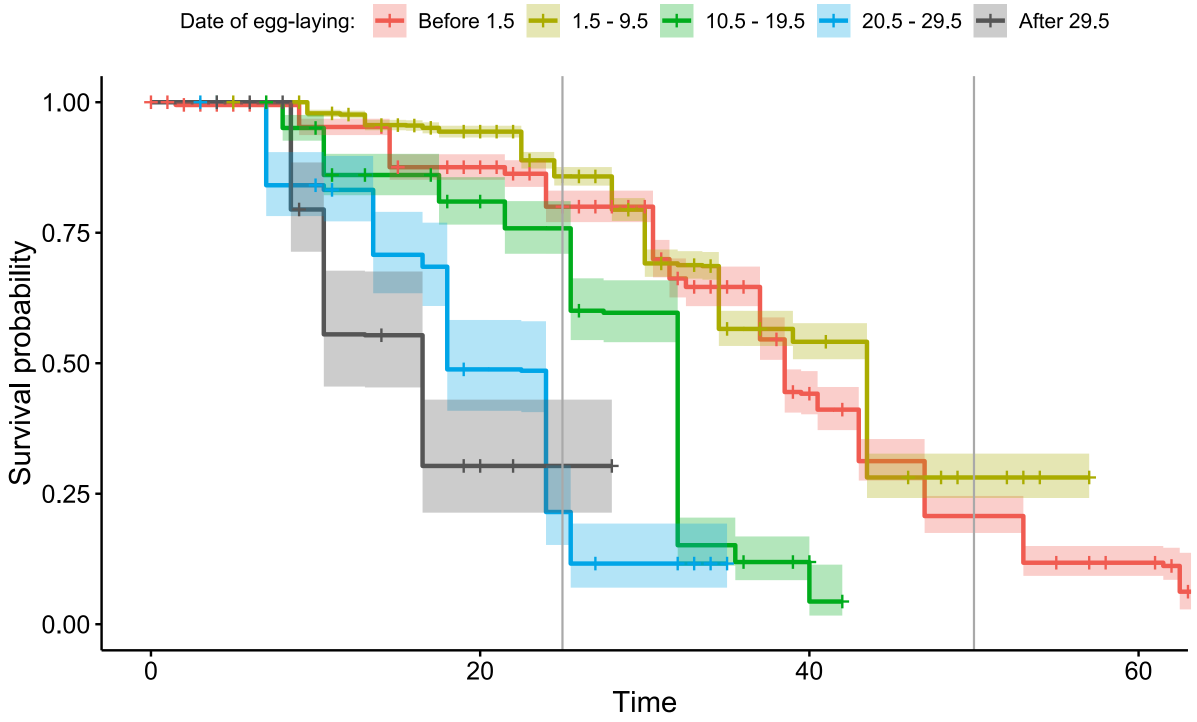

Figure 9. Survival plot based on data from all colonies divided into strata depending on when they settled their nests. The number of nests for each stratum (left to right) is 781, 1702, 320, 146, and 101. Values for confidence intervals can be seen in Table G2.

3.3 Known predators in the colonies

During the fieldwork, multiple different predators were observed in the colonies, either on nest cameras or when physically visiting the colonies. Night predators, such as Badger and Red Fox, were only observed on the nest cameras. As the different colonies were not visited for an equal amount of time, the known predators in Table 2 are likely biased so that "Main" colonies have the most detected predators since these were visited the most. If a colony was only visited once, there is very little data for estimation of predation pressure, and it is categorized as "NA". The predation pressure is judged from a combination of how much the colony was visited and how many predation events were observed. Dokkskjær was the only colony where no predation events were observed, but that, at the same time, were visited enough to judge predation pressure. Semsvannet was never visited and have also received "NA" in "Known predators".

Table 2. Summary of known predators for every colony in the study area. Colonies are not monitored equally, so no known predators do not mean that the colony is predation free. Coordinates for each colony is also included, which are mapped in Figure 1. Colony size is the maximum number of nests simultaneously in each colony.

Location	**Colony size**	**Colony type**	**Known predators**	**Predation pressure**
Bårudsdammen	42	Other	None	NA
Dokkskjær	21	Drone	None	Low
Feieskjær	56	Drone	Peregrine Falcon, Lesser Black-backed Gull	Medium
Flatskjær	11	Other	None	NA
Fyrsteilene	10	Other	None	NA
Geita	6	Other	None	NA
Geitungsholmen	249	Main	Herring Gull, Hooded Crow	Low
Kaffeskjær	14	Drone	None	Low
Killingen north	166	Main	European Badger, Peregrine Falcon, Hooded Crow	Medium
Killingen south	203	Main	European Badger, Peregrine Falcon, Lesser Black-backed Gull, Hooded Crow	High
Lagmannsholmen	15	Drone	None	NA
Langskjær	109	Drone	Great Black-backed Gull	High
Nakholmen	37	Drone	Lesser Black-backed Gull, Hooded Crow	High
Nakkeskjær	136	Drone	Lesser Black-backed Gull	Medium
Semsvannet	5	Other	NA	NA
Sognsvann	111	Main	Lesser Black-backed Gull	Low
Søndre Langåra	313	Main	Herring Gull, Great Black-backed Gull, Hooded Crow	High
Tjernsrudtjernet	22	Other	None	NA
Tuskjær	238	Other	None	NA
Ulvungene	41	Other	Peregrine Falcon, Lesser Black-backed Gull	Medium
Østensjøvannet	1255	Main	Red Fox, Hooded Crow	Low

Latin names: Red Fox (*Vulpes vulpes*), European Badger (*Meles meles*), Peregrine Falcon (*Falco peregrinus*), Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), Lesser Black-backed Gull (*Larus fuscus*), Hooded Crow (*Corvus cornix*)

4 Discussion

Overall, the breeding success in the study area in 2018 was low. In this thesis, breeding success was estimated as nest survival 25 and 50 days after egg-laying. On average, one in five breeding attempts produced chicks. The main reason for the low breeding success was likely a combination of food shortage and high predation pressure. However, the reasons for the high predation pressure is not clear. In the 1950s there were low predation rates in the colonies around Oslo (Ytreberg, 1956). At this time the colony sizes were comparable to what they are today, with an average of around 200 pairs, but some potential predators were controlled (by hunting) before each breeding season started (Ytreberg, pers. comm.). In a very large colony at Ravenglass in England, on the other hand, the predation rates were reported to be high in the 1960s (Kruuk, 1964). At the same time, local people collected eggs for consumption (Kruuk, 1964). This colony started to shrink some decades later and became deserted after 1985 (Anderson, 1990).

One factor which might increase the stress in the colony, and thereby the likelihood of predation, is lack of food (Anderson, 1990; Ashbrook et al., 2010). Parents search for food within a few kilometres from the colony, as seen from the shift lengths at the nest cameras, colour-ring sightings of the population in the Oslo Fjord (unpublished data, based on Norwegian colour-ringing database) and previous studies (Cramp, 1983). There might, therefore, be large variations in food choice and availability between the different colonies. The summer of 2018, from May to July, was the warmest, and the third driest, recorded since measurements began in 1937 at the weather station at Blindern, Oslo (eKlima, http://eklima.met.no, accessed May 2019). This meant that many colonies probably had less access to food than normal. Sognsvann, for instance, is located at the border between the city and the forest, and the birds in the colony are likely to be highly dependent on earthworms from surrounding lawns for part of the breeding cycle. When we ringed chicks at the colony in the morning of the 16th of June (unrelated to this thesis) the chicks seemed to regurgitate fewer earthworms than in previous years. One chick also regurgitated grass, and there were approximately 40 dead 3-week-old chicks spread across the island. Most of them were pecked in the neck and seemed to have been killed by other Black-headed Gulls. At least two chicks were pecked to death in the short time while we were in the colony. Adults pecking other chicks in the neck is rather common in Black-headed Gull colonies when chicks try to cross neighbouring territories (pers. obs.). This happens often when colonies are disturbed for a long time, and chicks try to run away from danger, but it is rather uncommon that this behaviour ends in chicks dying.

It is expected to be difficult for predators to access a colony due to an active colony defence from the inhabitants (Brunton, 1997; Kruuk, 1964). Many Black-headed Gull pairs in the colonies around Oslo seems to partly give up before the chicks are dead, and thereby heavily reduce their anti-predator behaviour (pers. obs.). This is likely due to the sum of stress elements as disturbance, lack of food, and the initial predation in the colonies. This again, will make the birds less willing to defend their nests, as the likelihood of successfully raising chicks that year decreases. Each individual bird might decide that it is not willing to risk its life and energy to save the current breeding attempt. If many birds make this decision and reduce their aggression in the colony defence, the colony will get more passive and it will be easier for predators to infiltrate it. Reduced aggression in the colony defence have been reported in multiple other Black-headed Gull colonies before they collapse (Anderson, 1990; T. Olsen, pers. comm.)[1]. Black-headed Gulls have an average breeding age of 6 years (unpublished data, based on Norwegian colour-ringing database), and in such a long-lived species, a better individual strategy in poor years may be to invest energy towards own survival or future breeding seasons (Ashbrook et al., 2010; Stearns, 1992). However, if the unfavourable years become too frequent, this individual strategy could be detrimental for the population over time.

4.1 Nest survival analysis

As the date of egg-laying used in the model was the midpoint between two weekly drone flights, the egg-laying dates are slightly inaccurate. This meant that different nests are slightly offset from each other in the analysis, which we can expect will smooth the survival curves slightly. Day 25 is a good estimate for hatching, as each egg is incubated for an average of 24 days, there are 1-3 eggs in each clutch, and the eggs hatch within an interval of hours to days (Cramp, 1983). This makes the total incubation period approximately 24 to 26 days long. Survival to day 50 was used as an estimate of the proportion of nests that fledged

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[1] T. Olsen, pers. comm.: Back in 1993 there were 974 Black-headed Gull pairs breeding in Hanangervannet, Lista, southern Norway (K. S. Olsen, 2001). After 1993 the colony started declining and producing fewer and fewer chicks every year, before it disappeared completely during the 2000s. If the colony was disturbed in the last few years, when no chicks were raised in the colony, the parents were only circeling high above the colony before they disappeared until the disturbance ended (T. Olsen, pers. comm.). This passive behaviour is the same as seen in the study area of this thesis, only more exaggerated.

chicks, which is a more uncertain estimate as the chicks have not fledged yet at this point. The ideal time point to measure the fledging success rate would be when they start to fly or when they leave the colony. It was not feasible to obtain an accurate estimate at this time point from the drone photos, as each individual nest was given a location and it was only noted whether the nest area was active or not. The older the chick is, the more likely it is to wander off and falsely get registered as a failed nest. At the same time, if the chick survival estimation point is set too early, the survival will be too high as there is likely to be failed nests after this day. Day 50 was used to balance over- and under-estimation of chick survival as best as possible.

We observe that pioneer nests have a higher survival probability than those settled later (Figure 9), which matches previous findings (Patterson, 1965). This is likely due to an increased predation rate after hatching, which arises from a higher number of predators (typically Crows and large Gulls) being attracted to the colony. These, in turn, are likely to predate eggs from later settled nests, in addition to the chicks they initially got attracted to. This would explain the earlier drop in the survival of later settled pairs in the survival analysis (Figure 9). The effect also seems to be present between colonies and based on the correlation plot (Figure 7), survival the first 25 days strongly correlates with settlement date. This correlation weakens and disappears during the chick phase (S50|25). This is probably because of the reason explained previously, where predators get attracted to the first hatchlings, and thereby reduces late settlers' incubation survival, while survival through the chick period would not be affected by this and is low regardless of the settlement date. As the effect also is present on an inter-colony basis, it is likely that the predation rate in the whole area is connected. Large Gulls might increase their predation rate in all colonies in the area when they start to find food in one colony. It is also possible that the increased predation from Crows and large Gulls are simply driven by an increased food demand from their own chicks.

Nests with more neighbours have a lower mortality rate (Figure 8), but as shown previously, this effect arises due to differences between colonies. Since the number of neighbouring nests correlates with colony size Figure 7, we can derive that larger colonies have higher survival as well, something which is further supported by the high correlation between colony size and survival (Figure 7).

The correlation between colony size and survival is mostly driven up by Østensjøvannet, due to its large colony size and high survival. Østensjøvannet consists of six sub-colonies that lie close to each other. This means they have the same food supply and most likely the same predators. Treating these colonies as different in the survival analysis would, therefore, result in pseudo-replicates. However, treating Østensjøvannet as one large colony also raises problems with this increased correlation in Figure 7. When we plotted the same correlation plot, but with Østensjøvannet divided into its different sub-colonies (Figure G1), the correlation decreases significantly.

4.2 Formation plots

According to the formation plots (Figure 4, Figure 5, Figure F1-F15), the nests in the middle of the colonies settled first in the majority of study colonies, while the following nests settled both in the middle of the colonies, as well as around the edges. When predation increased, the predation occurred across the whole colony and not first around the edges as central-periphery theory would predict (Hamilton, 1971; Vine, 1971). In that sense, the observed data fit better with central-satellite theory (Velando & Freire, 2001). However, both these theories presume that the quality of the pair determines the likelihood of predation. As observed in this thesis, many colonies experience an increase in predation rate when the first chicks hatch. The formation plots further show that the first predation often occurs in the middle of the colony just after the pioneer pairs hatch. Therefore, the predations seem to follow neither central-periphery nor central-satellite theory, but rather affect random pairs. For some colonies, the predation seems to start in the middle of the colony. This is likely to be because this is where the first chicks hatch and might be of higher interest to the predator.

It is important to note that these results are from a population in decline, likely with a weaker colony defence than normal for Black-headed Gull colonies in good years. With less active resistance against predators, it is not surprising that the predator is able to predate the first-hatched chicks in the colony, which are generally regarded as the highest quality nests. The extent of the predation and the effect vary between colonies. Judging by the formation plots in Appendix F (Figure F10-F15), in most sub-colonies at Østensjøvannet, the predation firstly occurs randomly throughout the colony, but the extent is not large enough to result in colony collapses. Most sub-colonies are large, and as they breed in one of the largest eutrophic lakes in the study area, with an additional high subsidy of bread from people feeding the birds, they are likely to be one of the colonies in this study with the highest and most secure food source. Østensjøvannet is also the colony closest to Oslo’s last waste treatment facility, which is still accessible for gulls, where at least some breeding Black-headed Gulls from Østensjøvannet are known to frequent during the breeding cycle (pers. obs.).

4.3 Disturbance and predation

From the disturbance results, we gain more insight into when predation in the colonies occurs. Because of my sampling regime, disturbances less than a minute or disturbances only affecting a part of the colony might not have been detected. The disturbance plots thus mainly illustrate the disturbances from ground predators, including humans. Among the main colonies, Søndre Langåra is an example of a colony with many undetected disturbances. The colony collapsed late in the chick phase but have very few detected disturbance events. On the nest cameras, multiple predation events were picked up, but all of them happened quicker than the 7 seconds between photos. This meant that the predator responsible for the predation event remained unidentified. Of seven camera monitored nests, four lost some or all eggs during incubation (Table D1). Such short predation events fit well with the predation events observed in the field at Søndre Langåra, which were performed very quickly from the air by Crows or large Gulls. The disturbance results do, however, indicate that there were not any ground predators in the colony, and that specialized Crows and Gulls are able to empty even large Black-headed Gull colonies.

From the results of this thesis, there is no reason to believe that disturbance in the colony directly affects breeding success. However, the character of the disturbance has a huge impact, which can mostly be derived from field observations and nest camera footage. As explained above, Søndre Langåra is an outlier in the disturbance analysis. For the rest of the colonies, disturbance during the night mostly indicated that there was a mammalian predator in the colony, which in all cases predated some chicks or eggs. At the formation plot of Killingen north (Figure F5), at the bottom of the top cluster of nests, there is a high degree of predation. This is the most easily accessible part of the colony for a ground predator, and it is highly likely that the same Badger that predated parts of Killingen south also accessed the northern colony on the island. Even though the nest cameras were not located where most of the predation was occurring at Killingen north (as shown when comparing Figure D1 with Figure F5), the Badger was observed at one of the nest cameras one time.

Disturbances during the day did not seem to be as negative to the nest survival, given that they were mostly not caused by predators. Most of these disturbances were likely caused by people that did not have any interest in the colony itself. At the same time, one could assume that disturbances during the day would allow easier access for bird predators, but there is no evidence that this ever happened. One of the colonies with many disturbances during the day is Sognsvann, which is located at one of the most popular bathing spots in Oslo. There were often people on the island, inside the colony when the colony was physically visited during the day. After a while, the colony quickly acclimated to these frequent disturbances and were incubating and defending chicks just a few meters away from bathing guests. This sort of disturbance seems to not do as much harm as one might expect, but it can be assumed that Crows and large Gulls get easier access to the colony during such disturbances. At Killingen south, the other colony with a lot of detected disturbance during the day, people were regularly seen walking closer than the colony excepted. This is likely the explanation for all the short disturbances. Local people have also reported that they often saw Crows and large Gulls predating chicks in this colony.

5 Conclusion

In the 2018 breeding season, Black-headed Gulls in the Oslo area hardly produced any chicks. Predation was the most apparent reason for this, effectively ending most of the breeding attempts. However, there are reasons to believe that many colonies had low food availability, weakening the colony defence in the study area. This might have been exaggerated in the dry year of 2018 where parents must have been away from the nest for longer periods of time to find enough food. For some colonies, e.g. Sognsvann, there were likely not enough food in their area to keep the chicks alive, and even though the predation pressure was low, many chicks died due to additional stress within the colony. Pairs and colonies that settle early in the season do generally have a lower mortality rate than those settled later. This is likely to arise from an increased predation pressure after hatching of the first pairs, something that becomes a problem when the colonies already are under pressure from both lack of food and disturbance.

6 Advice to nature managers

There are two possible approaches to managing the Black-headed Gull population in Norway. Either to do nothing and likely let them go extinct or to try to mitigate some of the problems the population is facing. If one should decide to attempt to mitigate the problems the population is facing, one highly probable positive measure is to recreate lost habitats. This has been done at Østensjøvannet by "Østensjøvannets Venner" for many years and judging from the result of this thesis it works. Østensjøvannet is by far the largest and most stable Black-headed Gull colony in Norway in the last few years, and to lose this colony would be detrimental for the population.

Both where habitats have been restored and elsewhere, monitoring of the colonies is very important. This thesis is unlikely to give the full picture of the situation, so there is always a possibility that other problems exists in the colonies. Monitoring should preferably be done so that it is possible to estimate the number of chicks produced by each colony, and with as little disturbance as possible. This can quite easily be done by using the same drone setup as in this thesis, or by a camera that monitors multiple nests. In addition, it is preferred to know something about the amount of predation in the colonies. This might be done best with a continuous video surveillance system, with the only drawbacks that it generates a lot of data and needs power.

Lastly, one can think about controlling some predators. As predation is unlikely the original problem for most colonies, controlling predators are unlikely to give long-term effects. That said, for some colonies, only one or a few problematic individual predators have large impacts of the breeding success of Black-headed Gulls. Removing these individuals might give more time to facilitate an increase in the Norwegian population. It is, however, very important that the predators to remove is selected with a high degree of care. This should be a last resort, and it is not advisable to uncritically control predators to save another species.

If nothing is done and the problems in the colonies continue, Black-headed Gull will most likely be removed from the Norwegian breeding bird list in some years' time. The final plunge to no breeding colonies might appear very quick, as the colonies often seem healthier than they actually are.

A final important point is that the counts of colony sizes presented in this thesis are unlikely to be directly comparable with previous work. Most of the counts presented here are done using drone photographs, while most previous works are ground based nest counts.

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8 Appendices

Appendix A Detailed description of nest camera setup

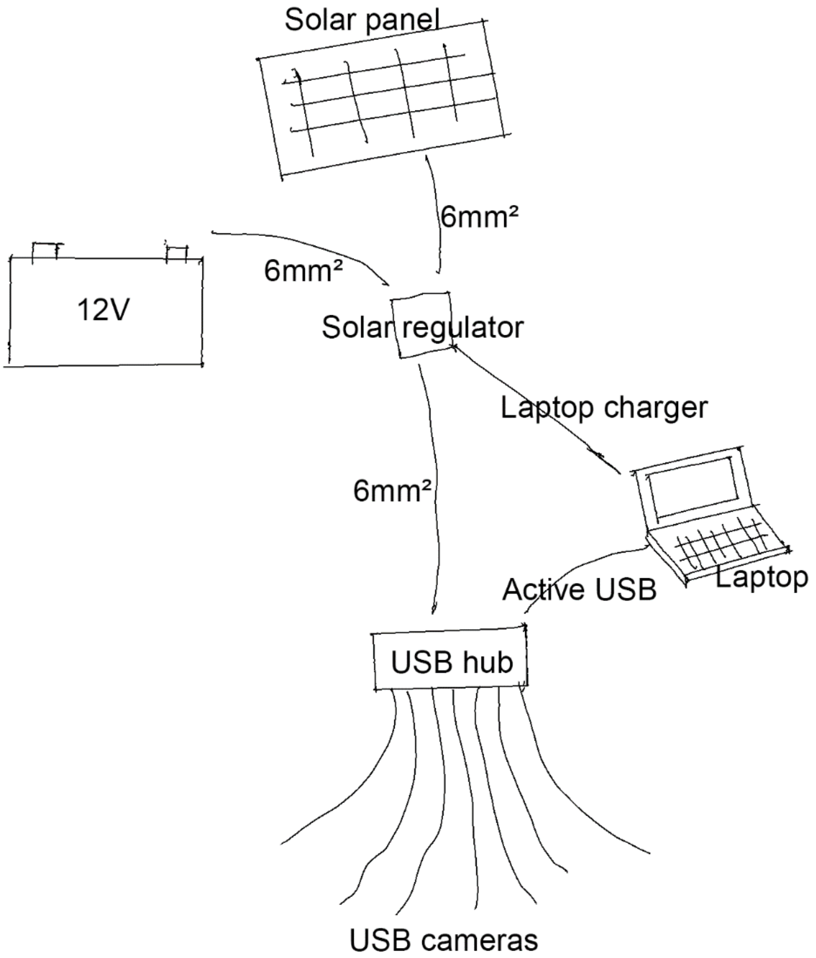


Figure A1. Schematic drawing of the setup

The setup (Figure A1) consisted of a laptop which ran a bash script looping through the seven USB cameras connected through a USB hub, capturing photos from each of them sequentially. As a power source, a 12V 120Ah car battery was connected to a 150W solar panel through a solar regulator. The solar panel was installed towards the south, at an angle of 45 degrees. The load terminal of the solar regulator was divided to a car charger for the laptop and a power cable directly to the 12V input of the USB hub as the cameras needed more power than a single USB port on the laptop could provide.

The laptop and battery were placed in a plastic box outside the colony, and the USB hub was connected to a 15 or 20 meters long active USB cable. An active USB cable amplifies the data signal making it possible to run USB cables longer than 5 meters. This meant that the cameras could be placed at individual nests, while the laptop and battery could be accessed and maintained without disturbing the colony. The USB hub used was a TP-Link UH700, which had the seven USB cameras connected to it. The USB cameras were generic waterproof USB cameras from AliExpress with their own infrared lighting (IR), originally designed for surveillance. The cameras had a resolution of 640x480 pixels, which was sufficient for determining what happened on the nest. Each camera had a five-meter USB cable included, which meant that all nests needed to be within a five-meter radius of the USB hub. The nests were selected so that at least one of the birds in the breeding pair was already colour-ringed. This would make it possible to distinguish which sex was on the nest at any given time. The group of nests were usually close to the edge of the colony so that the data central could be farther from the colony. When all cameras were placed at their individual nests, the USB hub was wrapped in a double plastic bag and taped shut to keep the water out.

The goal was that the setup would be self-sufficient with power. Unfortunately, the solar panels did not provide enough power even in the summer of 2018 which had unusually much sun. The solar panel did, however, give the system considerably extended operating time and much less transport of the 12V batteries for recharging. To extend the working life of the batteries even more, all camera's IR light had an 18 Ohm resistor added, as they did not need full power to illuminate the nests.

The operating system Ubuntu 16.04.3 LTS were installed on the laptops and the settings change so that the lid could be closed without turning off the computer. The software "fswebcam" were installed and a simple bash script was written to capture the photos (Script B1). The script looped through the seven cameras, capturing a photo at each camera. The script produced photos as fast as the CPU could handle, in my case meaning around every 7th second for each camera. When the laptops were heated by the sun, this was reduced to around every 20th second, probably because of the CPU's thermal throttling.

During the breeding cycle, the setup was checked regularly. In most cases, the laptops' hard drive was swapped for a new one with the same operating system to secure the photos taken up until that point in time.

In the six main study colonies, there were a few exceptions to the general setup described above. At Østensjøvannet and Sognsvann the colony is on such a small island that the laptop could not be visited without disturbing the colony. The laptops were therefore configured so that they would connect to a mobile WiFi hotspot and be accessible remotely. This does draw a bit more power, so the batteries would run out even quicker. At Østensjøvannet, a 220V outlet in a garage nearby was extended using two 50m cable drums. The now spare solar panel and 12V battery were then used at Sognsvann so that Sognsvann got two 150W solar panels and two 120Ah batteries in parallel. Also, at Sognsvann the laptop and battery had to be right in the middle of the colony, so there was no need for an active USB cable. Neither of these exceptions affected the data quality. At Geitungsholmen the USB data signal was sent over a 40-meter ethernet cable with USB to Ethernet converters, instead of the active USB cables. This affected the data quality as the transmission speed through the ethernet cable was slower. The photos during the day ended up being heavily overexposed so that they were unusable. The cable also did not manage to transmit the full resolution image from the cameras, and all images from Geitungsholmen ended up being 320x240 pixels. This obviously affected the data quality, and Geitungsholmen is therefore removed from most results below.

Appendix B Selected scripts

Script B1. Fswebcam bash script

```
while sleep 1;
do fswebcam -d /dev/video0 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video0/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video1 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video1/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video2 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video2/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video3 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video3/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video4 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video4/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video5 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video5/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
fswebcam -d /dev/video6 -r 640x480 --jpeg 50 -S 5
/home/user/Pictures/video6/$(date +\%Y\%m\%d\%H\%M\%S).jpg;
done
```

Script B2. Motion detection script (python)

```
# it consists of three parts, which are best run separately
# for easier bug testing and more control
import os
from os import walk
import cv2
import numpy
from shutil import copyfile
import sys

# create list of difference values
# useddays.txt is in the format:
#     colony/nest/YYYYMMDD
#     colony/nest/YYYYMMDD
#     colony/nest/YYYYMMDD
#     colony/nest/YYYYMMDD
#     etc.
# this is the same as the folder structure where the photos were stored,
# without the parent structure
# useddays is used to select just the days with photos of interest
useddays = open('useddays.txt', 'r').read()
useddays = useddays.split("\n")
log_file = open('out.txt', 'a')
for folder in useddays:
    dirpath = "(parent)"+folder #where (parent) is replaced with ie.
"C:/gulls/"
    print(dirpath)
    filenames = os.listdir(dirpath)
    for filename in filenames:
        try:
```

```
            firstfile
        except NameError: # if we are on the first iteration of the loop
            firstsrc = dirpath+"/"+filename
            firstdst = topath+"/"+filename
            firstfile = cv2.imread(firstsrc)
            continue
        else:
            secoundsrc = dirpath+"/"+filename
            secounddst = topath+"/"+filename
            secoundfile = cv2.imread(secoundsrc)
            diff = cv2.subtract(firstfile, secoundfile)
            diffvalue = numpy.mean(cv2.mean(diff)[0:2])
            log_file.write(dirpath+"/"+filename+": "+str(diffvalue) + "\n")
            firstfile = secoundfile
            firstsrc = secoundsrc
            firstdst = secounddst
log_file.close()


# select files to keep
difference = 8 #in my case 8 seemed about right
num_files_each_side = 5
include_every = 40#images, around 5min (will vary depending on image-
frequency)

motion = open('out.txt', 'r').read()
motion = motion.split("\n")
log_file = open('selectedfiles.txt', 'a')
i = 1

for line in motion:
    thisline = line.split(": ")
    if(float(thisline[1])>=difference):
        selected = motion[i-num_files_each_side:i+num_files_each_side]
        for select in selected:
            fromfile = select.split(": ")[0]
            log_file.write(fromfile+'\n')
    if (i%include_every==0):
        select = thisline[0]
        fromfile = select.split(": ")[0]
        log_file.write(fromfile+'\n')
    if (i%100000==0):
        print(str(i) + " - " + line) #to show progress
    i = i+1
log_file.close()


# copy selected files
motion = open('selectedfiles.txt', 'r').read()
motion = motion.split("\n")

i = 1
for file in motion:
```

```
    fromfile = file
    tofile = fromfile.split("/")
    # sets output folder, I decided to remove the date level
    topath =
tofile[0]+"/"+"selectedphotosfolder"+"/"+tofile[2]+"/"+tofile[3]
    tofile = topath+"/"+tofile[5]
    if not os.path.exists(topath):
        os.makedirs(topath)
    copyfile(fromfile, tofile)
    if (i%1000==0):
        print(str(i)+": "+file) #to show progress
    i = i+1
```

Appendix C Sub-colonies at Østensjøvannet

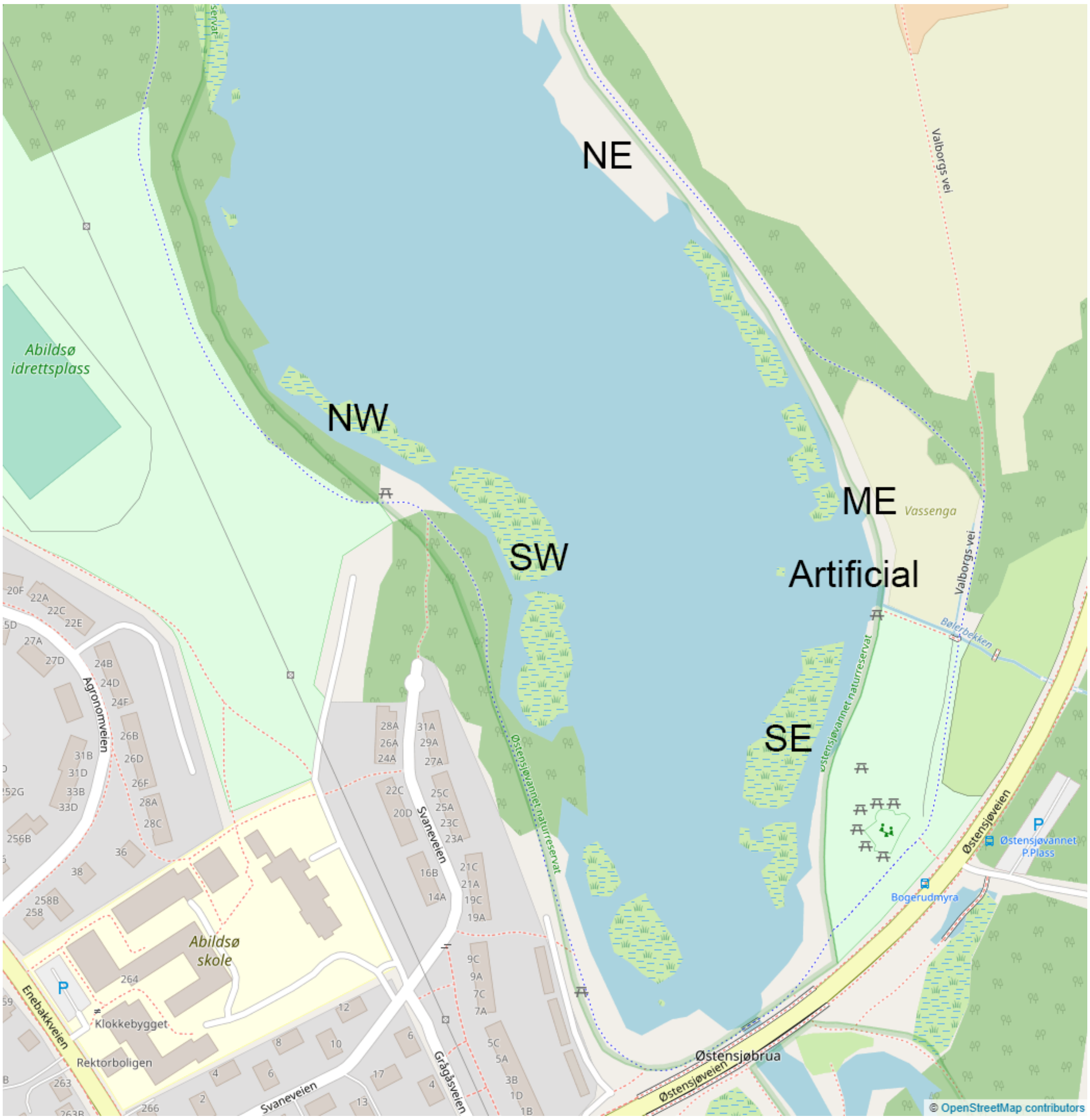


Figure C1. Map of sub-colonies at Østensjøvannet. Nest cameras were installed in the SW subpart. Background map copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org

Appendix D Nest camera data and incubation frequencies

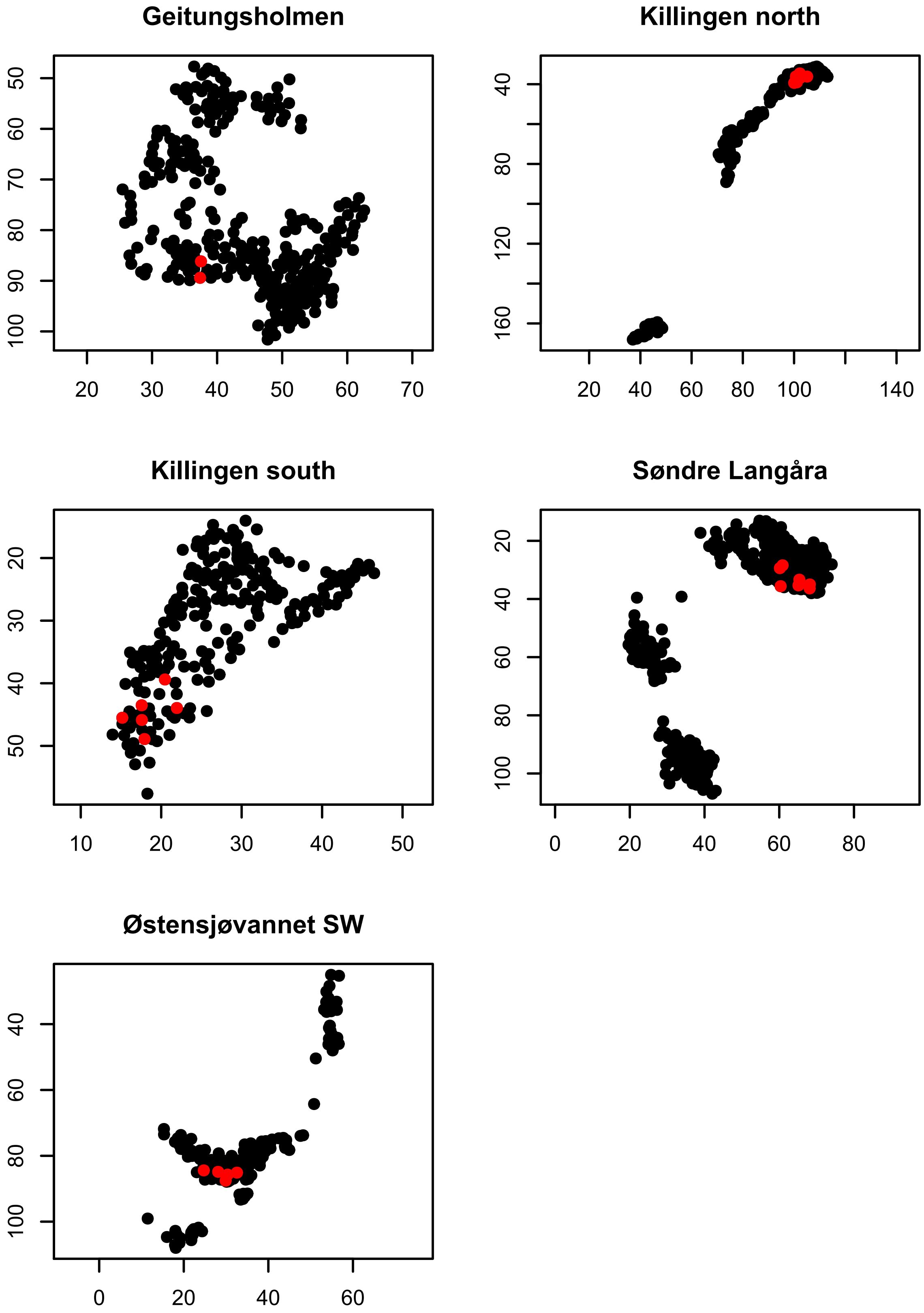


Figure D1. Locations of nest cameras within colonies (red points). Black points are all attempted nests within the colony based on drone photos.

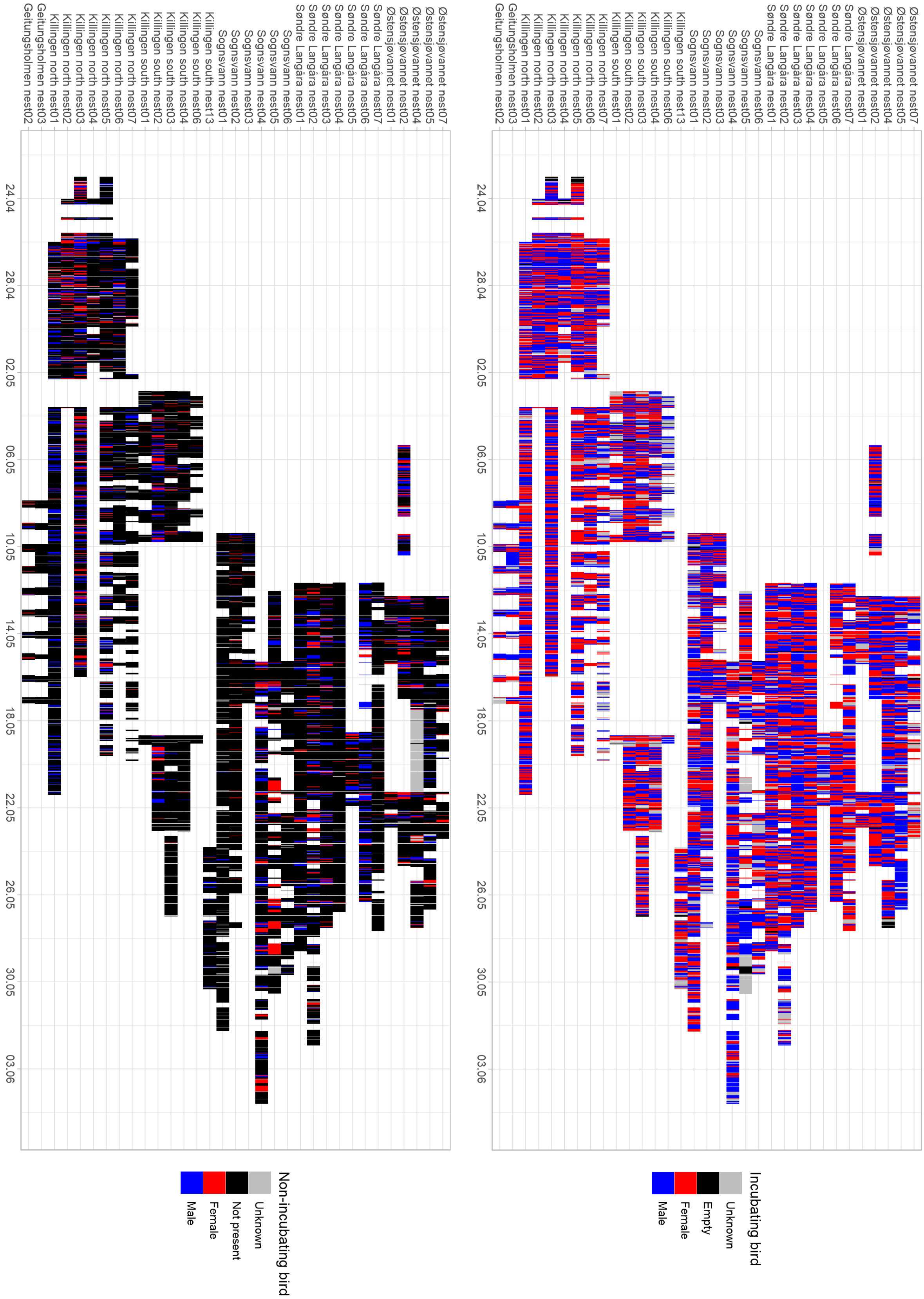


Figure D2. Incubation data, as well as the presence of the non-incubating bird at the nest cameras.

Table D1. Background data for all nest cameras. Contains information about the colour-ring number of the parents and breeding success derived from the nest cameras.

Nest	Male cr	Female cr	Laying egg1	Laying egg2	Laying egg3	Hatching egg1	Hatching egg2	Hatching egg3	Laid	Hatched	Comment
Østensjøvannet nest07	JC89		pre13.05	pre13.05	no	after24.5?	no	no	2	NA	1 egg falls outside the nest
Østensjøvannet nest05	J63E		pre13.05	pre13.05	no	after27.5?	after27.5?	no	2	0-1	?
Østensjøvannet nest04	J2UN		pre06.05	pre06.05	no	no	no	no	2	1	1 egg destroyed 18.5, possibily during a fight with another BHG 13:42. Last 2 eggs disappears 28.5 00:34 (Fox?)
Østensjøvannet nest02	J0JY		pre06.05	pre06.05	pre06.05	25.05 09:50	25.05 15:18	no	3	2	8.5 22:11 J0JY manages to to push its own egg out of the nest, not stressed situation. Still 2 chicks 16.6
Østensjøvannet nest01		J3PH	pre13.05	pre13.05	?	23.05 08:46	no	no	2	1	0, Fox 28.5 02:35
Søndre Langåra nest07	J4JY		pre13.05 16:32	pre13.05 16:32	pre13.05 16:32	26.05 19:00	27.05 19:42	28.05 10:02	3	3	chicks very mobile. 1 chick 2.6, end in 0 as the rest of the colony
Søndre Langåra nest06	JAN3		pre12.05	pre12.05	pre12.05	26.05 12:27	27.05 07:50	no	3	2	1 egg gone between 15.5 and 19.5
Søndre Langåra nest05	T-5		pre19.05	pre19.05	pre19.05	no	no	no	3	0	3 eggs gone in 7 secounds, 22.5 22:01, most likely Crow
Søndre Langåra nest04	JZ10		pre12.05 17:09	pre12.05 17:09	pre12.05 17:09	26.05 07:13	27.05 16:46	no	3	2	1 egg taken 24.5 19:57
Søndre Langåra nest03		J3K1	pre12.05	pre12.05	no	no	no	no	2	0	egg taken by Crow (most likely) 28.5 12:29
Søndre Langåra nest02		J66E	pre12.05 15:46	pre12.05 15:46	pre12.05 15:46	30.05 06:54	31.05 18:45	02.06 17:26	3	3	2, one chick gone during hatching(?), ends with 0
Søndre Langåra nest01	J44C		pre12.05	pre12.05	no	28.05 15:44	29.05 14:17	no	2	2	2 chicks 2.6-3.6, 1 chick 4.6-10.6, 0 chicks 11.6
Sognsvann nest06		J5U6	pre16.05	?	?	pre30.05 16:54?	?	?	NA	NA	poor visibility
Sognsvann nest05	JCU5		pre10.05	?	?	after09.06?	?	?	NA	NA	poor visibility, but incubating 9.6, 1 egg 10.5
Sognsvann nest04		JZ04	pre16.05	pre16.05	?	05.06 04:49	05.06 14:21	no	2	2	1 chick 6.6-15.6. They never return after the ringing session 16.5. Either dead or relocated. Parents do not use nest after ringing session as nest01, which might indicate relocation. Another pair (J7K1 + 2 chicks) uses the nest as of 16.6
Sognsvann nest03	J94N		pre10.05	?	?	after18.05?	?	?	NA	NA	?
Sognsvann nest02	J7K1		pre10.05	pre10.05	pre10.05	30.05 morning	30.5 evening	?	3	2	2 chicks 17.6, with colourrings
Sognsvann nest01	JCY6		pre10.05	pre10.05	no	01.06 14:24	02.06 04:28	no	2	2	2 chicks 11.6, 1 chick 13.6. The last one never returns after the ringing session 16.6. JCY6 are nest building 16.6 08:05
Killingen south nest13	JLP5		pre24.05 19:28	pre24.05 19:28	pre24.05 19:28	after31.05?	after31.05?	after31.05?	3	NA	?
Killingen south nest06	J4CY		pre03.05 20:29	pre19.05	pre19.05	no	no	no	3	0	0, Badger 20.5
Killingen south nest04	J7RC	J86A	pre03.05 20:29	pre03.05 20:29	04.05 17:56	no	no	no	3	0	0, Badger 20.5 and 24.5
Killingen south nest03		J6RU	pre03.05 20:29	pre03.05 20:29	05.05 07:29	25.05 18:16	26.05 14:36	27.05 18:43	3	3	at least 1 chick 31.5
Killingen south nest02		JHA4	pre03.05 20:29	04.05 23:50	no	no	no	no	2	0	still 2 eggs 19.5, Badger sniffs 20.5 (takes none). Badger takes first egg 23.5, and the last 24.5.
Killingen south nest01	J11E		pre03.05 20:29	pre03.05 20:29	pre03.05 20:29	no	no	no	3	0	0, Badger 20.5 01:13
Killingen north nest07	JKH0	J6L2	pre26.04	pre26.04	28.04 14:45	20.05 19:16	21.05 05:45	pre22.05 10:07	3	3	1 chick 7.6
Killingen north nest06	JY53		pre26.04 20:00	no	no	19.05	no	no	1	1	1 chick 7.6
Killingen north nest05		J7Y1	24.04 10:56	pre26.04 15:20	28.04 01:40	19.05 06:17	19.05 10:35	20.05 04:13	3	3	2(-3?) chicks 7.6
Killingen north nest04	J6LA		26.04 20:13	?	?	?	?	?	NA	NA	poor visibility
Killingen north nest03	JLL5	JY57	24.04 15:35	25.04 06:00	28.04 12:40	no	no	no	3	0	stray dog 16.5 takes all three eggs
Killingen north nest02		J1J1	25.04 06:26	27.04 02:35	28.04 18:41	yes	?	no	3	1-2	1 chick 7.6, parent at Dokkskjær 10.6, likely failed
Killingen north nest01	J3PA		27.04 04:35	pre30.04 03:14	pre12.05 19:45	22.05 04:54	no	no	3	1	stray dog 16.5, one egg gone, one other destroyed
Geitungsholmen nest03	gw		pre08.05 22:25	pre08.05 22:25	pre08.05 22:25	?	?	?	3	NA	?
Geitungsholmen nest02		J8UN	pre12.05 21:28	pre14.05 22:16	?	no	no	no	2	0	0, they try again 2 meters away

Table D2. Incubation frequencies for different nests, based on the same dataset as Figure D2.

Nest	Unknown	Empty	Female	Male	N minutes
Geitungsholmen nest 02	0.129	0.044	0.307	0.520	4628
Geitungsholmen nest 03	0.101	0.001	0.284	0.614	5665
Killingen north nest 01	0.086	0.008	0.464	0.443	34717
Killingen north nest 02	0.031	0.023	0.430	0.516	10310
Killingen north nest 03	0.009	0.018	0.445	0.529	29528
Killingen north nest 04	0.136	0.038	0.313	0.513	8723
Killingen north nest 05	0.072	0.020	0.535	0.373	28997
Killingen north nest 06	0.071	0.004	0.472	0.453	21746
Killingen north nest 07	0.237	0.004	0.364	0.395	20205
Killingen south nest 01	0.310	0.020	0.381	0.289	7770
Killingen south nest 02	0.031	0.024	0.499	0.445	16308
Killingen south nest 03	0.136	0.021	0.473	0.370	21032
Killingen south nest 04	0.163	0.021	0.387	0.428	15136
Killingen south nest 06	0.511	0.012	0.073	0.405	6097
Killingen south nest 13	0.132	0.027	0.486	0.355	8464
Sognsvann nest 01	0.145	0.018	0.395	0.442	30904
Sognsvann nest 02	0.078	0.008	0.375	0.539	22996
Sognsvann nest 03	0.122	0.012	0.368	0.498	7996
Sognsvann nest 04	0.130	0.007	0.338	0.525	26227
Sognsvann nest 05	0.130	0.056	0.314	0.501	19655
Sognsvann nest 06	0.219	0.006	0.366	0.409	13781
Søndre Langåra nest 01	0.086	0.009	0.439	0.466	24362
Søndre Langåra nest 02	0.128	0.003	0.430	0.439	26127
Søndre Langåra nest 03	0.011	0.003	0.406	0.580	22776
Søndre Langåra nest 04	0.030	0.005	0.540	0.425	21770
Søndre Langåra nest 05	0.243	0.000	0.326	0.431	4624
Søndre Langåra nest 06	0.036	0.001	0.548	0.414	16423
Søndre Langåra nest 07	0.133	0.002	0.520	0.346	20027
Østensjøvannet nest 01	0.144	0.014	0.495	0.347	6619
Østensjøvannet nest 02	0.015	0.020	0.467	0.498	17875
Østensjøvannet nest 04	0.025	0.034	0.380	0.561	21108
Østensjøvannet nest 05	0.109	0.011	0.257	0.624	19110
Østensjøvannet nest 07	0.263	0.019	0.401	0.316	10812

Appendix E Additional drone flight data

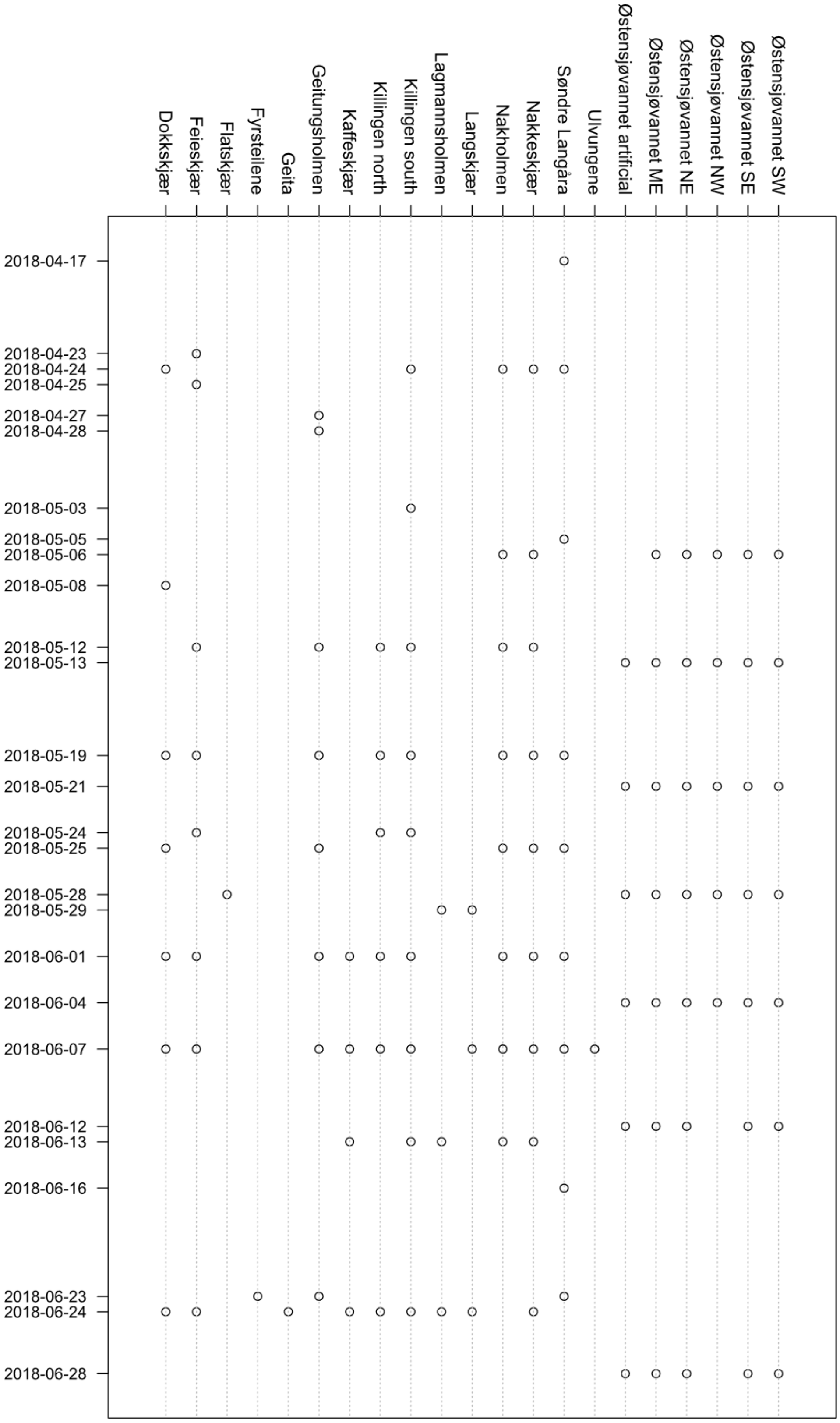


Figure E1. Dates of drone flights at the different colonies. Some colonies were only photographed ones and are not included in the main analysis in the thesis.

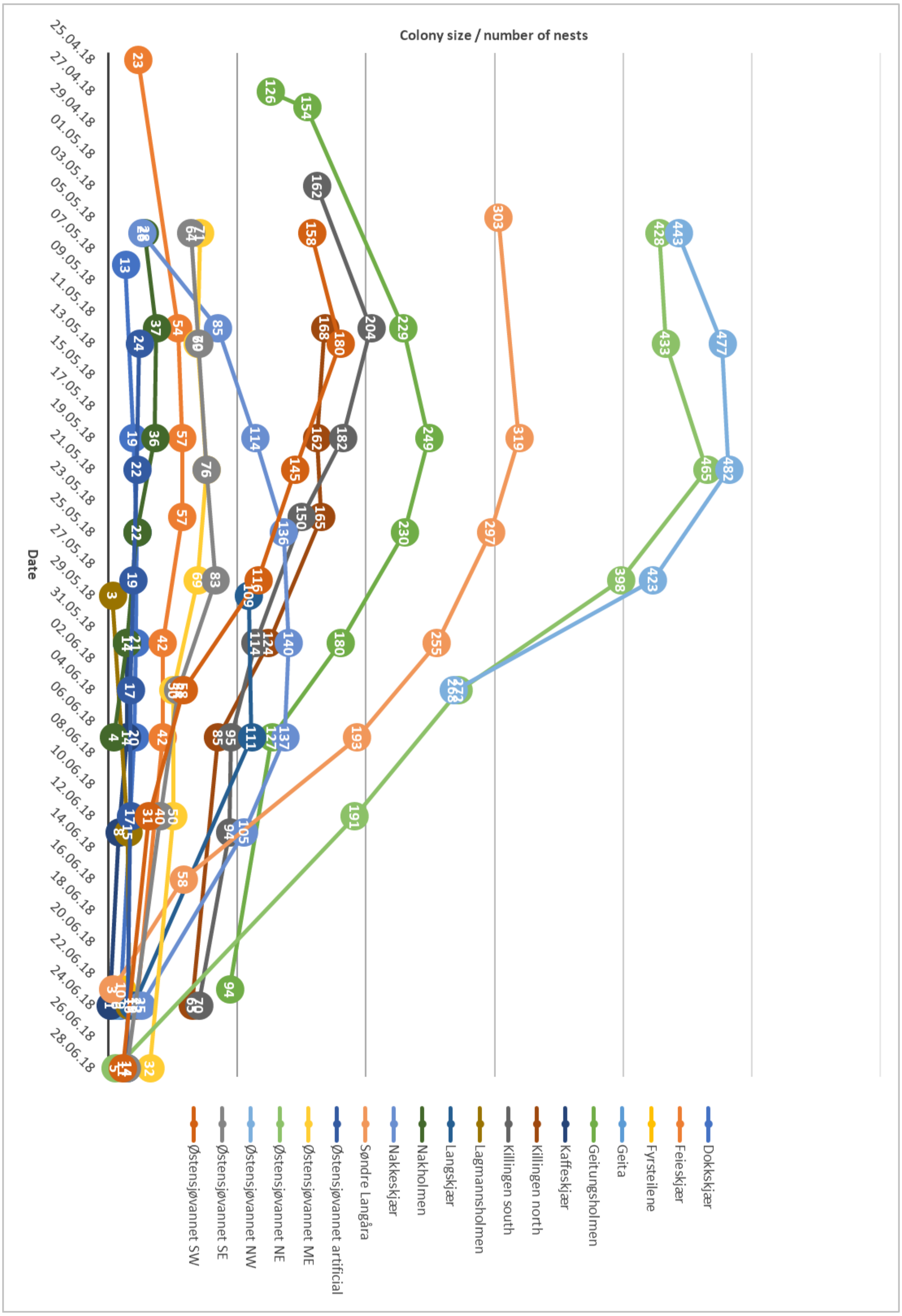
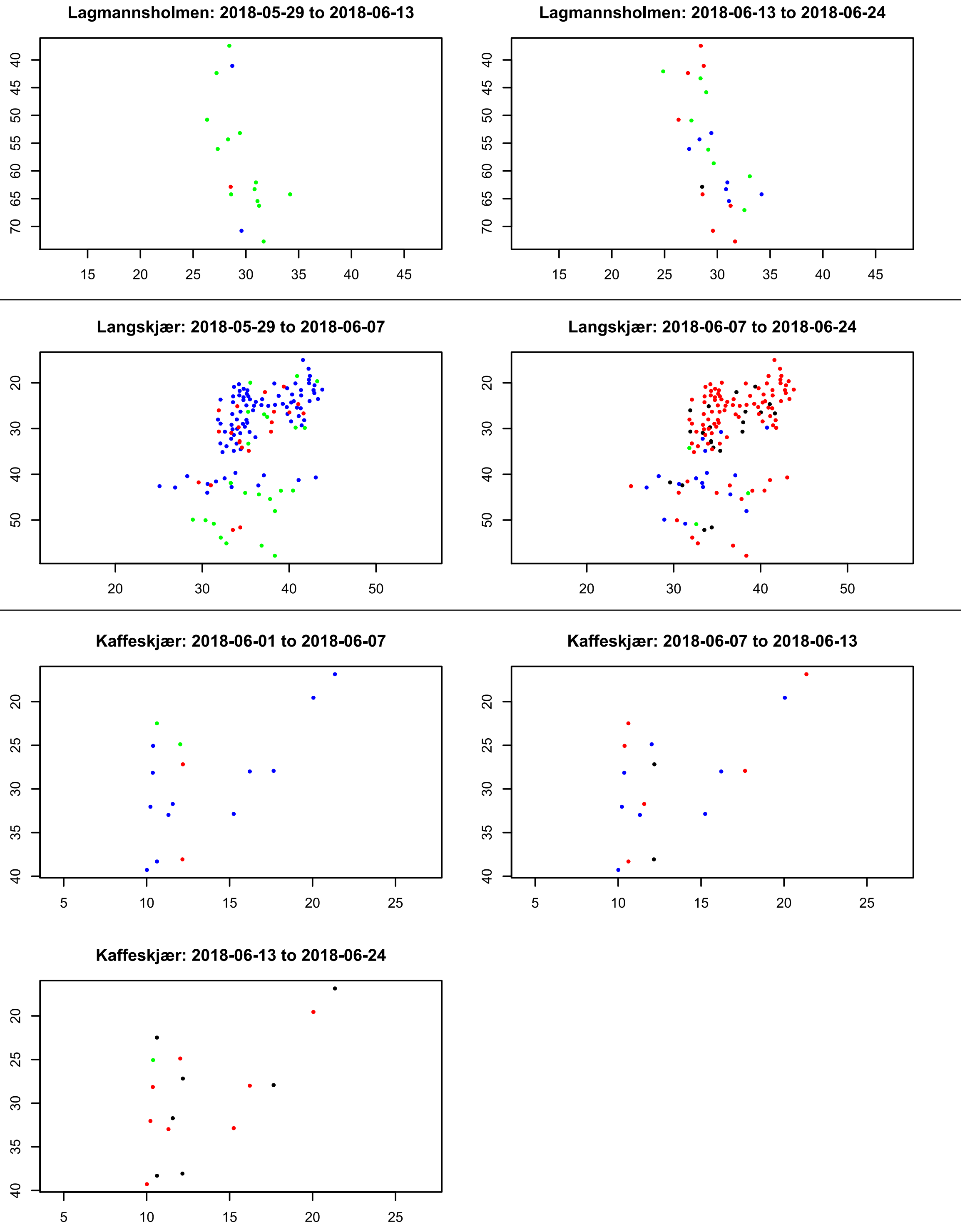


Figure E2. Nest counts for different colonies based on drone photos. We can see how much the colony size changes during the breeding cycle. Timing of single counts for population monitoring is thereby very important

Appendix F Additional formation plots

Following is all formation plots for each individual colony. Lagmannsholmen, Langskjær and Kaffeskjær are presented first due to their few periods with data. The rest of the colonies are presented alphabetically with one colony per page.



Lagmannsholmen: 2018-05-29 to 2018-06-13

Lagmannsholmen: 2018-06-13 to 2018-06-24

Langskjær: 2018-05-29 to 2018-06-07

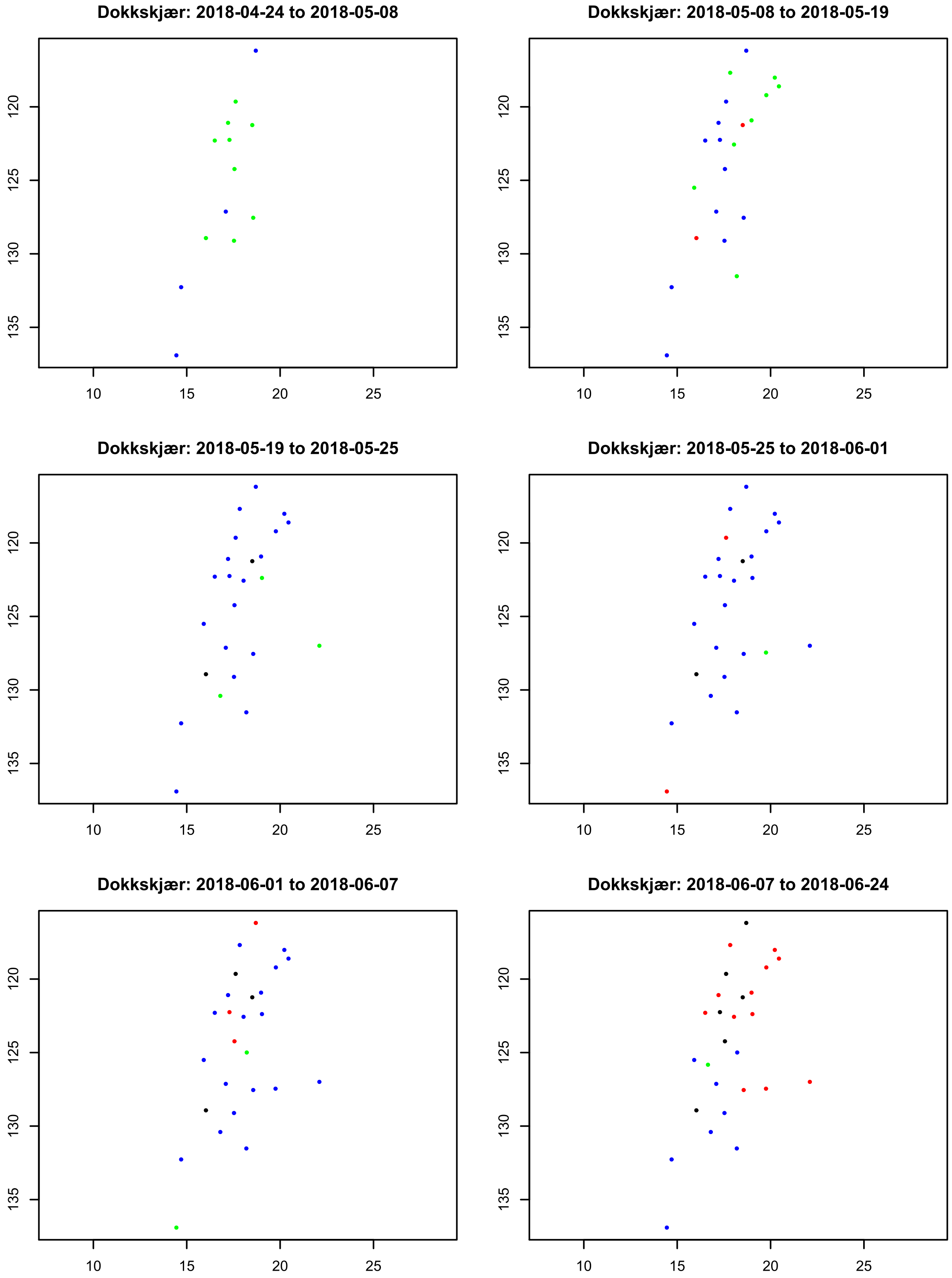
Langskjær: 2018-06-07 to 2018-06-24

Kaffeskjær: 2018-06-01 to 2018-06-07

Kaffeskjær: 2018-06-07 to 2018-06-13

Kaffeskjær: 2018-06-13 to 2018-06-24

Figure F1. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status



Dokkskjær: 2018-04-24 to 2018-05-08

Dokkskjær: 2018-05-08 to 2018-05-19

Dokkskjær: 2018-05-19 to 2018-05-25

Dokkskjær: 2018-05-25 to 2018-06-01

Dokkskjær: 2018-06-01 to 2018-06-07

Dokkskjær: 2018-06-07 to 2018-06-24

Figure F2. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

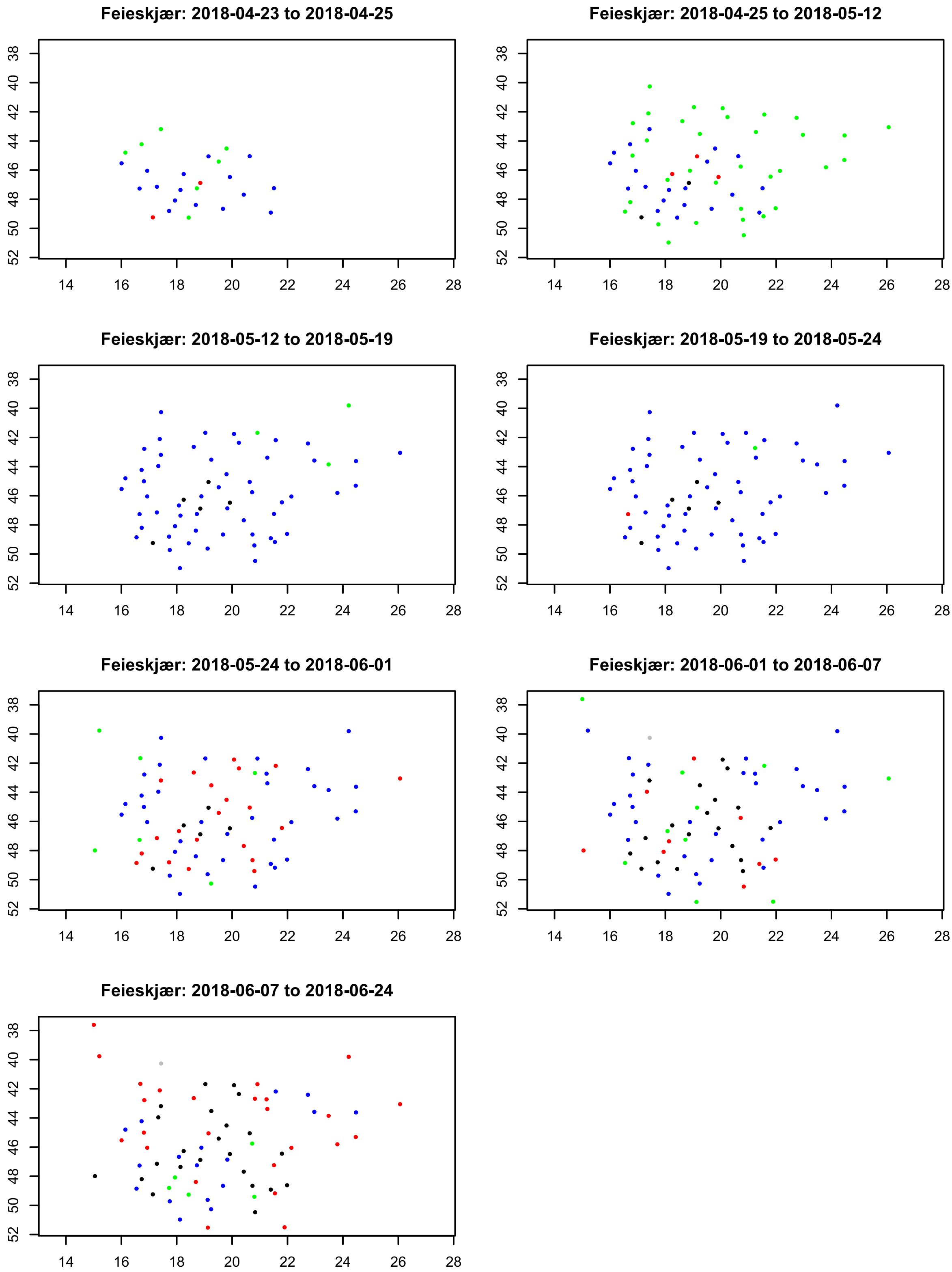


Figure F3. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

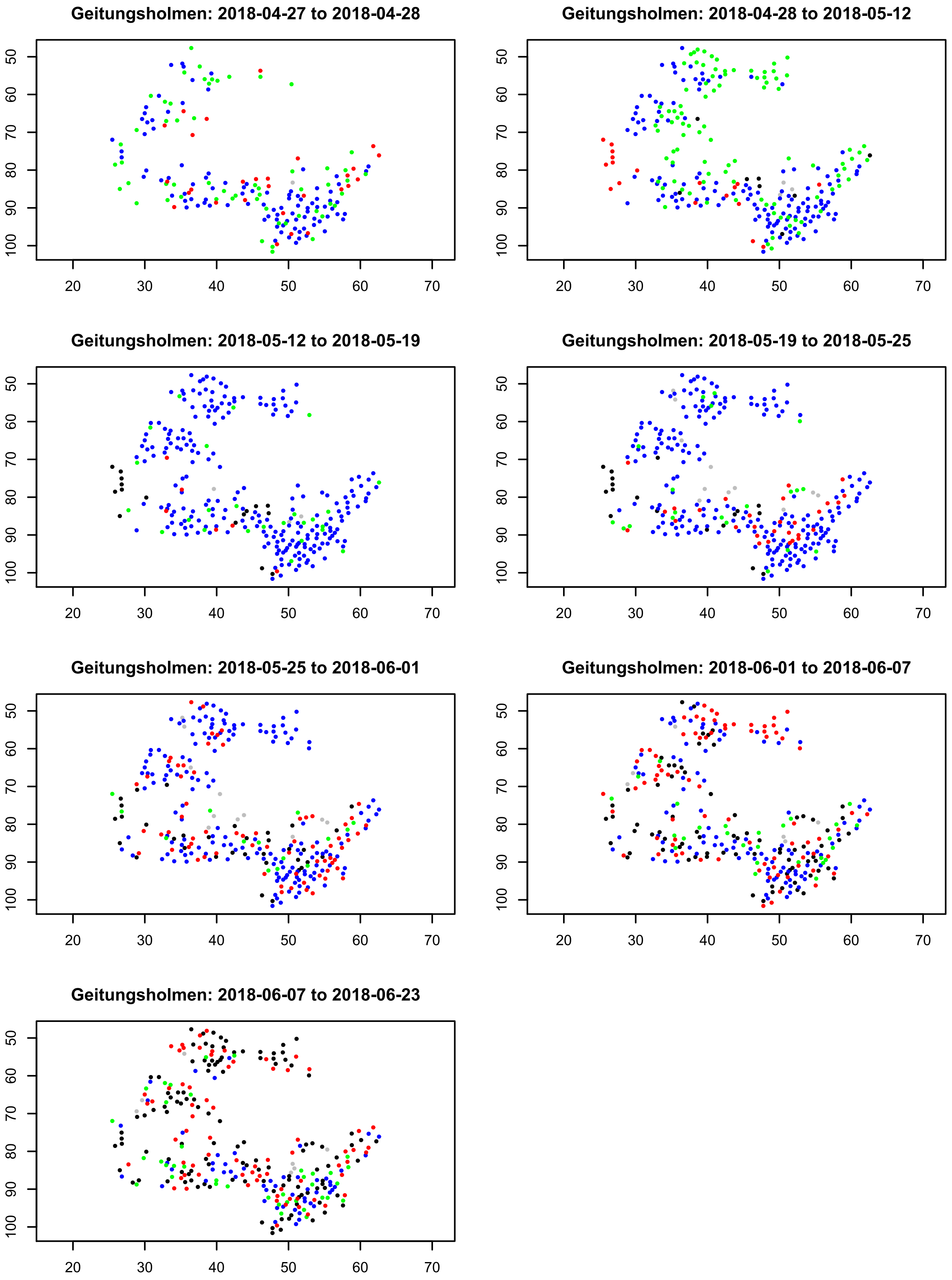
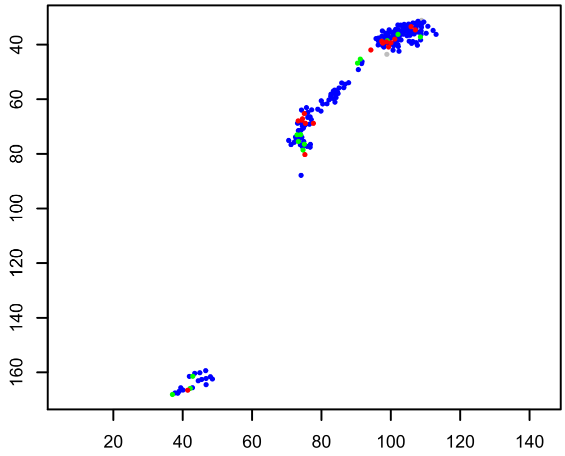
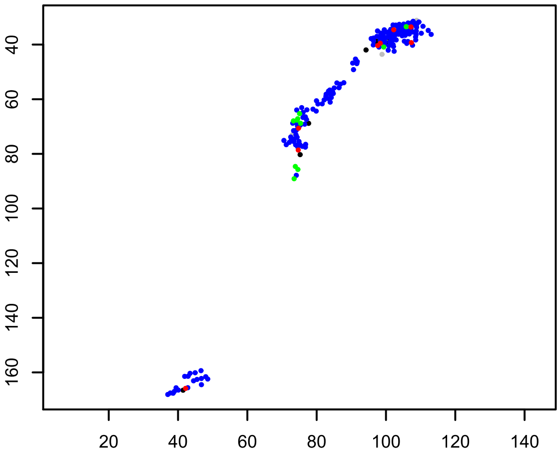


Figure F4. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

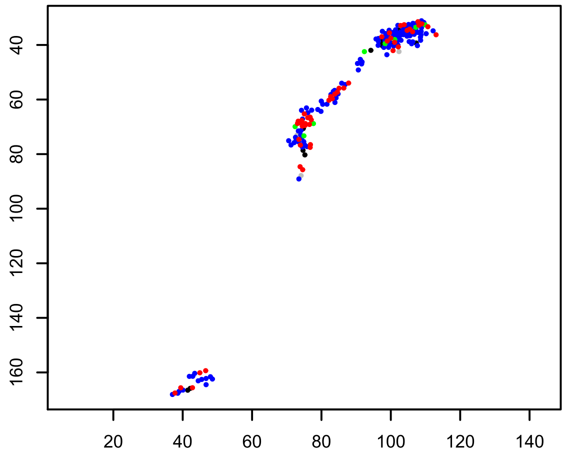
Killingen north: 2018-05-12 to 2018-05-19



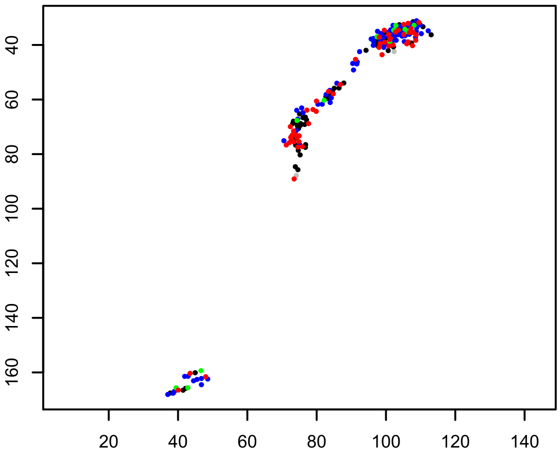
Killingen north: 2018-05-19 to 2018-05-24



Killingen north: 2018-05-24 to 2018-06-01



Killingen north: 2018-06-01 to 2018-06-07



Killingen north: 2018-06-07 to 2018-06-24

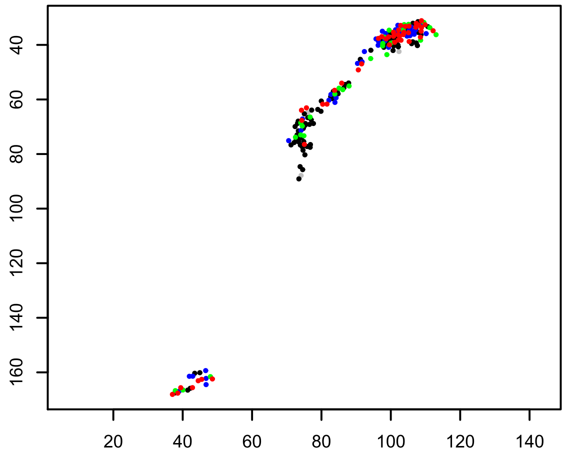
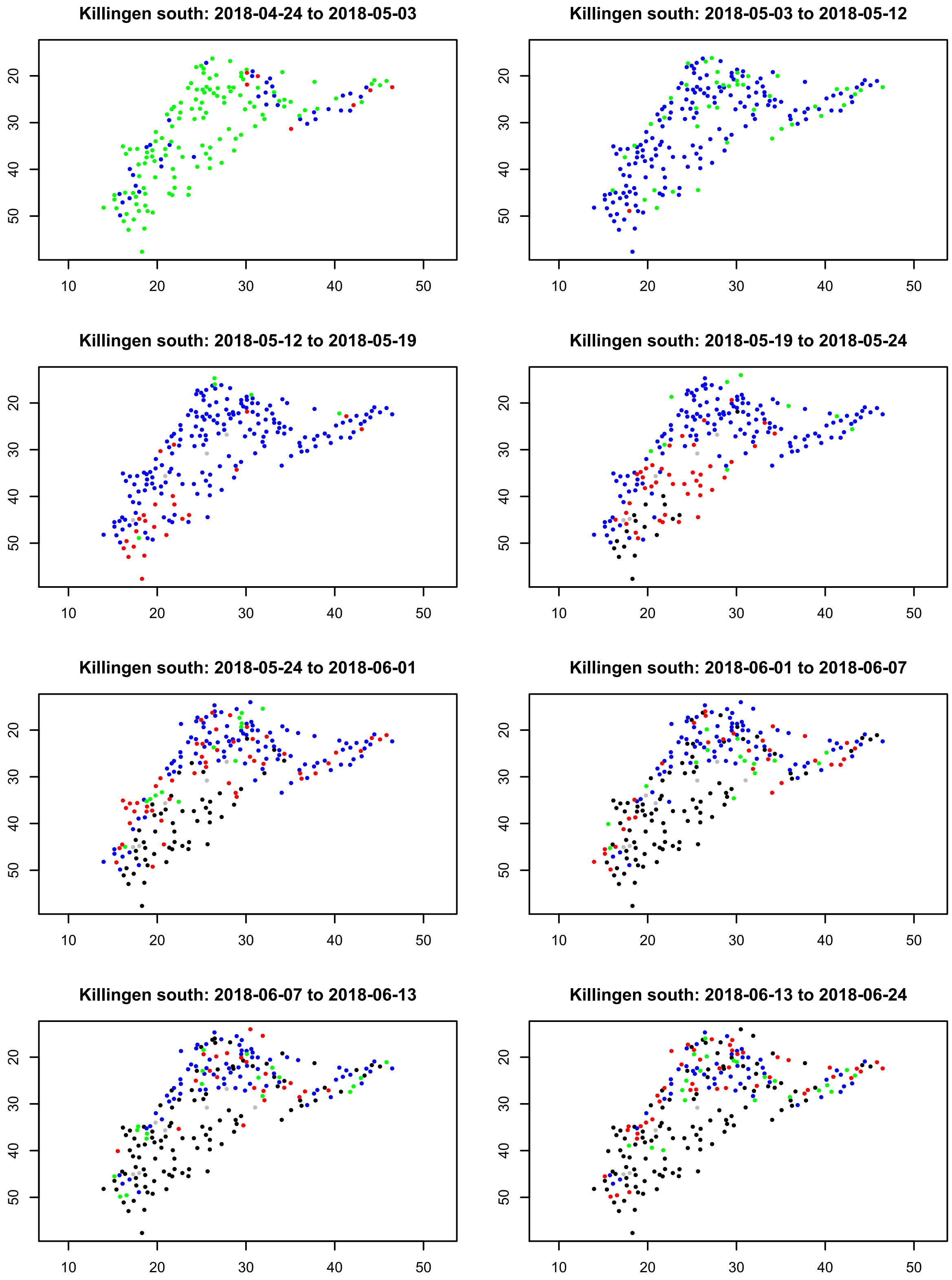


Figure F5. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status



Killingen south: 2018-04-24 to 2018-05-03

Killingen south: 2018-05-03 to 2018-05-12

Killingen south: 2018-05-12 to 2018-05-19

Killingen south: 2018-05-19 to 2018-05-24

Killingen south: 2018-05-24 to 2018-06-01

Killingen south: 2018-06-01 to 2018-06-07

Killingen south: 2018-06-07 to 2018-06-13

Killingen south: 2018-06-13 to 2018-06-24

Figure F6. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

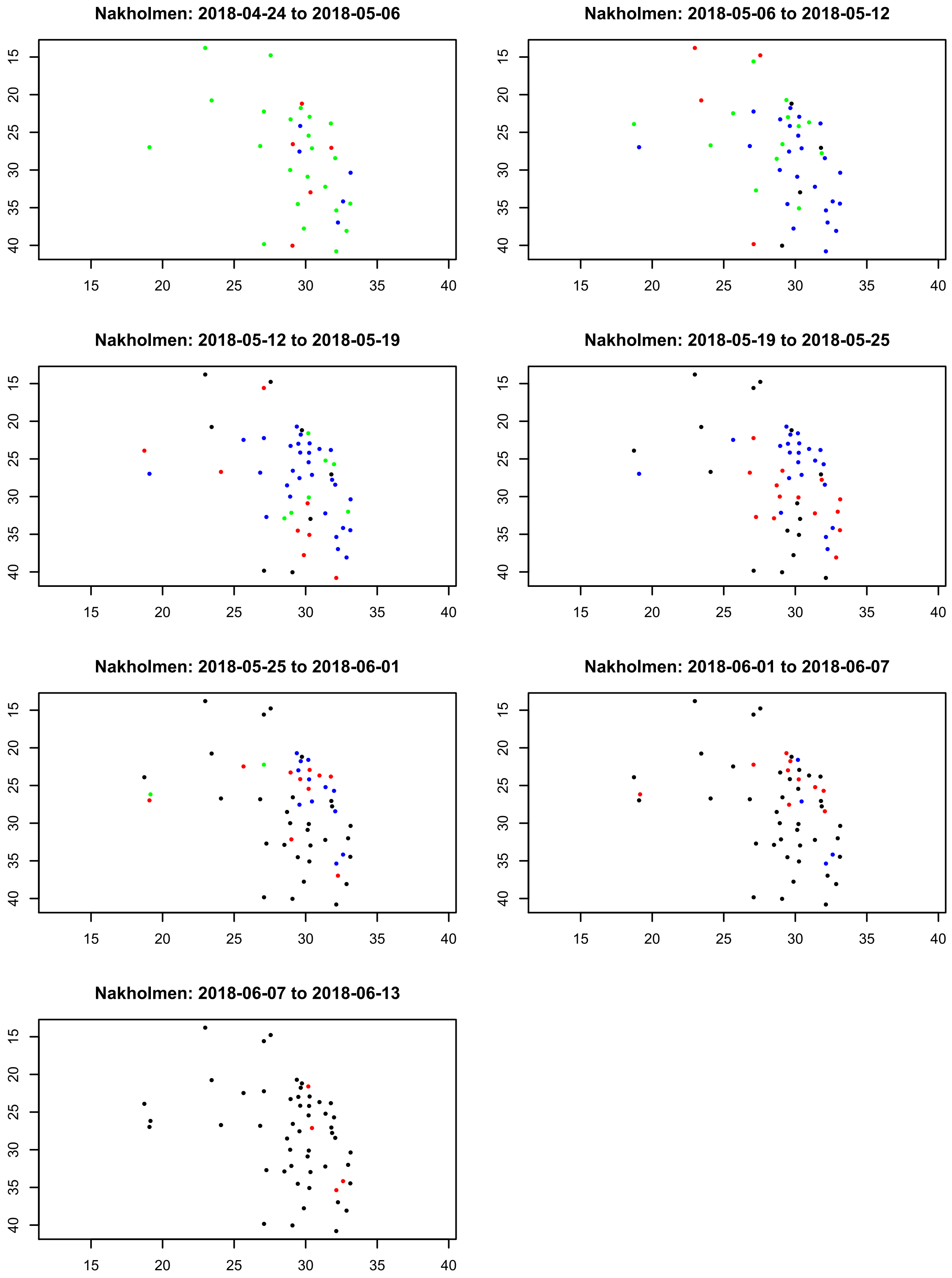


Figure F7. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

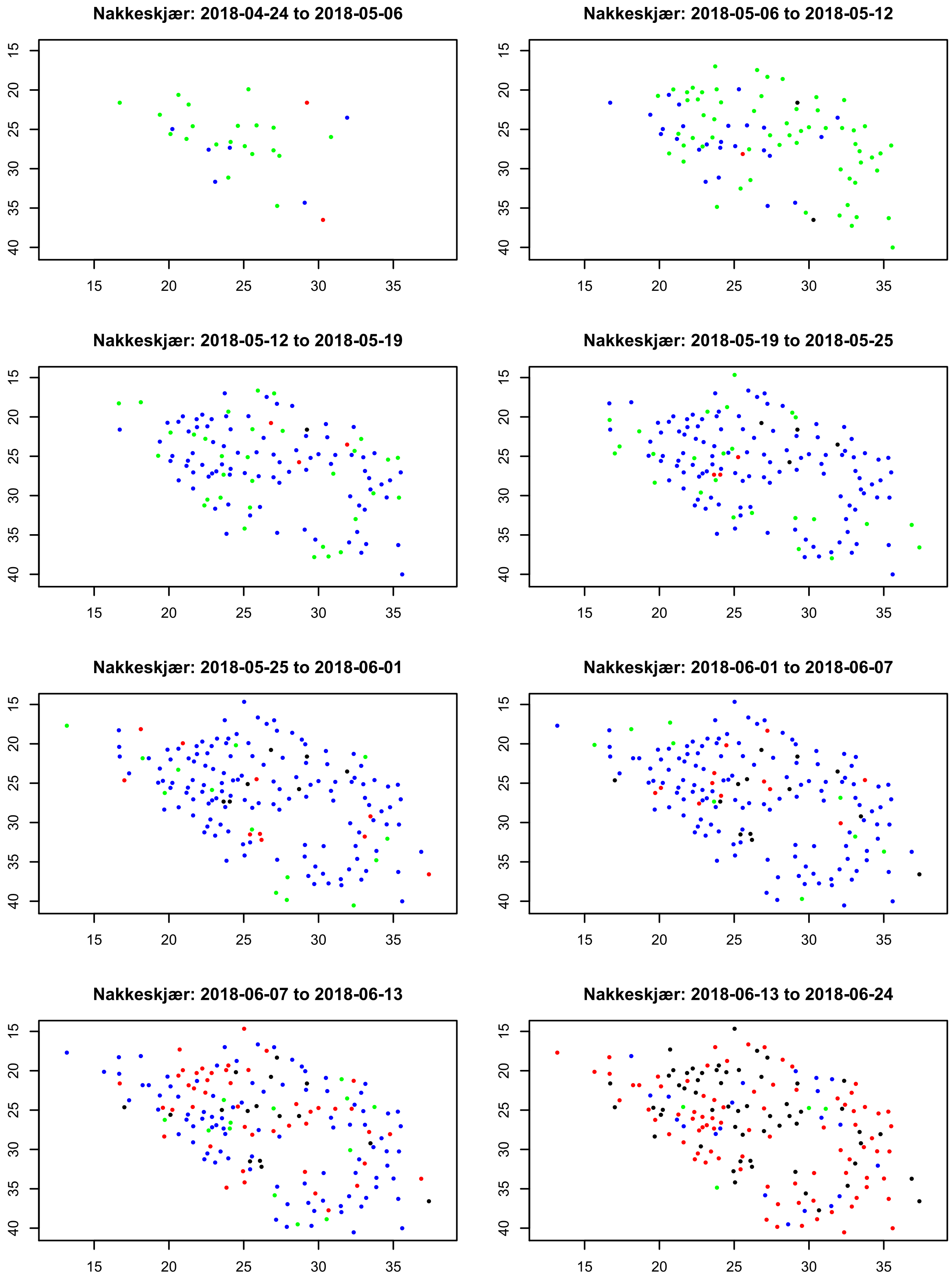
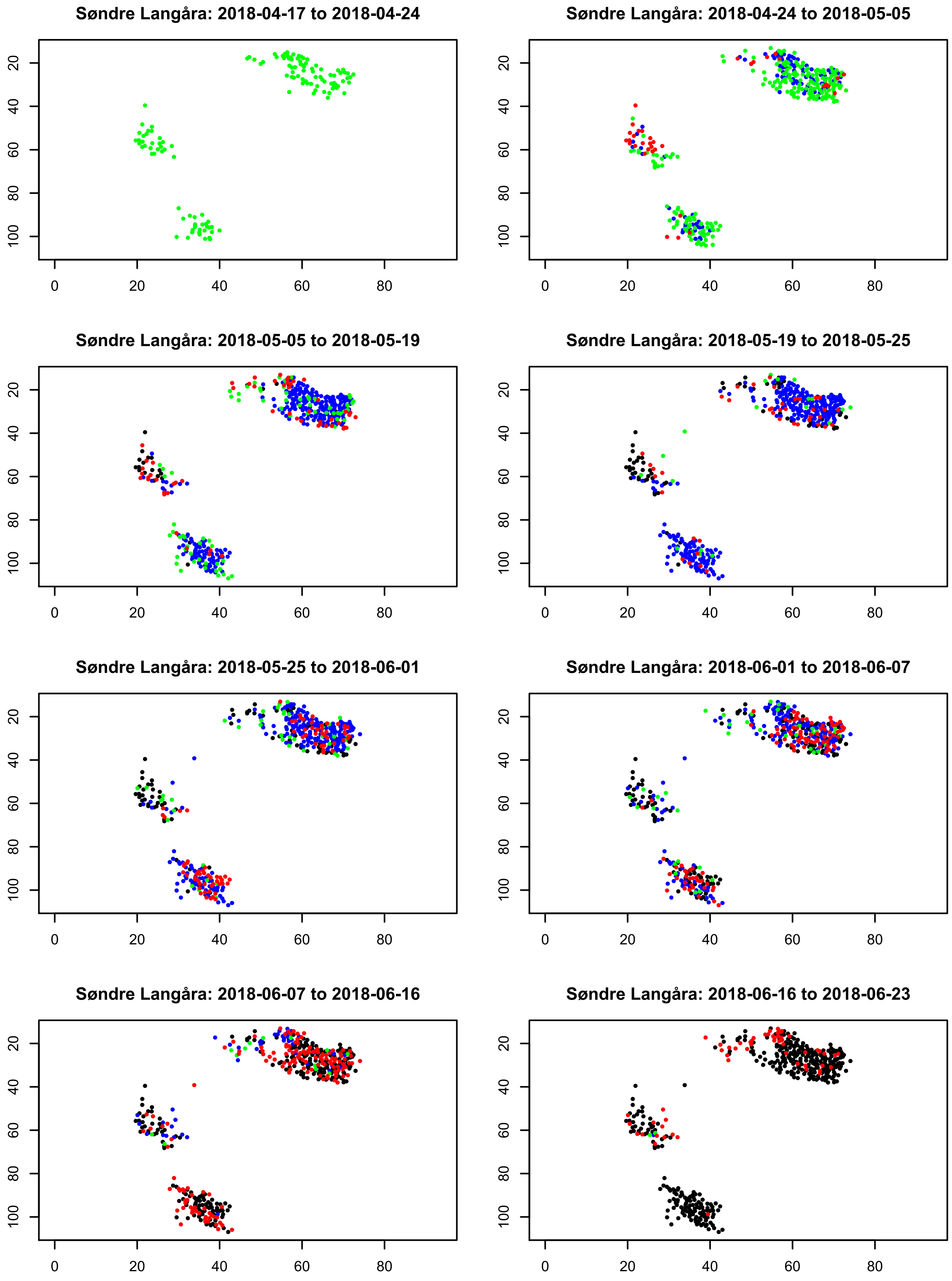


Figure F8. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status


Søndre Langåra: 2018-04-17 to 2018-04-24

Søndre Langåra: 2018-04-24 to 2018-05-05

Søndre Langåra: 2018-05-05 to 2018-05-19

Søndre Langåra: 2018-05-19 to 2018-05-25

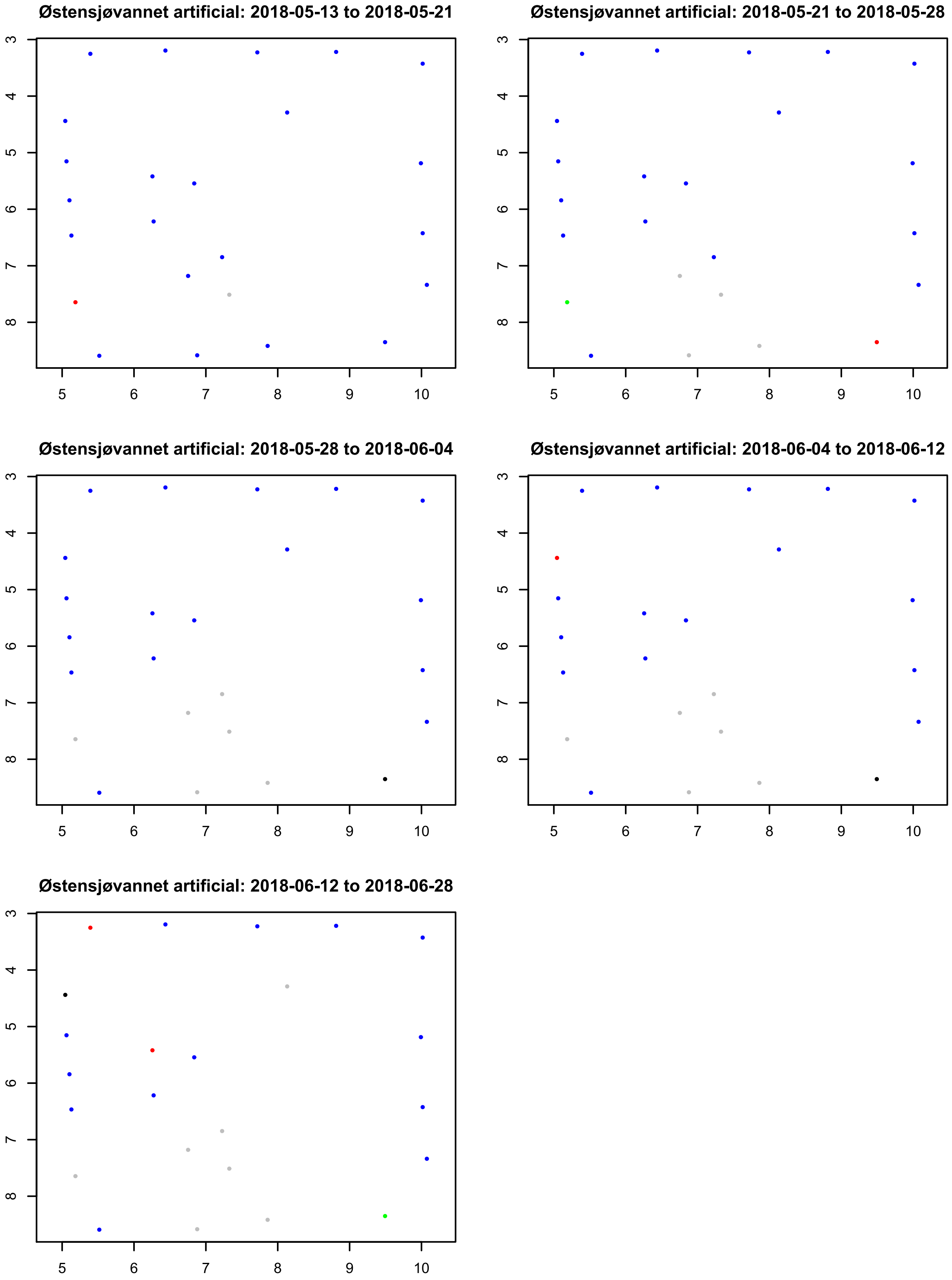
Søndre Langåra: 2018-05-25 to 2018-06-01

Søndre Langåra: 2018-06-01 to 2018-06-07

Søndre Langåra: 2018-06-07 to 2018-06-16

Søndre Langåra: 2018-06-16 to 2018-06-23

Figure F9. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status


Østensjøvannet artificial: 2018-05-13 to 2018-05-21

Østensjøvannet artificial: 2018-05-21 to 2018-05-28

Østensjøvannet artificial: 2018-05-28 to 2018-06-04

Østensjøvannet artificial: 2018-06-04 to 2018-06-12

Østensjøvannet artificial: 2018-06-12 to 2018-06-28

Figure F10. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

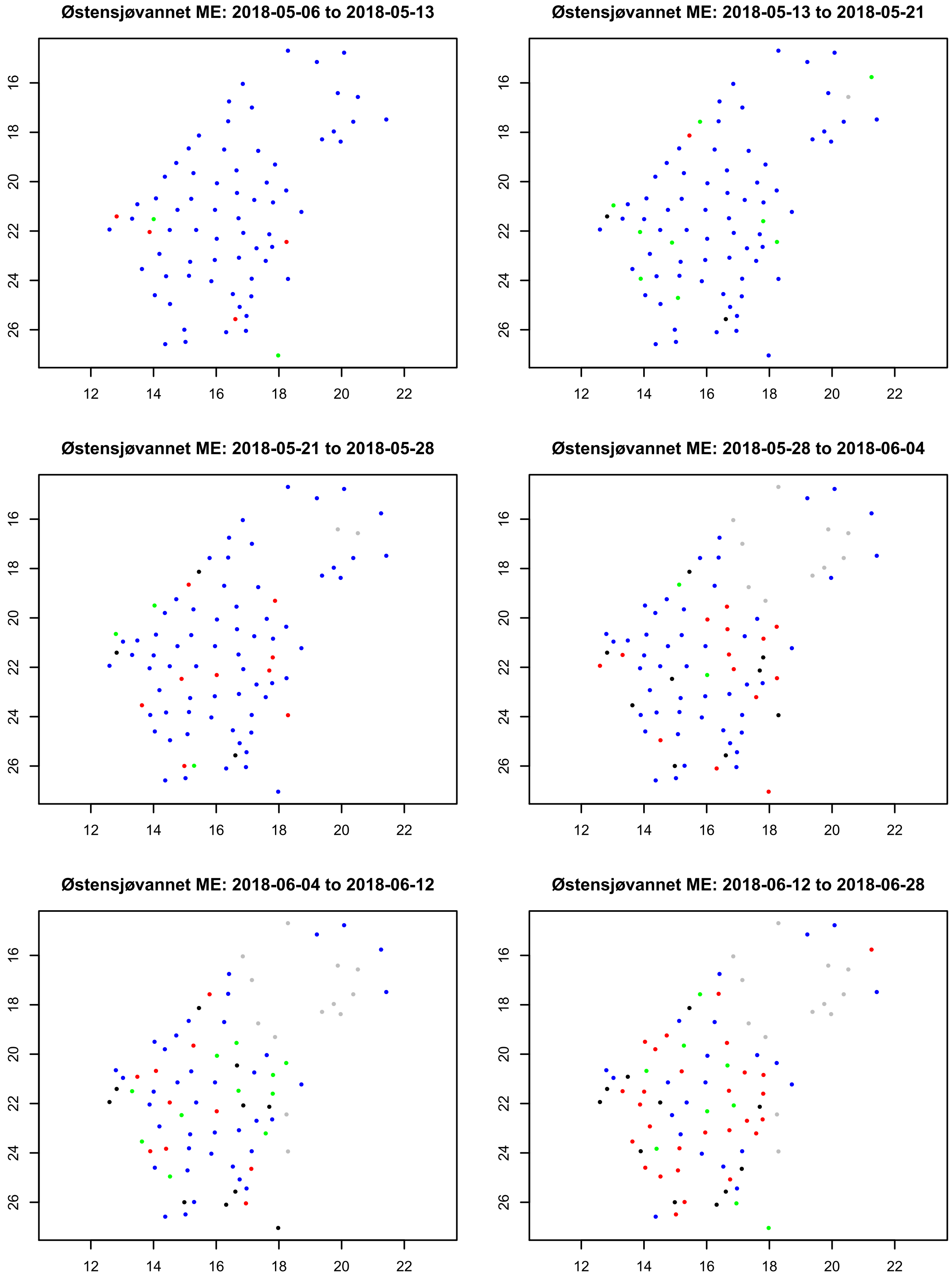


Figure F11. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

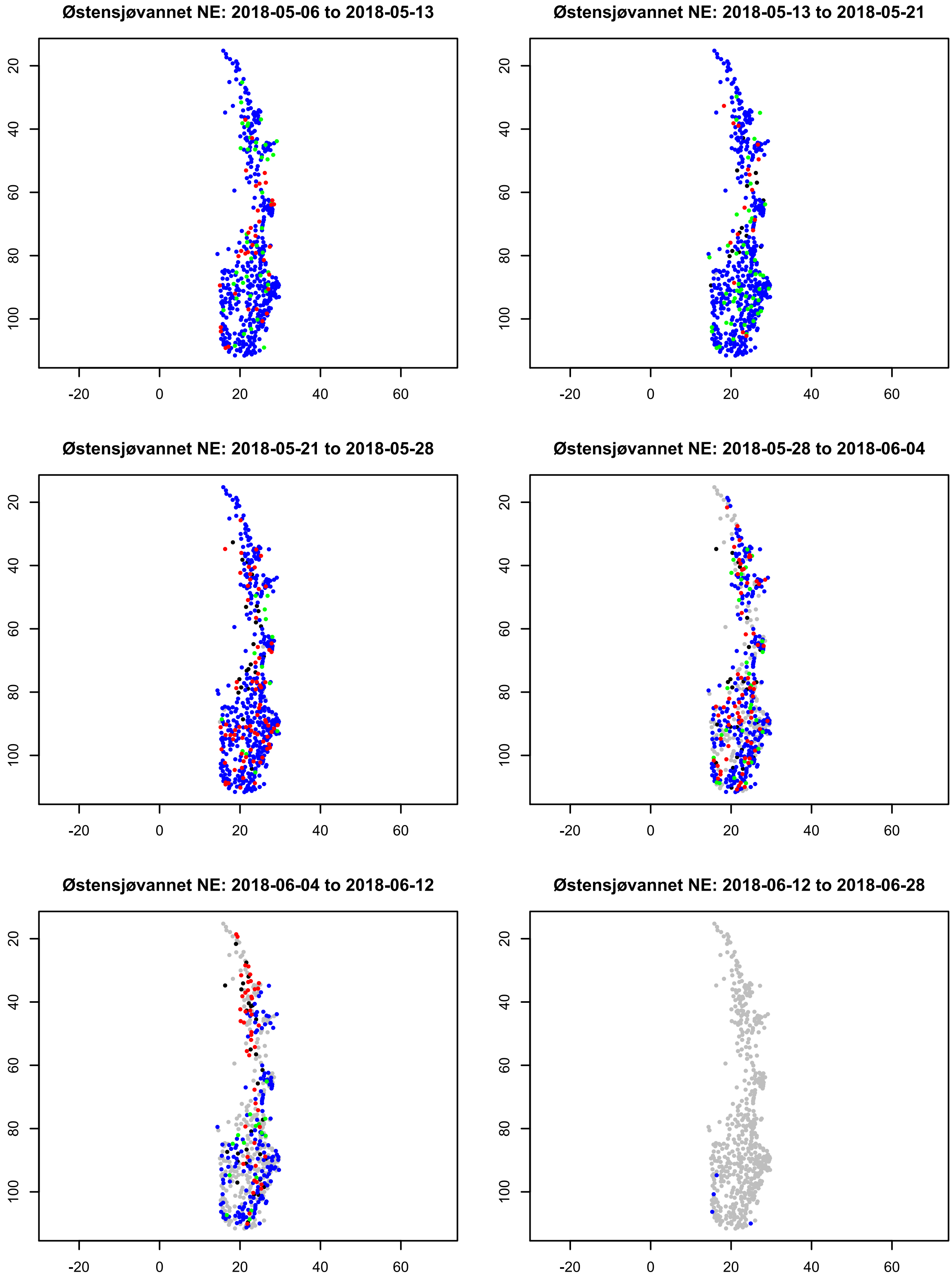


Figure F12. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

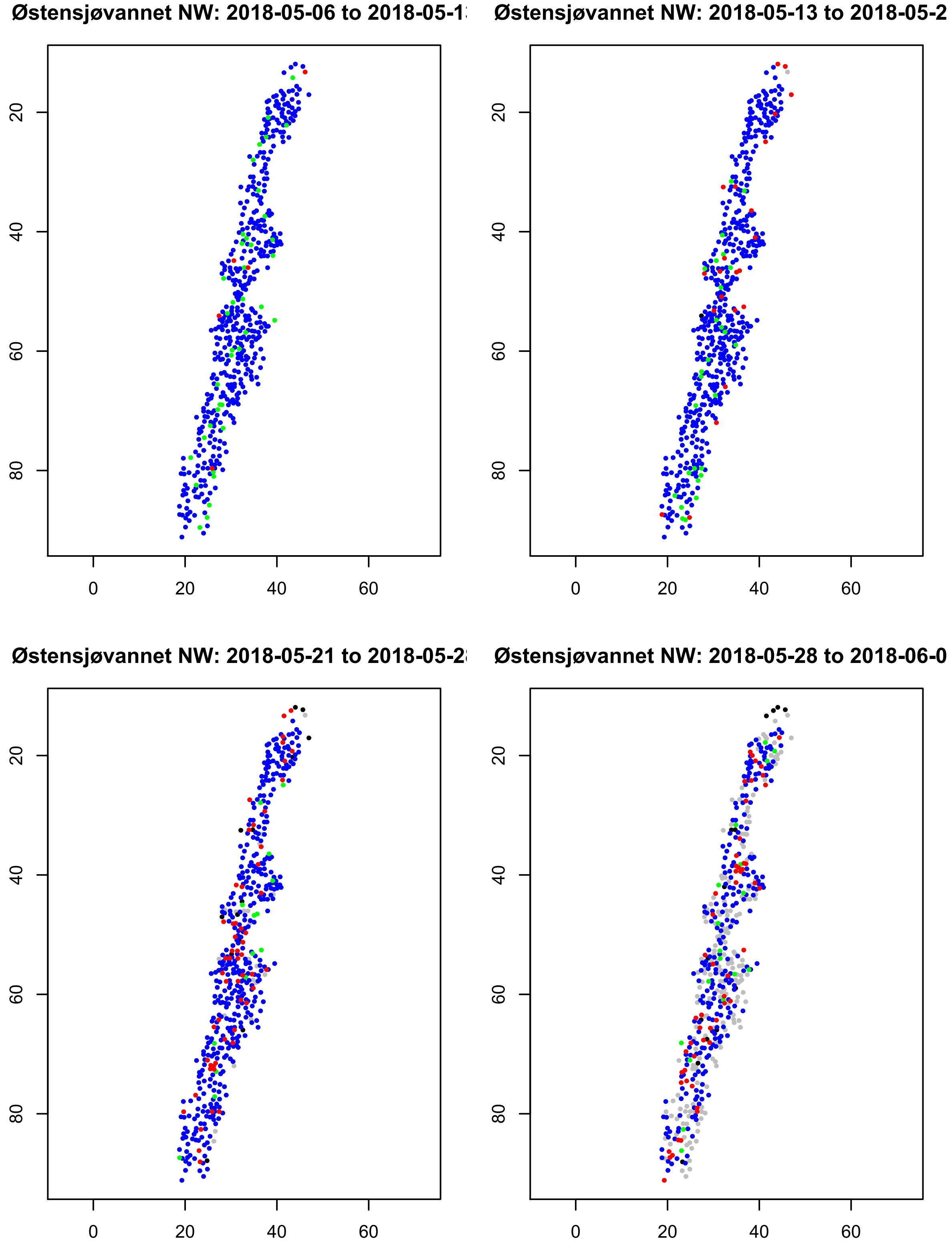
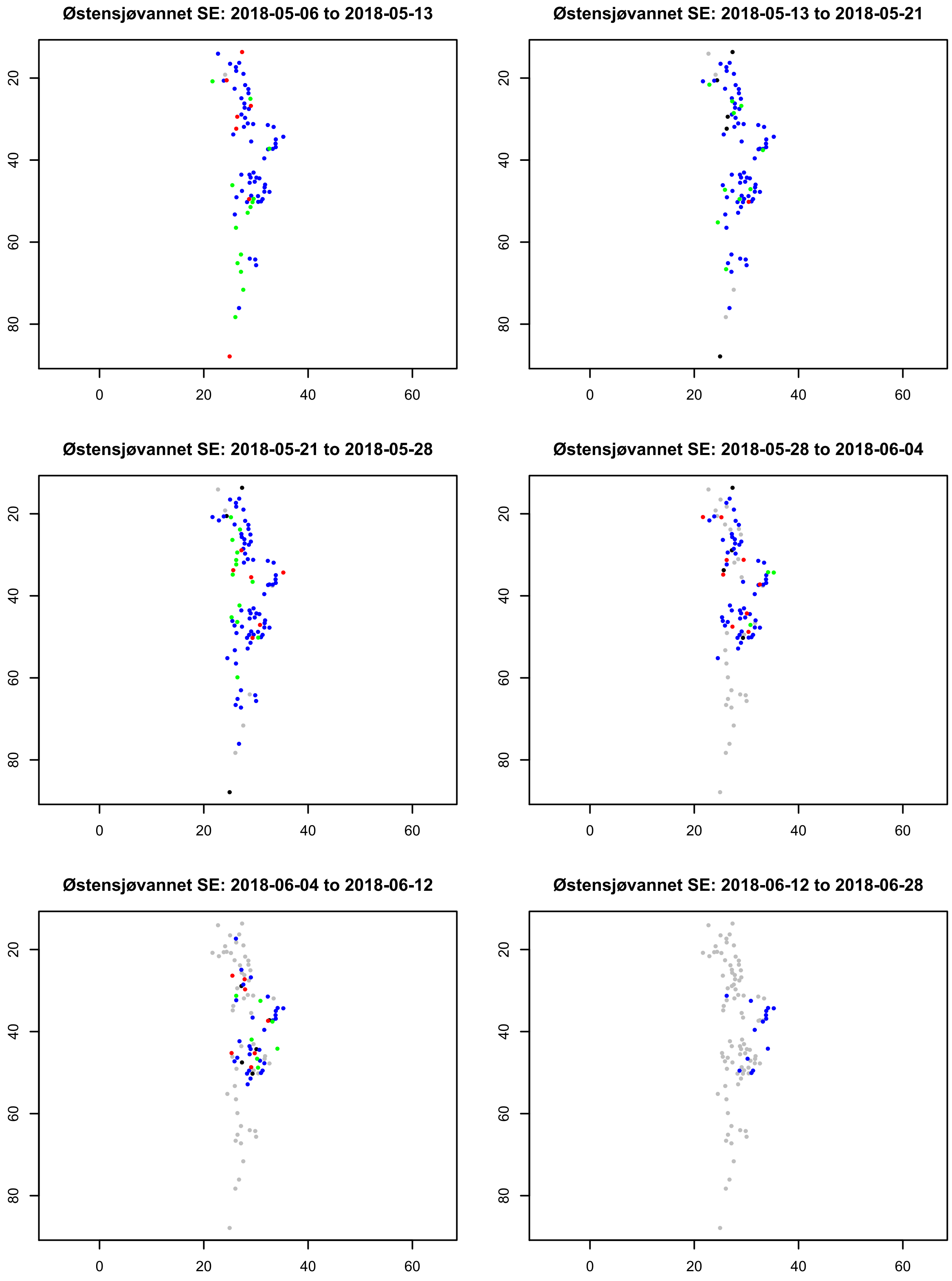


Figure F13. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status



Østensjøvannet SE: 2018-05-06 to 2018-05-13

Østensjøvannet SE: 2018-05-13 to 2018-05-21

Østensjøvannet SE: 2018-05-21 to 2018-05-28

Østensjøvannet SE: 2018-05-28 to 2018-06-04

Østensjøvannet SE: 2018-06-04 to 2018-06-12

Østensjøvannet SE: 2018-06-12 to 2018-06-28

Figure F14. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

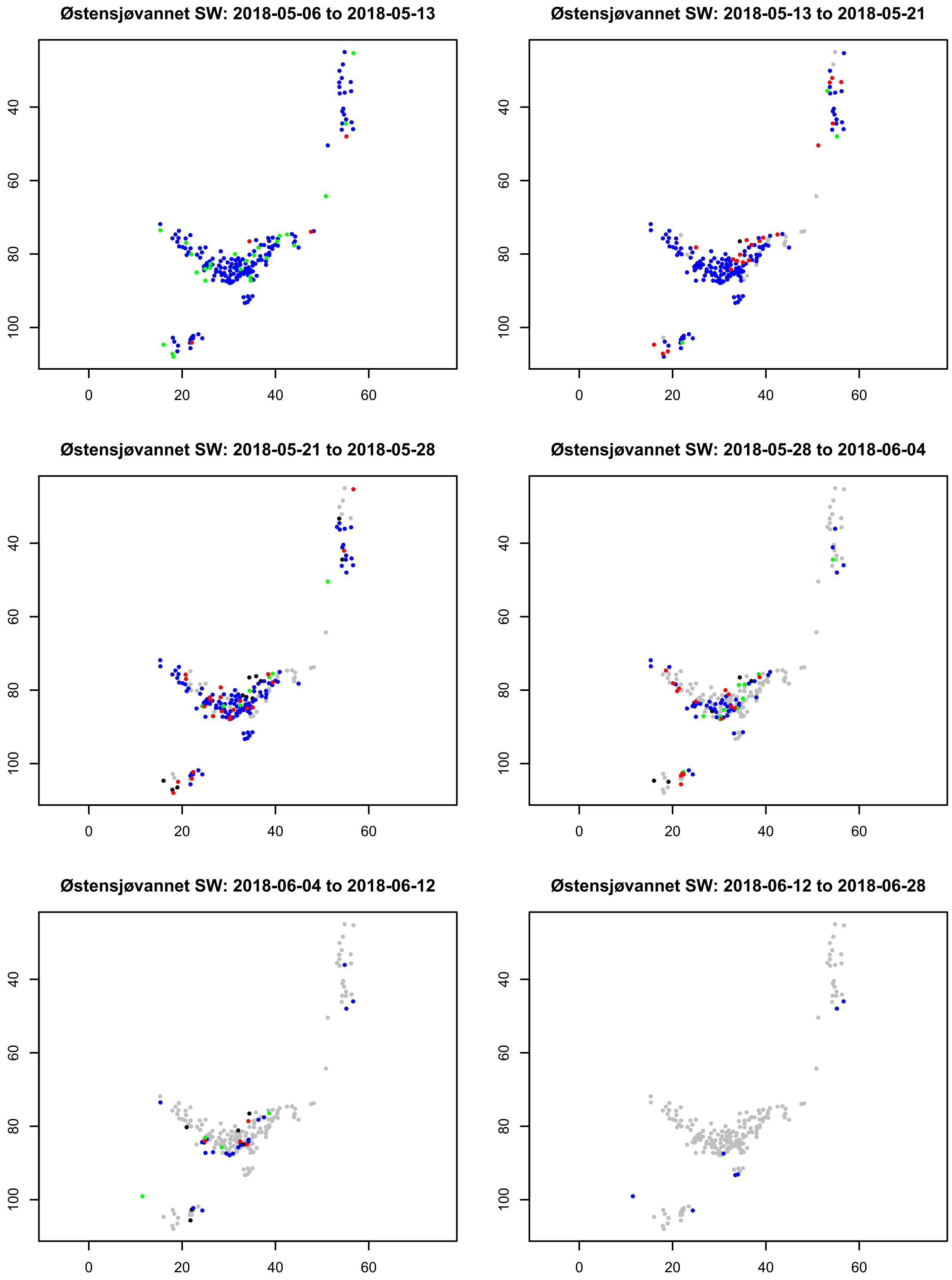


Figure F15. Green: nests settled in the date interval, blue: established nests that also was present last period, red: nests failed in the date interval, black: empty nest that have existed earlier, grey: nests with unknown status

Appendix G Additional survival analysis data

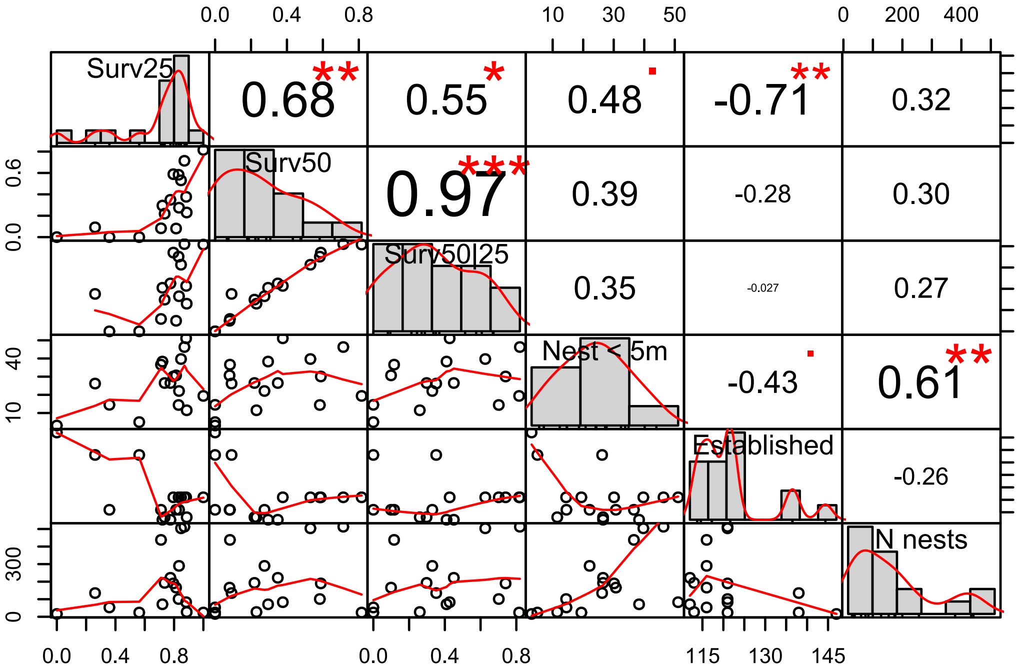


Figure G1. Correlation plot of data from Table 1. Similar to Figure 7, but with Østensjøvannet divided into its six sub-colonies.

Table G1. Table with survival estimates from Figure 8

Number of neighbours within 5 meters	***Number of nest attempts***	***Nest survival probability until day 25***	***Nest survival probability until day 50***	***Survival until 50 days, given survival 25 days***
0-4	78	0.51 (0.41-0.65)	0	0
5-9	173	0.72 (0.65-0.80)	0.28 (0.18-0.41)	0.39
10-19	517	0.73 (0.69-0.78)	0.18 (0.13-0.25)	0.25
20-49	1704	0.80 (0.78-0.82)	0.25 (0.22-0.28)	0.31
50+	578	0.81 (0.78-0.85)	0.14 (0.10-0.20)	0.17

Table G2. Table with survival estimates from Figure 9

Settlement date	***Number of nest attempts***	***Nest survival probability until day 25***	***Nest survival probability until day 50***	***Survival until 50 days, given survival 25 days***
Before 1.5	781	0.80 (0.77-0.83)	0.21 (0.17-0.25)	0.26
1.5 - 9.5	1702	0.86 (0.84-0.88)	0.28 (0.24-0.33)	0.33
10.5 - 19.5	320	0.76 (0.71-0.81)	NA	NA
20.5 - 29.5	146	0.21 (0.15-0.30)	NA	NA
After 29.5	101	0.30 (0.21-0.43)	NA	NA

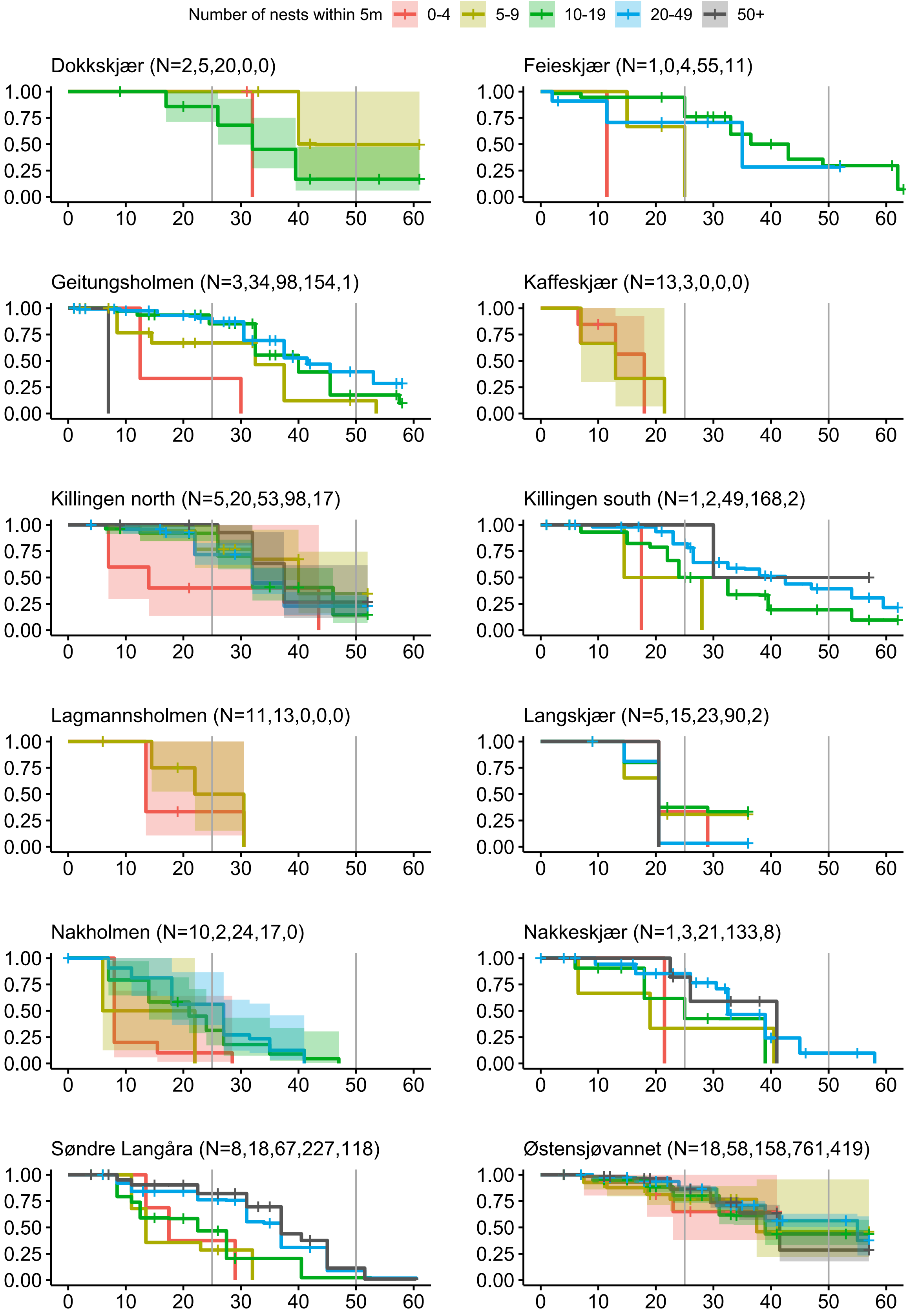


Figure G2. Survival plot based on data from one colony at the time. Divided into strata depending on how many neighbouring nests that were located within 5 meters. The number of nests for each stratum is shown in the individual plot titles.

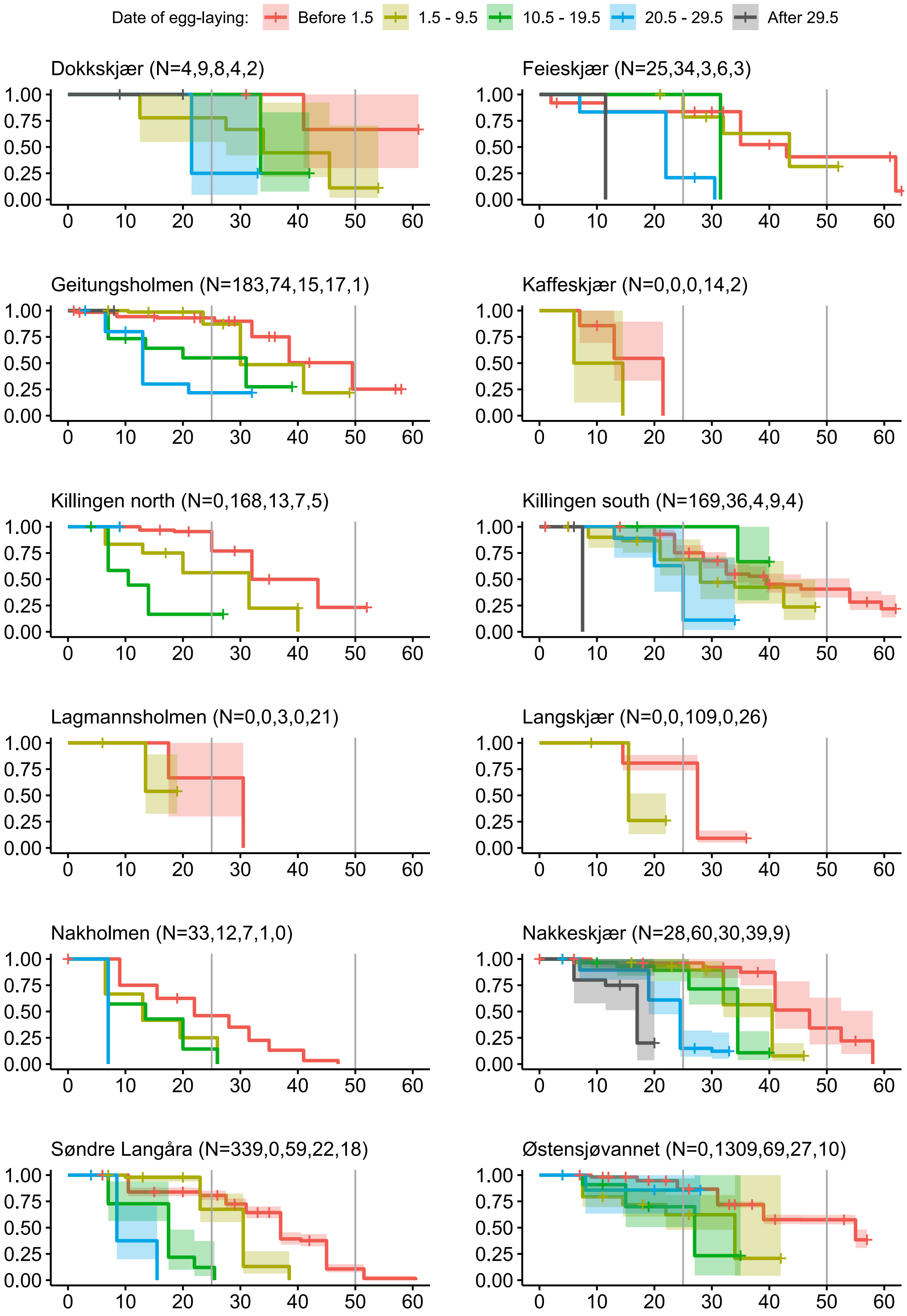


Figure G3. Survival plot based on data from one colony at the time. Divided into strata depending on when they settled their nests. The number of nests for each stratum is shown in the individual plot titles.