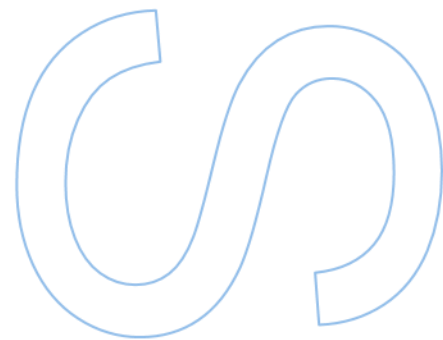
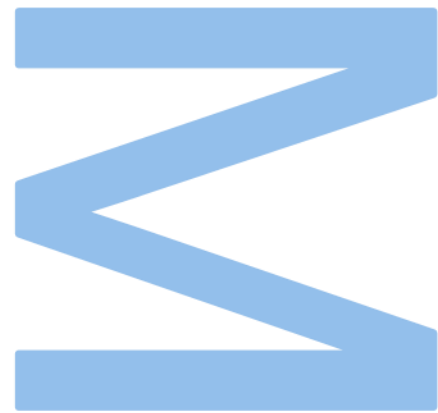




How does a catastrophic event influence demography and social associations in a colonial cooperative bird?

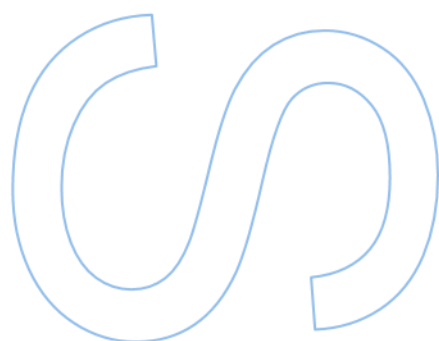
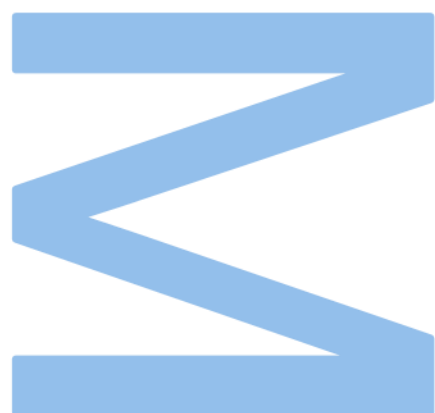


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Resumo

Fogos e outros distúrbios naturais estão a aumentar em frequência e intensidade devido às alterações climáticas. Estes eventos causam mortalidade súbita nas populações de animais, destruição de habitat e podem ter efeitos significativos na demografia e associações sociais. No entanto, estes efeitos estão mal documentados e raramente são quantificados, uma vez que são poucos os casos em que existem dados que precedem estes distúrbios, de forma a poder compará-los com o que acontece posteriormente.

Em setembro de 2021, um vasto fogo levou à destruição de 8 de 14 colónias de tecelão sociável *Philetaurus socius*. O tecelão sociável é uma ave cooperativa e estas colónias estavam a ser seguidas há mais de 10 anos, como parte de um estudo longitudinal de longo prazo sobre a evolução do comportamento de cooperação e dinâmica de populações. Dados detalhados sobre a demografia e estrutura social desta população estavam portanto a ser recolhidos desde antes do fogo. Aqui, eu descrevi e quantifiquei como o fogo afetou (i) parâmetros demográficos, (ii) o comportamento e (iii) as associações sociais.

(i) Esperava-se que as colónias que não arderam aumentassem o seu número de indivíduos devido à migração vinda das colónias que queimaram, o que foi confirmado pelos meus resultados, especialmente para as colónias mais próximas das que arderam. Em seguida, examinei se houve mudança na composição etária e na proporção dos sexos após o fogo, o que indicaria um enviesamento na mortalidade ou migração para fora da área de estudo, mas as diferenças não foram significativas.

(ii) Previu-se que a competição direta iria aumentar depois do fogo, uma vez que os recursos se tornaram mais escassos. Por isso, eu investiguei o número de interações agressivas entre os indivíduos, e observei um aumento acentuado após o fogo.

(iii) Por fim, esperava-se que os imigrantes e os indivíduos originalmente residentes nas colónias que sobreviveram ao fogo se associassem inicialmente com membros das suas colónias de origem, mas que progressivamente se comesçassem a associar a indivíduos de outras colónias (à medida que a familiaridade fosse aumentando). No entanto, este padrão não foi encontrado em todas as colónias.

No geral, os meus resultados mostram um aumento abrupto do tamanho das colónias, da migração e interações agressivas na maioria das colónias após o fogo. Além disso, a alteração na composição das colónias manteve-se a longo termo. Estes resultados

indicam que o fogo teve um efeito importante na dinâmica populacional e estrutura social desta população.

Palavras-chave: desastre natural, fogo, sociabilidade, dormitório comunitário, dispersão, tecelão sociável

Abstract

Fires and other natural disturbance are increasing in frequency and intensity under climate change. These events cause sudden mortality in animal populations and habitat destruction and are also expected to have profound effects on demography and social associations in wild animal populations. However, this is poorly documented and quantified as few studies have pre-disturbance data, which preclude comparisons with what happens afterwards.

In September of 2021, a vast fire led to the destruction of 8 out of 14 colonies of sociable weavers, *Philetairus socius*. These weavers are highly cooperative and were being studied for over 10 years, as part of a long-term longitudinal study on this species into the evolution of cooperation and population dynamics. Detailed data on the demography and social structure of this population was being collected prior to the fire and I described and quantified how the fire affected (i) demographic parameters, (ii) behaviour and (iii) social associations.

(i) I expected that colonies that did not burn would increase in size as a result of migration from burnt colonies. This was confirmed by my results, especially for the colonies that were closer to the ones that burned down. Then, I examined if there was a shift in age composition and sex ratio after the fire, which would indicate a bias in mortality or movement away from the study area, but the differences were not significant.

(ii) Direct competition was expected to increase after the fire as resources became scarce. I therefore investigated the number of the aggressive interactions between individuals at the colonies and found a steep increase after the fire.

(iii) Finally, I anticipated that immigrants and individuals originally residing at non-burnt colonies would initially associate with birds from their own colonies but would progressively start associating with others as the familiarity between these birds increased. However, this pattern was not found in all colonies.

Overall, my results showed a sudden increase in colony size, migration and aggressive interactions in most of the surviving colonies immediately after the fire. Furthermore, the change in the colonies composition was kept in the long-term. These results indicate that the fire had an important effect in this population's dynamics and social structure.

Keywords: natural disaster, wildfire, sociality, communal roosting, dispersal, sociable weaver

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List of Abbreviations

PIT	PASSIVE-INTEGRATED TRANSPONDER
DAF	DAYS AFTER THE FIRE
ID	IDENTIFICATION
PERS. OBS.	PERSONAL OBSERVATIONS
IN PREP.	IN PREPARATION

1. Introduction

The frequency and intensity of climate-related disasters such as wildfires, floods and droughts are increasing due to climate change (Schulz, 2022; Jolly et al., 2015). Wildfires can directly impact animal populations by causing mortality and habitat destruction (Mestre et al., 2013; Quintero & Mathur, 2011), but can also have profound indirect effects, for example, on demography and social associations (Amorim et al., 2022).

Habitat destruction can cause animals to flee and converge in nearby refuges or suitable areas, leading to increased population densities or overcrowding, especially in highly mobile species that rely on specific habitats or resources that are scarce in the surrounding landscape. This was the case for European free-tailed bats *Tadarida teniotis*, that roost in caves, crevices or trees along river valleys and thus have limited habitat available. The loss of habitat for this species due to flooding by a hydroelectric dam resulted in drastic increases in population size at nearby roosts (Amorim et al., 2022). Population increases at refuges after a sudden habitat loss have also been described in other groups, such as frugivorous and nectarivores birds (Robinson et al., 2013; Wunderle & Wiley, 1996; Wiley & Wunderle, 1993). A sudden influx of individuals at refuges can increase direct competition for scarce resources, thus increasing aggressive interactions, causing displacements and increased movements among refuges (Santos et al., 2008; Amorim et al., 2022). Crowding can also lead to density-dependent effects on survival and reproduction (Eberhardt, 2002), as already observed in bats species (Amorim et al., 2015; Rhodes, 2007). However, the initial density increase at the refuges is temporary and usually followed by a reduction in subsequent times (Debinski & Holt, 2000; Stouffer & Bierregaard, 1995; Darveau et al., 1995).

The forced movement from destroyed areas and influx of new individuals to refuges is also likely to alter the population's social structure in various ways (Kerth et al., 2002; Silvis et al., 2016). For example, it was seen that rhesus macaques (*Macaca mulatta*) widened their social networks and changed their affiliative behaviour after a hurricane (Testard et al., 2021), indicating that social factors can play an important role in how individuals cope with these extreme events. In a society, the bonds between the individuals can vary from weak to strong and can be stable or transient. Having strong and stable social associations has been found to be associated with several types of benefits for individuals, such as enhanced offspring survival, longevity and enhanced immune function (Silk, 2014). This means that disruption of social groups can lead to negative effects on fitness and individual condition (for primates: Silk et al., 2009; dolphins: Frère et al., 2010; Stanton & Mann, 2012; bats: Carter & Wilkinson, 2013; equids: Cameron et al., 2009). Furthermore, the strength and stability of social

relationships can help mitigate the negative effects of exposure to adversity. For instance, it was found that in chacma baboons (*Papio ursinus*), females with a network of strong and stable bonds showed attenuated physiological responses (less increase in glucocorticoid levels) during periods of social instability when compared to females with weaker bonds (Wittig et al., 2008).

The disruption of social relationships is also expected to have negative effects at the group, and possibly population level. For instance, changes in group membership have been shown to disturb cooperative activities such as allo-parental care (Gero et al., 2009; Ebensperger et al., 2016), group hunting (Gazda et al., 2005; Gilby et al., 2015) and communal territory defence (Port et al., 2011), which can in turn affect reproductive output, individual condition and survival.

The consequences of natural disturbances can therefore have repercussions at different scales. These are still poorly described and quantified, since these events are unpredictable in occurrence, and therefore the consequences are often undocumented. Given that the frequency of natural disasters events is increasing, it is crucial that we understand the effects of these events on animal populations and how individuals might adjust to these sudden changes. Specifically, documenting the population level changes - movements, the temporal dynamics of overcrowding and possible changes in age structure and sex ratio – provides an understanding of how populations are affected and how they might recover. Studying social associations, can help us to understand how social structure is affected, whether some species or types of social structure are more resilient than others, and whether individuals can adopt strategies that help them coping with these events. This in turn can help us identify more vulnerable systems and possibly guide any management interventions (Amorim et al., 2022; Testard et al., 2021; Ensbey et al., 2023).

In this study, I investigated how a major habitat disturbance event influenced demography, behaviour and changes in social structure of the surviving population before and after a major fire. I studied a colonial, cooperatively breeding bird, the sociable weaver, *Philetairus socius*. These weavers live in very large nest structures (hereafter 'colonies') that are built communally, and where they reproduce and roost all year-round. These structures take time to build (ca. a week to produce a single, unfinished chamber (Collias & Collias, 2008; Covas & Doutrelant pers. obs.)) and are usually occupied for several decades (e.g. before the fire nearly half of the colonies in the study area were known for nearly 30 years and there are unpublished accounts of colonies that have been known for nearly a century). Hence, colonies represent an important resource for this species.

A long-term study at the Benfontein Nature Reserve, in South Africa, has been collecting detailed data on this population's demography and reproductive behaviour since 2010, and on social associations since 2017.

On the 27th of September 2021, an intense fire completely burned all the grass and several trees in the study area, burning down entirely 13 out of the 23 sociable weaver colonies known to exist in the area (for more information see Lee et al., 2023). Long-term data on demography and social associations were available for 14 of these colonies, eight of which burned down. The changes that occurred immediately after the fire were recorded at the six surviving colonies that had been studied previously. The aim of my masters' thesis was to describe and quantify how the fire and the associated destruction of eight colonies affected demographic parameters, behaviour and social associations.

I first examined changes in colony size expecting that the size of the surviving colonies would increase suddenly after the fire, due to the fleeing individuals from destroyed colonies. Colony size was then expected to decrease and stabilise in the following weeks, as birds either settled or moved to other areas. Second, I examined changes in sex and age ratio at the colonies to understand if there was a bias in the birds that went missing (either because they died or moved outside the study area). It has been shown previously that male sociable weavers are dominant over females in Rat et al. (2015), and adults over young (Silva et al., in prep.). Hence, considering that crowded colonies should experience increased competition and aggression among the birds, I expected that older birds and/or males would be more successful at staying at their colony. So, I investigated the sex ratio and age structure of different categories of birds present at the colonies after the fire (birds from unburn colonies that stayed in their colony, birds from unburn colonies that had to move and birds from burned colonies). Third, I investigated whether birds moved in groups or were scattered among the surviving colonies. For this, I quantified the number of immigrants that moved into each colony before and after the fire considering their colony of origin.

Fourth, I examined aggressive behaviour at the colonies at roosting. Under normal conditions, sociable weavers always roost in one of the colony chambers and not out in the open (Maclean, 1973b; Covas pers. obs.). Because a sudden increase in colony size should lead to increased competition for roosting chambers, I examined whether there were changes in the number of aggressive interactions at roosting by comparing data obtained before and after the fire. I predicted that the levels of aggressive interactions would increase after the fire, due to increased competition for space.

Finally, I examined social associations between immigrant and resident birds. I expected that the immigrants and the birds originally residing at the surviving colonies would associate with birds from their own colony initially but would start associating with others as time passed. For this, I used a social network analysis.

2. Methods

2.1. Study Species and Site

Sociable weavers are colonial, cooperative breeding passerines endemic to the semi-arid savannahs of the Kalahari region of southern Africa. They live in large, communally built, nest structures (i.e., colonies) housing from ca. 5 to over 500 individuals (Maclean, 1973a). The most common support used for these structures is the camelthorn tree *Vachellia erioloba* and the material is *Stipagrostis* and other grasses (Maclean, 1973b).

Sociable weavers breeding periods are variable, but usually occur during the austral summer from September to April, which coincides with the rainy season. The rains influence seed germination and insect activity, the latter being the main sources of food for adults and nestling sociable weavers (Maclean, 1973c; Covas et al., 2008). Rainfall in this region is usually low and unpredictable and sociable weavers normally lay several clutches during a single breeding season, while the conditions are suitable (Covas et al., 2008).

Pairs can breed alone or can be assisted by “helpers”, which are sexually mature individuals that forgo reproduction and assist raising the offspring of other birds in the colony. Helpers contribute feeding the nestlings, but also with brooding, nest sanitation and nest building (Ferreira, 2015). Helpers are usually offspring of one or both breeders from previous years, although less often there can be distant relatives or seemingly unrelated birds helping (Covas et al., 2006; Fortuna et al., 2021). Both female and males can be helpers (Doutrelant et al., 2004).

The sociable weaver colonies contain several independent nest chambers wherein individuals breed and roost throughout the year (Fig. 1). Pairs or groups (of pairs and their helpers) can occupy one to three chambers, and an individual may roost in any chamber occupied by its group. The roosting group size varies between 1 and 8 (Paquet et al., 2016) and roosting group composition is associated with breeding group composition (Pacheco, 2021).



Figure 1 – Nest structure with visible nest chamber entrances (Photo by Franck Theron).

This study is part of a long-term research project conducted at Benfontein Nature Reserve in the Northern Cape Province. Capture-mark-recapture data goes back to 1993 and detailed data on demography, reproductive behaviour and cooperative breeding has been collected since 2010. Data on social associations during foraging has been collected since 2017 and on roosting associations since 2018. 14 colonies were being monitored before the fire of 27th September 2021 and each colony is identified with a unique number (mentioned hereafter as colony ID).

2.2. Data Collection

Annual colony captures and Individual Identification

Every year, as part of the sociable weaver long-term study, all the birds in the study colonies are captured using mist nets (Fig. 2), usually before the breeding season (i.e. from late August to early September). Before the fire, this meant a total of ca. 400-500 individuals. During these captures, all new individuals are ringed with a unique numerical metal ring and unique colour combination (with three coloured rings). This colour combination allows individual identification in video recordings and through direct observations. The birds are also measured (tarsus, intertarsal joint and wing length), weighed, and a blood sample is collected for DNA analyses (i.e., sexing and relatedness). In six of the study colonies, one of the colour rings is a passive-integrated transponder (PIT-tag) that allows for automatic detection when feeding at an artificial station. The captures also provide information on colony size, allow to mark new immigrants and to track dispersal between colonies. Note that in 2020 the annual captures did not take place due to COVID19 restrictions.



Figure 2 – Mist net used for the captures.

Counts of colony size after the fire

Immediately after the fire, an effort took place at the six colonies that survived in the study area to record the changes in colony size, record the birds that were still alive in the population, and to document the influx of immigrants into the surviving colonies, and possible changes in behaviour (Fig. 3 and Fig. 4).



Figure 3 - Burned vegetation surrounding one of the sociable weaver colonies (colony 8) after the fire.

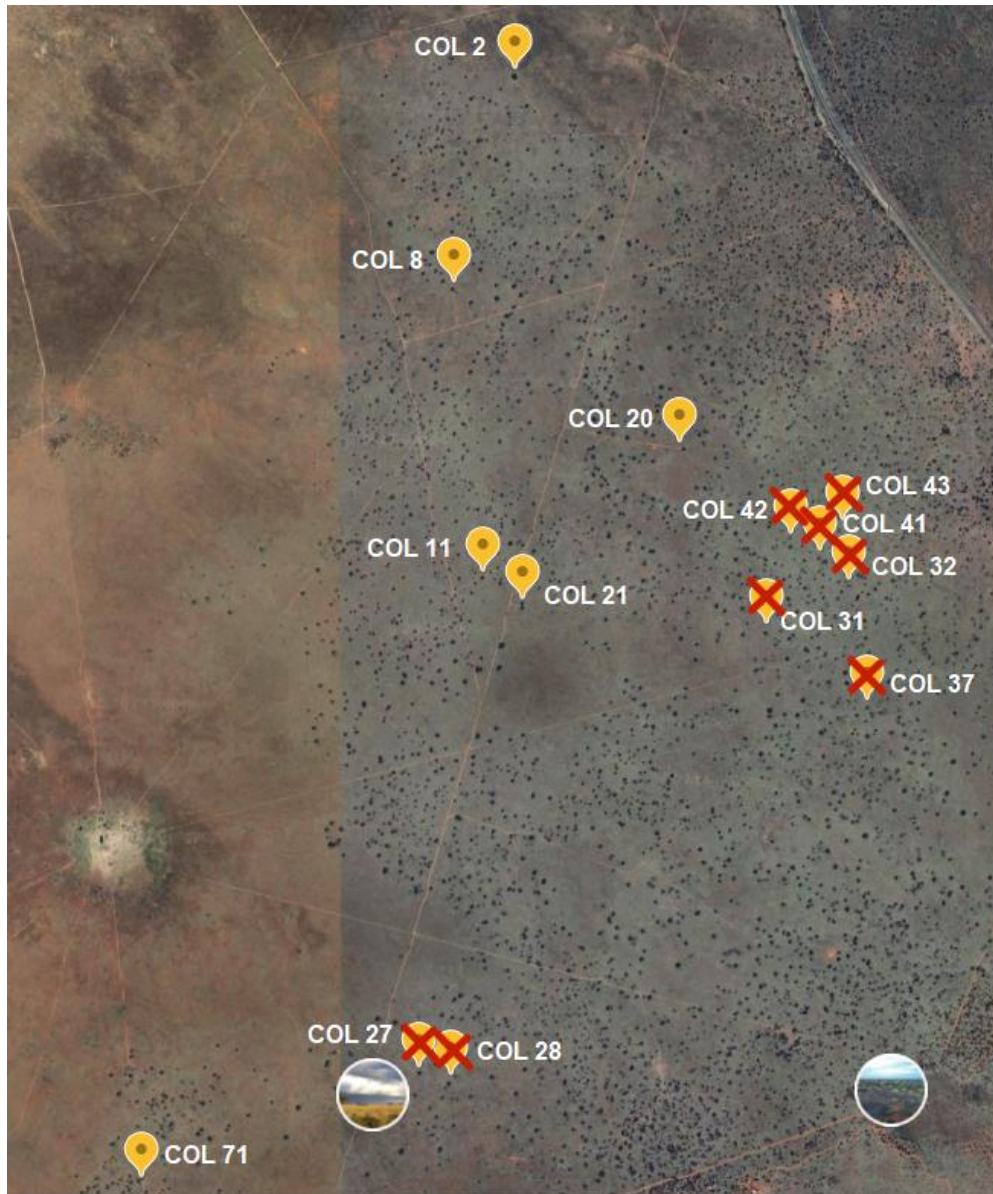


Figure 4 - Map of the study site. The yellow marks represent the location of each colony. The red crosses indicate the colonies that burned during the fire.

To obtain information of colony size after the fire, direct counts and video recording were conducted at the six surviving colonies. Direct counts were conducted by observers that arrived at the colonies before sunrise and counted the number of birds leaving the colony in the morning. In addition, video recordings were obtained by placing cameras 20 metres away from the colony to have a view of the entire tree where the colony was located, allowing to count the birds seen leaving. Both methods used (direct counts and video counts) collected very similar values and, for each count, I decided to keep only the higher value out of the two.

Table 1 summarizes the colonies observed on each day and the type of count that was made. Each colony was counted three times in the month of October of 2021.

Table 1 - Types of counts made for the colonies after the fire per date. Direct count is based on the observers and camera is based on the video footage.

Date	Colony ID	Count type
01/10/2021	2	direct+camera
	8	direct
	20	direct
02/10/2021	11	direct+camera
	21	direct
	71	camera
14/10/2021	2	direct
	8	direct+camera
	20	direct+camera
18/10/2021	11	direct
	21	direct
	71	direct+camera
25/10/2021	2	direct+camera
	8	direct+camera
	20	direct+camera
31/10/2021	11	direct
	21	direct
	71	direct+camera

Roosting Data

Roosting Videos

a) Roosting Videos Recording Protocol

The identities of the individuals that compose the different roosting groups have been recorded at several colonies during the non-breeding season as part of a broader study into the social structure of sociable weavers. The roosting recordings usually take place from March until August or September. After the fire, additional recordings were collected in October/November (see below).

Before each roosting recording season, we do a full nest check at all colonies using LED lighted mirror to inspect each chamber to confirm that the breeding activity has ceased. All the chambers in a colony are marked with a numbered tag (Fig. 5). We can identify abandoned chambers because they lose their usual shape or have evidence of being used by other bird species (e.g., droppings), most commonly, the Red-headed finch (*Amadina erythrocephala*). Chambers that have signs of being abandoned are not recorded.



Figure 5 - Vehicle with a canopy platform used to access the colony for nest checks.

The roosting protocol is the following (in September/October 2022 the fieldwork was conducted by myself).

Cameras are placed under the nests using tripods, each focusing on the entrance of a chamber (necessary to get videos with high quality for colour ring identification) (Fig. 6 and Fig. 7). Sociable weavers usually leave the nest after sunrise and can come back to the colony multiple times during the day to feed nestlings (if reproducing), to build/maintain the nest structure, to rest or to seek shelter from predators. Roosting can start as early as one hour

before sunset, so the cameras are set ca. 1h30 to 2h before sunset, to ensure they are ready when the sociable weavers start returning to their colonies to roost. For each video, we record the date, the chamber number and the colony. The cameras are collected after dark to avoid disturbing the weavers in their chambers.



Figure 6 - Roosting recording set-up. On the left, near the tree, is one of the tents used for roosting observations.

b) Video Analysis

The first step of the video analyses is marking the videos using an artificial intelligence program developed by Liliana R. Silva that creates a list of times for birds entering or leaving the nest chamber. This makes it easier to track every bird movement without having to watch the full video, reducing substantially the amount of time required for analysis.

After all the videos are marked, the colour combination of each bird is noted on a excel file, indicating in which chamber(s) it was seen at and the time(s) the bird entered or exited the chamber (also the date and colony). Other possible relevant interactions such as aggressions (here defined as pecking or actively preventing an individual from entering the nest chamber) are also noted. When the full colour identification was not possible, we attributed an unknown

identification. This happens when some of the colour rings are not seen on the videos or the video was not enough quality to see it clearly, especially as the sociable weavers are active until late and the visual identification becomes constrained by the light availability. Missing data can also arise from video failures.



Figure 7 - Example of a full colour combination of rings (total 4 rings, 3 colour and one metal) (Photo by Liliانا Silva).

After the videos are analysed, the colour information is crossed with the sociable weaver project long-term database' in order to attribute the unique metal ring number. This allows us to have access to important information for each individual, such as sex, age and colony capture history.

c) **Analysed Roosting Videos**

In this project I used videos that were collected in previous seasons and some had already been analysed (the rest I analysed myself; ca. 500 videos). For ease of reference, these were divided into six time-related periods (Table 2; Post-fire and 2022 have a limited sample size of analysed recordings which will limit some of my conclusions here). Note that larger colonies (more than 25 active chambers) were recorded usually over consecutive days, in order to film all the chambers (since there were only 25-31 cameras available).

Table 2 - Overview of the six periods into which the video data was divided, and the colonies recorded for each category. The recording days for each colony corresponds to the first and last day when a recording was made for that category. The recorded nests are the ones that were deemed active during the full nest checks. The average days correspond to the average number of days recorded and analysed for that colony during that period.

Period	Colony ID	Recording days	Number of recorded nests	Average days per nest
2018	20	03-12-2018 – 12-12-2018	21	4.667
2020	20	17-11-2020 – 05-12-2020	21	9.810
	41	24-11-2020 – 13-12-2020	21	9.904
2021	11	28-03-2021 – 03-04-2021	34	2.353
	41	23-03-2021 – 27-03-2021	21	4.714
Pre-fire	11	23-08-2021 – 20-09-2021	26	3.154
	20	11-09-2021 – 13-09-2021	8	3.000
	27	21-09-2021 – 23-09-2021	22	2.591
	41	12-09-2021 – 14-09-2021	14	2.714
	43	14-09-2021 – 17-09-2021	28	2.893
Post-fire	2	03-10-2021 – 02-11-2021	19	2.895
	8	09-10-2021 – 20-10-2021	55	1.891
	11	04-10-2021 – 03-11-2021	37	3.273
	20	02-10-2021 – 11-11-2021	22	2.909
	21	03-10-2021 – 02-11-2021	9	3.000
	71	06-10-2021 – 19-10-2021	49	2.061
2022	11	13-09-2022 – 03-10-2022	30	2.567

Roosting Observations

From October 2021 to November 2021, immediately after the fire, observations in the field were conducted before roosting with the aim of assessing whether there was an increase in aggressive behaviours, (which was expected to arise through increased competition for roosting chambers) and whether there were birds forced to roost outside. Observations were conducted by a team of 1-2 people from a tent placed 2-3 m from the colony tree. These observations were conducted at only three of the colonies monitored and started ca. one hour before sunset.

We recorded the 1) total number of chases around the nest, 2) total number of chasings from the chambers and 3) number of individuals that seemed to roost outside. Notes about other

behaviours (attacks from other species of birds, number of individuals arriving in the first flock) or other important information (other bird species using the weavers' chambers, colony, date, sunset time and weather) were also collected, but not used in the present study. Colonies 11 and 71 were observed for a total of 5 days and colony 20 for 2 days. The observations were conducted between 6 to 14 days after the fire and the days of the observations were chosen opportunistically.

From September 2022 to October 2022, I repeated similar observations at the same colonies, following the same protocol. The aim of these observations was to compare the number of aggressions immediately post-fire with what might be found under normal conditions in the same colonies at the same time of the year. Colony 11 was observed for 7 days, colony 71 for 5 days and colony 20 for 3 days.

The aggressive/displacement interactions were defined as follows in table 3. For simplicity, hereafter I will refer to these interactions as aggressive interactions but note that they can also just indicate a displacement of an individual by another (instead of physical aggression).

Table 3 – Different aggressive interactions that happen in the colony and specifically at the chambers during roosting observations. If any of these aggressive interactions are seen, they count as an aggressive interaction in my study.

Aggressive/displacement interaction around the colony	Aggressive/displacement interaction around the chambers
• Individual A chased actively individual B around the branches, ground, or tree. • Individual A landed close to individual B and B moved away, without individual A actively chasing him.	• Individual B tried to enter a chamber and individual A went outside of this chamber and collided with individual B. • Individual B entered chamber X and individual A went outside a nearby chamber and chased individual B from chamber X. • Individual B was pushed out of a chamber by individual A.

2.3. Statistical analyses

All the statistical analyses that follow were done using R v 4.2.3 (R Core Team, 2021).

Demographic changes

a) Changes in colonies size

I expected that the birds from burned colonies would seek refuge in the six surviving colonies, which could lead to a drastic increase in the number of birds present at the surviving colonies.

To better characterise the changes in colony size, I tested if there was a difference between the size of the colonies at the 2021 captures (ca. one month before the fire) and the first count made after the fire (4 or 5 days after the fire depending on the colony). For this, I used a paired samples Wilcoxon test (function 'wilcox.test' included in the "stats"), because the assumptions for a paired T-test were not met (See the data used here in Table 4). Then, to quantify the biological relevance of the change, I calculated the Cohen's D (function 'cohens_d' included in the "rstatix") to estimate the effect size of the possible change.

Moreover, I conducted a repeated-measures ANOVA test for the counts made after the fire to test if there was a difference between any of the counts made (17 or 21 days after the fire for the second count and 28 or 34 days after the fire for the third count) (the assumptions for this parametric test were met; function 'anova_test' included in "rstatix").

In previous years to the fire, counts similar to the ones done after the fire were conducted to estimate the colony size of some colonies for other studies undertake. During this experiment, it was seen that the number of birds captured during annual captures was quite similar to number obtained during counts, indicating that both methods are quite accurate and comparable.

b) Changes in sex ratios and age composition after the fire

Since one sex might be more successful at remaining at the surviving colonies (because it is more dominant or the other has disproportionately died or migrated (displaced or not)), I tested for a sex difference in sex ratios between the capture before the fire (2021) and the videos post-fire. Here I analysed the sex ratios as the proportion of males out of the total number of individuals sexed. I conducted a two-sample test for equality of proportions with continuity correction (function 'prop.test' included in "stats") for the sex ratio of all six surviving colonies together (See Table 5).

Similarly, to investigate whether older birds might be more successful in staying at the surviving colonies, I decided to investigate if there was a shift in age composition after the fire. Since I was interested in seeing if the age composition changed because some individuals went missing (died or migrated) and not because individuals became older, I calculated the age that each individual captured/seen would have on the 3rd of September of 2022, so that the same individuals would have the same age in both time periods.

The exact age is known for birds ringed in the nest as chicks. After they fledge, sociable weavers can be aged with ca. 1 month accuracy until they are ca. four months old and obtain a fully developed patch, after which they cannot be accurately aged (Covas pers. obs.). This means that I only attributed an age to birds that were captured for the first time when younger than 4 months. By doing so, I lost 31 females and 11 males before the fire (out of a total of 251 individuals) and 39 females and 9 males after the fire (out of a total of 307 individuals). The ones I lost are mostly females because they are the dispersal sex and immigrate to our study area usually when they are already adults.

Then, to explore if there was a shift in age composition from before to after the fire, and if the two sexes have different age compositions, I conducted a generalized linear mixed-effects model (GLMM) with a Poisson family using the function 'glmer' included in the "lmea4" package. The dependent variable was the age of the individuals, the independent variables were "when" (before the fire using data from captures 2021 or after the fire using the post-fire videos) and "sex". I included the interaction between "sex" and "when" because the age composition may vary differently before and after the fire for males and females. As random factors I added the "ID of the last colony where the bird was seen before the fire" and the "ID of the colony where the bird was seen after the fire" (the description on how I attributed these variables to each individual comes in the next topic).

To determine if there were age differences between (i) the residents that stayed in their colony, (ii) residents that moved and (iii) birds from burned colonies, I conducted a linear mixed-effects model (GLMM) with a Poisson family. The dependent variable was the age of the birds, the independent variables were "type" (the three mentioned above) and "sex". I included the interaction between "sex" and "type" because the age composition may differ with types for males and females. As random factors I added the "ID of the last colony where the bird was seen at before the fire" and the "ID of the colony where the bird was seen after the fire".

For both GLMMs, I checked for overdispersion and extreme outliers and visually inspected the QQplots.

c) **Migration between colonies**

After the fire, individuals from burned colonies had to move to other colonies for refuge. To understand how the number and origin of migrants varied after the fire, I quantified the birds present in the videos' categories pre-fire and post-fire, and in the captures of 2021 and 2022. For colonies where there were no recordings before the fire, the only data for the period preceding the fire is the capture of 2021. One colony also includes information from video recordings obtained in 2022.

I saw that the differences between the individuals seen in the captures and in the videos around the same time is very low (the differences between captures of 2021 and pre-fire videos and between capture 2022 and videos of 2022 for a better understanding). This indicates that the videos depict a similar number of individuals to captures and therefore, the two data types are comparable.

All the birds seen before the fire (on the videos pre-fire or at the captures of 2021) were attributed the last colony where they were captured before the recording or the capture of 2021.

All birds seen after the fire (on the videos post-fire and capture of 2022) were attributed the ID of the last colony they were captured at before the date of the fire, because I am interested in where the birds of the burned colonies went for refuge and if any of the residents of the surviving colonies travelled to a different one.

If the last time a bird was captured or filmed was before 2019, I corrected their last colony to "Unknown", since it is a large time gap and the bird might have moved across other colonies during that time. Additionally, if a bird from a colony that I knew to have disappeared was seen or captured for the first time after the colony collapsed, I also attributed it "Unknown colony", because I cannot be sure of the bird's origin. Furthermore, if a bird was captured for the first, I also attributed it "Unknown", since I do not know its previous history.

i) Movement network - To obtain an overall view of the movements that occurred between the colonies after the fire, I used data obtained from the videos collected post-fire. I computed a movement network, in each the nodes are the colonies, the edges represent the movements of the immigrants (please note that one individual might be represented in more than one edge if it changed colonies several times), and the thickness of the lines indicates the number of birds that undertook that movement. I computed the network using the function 'graph_from_data_frame' from the package "igraph".

ii) Immigration bar plots - Additionally, I complemented this information with a bar plot per colony representing the immigrants and residents present at each time period.

iii) Factors influencing the group size of immigrants - Finally, to explore which factors might be related to the number of birds migrating together, I conducted a generalized linear mixed-effects model (GLMM) using the function 'glmer' included in the "lmea4" package. The dependent variable was the number of birds from the same colony present in another colony ("group" size of the immigrants from each colony). Since this is a count variable, I used a GLMM with a Poisson family. The independent variables were "distance between colonies" and the "size of the original colony". As random factor I added the ID of the original colony and the ID of the colony where the birds migrated to. For this GLMM, I also added an observation level random variable to correct the overdispersion seen in the model. Additionally, I ran this model with an extra independent variable "size of the destination colony", however this variable was non-significant ($P > 0.050$) and therefore this model was not presented. This variable was used as a proxy of how hard it might be for the immigrants to remain in the colony, as there will be more resident birds to fight the "intruders" off. Ideally, I wanted to use the size available, but it is not possible at the moment to do so.

Behavioural changes

To explore changes in the aggressive behaviour of sociable weavers following the fire, I used two data sets: (i) the direct observations done during roosting immediately after the fire and in 2022 and (ii) video recordings from pre-fire and post-fire, although for pre-fire there is only videos for two of the six colonies (see table 2). The videos were analysed by five different people and to reduce the possible differences arising due to an observer effect, I divided the number of aggressive interactions seen into 4 categories. The categories chosen were low (less than 10 aggressive interactions), medium (from 10 to 49 aggressive interactions), high (from 50 to 99 aggressive interactions) and very high (100 aggressive interactions or more). These categories were defined following the distribution of aggressions (reference plot from supplementary material). Afterwards, to visualize how the aggressive interactions changed, I used each data set to create a line graph.

Changes in social associations

I expected that immigrants and residents would not roost together immediately after the fire, but would mix more with time, as their familiarity increased. I tested this using roosting associations seen in the post-fire videos. These analyses aimed to assess if the network assortment (a measurement used to indicate how mixed the different colonies are in terms of roosting groups) changed with time after the fire.

I constructed social networks for each colony on different time periods after the fire (c.a. one week, two weeks and one month later (only available for three colonies)), based on a time-overlap criteria (the cumulative overlap time that two individuals stayed together inside the same nest) to create the edges of the network. Using the video data, I converted the time of all entrances and exits for all successful individual identifications into decimal minutes using the R package “chron”. Then, I used a binary approach in which a time threshold defines if a connection between two individuals existed or not. The time threshold is a parameter that allows to turn the overlap time values of the matrix into 1 or 0, creating a binary network (Farine & Whitehead, 2015). If the overlap time is higher than the time threshold, the value is turned into 1, meaning that a connection exists between the two individuals. If the overlap time is lower than the threshold, the value is turned into 0 meaning that there is no connection between the two individuals. I used 0.5 minutes time as the time threshold, as it was tested previously by Pacheco (2021) and this was the value with higher correlation between the roosting networks observed in different days (for more information see Pacheco, 2021).

After the matrices were created, I plotted the networks using the function ‘graph_from_adjacency_matrix’ from the “igraph” package. The nodes represent the individuals and the edges the associations among them. I then attributed to each individual in the networks the colony they were last seen at before the fire.

Finally, I calculated the assortment of the roosting groups formed at the different times mentioned before, using the function ‘assortment.discrete’ from the “assortnet” package. Assortment is the tendency for nodes that share an attribute (in this case the last colony) to be connected and the assortment coefficient can be used to examine whether discrete node types are more or less connected to each other. The assortment coefficient varies from -1 to 1. An assortment value of -1 indicates that the individuals don’t assort by the last colony they were captured at (different colonies are mixed), 0 means there is no trend and 1 indicates that the individuals are assorting exclusively by their attributed colony (different colonies are not mixing).

I performed permutations of the node-labels in the network. Node-label permutations involve shuffling the node type (in this case the last colony the birds were captured at) randomly across all nodes in a network, while keeping the edges the same. This ensures that the inherent structural pattern of the network remains the same, but the node attributes are randomized, allowing us to use it as a null model for the assortativity. I performed 10,000 data stream permutations with no replacement, so that each individual would only appear once per permutation. I tested the significance of the observed values of assortativity by comparing them to the assortativity values expected by chance that were generated through the permutations.

Since the assortment is very dependent on having individuals from different groups to calculate the proportions of the connections and I am interested in understanding the relations between the residents and all the immigrants from different origins, I decided to remove from this analysis the colonies with very few immigrants (colony 2 and colony 71).

3. Results

Demographic changes

a) Changes in colony size

Overall, the number of birds in the six surviving colonies increased 63% (Table 4; Fig. 8). When considered individually, four colonies increased between the captures pre-fire and the first counts made 4-5 days post-fire (colony 8, 11, 20 and 21; increased respectively 34%, 125%, 346% and 458%; See Table 4) while two decreased (colony 2 and 71; decreased respectively 32% and 44%; See Table 4). This increase was not significant statistically (Wilcoxon signed ranked exact test, $P = 0.156$). However, I found indication that this effect was biologically relevant, since the effect size of the change was of large magnitude (Cohen's $d = 0.811$),

I also found no significant statistical difference in the colony size between the different counts that were made (total of three counts per colony) ($F_{(2,10)} = 3.650$; $P = 0.065$). However, the total number of birds between the first count and the second count decreased by 25% while between the second and third count the decrease was only of 2% (See Table 4).

Table 4 - Overview of the colony size for each capture and the counts made after the fire. The column colony ID indicates the six surviving colonies and the last row gives the totals for the six colonies combined. DAF is an abbreviation for 'days after the fire'.

COLONY ID	2018	2019	2021	4 DAF	5 DAF	17 DAF	21 DAF	28 DAF	34 DAF	2022
2	30	25	44	30	-	34	-	41	-	31
8	81	91	122	164	-	130	-	122	-	86
11	48	45	56	-	126	-	75	-	78	53
20	37	26	13	58	-	51	-	40	-	37
21	9	11	12	-	67	-	34	-	26	30
71	66	59	41	-	23	-	26	-	36	40
ALL	271	257	288	468		350		343		277

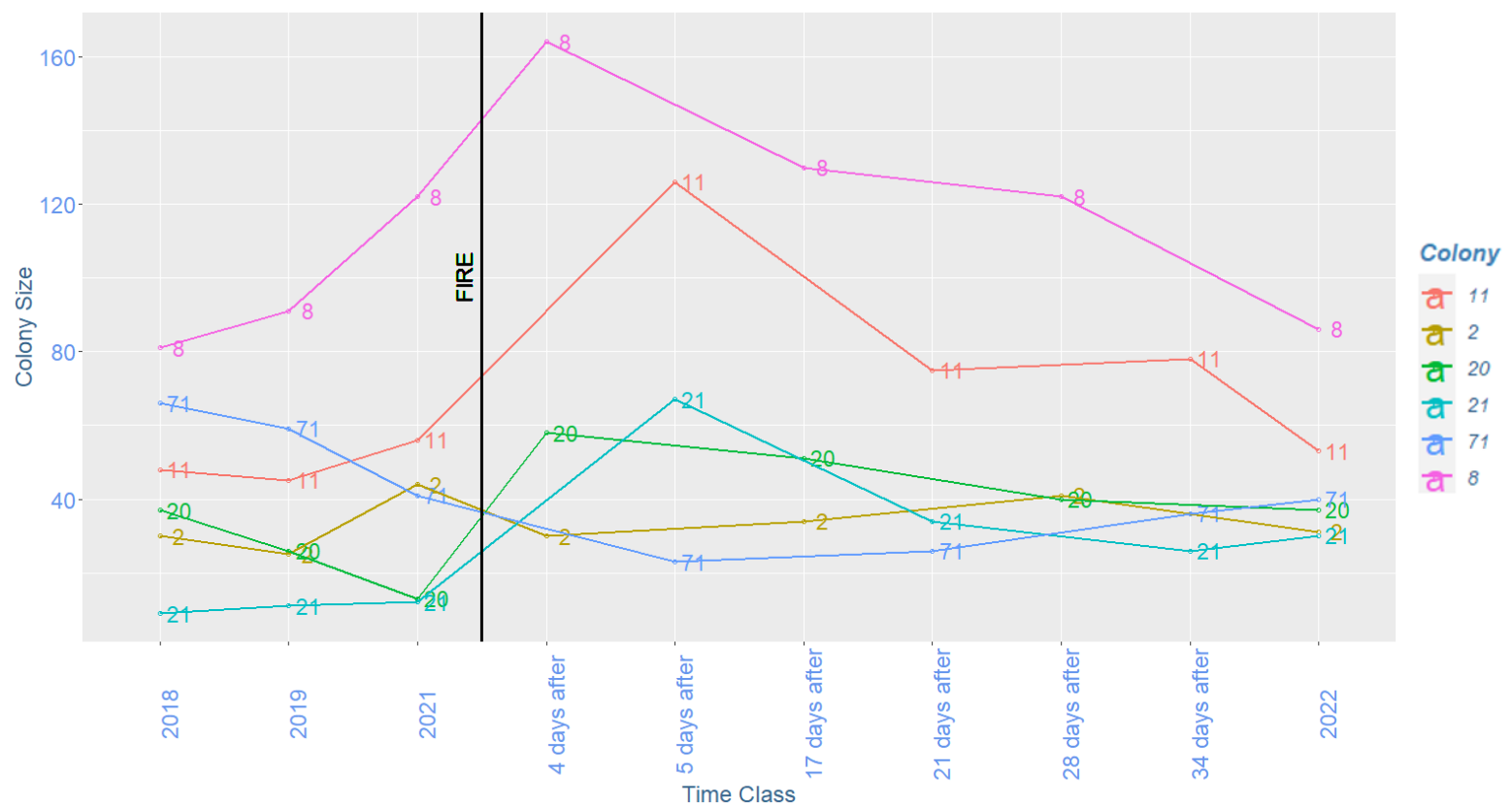


Figure 8 - Line graph representing the colony size (y) in each time class (x). Each different coloured line represents a different colony with the ID number represented in the legend "Colony" on the side and above the points each line connects. Please note that each unit on the Time Class axis might not represent the same duration of time. The years in the x axis represent captures and the days represent the counts made after the fire.

b) Changes in Sex Ratios and Age Composition

I found no significant difference in the sex ratios in the colonies before the fire (capture of 2021) and after the fire (post-fire videos) ($\chi^2 < 0.010$; $df = 1$; $P = 1$; Table 5). The sex ratio before the fire was based only on the six surviving colonies because the difference with all or with only the six was extremely small.

Table 5 - Number of females and males and the sex ratio obtained from captures in 2021 and from the videos post-fire. Note that here the number of birds on this table does not match the number of individuals captured (Table 4) because there are some individuals that were not sexed.

Class	Capture 2021	Post-fire videos
Males	136	165
Females	116	142
Sex Ratio	0.540	0.538

From the captures of 2021, there were a total of 209 birds with an exact age and sex determined (84 females, 125 males). From the videos post-fire there were a total of 259 individuals (103 females, 156 males). Age composition did not appear to undergo any changes after the fire (GLMM estimate= 0.010 + 0.083, $P = 0.903$; Table 6, Fig. 9). Sex had a significant effect on age, with males being older than females (GLMM estimate = 0.245 + 0.068, $P < 0.010$; Table 6, Fig. 9)

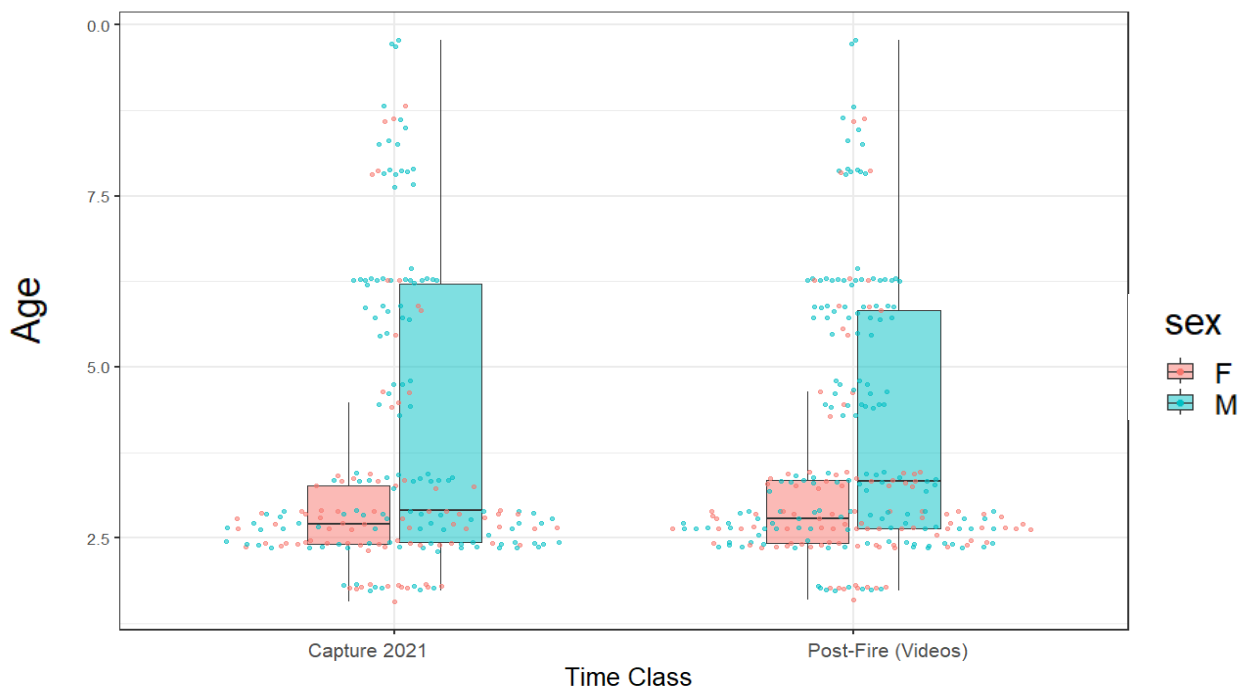


Figure 9 - Age composition of six surviving colonies (ID 2, 8, 11, 20, 21 and 71) by sex at the capture of 2021 and in the videos post-fire

Table 6 - Results of the GLMER to detect if the age composition is different before and after the fire and in the different sexes. When: before or after the fire.

Fixed effects	Estimate	Std. Error	Z value	P-value
(Intercept)	1.175	0.076	15.517	<0.010
When	0.010	0.083	0.122	0.903
Sex	0.245	0.068	3.613	<0.010
When * Sex	0.003	0.101	0.025	0.980

The age composition was similar between the different types (non-significant), i.e. the birds from the surviving colonies that stayed, those from the surviving colonies that moved to other colonies, and the birds from the burned-down colonies (Table 7 and Fig. 10). The interaction between the sex and the types of birds was also statistically non-significant, meaning the different types also do not clearly differ their age composition by sex.

Table 7 - Results of the GLMER including the random factors 'ID of the last colony the bird was seen at before the fire' and 'ID of the colony where the bird was seen after the fire' to detect if the age composition is across the types of birds alone and in interactions with the sex.

Fixed effects	Estimate	Std. Error	Z value	P-value
(Intercept)	1.087	0.101	10.770	<0.010
Sex	0.356	0.106	3.375	<0.010
Resident birds that moved	0.086	0.215	0.401	0.689
Resident birds that stayed	0.172	0.129	1.328	0.184
Sex * Resident birds that moved	-0.210	0.339	-0.619	0.536
Sex * Resident birds that stayed	-0.196	0.143	-1.373	0.170

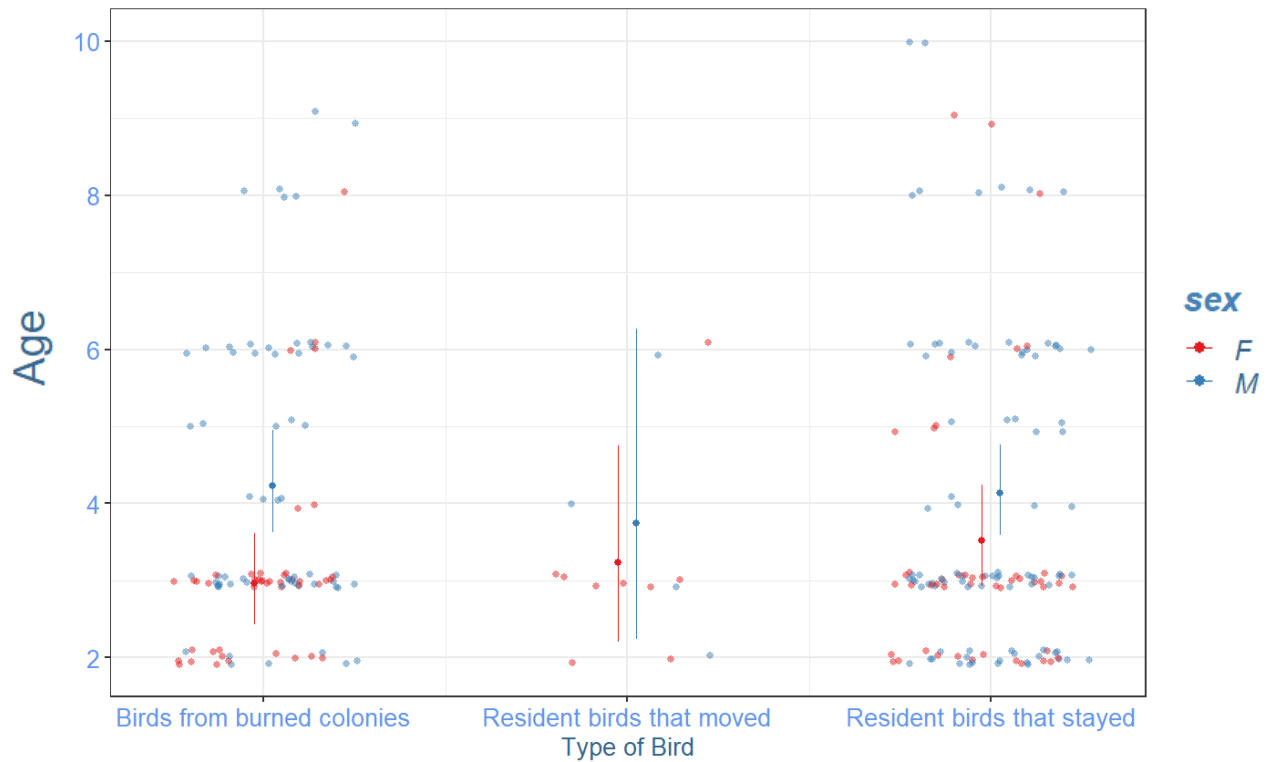


Figure 10 - Age composition of the different categories of birds (that stayed in their colony after the fire, moved or immigrated into a surviving colony after losing their colony) by sex of birds in the post-fire videos. The line represents the 95% confidence interval. The point in the middle of the line represents the estimated mean.

c) Immigration

i) Movement network

I had a total of 14 different origins for the immigrants (13 known colonies and an “unknown” category; note that colony 2 was the only colony that did not have birds emigrating from it; Fig. 11). In total, I recorded 182 movements of individuals between colonies (note that individuals can represent more than one movement if they change colonies more than once; in my data set 30 individuals moved twice). We can see that four colonies received the majority of immigrants: colonies 8, 11, 20 and 21 (Fig. 11).

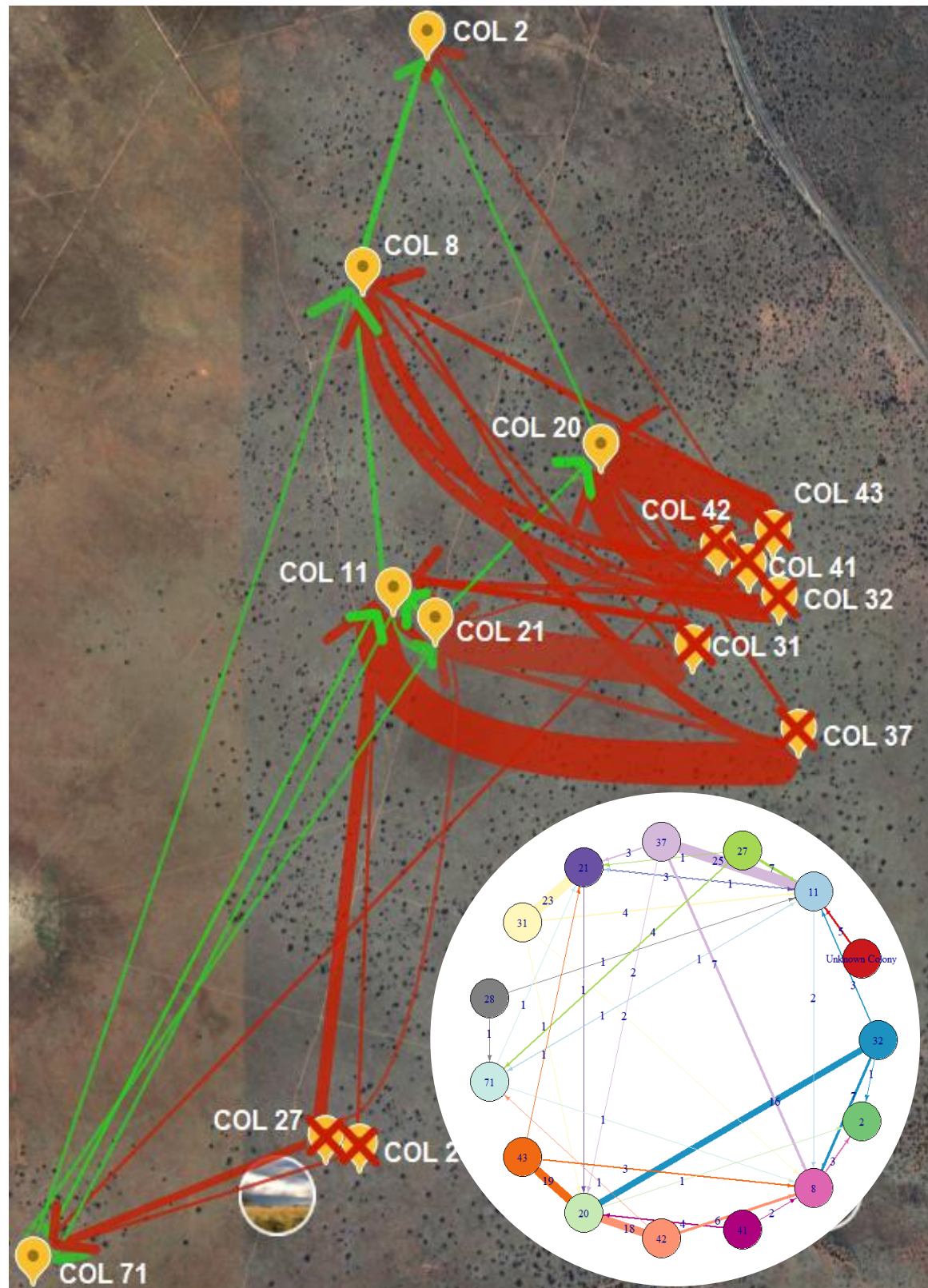


Figure 11 - Movement between the colonies observed in the videos after the fire. Note that the colour of the arrows/connections in the circle on the bottom right represent the colour of the colony where the birds are moving away from. The number of movements on the connections is closer to the colony where the birds are moving away from. One bird can be represented in more than one arrow if they moved more than once between colonies, however they will be represented by an arrow leaving the original colony and not the movement between the colonies that they later moved in between. The colours in the circle are not related to the colours in the map. The green arrows in the map represent movements from colonies that did not burn and the red arrows represent movements from the colonies that did burn. The thickness of the lines in the arrows is representative of the number of birds that did that movement.

ii) Immigration bar plots

After the fire, all the colonies were composed of more migrant birds than before the fire. (Fig. 12 to 17). Compared to what happen before the fire, these migrants were also from a larger range of different colonies. These differences were very visible after the fire but were still detectable one year later. These results were more noticeable for colony 20 and 21, that were the smallest colonies before the fire. In addition, it can be seen that all colonies kept some immigrants even one year after the fire (captures of 2022), and that 4 out of 6 colonies did not increase in size between the two captures.

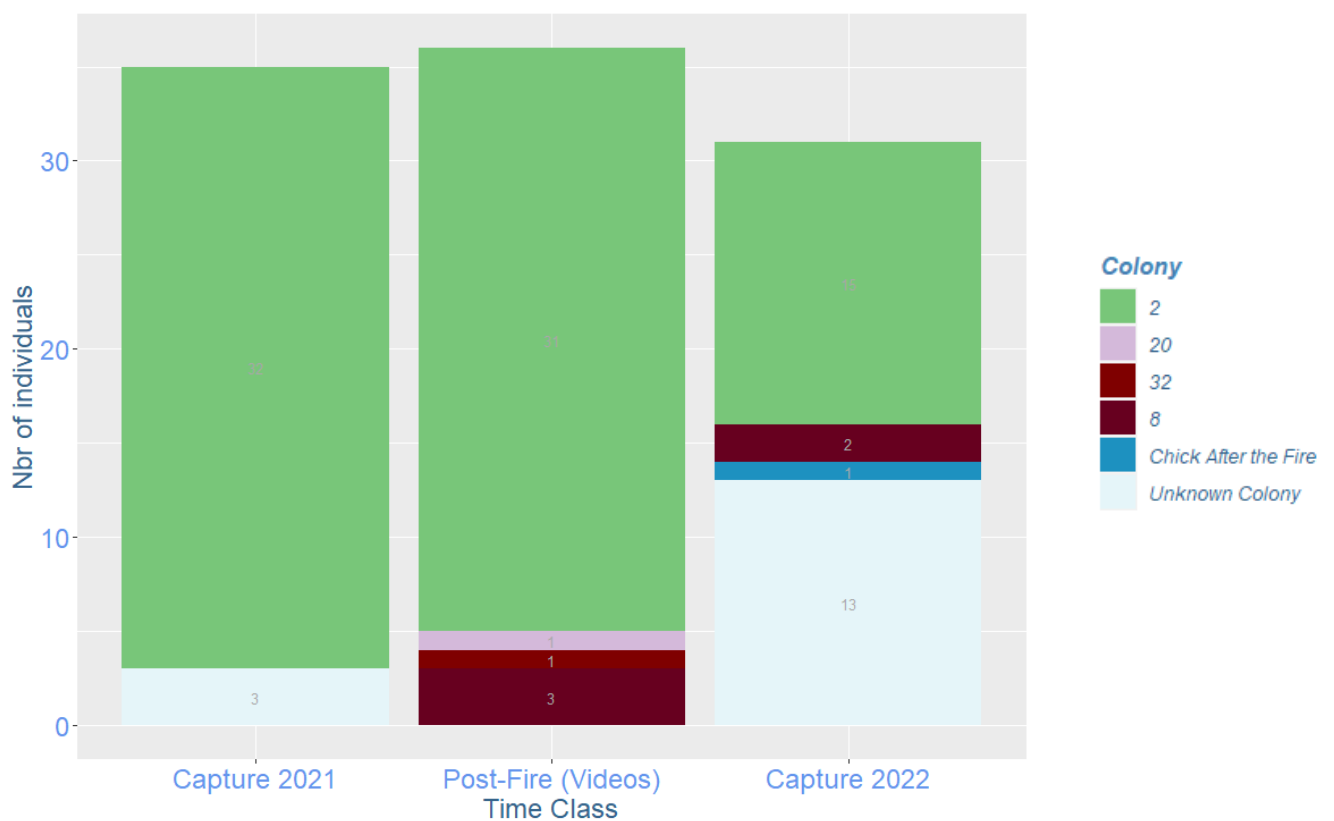


Figure 12 - Residents (in green) and immigrants (other colours) present at colony 2 in different times of data collection (capture 2021, after fire (videos) and capture 2022).

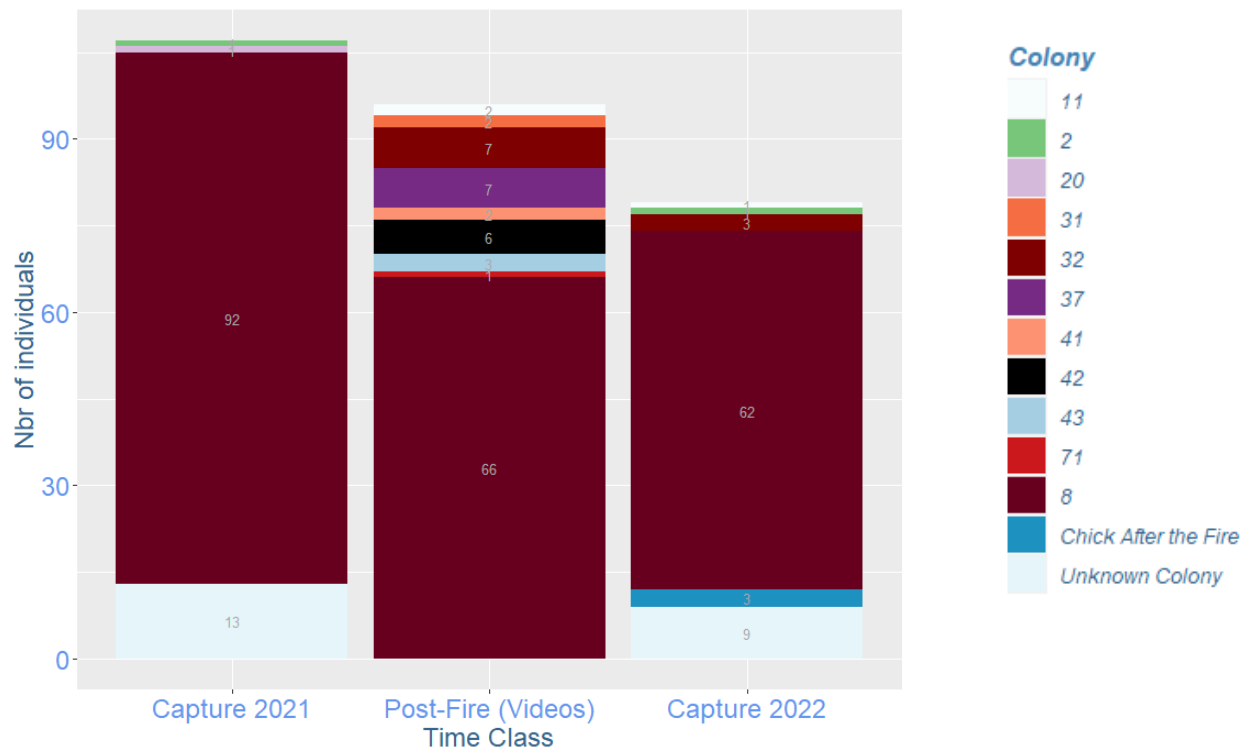


Figure 13 - Residents (in brown) and immigrants (other colours) present at colony 8 in different times of data collection (capture 2021, after fire (videos) and capture 2022).

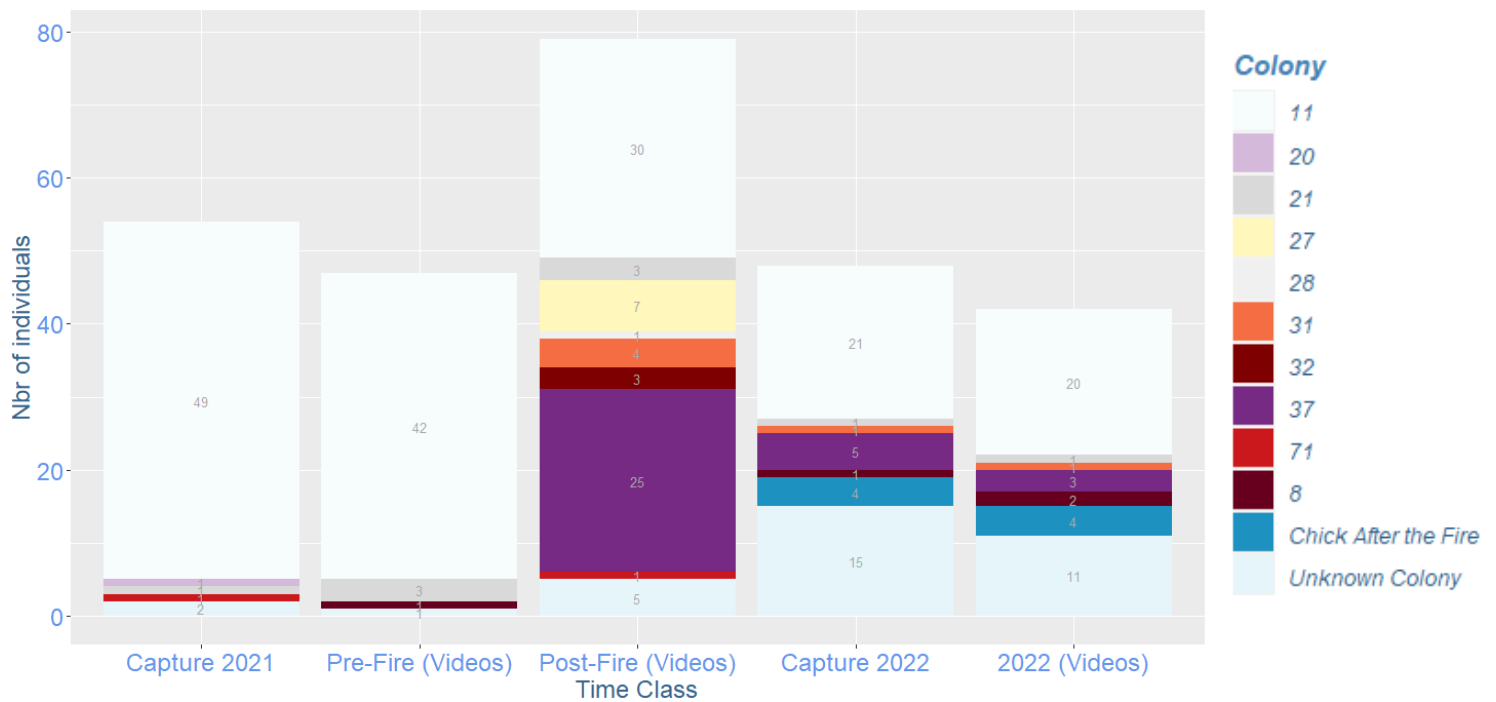


Figure 14 - Residents (in white) and immigrants (other colours) present at colony 11 in different times of data collection (capture 2021, before fire (videos), after fire (videos), capture 2022 and 2022(videos)).

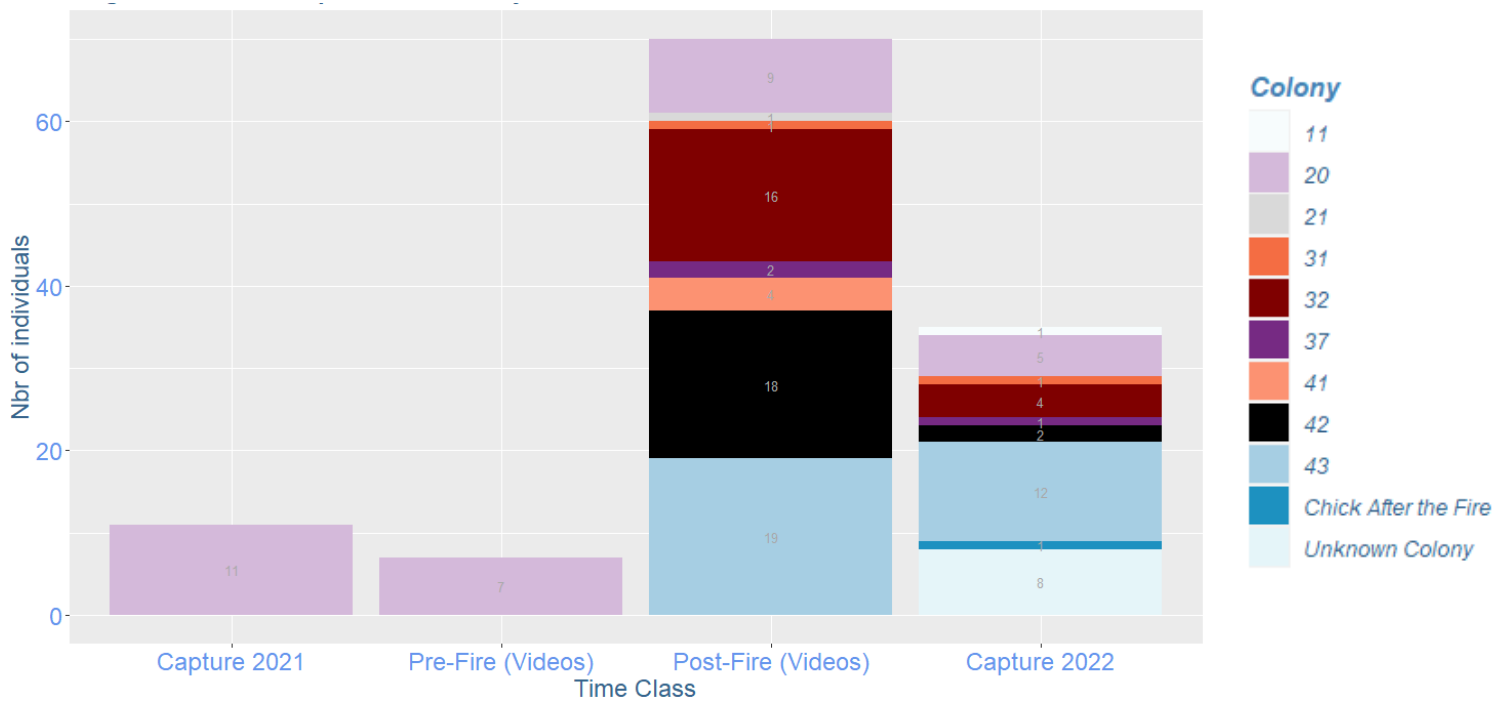


Figure 15 - Residents (in violet) and immigrants (other colours) present at colony 20 in different times of data collection (capture 2021, after fire (videos) and capture 2022).

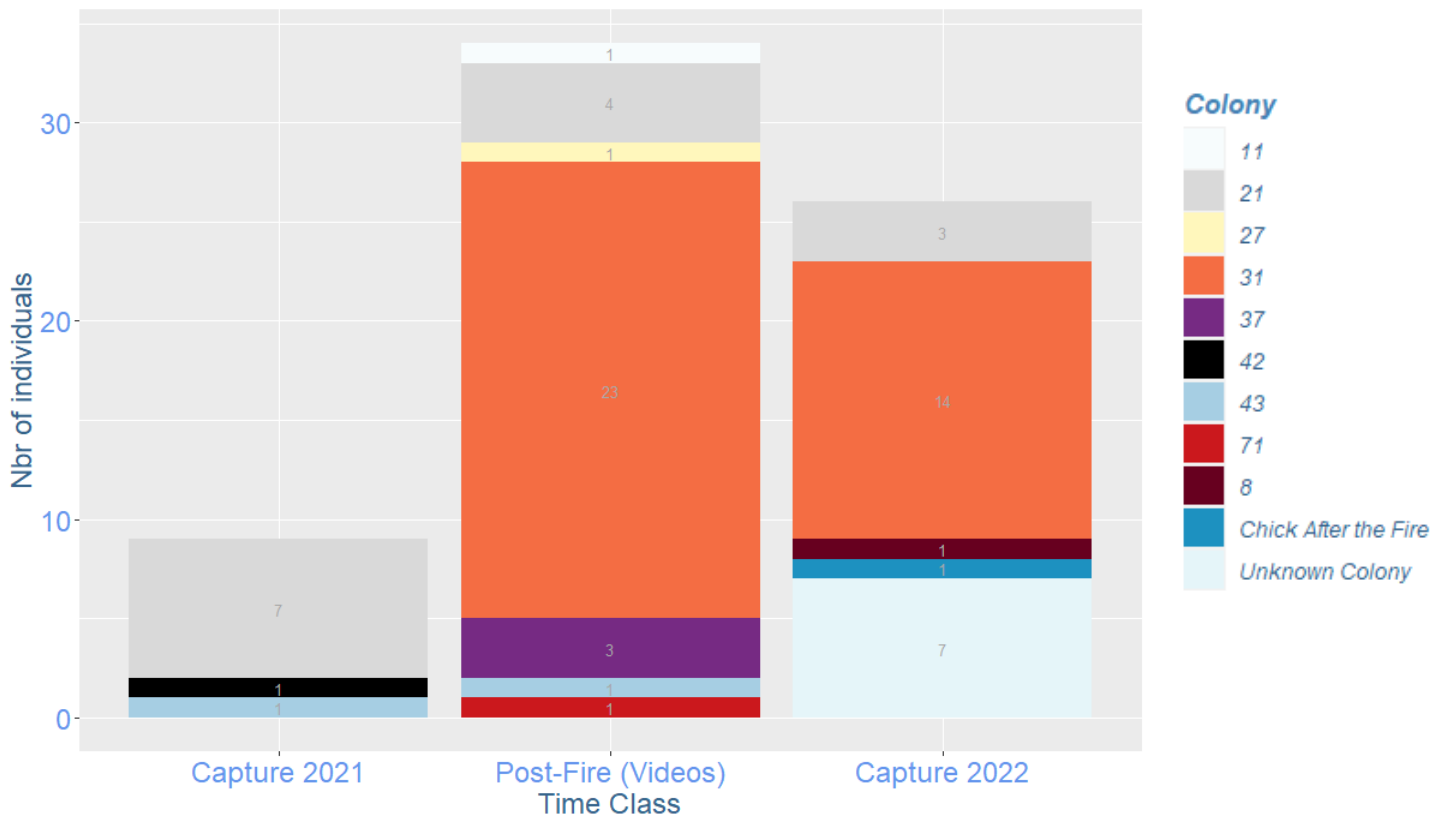


Figure 16 - Residents (in grey) and immigrants (other colours) present at colony 21 in different times of data collection (capture 2021, after fire (videos) and capture 2022).

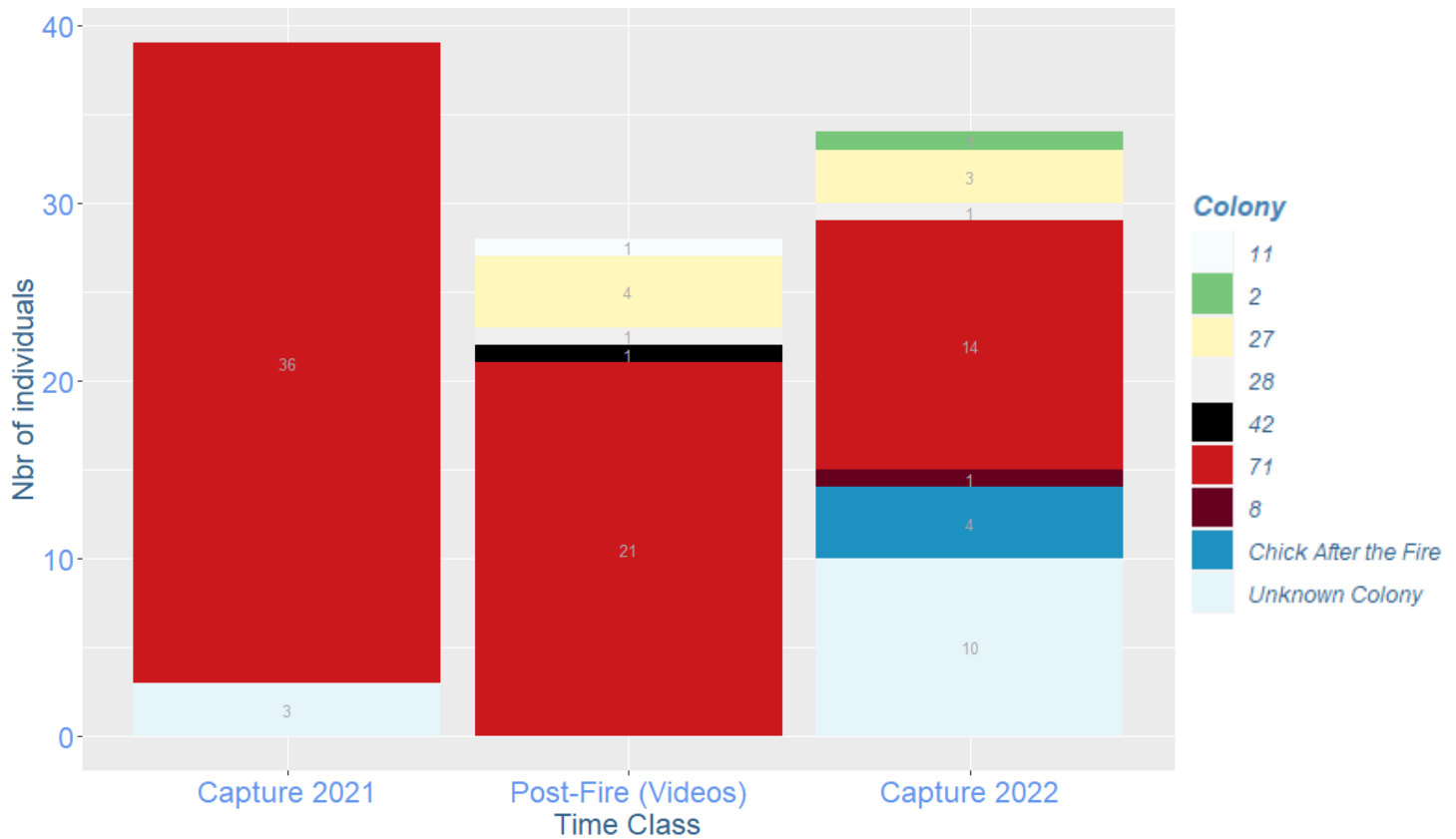


Figure 17 - Residents (in red) and immigrants (other colours) present at colony 71 in different times of data collection (capture 2021, after fire (videos) and capture 2022).

iii) Factors influencing the group size of immigrants

The size of the original colony where the immigrants moved from did not have a significant effect on the number of individuals that arrived at other colonies (GLMER estimate= 0.163 ± 0.186 , $P = 0.380$). The distance between the colony the birds were leaving and the colony the birds were migrating to was negatively associated with the number of birds arriving at the destination colony (GLMER estimate = -0.450 ± 0.203 , $P = 0.027$).

Table 8 - Results of the GLMER including the random factors 'ID of original colony' and 'ID of destination colony' to detect which factors are associated with the number of immigrants that arrived at the destination colony for 182 movements. Note that one birds can represent more than one movement if they were recorded in more than one colony.

Fixed effects	Estimate	Std. Error	Z value	P-value
(Intercept)	1.071	0.195	5.505	<0.010
Size of original colony	0.163	0.186	0.878	0.380
Distance between colonies	-0.450	0.203	-2.216	0.027

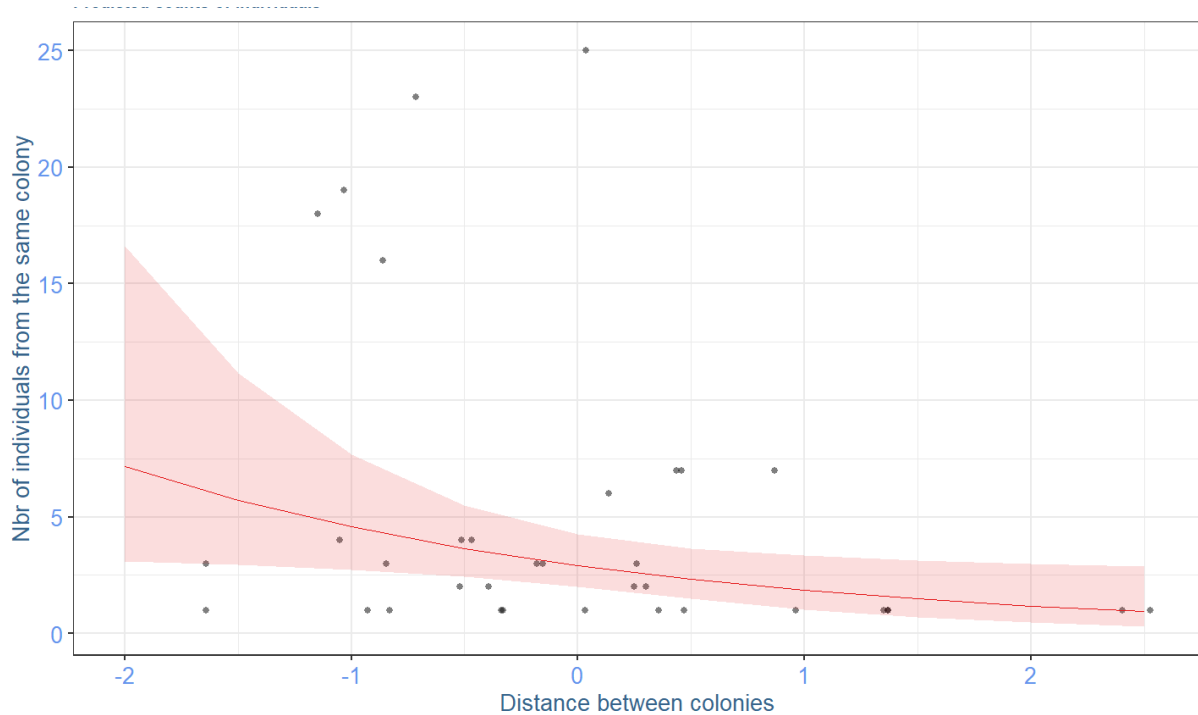


Figure 18 - Predicted counts of individuals in function of the distance between the colonies. Please note that distance is scaled. The red shading represents the 95% confidence interval.

Behavioural changes

Both methods of data collection showed that under normal conditions (pre-fire for the videos and one year after the fire for the observations (2022)) the level of aggressive interactions at roosting are always low, with less than 10 per night (Fig. 19 and Fig. 20). After the fire, most colonies showed a sudden increase in their aggressive encounters and then a decrease as time passed (Fig. 19 and Fig. 20). We also see that colony 2 and 71 are the only ones in which the level of aggressive interactions never went higher than medium. Additionally, we can observe that in the results for post-fire with the videos (Fig. 19) the level of aggressive interactions for colony 11 and 20 decreases faster than when looking at the results based on the observational data (Fig. 20).

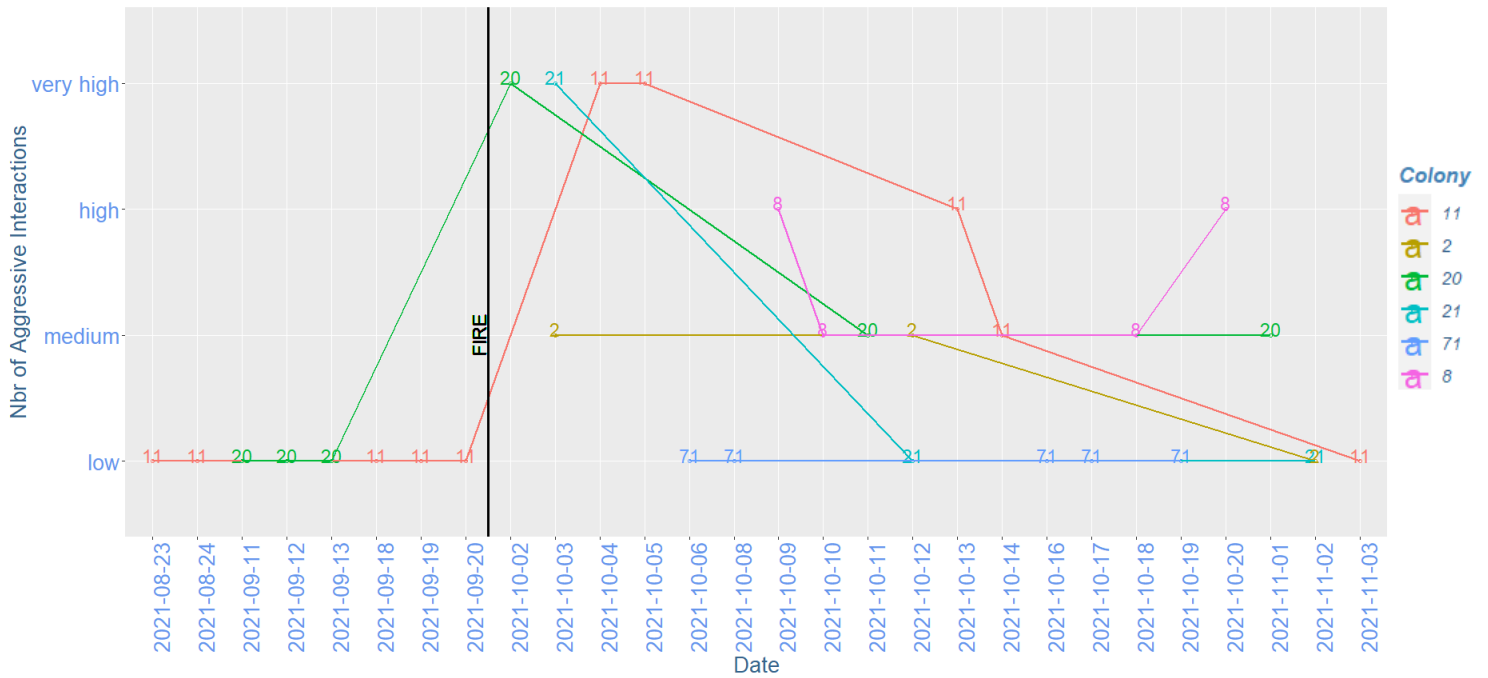


Figure 19 - Level of aggressive interactions in the colonies based on the video data per date. The black line separates the dates pre-fire and the post-fire.

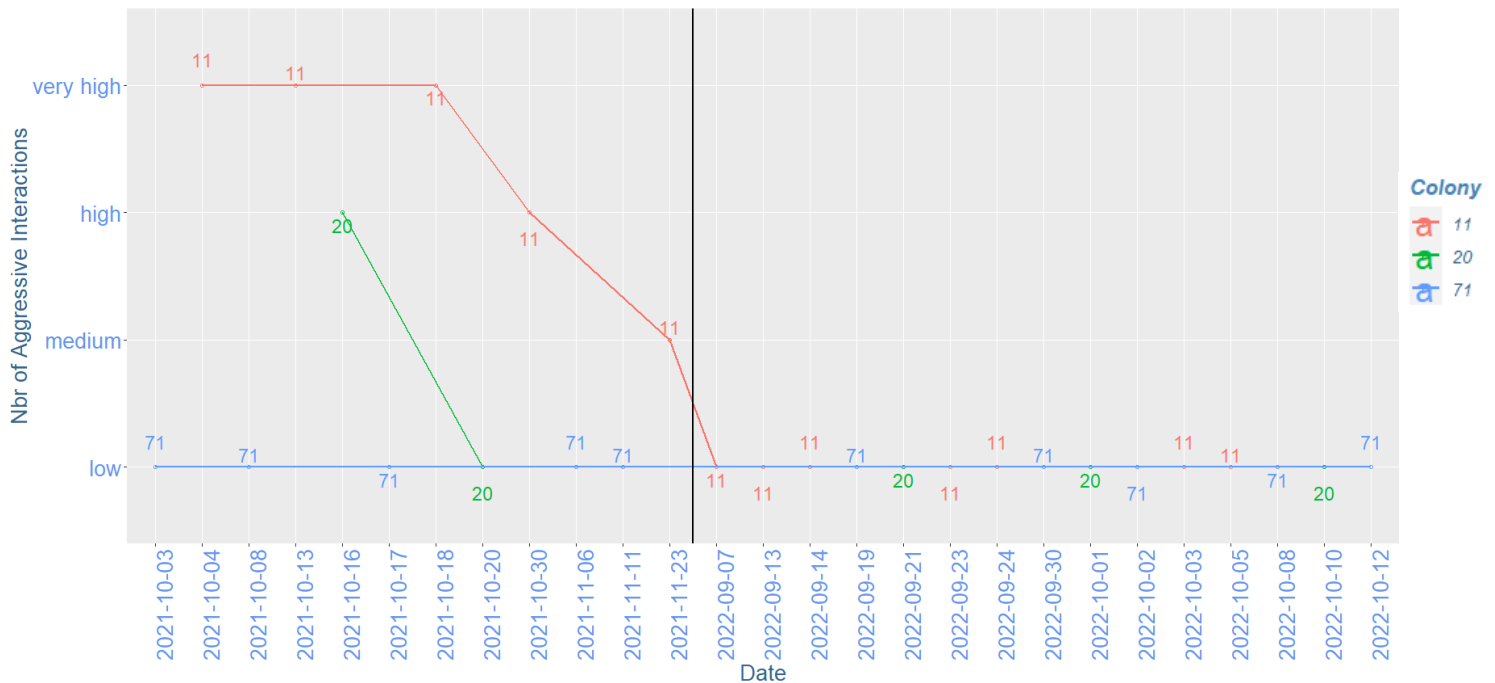


Figure 20 - Level of aggressive interactions in the colonies based on observations after the fire (October and November 2021) and one year after (September and October 2022). The black line represents the separation between the observations done in 2021 and 2022.

Social Associations

Pacheco, 2021 saw stability between daily roosting networks, which means the connections between individuals are likely not random and the birds do actively choose who they roost with.

From Table 9 and Fig. 21, we see that all assortment values are positive, which indicates that the birds do actively assort by their original colony. No clear patterns emerge from the changes in the assortment values between the networks in different time periods. From the Fig. S 3, S 5, S 7 and S 9 available in the supplementary material, we observe that all observed assortment values seem to be on the edge or outside the distribution of the values that occur by chance under the null hypothesis (random mixing) (the p-values between the observed and values from permutations were always lower than 0.050).

Table 9 - Assortment values per colony for each period considered. Note that some colonies are missing values because the data as not been analysed yet.

Colony ID	c.a. 1 week after	c.a. 2 weeks after	c.a. 1 month after
8	0.536	0.201	Data not analysed
11	0.153	0.259	Data not analysed
20	0.346	0.424	0.301
21	0.573	1.000	1.000

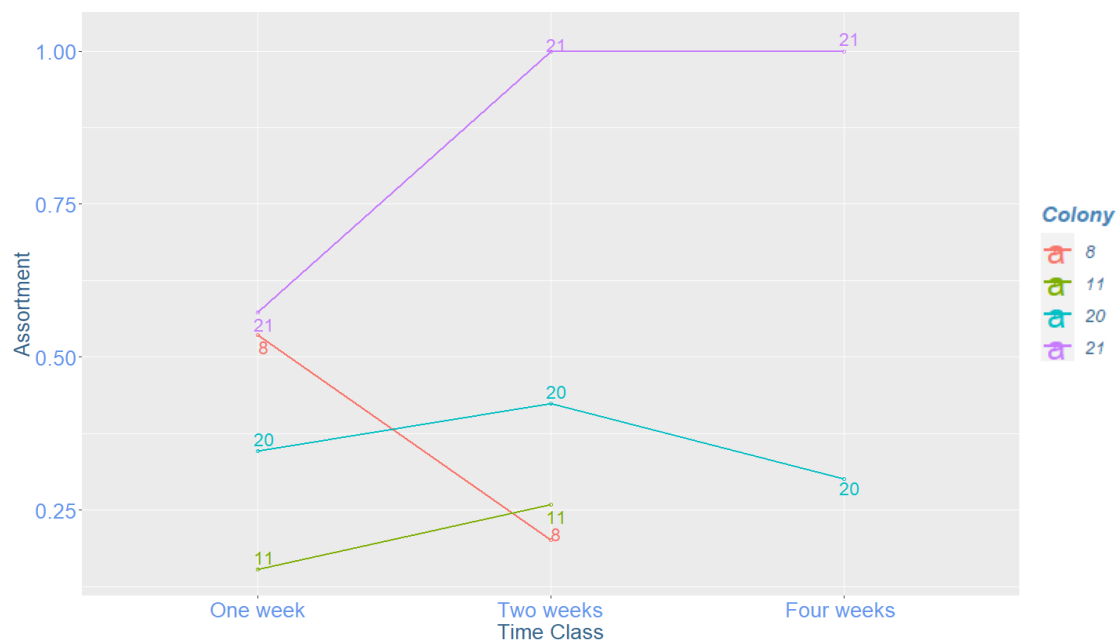


Figure 21 - Assortment values (y) for the social networks for time class (x). Four weeks here represent the network done for ca. 1 month. Each different coloured line represents a different colony with the ID number represented in the legend "Colony" on the side and above the points each line connects. Please note that each x unit might not represent the same duration of time.

4. Discussion

In this study, I investigated the demographic, behavioural and social changes associated with a wildfire that affected a sociable weaver population, destroying half of the colonies known in the area. I found that four out of the six surviving colonies, the ones closer to the burned colonies, increased their number immediately after the fire. These also corresponded to the colonies that received most immigrants and from more origins. I also found evidence that the group size of birds migrating from the burned colonies after the natural disaster is negatively correlated to the distance between their colony and their destination colony. I did not find a change in the sex ratio and age composition at the surviving colonies, suggesting that there is no age or sex bias in coping with post-fire crowding. Additionally, we saw that most colonies had a higher level of aggressive interactions at roosting after the fire, indicating strong competition as a consequence of the fire. I did not find a general pattern in the changes of the assortment values for the networks at different times after the fire for each colony. This means that, in some colonies, immigrants and individuals originally residing at non-burnt colonies might not have progressively started associating with other colonies.

Demographic changes

I found that the effect size of the change of the number of birds present in the six surviving colonies at the first count done after the fire was large (63% increase between captures in 2021 and first count after the fire). A marked increase was seen in four out of the six surviving colonies (the other two decreased). The fact that the observed patterns are not statistically significant is probably due to lack of statistical power since I only had 6 replicates (colonies). The increase of the total number of birds present at the six surviving colonies and the fact that all the surviving colonies had more immigrants and from more diverse origins when we compare with before the fire, concurs with previous literature and with my predictions that animals flee and converge in refuges nearby, leading to increased densities in these locations. Hence, my results for sociable weavers are similar to what was previously found in bats, other birds and insects (Amorim et al., 2022; Debinski & Holt, 2000). Therefore, I provide additional evidence of overcrowding effects at refuge areas after natural catastrophes. This overcrowding is expected to have detrimental effects through increased competition and associated aggression (see below).

I found that the two colonies in the periphery of the study area (colony 2 and 71) received less immigrants and were the only ones that decreased in size just after the fire. The periphery of the study area might be less familiar to birds from the burned colonies (which were located

mostly in the central area), making these colonies harder to find or the birds more reluctant to move into less familiar locations, if they are tired, confused and stressed due to the fire. Because of this, the number of immigrants these two colonies received might not compensate the number of fatal losses they suffered. Additionally, I found evidence that the distance between the colonies that the migrants had to travel from was negatively associated with the size of the group that arrived at a surviving colony, which reinforces the idea that most individuals will look for refuge in close by areas.

The counts made at the colonies in the weeks following the fire revealed no statistically significant differences in colony size. However, we do see that between the first count and the second count there was a decrease of 25% of individuals. Between the second and third count the decrease was only of 2 % of individuals. This suggests that after the fire the colonies quickly lost some birds and tended to stabilize, which could result either from mortality following the wildfire or birds leaving to seek colonies outside the study area. This latter possibility could be motivated by the colonies' overpopulation leading to increased competition for now scarce resources, such as roosting chambers or food. This temporary increase followed by a decrease has been seen before by Darveau et al. (1995) and Schmiegelow et al. (1997) in communities of birds after fragmentation, although over a longer time frame (two/three years instead of weeks) (Schmiegelow et al., 1997; Darveau et al., 1995).

The size of the colonies continued to change, and one year after the fire (captures of 2022) only 2 out of the 6 colonies had increased size in comparison with the captures of 2021 (just before the fire). The number of original residents had decreased in all colonies, meaning that many residents had to leave their colonies following the massive immigration, or had died. I also saw that the colonies kept some immigrants even one year after the fire, which indicates that the change in the composition of the colonies is a long-term effect. This suggests the fire affected the survival and migration of all individuals across both burnt and non-burnt colonies as well as having long-term implications for population dynamics.

In spite of the sudden increase in size of several colonies after the fire, I did not find changes in sex ratio or age composition. This suggests that there might be no age or sex bias in mortality or in migrating outside our study area. In various passerine birds, older birds and males have been found to be dominant over young birds and females (Chiarati et al., 2010; Izawa & Watanabe, 2008; Balph, 1977)). Therefore, I expected that males and older birds could have higher chances of remaining at the surviving colonies, by evicting younger birds and females. To understand if the movements inside the study area reflect this prediction, I examined the age composition of different categories of birds (residents that remained in their colonies, residents that moved from their colonies and the birds from burned colonies). I found

no significant difference between the three categories. However, the estimated mean age of the resident birds that moved, for both sexes, was slightly lower than the mean for the resident birds remaining in their colonies. Nonetheless, the confidence interval is too large and the number of birds displaced is quite low, preventing any firm conclusions.

Behaviour changes

Sociable weaver chambers are a crucial resource, as birds do not sleep out in the open. After the fire, the sudden increase in colony size was expected to lead to increase aggressive interactions at the colonies at roosting, since the more birds would be competing for the same chambers.

This prediction met, as I observed an increased level of aggressive interactions immediately after the fire. In contrast, under normal conditions, the level of aggressive interactions was always low (regardless of the method used, observations and video recordings), which indicates that any differences we see after the fire is likely a result of the fire-induced crowding.

The results obtained with observations and video data suggest that the level of aggressive interactions decrease more rapidly in the video data compared to the observational data. This is likely because we can only see aggressive interactions at the chambers in the video recordings, while in observations we can also track aggressive interactions around the nest. This reflects the importance of also having roosting observations when following events that might increase the competition between the birds, since the chance of aggressive interactions happening outside the colony will be higher than under normal conditions and therefore missed if we only collect video recordings.

I found that the levels of aggressive interactions decreased as time from the fire passes by. This is probably because colonies decreased in size as time passed by, leading to a subsequent decrease in competition, in particular for roosting chambers. Another possible explanation is that the familiarity between the birds increased, which can result in the migrants being included in residents roosting groups, therefore decreasing competition for space. However, my results at the moment seem insufficient to support this later justification (see below).

Social Associations

I used 'assortment' in relation to the colony of origin to investigate social associations after the fire. I expected that the assortment values would decrease for all colonies if the resident birds at the surviving colonies would start to mix with the immigrants from other colonies as time passed. However, I did not see a decrease for all colonies. Looking individually at the networks of each colony provides additional element to understand why my prediction was met on some colonies and not others (all the networks are provided in the supplementary material).

Starting with colony 11 and 21, where there was an increase in the assortment values, which goes against my prediction. For colony 11, we see that the total number of birds and the number of different colonies represented in the last network (ca. two weeks after the fire) reduced quite a lot in comparison with the first network (ca. one week after the fire). This means the increase in the assortment might reflect the disappearing of this huge number of individuals from several origins, and not that the birds from different colonies are not associating. The case is the same for colony 21, where in the last two networks (ca. 2 weeks after the fire and ca. 1 month after the fire) the vast majority of individuals from the first network are missing and the different colonies presented are much less.

Then, looking at colony 20, we see that between the first network after the fire and the second, the number of immigrant birds decreased a lot. Which means, once again, that the increase in assortment between these two networks might reflect the loss of individuals from outside colonies. If we then look at the second and third network, we see that they have very similar number of resident birds and immigrants and origin of the immigrants. This example seems like a good case of what might happen to the associations between the birds as time passes, as most individuals are present and analysed in both networks. Here, the assortment value decreased, which might correctly indicate that the birds of different origins are mixing more in the roosting groups.

Finally, in colony 8 we also see that the number of residents and immigrants and the immigrants' origins between the two networks is extremely similar. This means that this colony might also be a good representative of what happens in terms of associations between the different immigrants and resident birds for the same reason above. Here, the assortment value also decreased between the two networks and more immigrants seemed to be integrated in the roosting groups of the residents in the network ca. two weeks after the fire.

Overall, my social associations' results suggested that, if individuals remain in the colony, different colonies might associate with other colonies more as time passes by. My results also indicate that assortment is dependent on too many factors that we cannot control for and that

we should try also other approaches in the future, to better understand what happens to social associations in animals at refuges after a natural disaster. In the future, we should try to look at the individual level of the composition of the roosting groups before the fire and at different times after the fire, to understand what happens at the individual level in terms of strength, stability and degree of associations. We should also investigate other ways of testing if the threshold that defines an association is adequate (alternative approaches to what Pacheco (2021) conducted). Additionally, it might be interesting to look at the factors related to being integrated into other colonies roosting groups, as we saw that some individuals get integrated into other roosting groups and others did not. The number of individuals from their previous colony might play an important role here, as in some colonies a lot of individuals went missing as time passed, which might indicate they left in groups.

5. Conclusion

This study provides insights into the impact of a fire on a highly sociable and cooperative bird species. My results showed how a fire can deeply influence populations dynamics, as most surviving colonies had a marked increase in size, number of immigrants and aggressive interactions. I also saw that some effects of the fire, specifically the change in the composition of the colonies, seem to continue up to one year after, which suggests that future work should be done to study the long-term effects of this fire on our population's demography and social composition, so that we further understand how affected our population is and how they might recover. One variable that should be investigated is the reproductive success following the fire, as it is an extremely important parameter for the population recovery. Other important parameters to look at are the long-term survival and stress effects, as the increased aggressions and therefore stress may lead to physiological costs and decreased physical condition. The factors associated with being able to remain at the colonies one year after the fire should also be investigated, especially the social associations on the individual level composition of the roosting groups, since it will give us more complex details about the individuals that managed to remain and additional context on the ones that I saw managed to integrate roosting groups from other colonies. Some other variables that might be important to look at in this context are space availability, mate presence and number of individuals from the same roosting group present.

All this future work will allow us to understand which individuals are more resilient when facing a natural disaster, so that we can identify more vulnerable systems and possibly guide any management interventions.

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Supplementary material

Colony 2

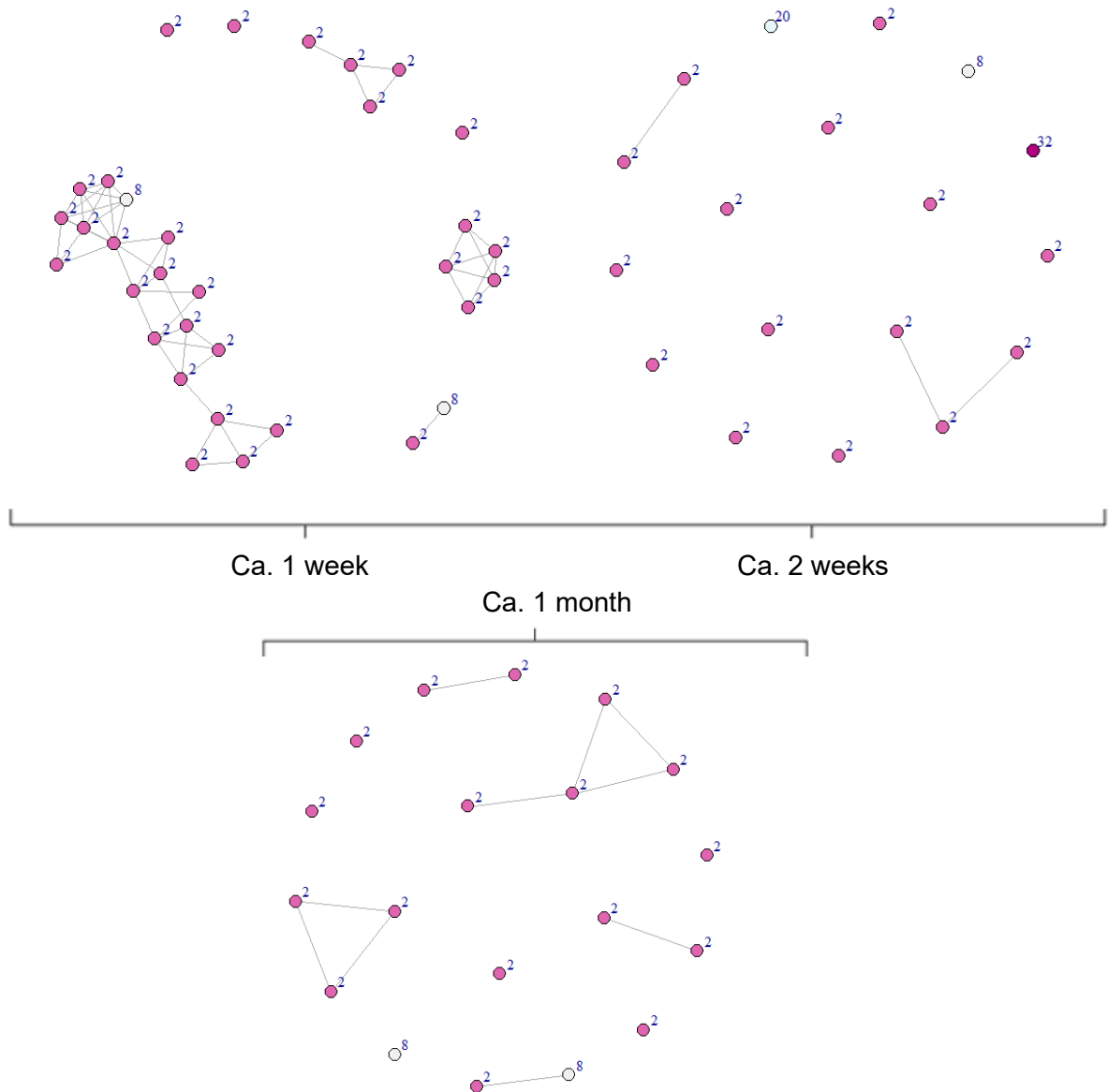


Figure S 1 - Roosting social networks obtained for colony 2 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.

Colony 8

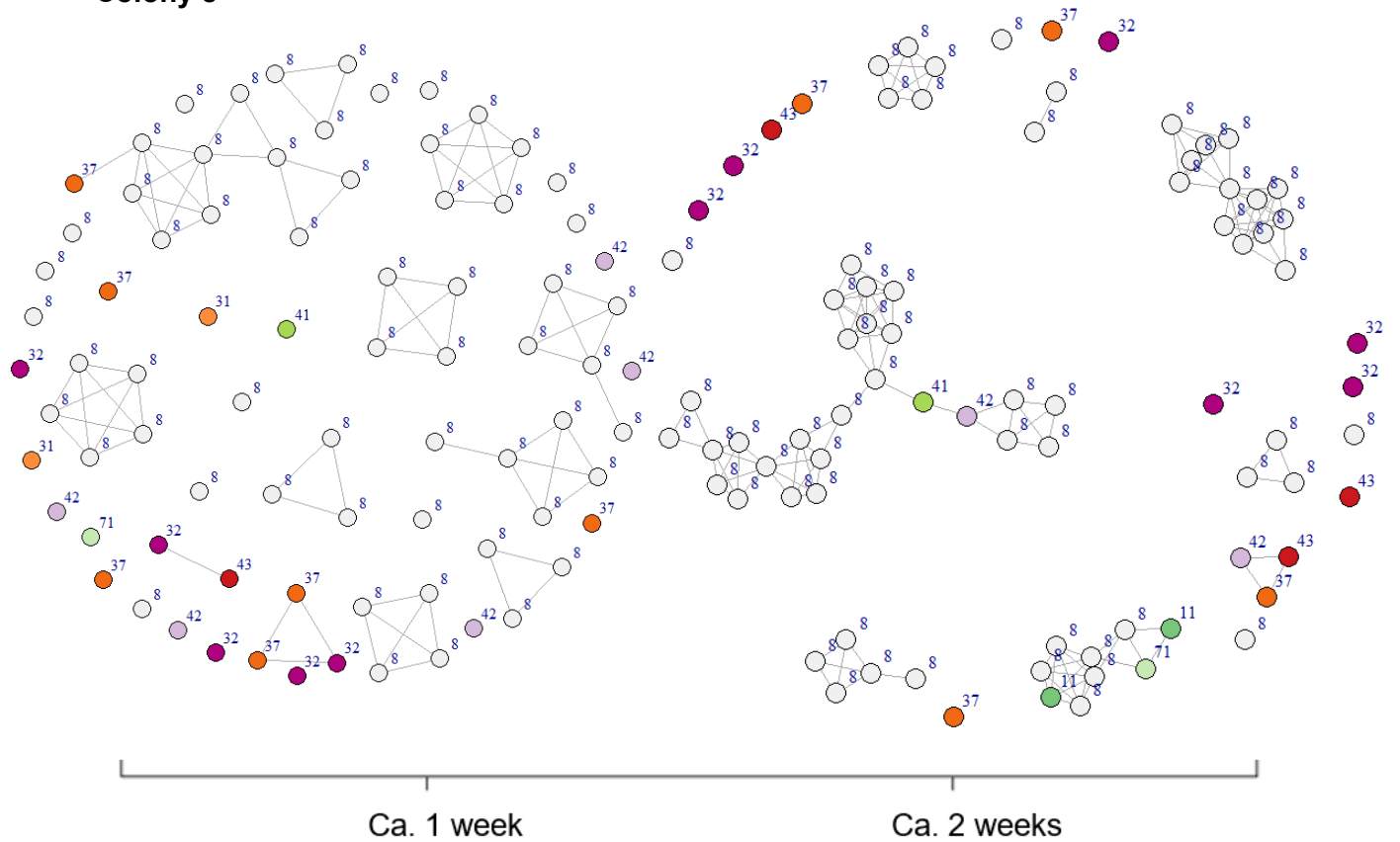


Figure S 2 - Roosting social networks obtained for colony 8 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.

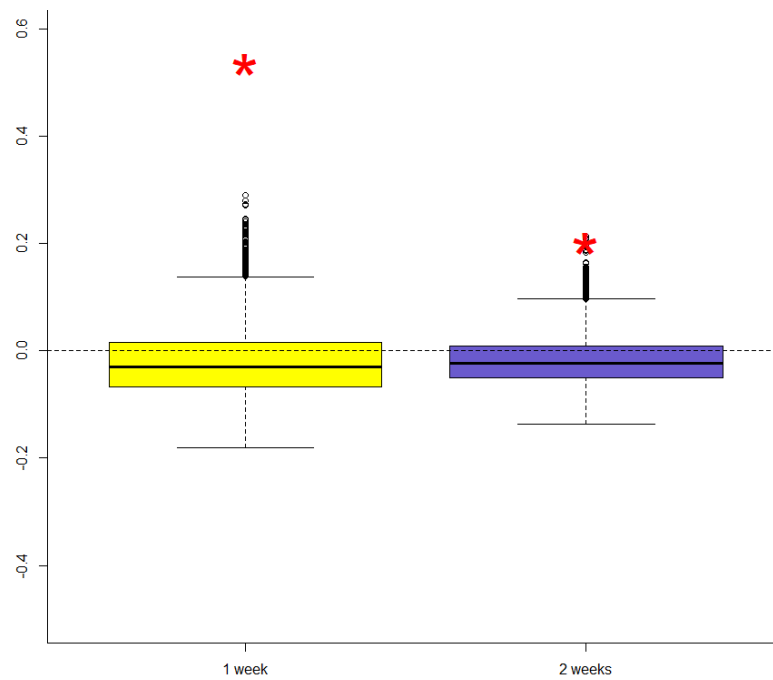


Figure S 3 - Distribution of the assortment values generated through the permutations of the node attributes in the networks at different time periods (ca. 1 week after the fire and ca. 2 weeks after the fire) for colony 8. The observed values are represented by the red asterisk.

Colony 11

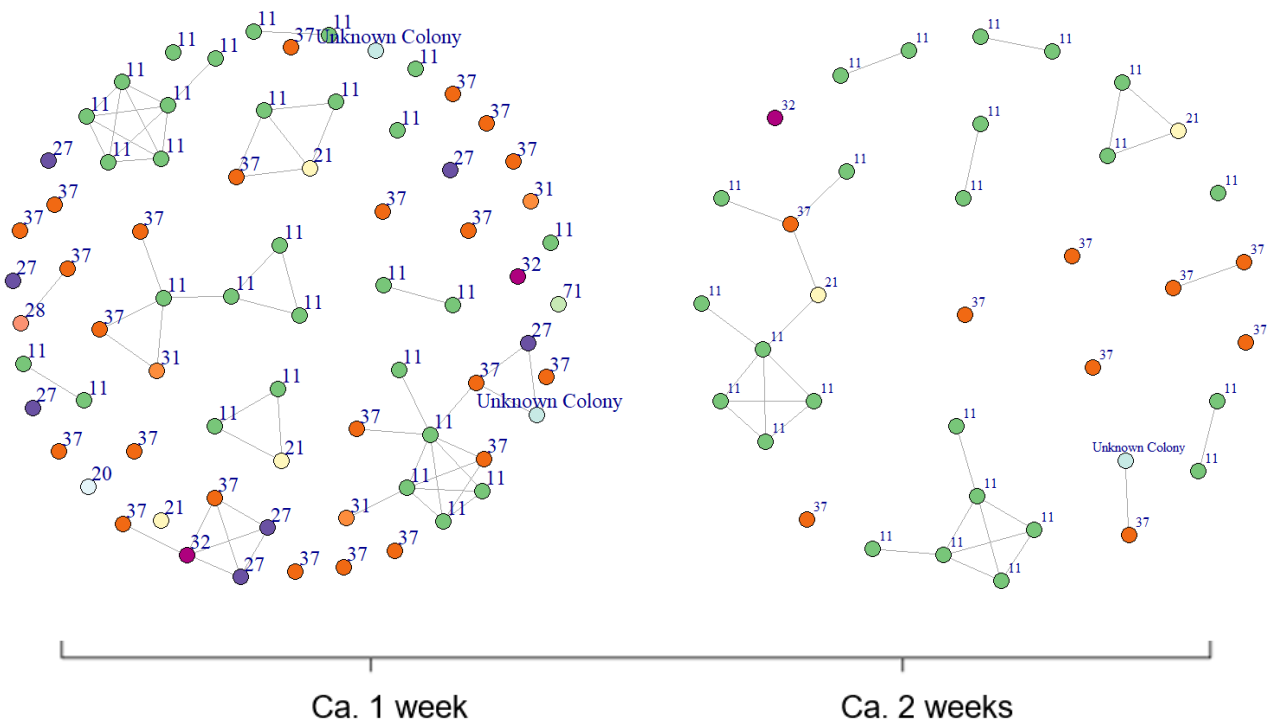


Figure S 4 - Roosting social networks obtained for colony 11 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.

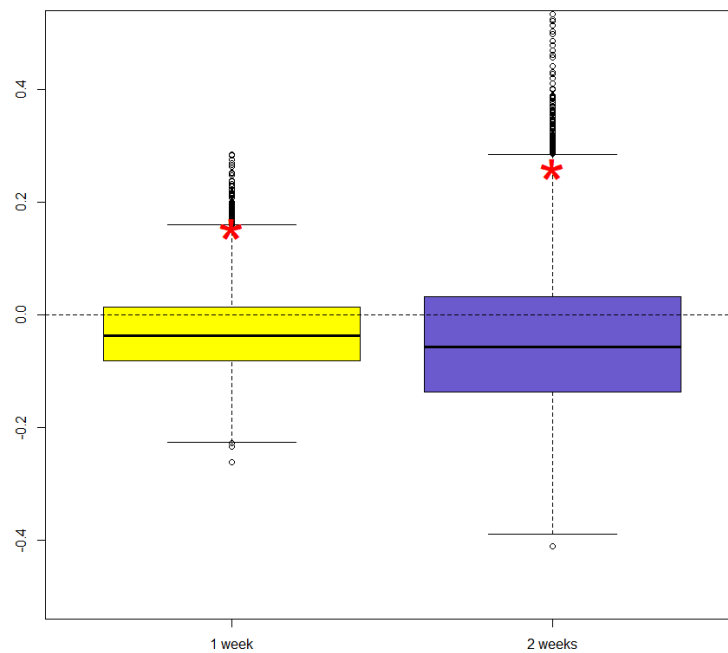


Figure S 5 - Distribution of the assortment values generated through the permutations of the node attributes in the networks at different time periods (ca. 1 week after the fire and ca. 2 weeks after the fire) for colony 11. The observed values are represented by the red asterisk.

Colony 20

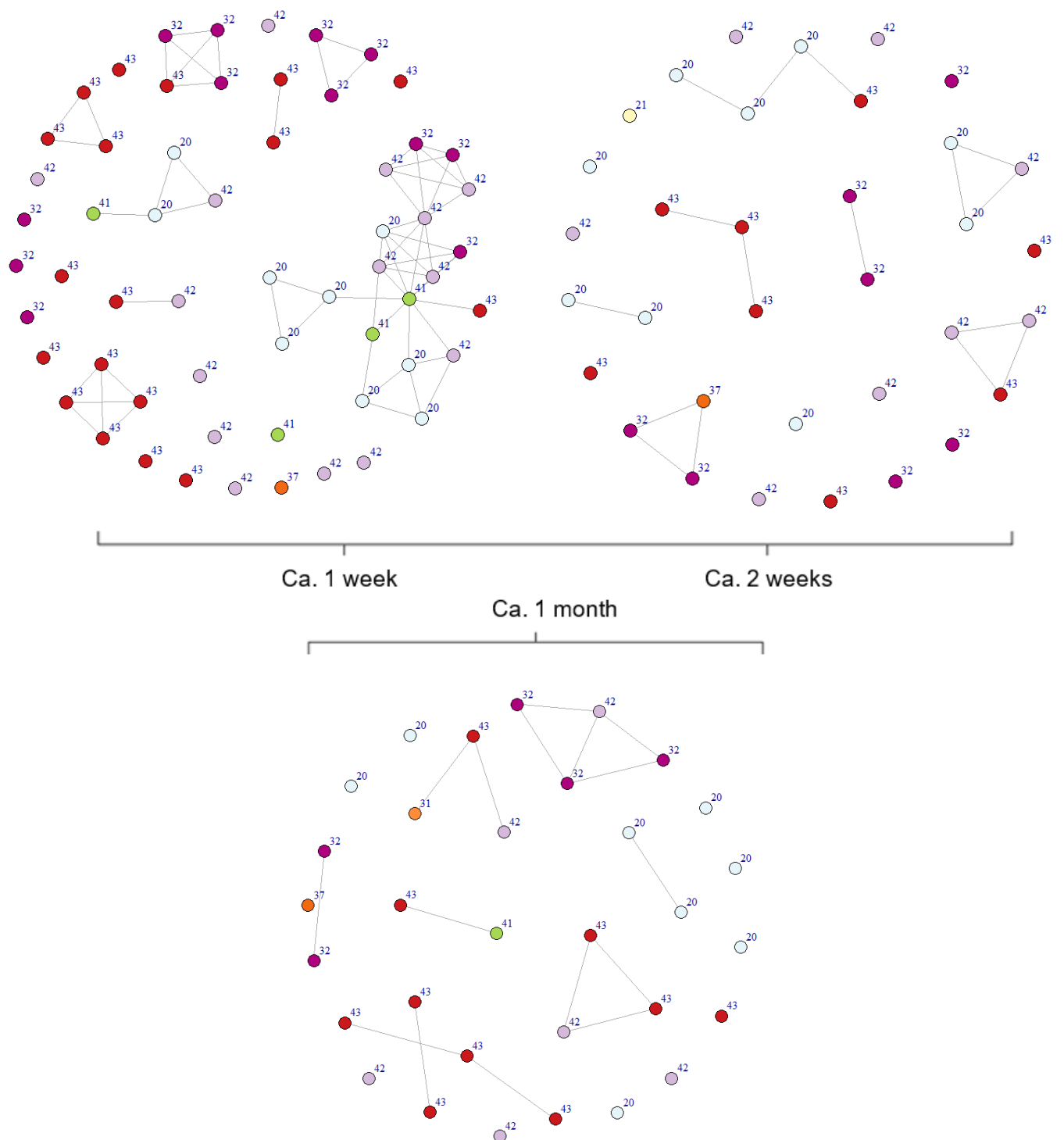


Figure S 6 - Roosting social networks obtained for colony 20 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.

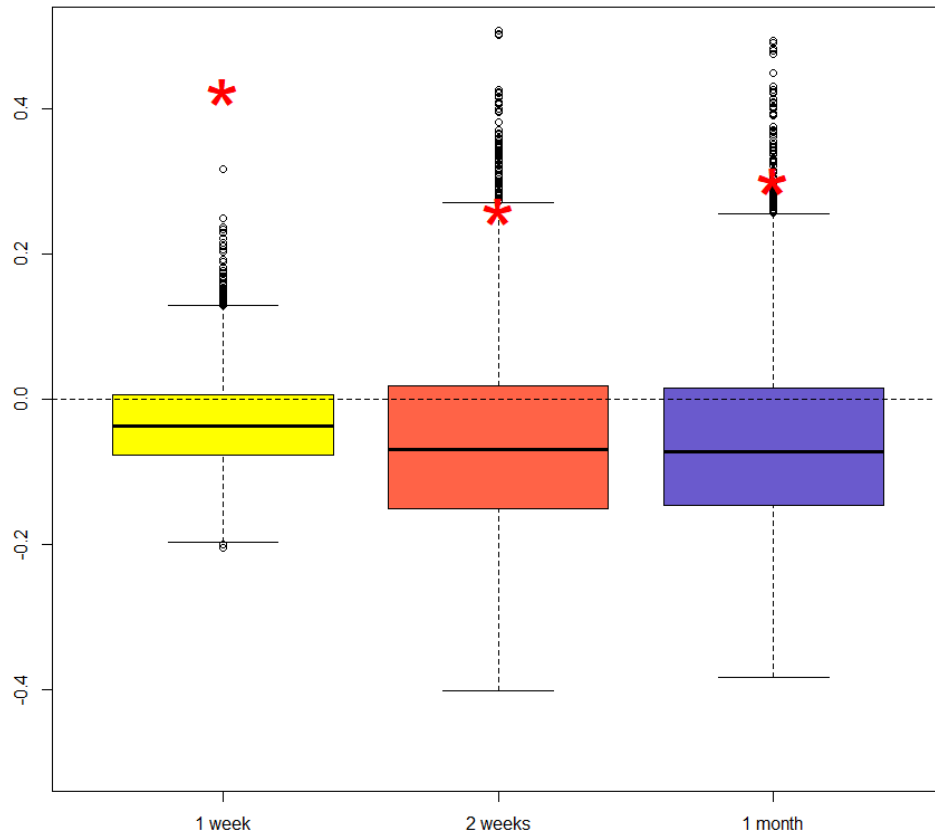


Figure S 7 - Distribution of the assortment values generated through the permutations of the node attributes in the networks at different time periods (ca. 1 week after the fire, ca. 2 weeks after the fire and ca. 1 month after) for colony 20. The observed values are represented by the red asterisk.

Colony 21

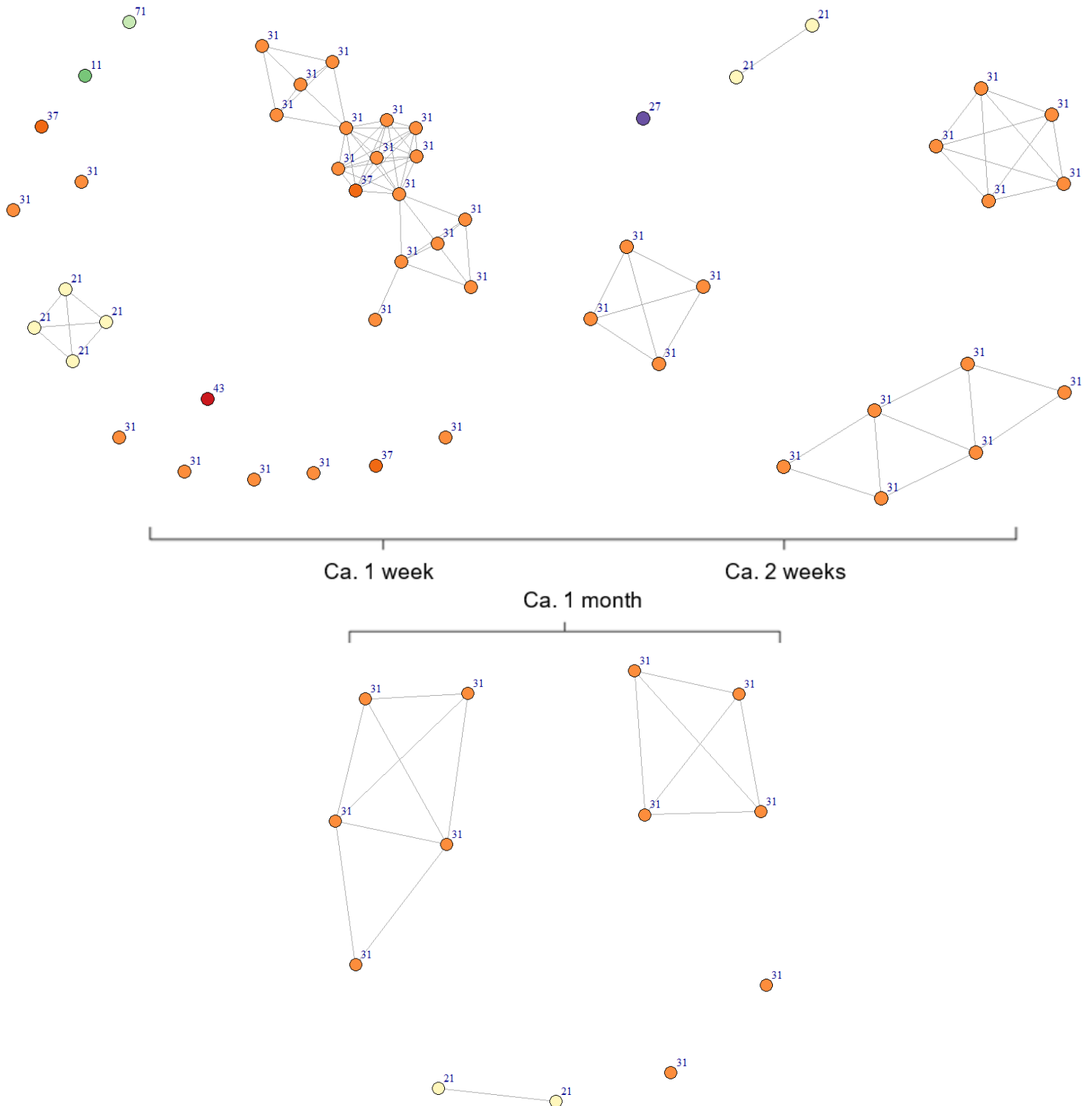


Figure S 8 - Roosting social networks obtained for colony 21 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.

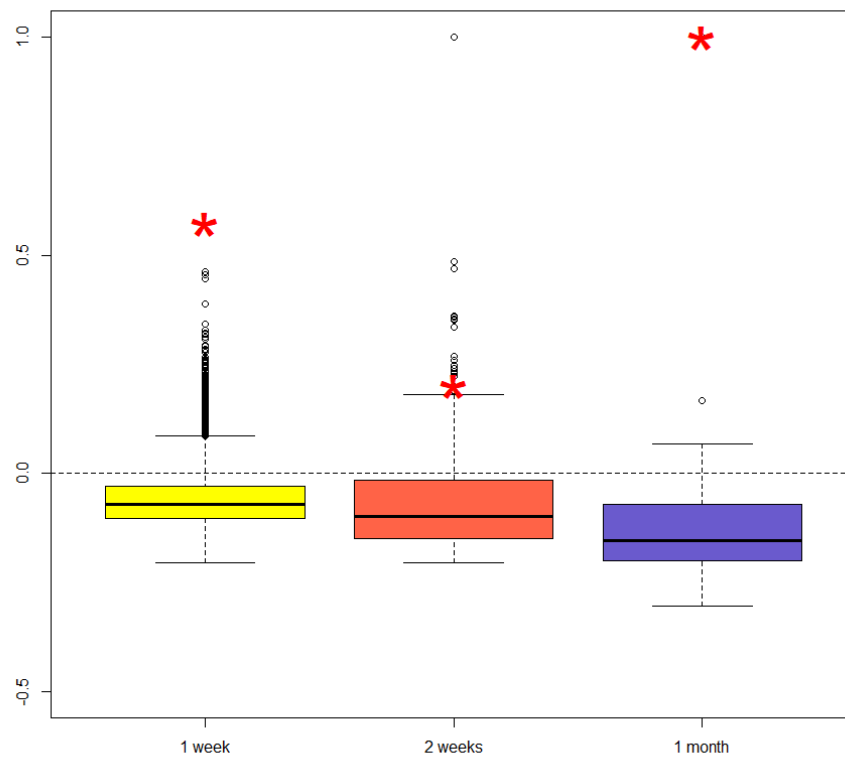


Figure S 9 - Distribution of the assortment values generated through the permutations of the node attributes in the networks at different time periods (ca. 1 week after the fire, ca. 2 weeks after the fire and ca. 1 month after) for colony 21. The observed values are represented by the red asterisk.

Colony 71

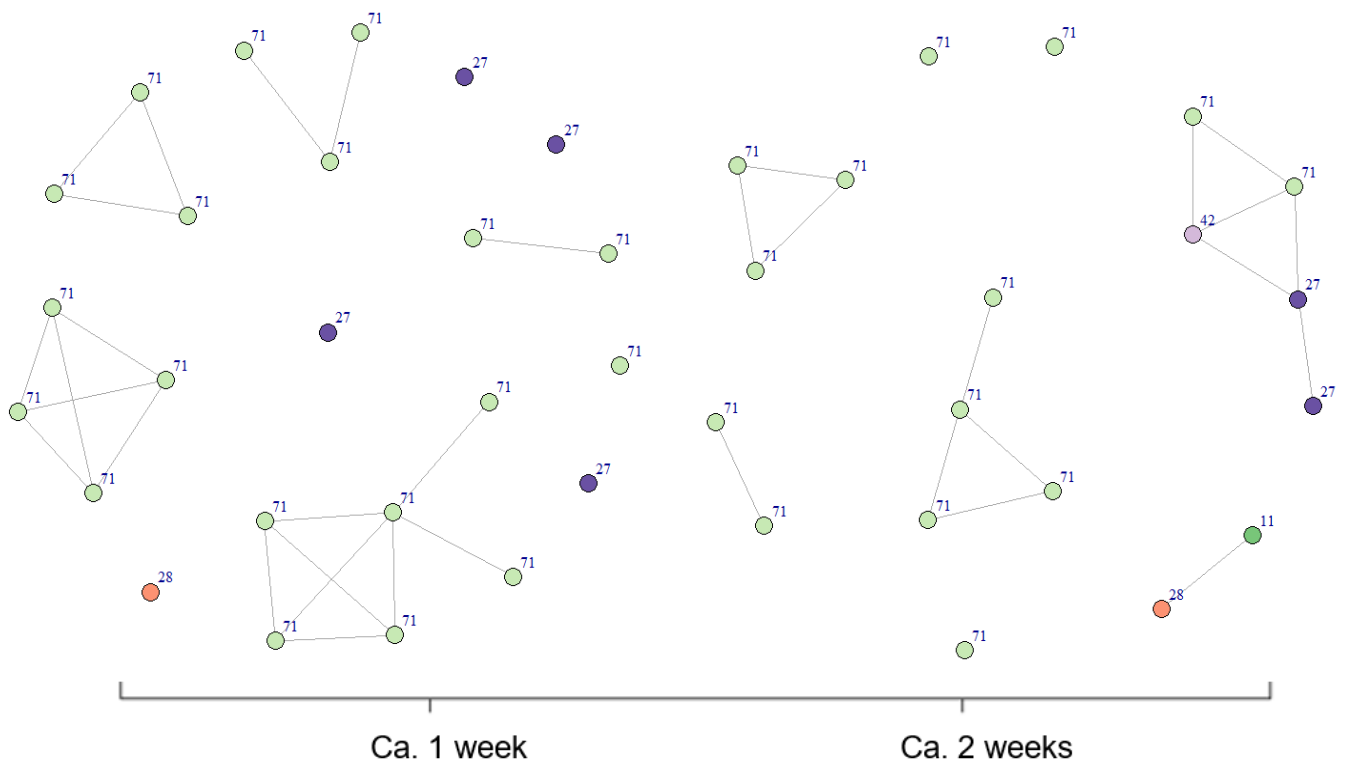


Figure S 10 - Roosting social networks obtained for colony 71 at different periods after the fire. Each individual (node) is coloured in accordance with the last colony they were captured at. Each individual also as the number of the last colony they were captured at next to it.