Roosting Dynamics: Assessing the 'pay-to-stay' hypothesis using a social network approach

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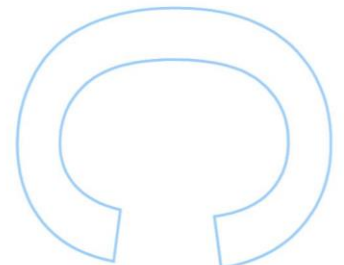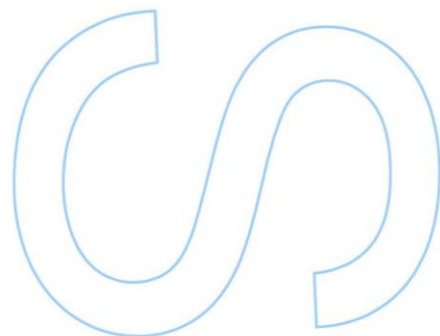
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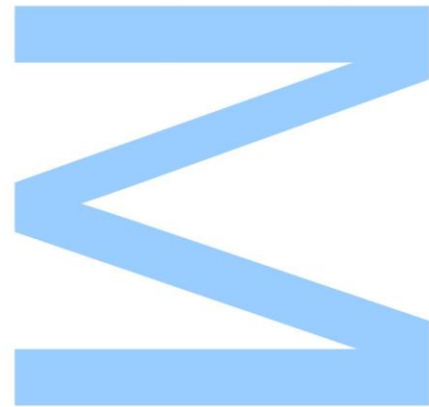
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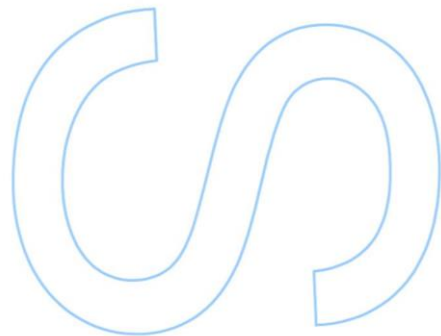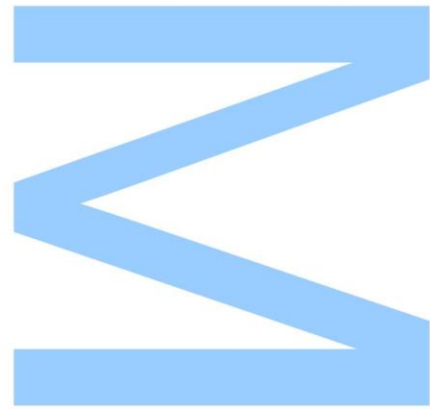FC FACULDADE DE CIÊNCIAS
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pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Duílio Silveira, 2014

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Abstract

In cooperatively breeding animals, sexually mature individuals postpone reproduction to assist other individuals with their breeding efforts. This costly cooperative behaviour is commonly explained by kin selection but could also be explained by natural or social selection if helping gives access to commodities beneficial for the fitness of the co-operators, the so called 'pay-to-stay' hypothesis. We investigated here whether helping-at-the-nest has the potential to be associated with social benefits in the sociable weaver *Philetairus socius.* This colonial cooperatively breeding bird builds massive communal nest structures that are used for breeding and for roosting throughout the year. A potentially important benefit of group membership in this species is the access to communal nests to roost during the winter, since temperatures frequently drop below 0 degrees Celsius and communal roosting effectively keeps the temperatures higher inside the nest. I measured this roosting behaviour in the field, described it and used a social network analysis approach to determine if roosting associations can be detected in this species. Lastly, I compared the roosting network with the breeding network constituted by the list of all individuals, helpers and breeders provisioning the nestlings.

My work showed that recording animals at roosting time is feasible even though some observations are missed due to low light conditions. It revealed that sociable weavers use different nests, and this is not related with sex or age. It also showed that there is some level of stability in the daily roosting associations, indicating that preferred roosting association exist in this species. Finally, my work documented a positive correlation between the roosting network and the nestling provisioning network. Together these results suggest that helping breeders is associated with having access to a roosting group, a result in agreement with the 'pay-to-stay' hypothesis.

Keywords: Cooperative breeding, communal roosting, 'pay-to-stay', social network.

Resumo

Em animais que apresentam comportamento de cria cooperativa, indivíduos sexualmente maduros adiam a sua própria reprodução de forma a ajudar outros indivíduos nos seus esforços reprodutivos. Este comportamento cooperativo apresenta um custo para o ajudante, sendo normalmente justificado segundo a teoria da seleção de parentesco, mas podendo também ser explicado como uma forma de seleção natural ou social, se o comportamento altruísta do indivíduo permitir aceder a comodidades que tragam benefícios que contribuam para melhorar a sua aptidão (i.e. *fitness)*. Quando estes benefícios resultam de acesso a um grupo social e/ou território, dá-se a esta hipótese o nome de '*pay-to-stay'*, indicando uma contrapartida, em forma de ajuda, pelos benefícios obtidos ao fazer parte de grupo. Neste trabalho investiguei se ajudar no ninho poderá garantir acesso a benefícios sociais na espécie Tecelão sociável *Philetairus socius*, uma ave colonial com hábitos de reprodução cooperativa, que constrói ninhos comunitários colossais que são utilizados para fins reprodutivos e de dormitório - *roosting-* durante todo o ano.

Um potencial benefício de elevada importância nesta espécie é o de pertencer a um grupo que garante acesso a um ninho comunitário durante o inverno, visto que as temperaturas podem descer abaixo dos 0 graus Celsius, e dormir com mais indivíduos dentro do ninho é uma forma eficiente de manter a temperatura mais elevada no interior do ninho. Este comportamento de *roosting* comunitário foi medido no campo, descrito e alvo de uma análise de rede social para determinar se é possível detetar conexões derivadas do comportamento de *roosting* nesta espécie. Por fim, foi feita uma comparação entre a rede social obtida para o comportamento de *roosting* com a rede social obtida a partir da informação que contém todos os indivíduos, incluindo ajudantes e casais reprodutores, que ajudaram no processo de alimentar as crias.

O meu trabalho demonstrou que obter dados sobre as dormidas através de gravações vídeo é possível para esta espécie, apesar de algumas observações poderem falhar devido às más condições de iluminação. Este trabalho revelou também que os tecelões sociáveis usam ninhos diferentes, e que esta característica não depende do sexo nem da idade. As associações diárias de *roosting* mostraram alguma estabilidade, traduzindo uma associação preferencial entre alguns indivíduos. Por fim, foi possível obter uma correlação positiva entre a rede referente às associações de *roosting* e a rede referente aos indivíduos que alimentam as crias. O conjunto destes resultados sugere que ajudar os casais reprodutores pode garantir acesso a dormir com um grupo maior de indivíduos, estando de acordo com a teoria '*pay-to-stay'*.

Palavras-chave: reprodução cooperativa, dormitório comunitário, '*pay-to-stay*', rede social.

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Figure 1S.Sample size for the comparison of networks between consecutive days of recording for colony 41. The red line divides the values obtained for the first round of recordings and for the second round of recordings.

Introduction

Animals frequently engage in altruistic behaviours, benefiting other individuals with no apparent benefits to themselves (Dugatkin. 2002; Schino and Aureli. 2010). This type of cooperative behaviour is widespread across different taxa, including insects, fish, birds, and mammals. Under the classic Darwinian view of evolution, this type of strategy seems paradoxical, since selfish behaviours, which rise the reproductive output of the individual, should be favoured against altruistic behaviours that are costly to the actor and beneficial to other individuals (West et al. 2007).

W.D. Hamilton formulated the first major breakthrough in solving this paradox by developing the inclusive fitness theory (Hamilton. 1964). This theory states that an individual can gain indirect fitness benefits by improving the reproductive output of close relatives with whom it shares a large quantity of genetic material. The fitness of the individual is therefore dependent on the individual reproductive output (direct fitness), as well as the reproductive output of its relatives (indirect fitness) (Hamilton. 1964). This information was translated into a simple rule (rb-c>0) showing that this type of behaviour will be selected if the fitness costs(c) for the individual are outweighed by the benefits(b), which are weighed by the degree of relatedness(r) between both individuals (Hamilton. 1964; West et al. 2007).

Helping close kin might allow the individual to gain direct and indirect fitness at the same time, but in nature there are also cases where cooperative behaviours take place between non-related individuals (Riehl. 2011) or even between individuals from different species (Barker. 2017). In these cases, cooperation is explained through direct fitness benefits that increase the survival or reproductive output of the actor. For example, engaging in cooperative mobbing brings higher survival chances for all group members, as the individuals join together in order to face the common predator, with all of the actors gaining in return direct fitness benefits (Wheatcroftand and Price. 2008).

Direct benefits can also be related to the choice of a sexual partner and be linked to sexual selection if more cooperative individuals are preferred as sexual mates and thereby have a higher probability of gaining access to reproduction, than non-cooperative individuals (Covas and Doutrelant. 2019). Direct benefits could also be obtained by social choice and reciprocation. For instance, studies with vampire bats (*Desmodus rotundus*) showed that individuals may share their blood meal with others that were not able to find a meal. Remarkably, individuals share with both kin and non-kin (Carter and Wilkinson. 2015) and it was shown that, when individuals shared meals with a larger number of partners, including non-kin, they are able to create a wider social network, which resulted

in greater chances of receiving a meal when they failed to obtain a blood meal than they would have if they only depended on close kin for back-up meals (Carter et al. 2017).

In cooperatively breeding species, non-breeding 'helpers' aid breeding couples by providing care and food to their young (Cockburn. 2006). Kin selection is a powerful explanation for this behaviour when this type of helping is directed towards kin. However, studies have shown that these breeding groups can also be composed by unrelated birds (Riehl. 2013), implying that other selective forces besides kin selection might be in play and demand further investigation. In addition, even in groups of kin, direct and indirect benefits might add up. One of the proposed mechanisms that may give direct benefits is the "pay-to-stay" (Mulder and Langmore. 1993; Koening and Walters. 2011). It suggests that helpers may tend for the nestlings in order to be tolerated in the territory of the dominant breeders (Gaston. 1978). This social preference of the territory owner can allow the helpers to have access to foraging grounds and shelter, foraging groups, and associated benefits including predator vigilance dilution. This is expected to improve the helpers' survival and might lead to increased access to breeding in the future (Taborsky et al. 2016). Previous studies have demonstrated that "paying the rent" is more common among non-related individuals (Zöttl et al. 2013; Clutton-Brock. 2009) but under harsh conditions, related individuals can also be subjected to this requirement of "paying rent" (Kokko. 2002). Another study performed in cichlids showed that helpers tend to help more if they are experimentally prevented from doing so, overcompensating the time in which they were not allowed to help, suggesting that an individual can have disadvantages if not engaging in cooperative behaviours, and that cooperative traits can be under social selection (Bergmüller and Taborsky. 2005). In fact, in this cichlid species, individuals that help more have a higher chance of being tolerated in a group's territory as a subordinate, gaining direct fitness benefits, such as protection from predators.

Currently the different forms of payoffs that individuals can receive from cooperation remain relatively unexplored. Access to communal roost, for example, is one of them. Communal roosting or huddling are commonly seen in different species (Gilbert et al. 2010). This type of behaviour consists of individuals gathering together and can bring different type of benefits, including a reduction in thermoregulation demands and a decrease in predation risk (Beauchamp. 1999). A known example of huddling is performed by the emperor penguin (*Aptenodytes forsteri*). A previous study showed that when huddling, the temperature inside the group often reaches values higher than 20 degrees Celsius, with the maximum temperature recorded being 37 degrees Celsius, in contrast with the constant environmental temperature with values below 0 degrees Celsius. (Guilbert et al. 2006). Another study performed with the common degu (*Octodon degus*), a small mammal, showed that huddling can also help to reduce the basal

metabolic rate, helping the individual to save energy. This reduction is proportional to the number of individuals huddling together, meaning that huddling in a larger group can bring more benefits than huddling in a smaller group (Nunez-Villegas. 2014). Another study on a cooperatively breeding passerine bird, the long-tailed tit (*Aegithalos caudatus*) showed that roosting in groups can help individuals to decrease their weight loss when facing low temperatures during night-time, but that this reduction in weight loss is asymmetrical and is related to the individual position inside the flock (Hatchwell et al. 2009). Similar results were obtained in white-backed mousebird (*Colius colius*), where communal roosting led to significant energy savings, and that these savings were dependent on the number of birds roosting together (McKechnie and Lovegrove. 2001).

In a first step to understand whether cooperation and roosting may be exchanged in some species (pay–to-stay hypothesis), I studied here the roosting behaviour of the sociable weaver. More precisely, we observed roosting to determine whether roosting associations are consistent and whether they are linked to breeding groups (i.e. the adult birds, breeders and respective helpers, providing to the nestlings). This bird species is a colonial and facultative cooperative breeder endemic to the semi-arid savannahs of southern Africa (Maclean. 1973; Mendelsohn and Anderson. 1997). This specie builds very large communal nests (colonies) with the colonies varying in size, from ca. 10-300 individuals living together in the nest in different nests (Maclean. 1973). These weavers can breed in pairs or with up to nine helpers, that will contribute to feed the nestlings (Covas et al. 2008; Fortuna et al. 2021). Although less common, unrelated birds can also be helpers (Covas et al. 2006). These nests are the place where breeding and roosting takes place all year round (Doutrelant and Covas. 2007). It is also known that the colony nest's temperature during the night is strongly related to the number of birds roosting together, suggesting that being in larger groups confers thermoregulatory benefits (Paquet et al. 2016). Nevertheless, it is still unknown if individuals of the same colony organize in smaller and consistent sub-units ("roosting group") or if roosting associations are randomly determined. Understanding the roosting dynamics is a crucial step to use this species as model for testing the predictions of the pay-to-stay hypothesis, specifically to test if roosting groups and breeding groups are correlated or if individuals that help more have more chances of being part of a roosting group.

In order to study the communal roosting behaviour in the sociable weaver, I first validated a method to collect roosting associations using video cameras. Collecting roosting associations is particularly challenging under wild conditions as most cooperative breeding birds roost during the low light part of the day where visual tags used for individual identification (e.g. colour rings) are hard to see. Furthermore, animals are usually unpredictable regarding the place chosen to roost. I took an intensive recording

approach in which all nests of the colony (i.e. all places where birds could roost) were recorded simultaneously and verified that an acceptable number of individuals could be recorded even when light conditions where low.

After validating the method for collecting roosting association data, I described the roosting behaviour considering the number of nests visited per individual, and what differences could arise when comparing individuals with different sex, different age and from different colonies. This description was followed by a social network analysis (Cantor et al. 2021). This type of analysis allows to describe the roosting connections between individuals, giving us information of the composition of the roosting groups, including the number of birds roosting together. The data collected through the observation of the interactions between animals, produces information that is translated into matrices, which can later be graphically displayed into nodes (individuals) and edges (connections between individuals) in order to facilitate results interpretation and enabling further processing (Krause et al. 2002). I used this approach to determine the consistency of the roosting groups composition by correlating networks taken on different days. Additionally, I also infer about the potential of roosting to be used as a payoff for helping behaviour (under the pay-to-stay hypothesis) by correlating the roosting networks with the helping networks. I predict that if helping can bring direct benefits through roosting to co-operators, the individuals that are found feeding the same chicks should also be found roosting together.

Methods

Study species and field methods

Sociable weavers are cooperative breeders, with non-breeding individuals assisting to raise the offspring of others (Maclean 1973). The breeding group size is variable, composed of only the breeding couple, or the breeding couple plus up to 9 helpers (Covas et al. 2008; Fortuna et al 2021). Usually, helpers are the offspring of the previous year, but up to 20% can be distant relatives or even unrelated individuals (Covas et al. 2006). Females typically help during the first year, while older unrelated individuals are mainly males (Doutrelant et al. 2004). Helping predominantly consists of food provision, but it also consists of brooding, nest sanitation and nest building (Ferreira. 2015). Breeding activity and success is highly dependent on food availability, which is mostly determined by rainfall, making rainfall one of the most important factors for reproduction (Maclean. 1973c; Covas et al. 2008). The sociable weaver has a diet consisting mostly of seeds and insects (Maclean. 1973c).

This project was part of a long-term research project that investigates the cooperative behaviour and social dynamics of the sociable weaver. It was conducted at Benfontein Game Farm near Kimberley in the Northern Cape Province, South Africa. In the study site (of approximately 18 km^2), there are ca. 20 sociable weaver colonies, of which 15 are included in the long-term research and 2 of those were used in this work. Every year, these 15 colonies are captured using mist nets, usually before the beginning of the breeding season. During these captures, all individuals are ringed with a unique numerical metal ring and three colour rings, providing a unique colour combination for each individual (previously ringed individuals are recorded and any missing rings are replaced). They are also weighed, measured (tarsus and wings), and a blood sample is collected in order to genetically determine sex, parentage and relatedness. Sex was determined by amplification of chromo-helicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers (Griffiths et al. 1998). The genetic analyses were conducted at CTM (Center of Molecular Tests), CIBIO (Vairão).

During the breeding season, that usually starts in September and lasts for 6-8 months (sometimes longer), all colonies are inspected every three days in order to detect the appearance of new clutches. Nests with new clutches are then considered active and are monitored to determine the hatching date, allowing to attribute a precise age to the nestlings. When nestlings are 9 days old, the nest is visited in order to ring the birds with a unique metal ring, take a blood sample and weigh the chicks. When chicks are 17 days old, the nests are visited again in order to ring the birds with a unique colour combination of 3 rings, and wing and tarsus are also measured. This colour combination is essential, allowing individual identification in video recordings. All active nests are filmed for four hours (over two days) during the incubation stage, and for 4 to 8 hours (over two to four days) during the nestling stage. This allows to determine the breeding group identity and size, including the breeding couple and the number of helpers if there is any. These recordings also allow to quantify the helpers' investment in feeding the nestlings. Females usually lay 3 to 4 eggs asynchronously per clutch (1 per day) and can lay several clutches per breeding season, followed by an incubation period of 15 days (Maclean. 1973a; Covas et al. 2008).

Due to the covid-19 pandemic, and associated traveling restrictions, the field season of 2020/2021 was strongly impacted. The annual colony captures that require a large team of people could not be conducted. Since one of the main functions of the annual captures is to colour-ring any new immigrants and to replace missing rings, the failure to conduct captures meant that our capacity to individually identify the birds in the population was, to some extent, compromised, and that my work was directly impacted. In addition, I was

only able to go to the field for a month, from the 14th of November 2020 to the 14th of December 2020, instead of the 3 months that were initially planned. For these reasons, I was only able to use two study colonies for my project, colony 41, which we were able to capture while I was in the field, and colony 20, which was captured about 3 months later in March 2021.

Roosting data

Roosting data was collected from video recordings using Sony Handycams HD, during the sociable weavers breeding season. Each single nest had to be filmed by a single camera in order to obtain recordings of sufficient quality. We targeted two colonies of medium size (32 and 38 individuals), given the range size distribution of colonies in the study area.

Before starting the roosting protocol, we did a full nest check for both colonies to assess whether some of these nests were not active and should thus not be part of the study. All nests have a tag number assigned. For these nest checks, we used an extendable LED lighted mirror to be able to look inside each nest and determine if the nest was active or not. We were able to distinguish abandoned nests from used ones as they start to lose their usual shape and form, and some of them can even show evidence of being used by other bird species, most commonly, the Red-headed finch (*Amadina erythrocephala*).

Each colony was subjected to 10 days of recordings, divided into two rounds. In the case of colony 20, 5 days with a 10-day break followed by another 5 days, and in the case of colony 41, 4 days of recordings with a 10-day break followed by another 6 days of recordings. The break between both rounds of filming allowed us to test if the roosting connections between individuals were stable with period of time.

For each day of recordings, we set-up the 21 cameras using tripods (see Figure 1), each one pointing to the entrance of a specific nest (see Figure 2). We recorded for about 2 hours before sunset, when the sociable weavers started to get back to the nest to roost together. The process was extremely meticulous because when dealing with so many cameras it is easy to lose track of which ones are recording and which ones are not. To avoid mistakes, we first pointed every single camera to the intended nest (a planning was made every day before going to the field) leaving the screen opened. After that, we would go camera by camera and start the recording, in order to see if all the cameras were still pointing to the correct nest. After starting the recording, the colony number and the nest number were mentioned in the beginning of the recording in order to identify the

video. After this process, the screen was closed meaning that the recording had started. After all cameras had started recording, we shouted the date and time. This way, if for any given reason we lost track of the recording, we would be able to identify it since for each video we would have the date, time, colony number and nest number. Some days of recording were also complemented with field observations to better understand, on the personal level, the sociable weaver behaviour.

Figure1. Camera set up used for roosting behaviour recording.

Figure 2. Ideal camera recording of a sociable weaver nest entrance.

After sunset and once it got dark, we picked up the cameras using only red light to avoid disturbing the weavers in their nest. In the morning of the following day, all the recordings were downloaded to a specific folder and were attributed a unique name containing the day, time of the beginning of recording, the nest number and the colony number.

Video analysis

The aim of the video analysis was to identify the colour combination of every bird that entered or left a nest, as well as when these movements are made. In order to achieve this task, the first step was marking (by noting the time) every recording for the bird's movement. This marking was done using an artificial intelligence program developed by Liliana R. Silva that produces a "Bookmark" containing the recording time every time it detects a bird entering or leaving the video frame. This represents a significant decrease in the time required for these analyses, allowing to focus only on the frames with activity instead of watching the 2 hours of recording obtained for the 21 nests recorded per day.

After having all the videos marked, we noted the colour ring of all roosting birds in an excel file for each of the nests for each specific day. We used this file to record the time when a bird enters the nest, as well when it exits the nest, attributing the colour ring combination in order to identify the bird, every time it was possible. When bird identification was not complete, we would attribute a partial colour combination or an unknown identification if full identification was not possible. We obtained 10.2% of incomplete or unknown identifications. These were mainly a result of incomplete colour combinations or the cameras, but there were also cases when the sociable weavers were active until later in the day when the visual identification is constrained by the light availability.

After analysing all the videos, I crossed the information obtained with the sociable weaver project-s long term database in order to attribute the unique metal ring number to every sociable weaver that we completely identified using the colour ring combination. Obtaining the metal ring number allowed us to have access to important information for each individual, including sex and age.

Statistical analyses

General roosting description

I started by describing the roosting dynamics of the sociable weaver by determining the number of individuals roosting in the colonies' nests as well as their age category (juvenile or adult) and their sex distribution. I then estimated the number of different nests that each individual used. Having found that sociable weavers can use multiple nests to roost (see results) I used Wilcoxon nonparametric test to test if there were statistically significant differences between individuals with different sex.

Roosting Social Network Analysis

In order to carry out social network analyses, the most important step is to define the parameter that will be used to create the edges that connect the nodes of the social network. This edge definition is the criterium used to define what can be considered a connection (edge) between two individuals (nodes) (Farine et al. 2015). The edges represent an interaction or connection between individuals, placing them in specific positions inside the group, allowing to test if this positioning inside the network is influence by the individual characteristics, or what type of individuals tend to associate (Farine et al. 2015). Edge definition can be complex, and the decision of which parameter used to define these edges, should take into account the a priori knowledge of the study species, and should always be independent from the hypothesis that the network will analyse (Ferreira et al. 2020). Networks can be constructed using any type of social interaction and can give information regarding the frequency or intensity of the interaction, their direction and the order in which they took place (Croft et al. 2008). Building a binary network is also possible by defining a threshold that by being crossed will translate into an association, but by not being crossed, will translate into the absence of an association (Farine et al. 2015).

The ideal criteria would have been to consider the connection that existed between two individuals if, by the end of the camera recording, they were together on the same nest. We found out that this was not possible due to the number of unknown identifications of the roosting individuals (673 identifications/10.2%). This number is high because for example, when we know the identity of 3 sociable weavers inside a nest, it only takes one individual exiting the nest, when is too dark to identify it, to lose track of which individuals stayed inside.

We decided to use a time-overlap criteria to create the edges of our social networks. From previous studies (Maclean, 1967) and our own observations, we know that the sociable weaver is prone to aggressive behaviour towards apparent "non-nest" members. This aggressive behaviour is common and happens quickly, meaning that "non-nest" members are attacked as soon as they are detected inside the "wrong nest" and are forced to exit it. Hence, we decided to create the edges considering the cumulative overlap time that two individuals stayed together inside the same nest.

We first converted all entrances and exits time for all successful individual identifications into decimal minutes using the R package "chron". In the previous case of having 3 identified sociable weavers inside a nest, followed by an unidentified exit of one of the individuals, we attributed the exiting time of the unknown sociable weaver to all three

individuals that were inside. This allowed us to have an entrance and exit time to all known individuals and to estimate a minimum time inside the nest.

Having all the times in decimal minutes, enabled us to calculate the cumulative overlap time between every sociable weaver, allowing to use this parameter to build the edges of the social network connecting the nodes (represented by a single individual).

I then used a binary approach in which a time threshold defined if a connection between two individuals existed or not. This was done since if two sociable weavers do not tolerate each other they will resort to attacks to expel one another, and this often happens within seconds. 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 et al. 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. In order to determine this time threshold, we created 10 different networks for each of the two colonies, one for each day of recording. This is possible by converting the overlap times into a matrix. When comparing the social network of two different days, the two matrixes that originated each of the networks must have exactly the same size and the same individuals. The sample size when comparing two social networks, is made of all the common individuals seen in both days, meaning that if an individual is seen in only one of these two days, it is left out of the sample. For this reason, I calculated the proportion of days seen for each individual.

Although I expected that a small-time threshold would be suitable for considering individuals to be or not connect it was not possible to know a priori exactly which time to use. On the one hand, using a too small threshold could capture much noise from the dataset (e.g. considered two individuals that attacked each other but did not do so immediately after entering the nest). While using a value too large might exclude potentially associated individuals from nests in which an "unknown" bird left very early in the recording, making the data about the birds remaining in the nest useless. I therefore built several networks that differed on the time threshold used to convert the edges to a binary value of 0 or 1 (0.5, 1, 1.5, 2, 2.5, 3, 6, 9 and 12 minutes). I then correlated networks collected on the first and second day of the data collection and of the same time threshold using mantel correlation tests (Smouse et al. 1986). The mantel test can give a correlation value ranging from -1 to 1. A value above 0 is considered a positive relationship. I expected that if roosting associations are non-random that networks collected on day 1 and day 2 should be correlated and the time threshold with the highest correlation value should be the most suitable one to use as noise in the data is expected

to produce smaller correlation coefficients. I ran a similar test, by comparing all the daily networks with the network obtained from day 1 of filming, as an alternative way of testing consistency.

All the overlaps time turned in a similar positive correlation, so we decided to use the time that showed the highest correlation value (see results). This time threshold was then used to test the stability throughout the 10 days of filming and for relating nestling provisioning network with roosting network (see below). I determined the stability of the roosting associations by correlating pairs of networks collected on consecutive days (including pairs of networks that were crossed by the 10 days interval).

Nestling provisioning network vs Roosting network

A network of nestling provisioning visits was created using the data obtained from the daily protocol on reproduction monitoring used for the long-term research project. I used the individual identification and behavioural annotations of the analysed videos obtained around the D9 (i.e. 9 days after the chicks hatched) and D17 of the chick of the closest breeding event. We created this network using the information obtained in the same time period of my roosting project. This was only possible to do for colony 20, were we had information of nestling provisioning for 7 different nests. In the case of colony 41, this type of analysis was not possible to preform since there was no nests with chicks during this time period. To build the edges of the feeding visits network, we defined that a connection between two individuals existed if they were seen providing the same chicks, which is an indication of belonging to the same breeding group. Similar to the previous roosting network, the matrix values were also composed of 1 and 0, with 1 representing a connection, and 0 representing the lack of connection. The feeding visits network was then compared to the Roosting network using the mantel correlation test. After obtaining this nestling provisioning network, I also built a network containing all roosting data and thresholding the edges with the best time value obtained in the analysis described above. I then used the mantel correlation test to correlate the nestling provisioning network with the roosting network.

All statistical analyses were conducted in R v.4.0.5.

Results

General roosting description

For roosting I was able to collect data on a total of 70 individuals from 42 nests. Table 1 describes how these were distributed in the two studied colonies according to age and sex.

Table 1. Description of the information extracted from the roosting sample.

	Number of individuals	Number of adult birds (>200 days-old)	Number of chicks (<200 days-old)	% Females
Colony 20	38	26	12	52.63
Colony 41	32	32	0	50
Total	70	58	12	51.51

In both colonies studied, the majority of individuals was seen using more than one nest, with some individuals visiting up to 10 different nests during roosting time (Figure 3).
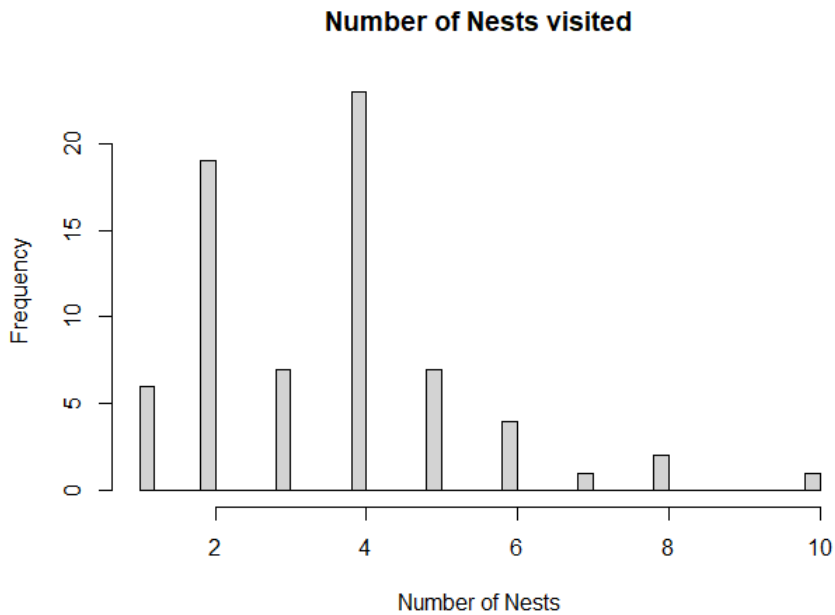
Number of Nests visited

Figure 3. Number of nests visited per individual. Frequency represents the number of individuals that visited a specific number of nests during the 10 days of recording.

There were no significant sex differences in the number of nests used by adult sociable weavers (Fig.4 Wilcoxon test p=0.2594) and adults did not significantly visit more nests than the juvenile birds although there was a positive trend (Fig.4 Wilcoxon test p=0.2101).
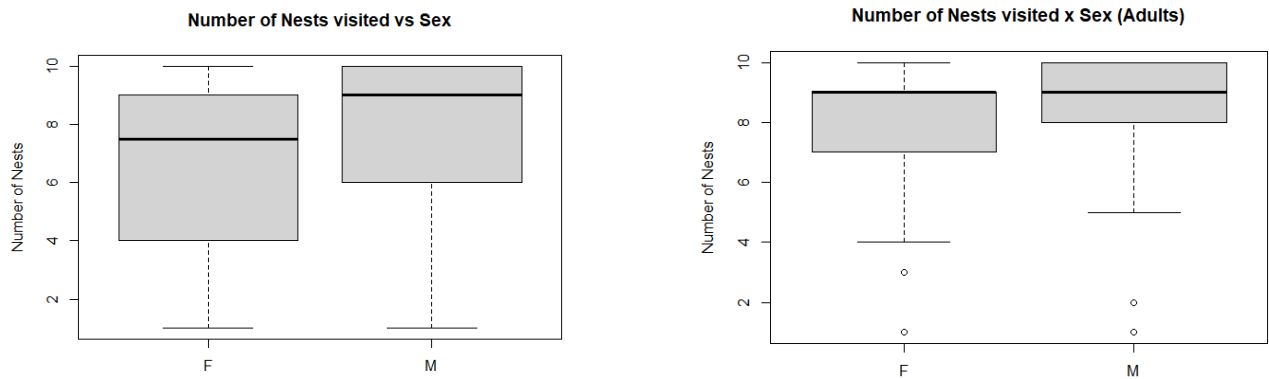

Figure 4. Box plot representation for the number of nests visited per individual considering sex (F=Female, M=Male). On the left, comparison between the entire sample (p= 0.2594), on the right, comparison using only adult individuals (p=0.2101). The gray box represents the central quartiles, and the black line the median. The horizontal line represents the range of the values, with the outliers being depicted as dots.

This was reflected in the differences between colony 20 with colony 41 (colony 20 was composed of 26 adults and 12 chicks, while colony 41 was only composed by adults: Wilcoxon test p=0.0082; Fig.5).
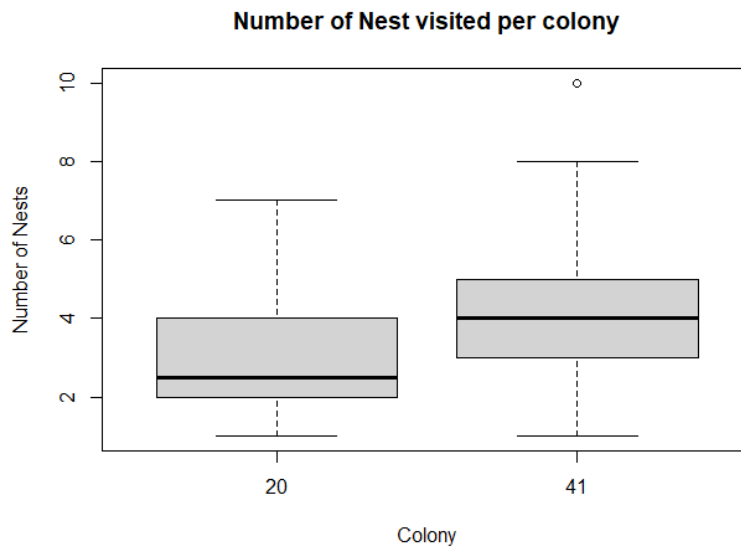

Figure 5. Box plot representation for the comparison of the number of nests visited per individual for each colony (p=0.0082). The gray box represents the central quartiles, and the black line the median. The horizontal line represents the range of the values, with the outliers being depicted as dots.

Roosting social network analysis

Analysing Figure 6, it's possible to see that only 15 out of 70 individuals were seen every day of filming, however most of the birds were seen in the recordings in more than 50% of the days.

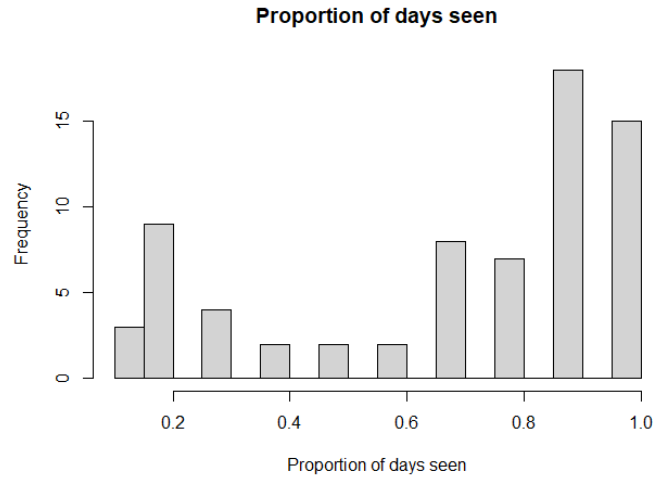**Proportion of days seen**

Figure 6. Proportion of days seen per individual throughout the 10 days of recording.

Having all the overlap times calculated, I started by estimating the correlation value between social networks of consecutive days, using different overlap times thresholds to create the daily social networks. In Figure 7 we have an example of the comparison between network of day 1 and day 2 for colony 41, with the correlation values for different time thresholds.
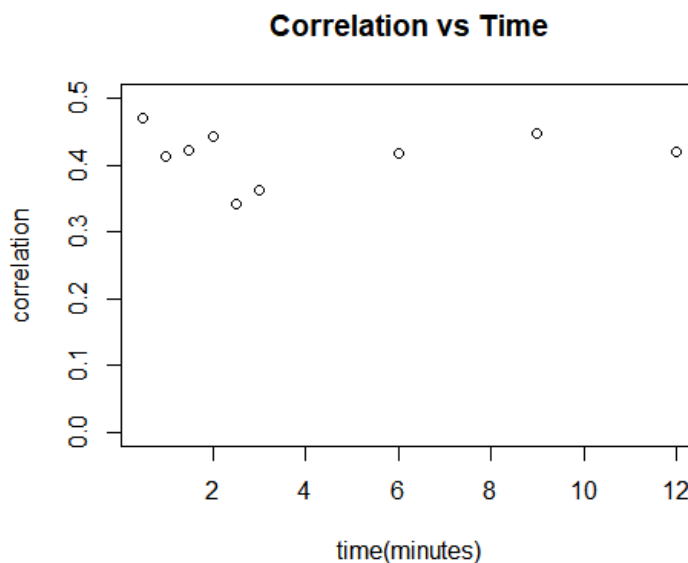
Correlation vs Time

Figure 7. Correlation between the daily social network of day 1 and day 2 of recording for colony 41, using different overlap time thresholds to build the social networks.

The correlation values were always positive, with 0.5 minutes being the time value with the highest correlation. This was also true for colony 20.

To test the stability of the roosting networks throughout all days of filming, I first applied the mantel correlation test for consecutive days of filming. The results are shown in figure 8, where each dot represents the correlation value for two consecutive days. All correlations turned in a positive value for both study colonies, showing that a percentage of the network structure is kept between days.

Colony 41   **Colony 20**
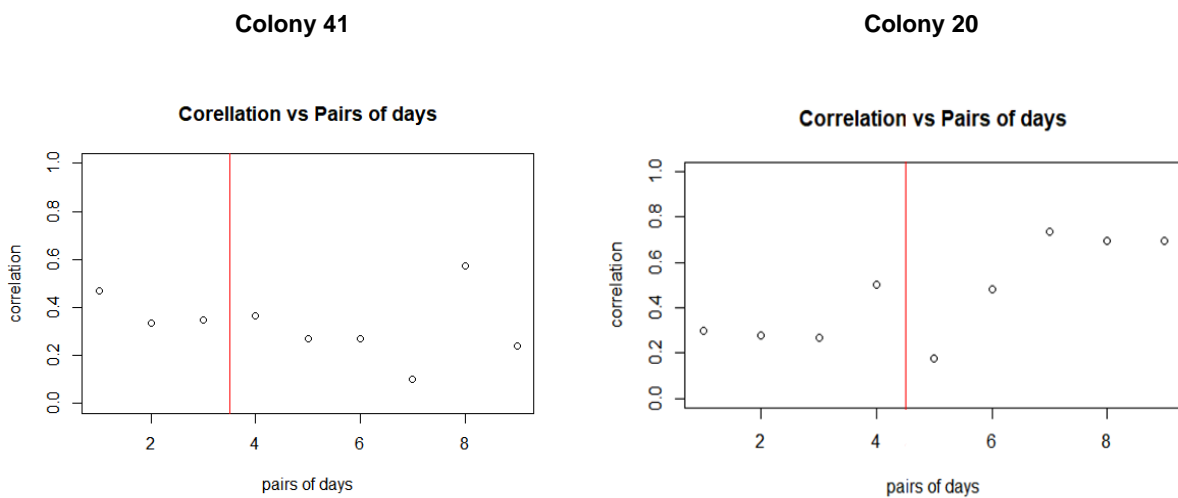

Figure 8. Correlation values obtained for the comparison between consecutive days of recording for colony 41 and colony 20 using the mantel correlation test. The red line divides the values obtained for the first round of recordings and for the second round of recordings.

As an alternative way of testing consistency, I ran a similar test, but this time I compared all the daily networks with the network obtained from day 1 of filming. The results are shown in Figure 9, where each dot is the correlation between the network of day 1 and the networks obtained from the rest of the days. As in the previous analysis, all correlations were positive, showing that a percentage of the network is kept from day 1 of filming until the last day of filming.
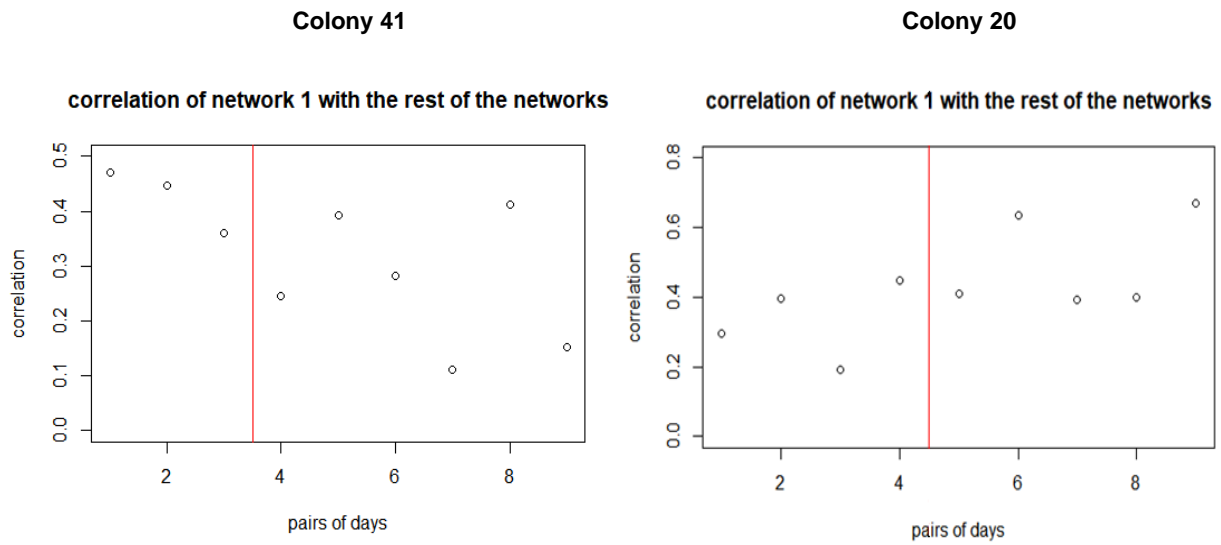
Colony 41

Colony 20

Figure 9. Correlation values obtained for the comparison between day 1 of recording and the rest of the days, for colony 41 and colony 20 using the mantel correlation test. The red line divides the values obtained for the first round of recordings and for the second round of recordings.

Both analyses show some stability between the daily roosting networks, showing that the connections between individuals are not random.

The last step was to build the roosting social network using the overlap time considering all ten days of filming. The matrix that originated the following networks was created using the sum of all overlap times from the ten days, and the 0.5 minutes time threshold. This allowed to build a social network with every successfully identified individual (throughout the ten days) being depicted in the graphic representation.

The network for colony 20 is shown in figure 10, and for colony 41 on figure 11. In these figures, a group of individuals surrounded by different coloured ellipses represent different roosting groups. It is possible to detect different roosting groups inside the same colony in both cases, and in the case of colony 41, 2 isolated individuals.
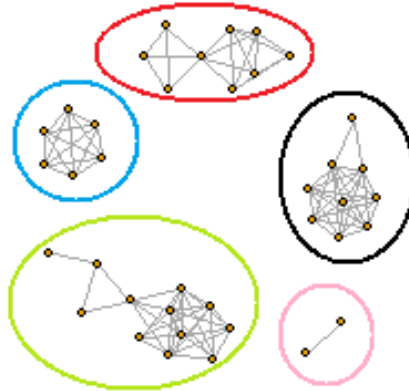
Colony 20

Figure 10. Graphic representation of the roosting social network obtained for colony 20 using a 0.5-minute threshold. Coloured ellipses represent different roosting groups.

Colony 41
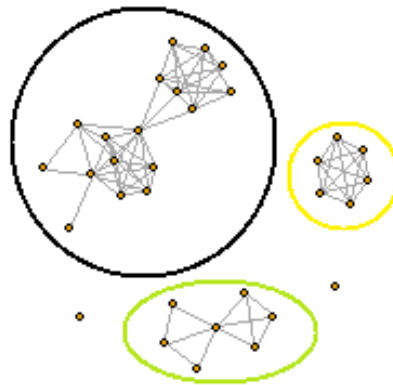
Figure 11. Graphic representation of the roosting social network obtained for colony 41 using a 0.5-minute threshold. Coloured ellipses represent different roosting groups.

Nestling provisioning network vs Roosting network

After building the roosting social network, I used the information from the nestling provisioning data to create a network and compare it with the previous obtained roosting network. This was only possible to do for colony 20, since colony 41 did not produce any chicks in this season, consequently not having information to build a nestling feeding network.

In order to compare both networks for colony 20, I ran a correlation test obtaining a positive correlation value of 0.36. In Figure 12 we have the graphic representation of both networks side by side using the 0.5 minutes threshold. The individuals have the same spatial coordinates in both networks, meaning that each individual is depicted in the same edge in both the nestling provisioning network, and the roosting network.

Nestling provisioning Network   **Roosting Network**
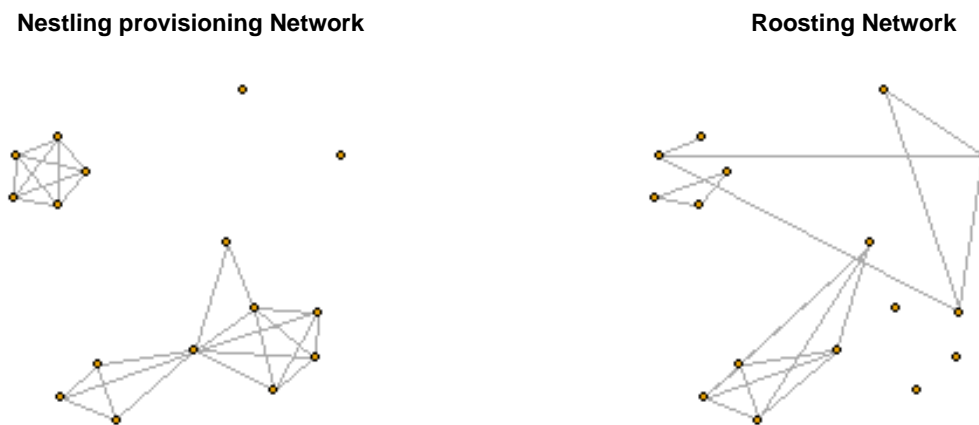

Figure 12. Graphic representation of the nestling provisioning network and the roosting network using the 0. 5 minute threshold. Nodes that ocuppie the same position in both networks represent the same individual.

Discussion

The aim of this project was to study the social associations at roosting in order to better understand the social component of this important behaviour. In addition, I was interested in using these results to investigate the "pay-to-stay" hypothesis, by comparing the roosting network with the social networks obtained from another cooperative behaviours (helping-at-the-nest). I found that recording sociable weavers at roosting time is a valid way of obtaining roosting associations, even though some identifications are missed due to low light conditions or incomplete ring combinations. I found that sociable weavers use different nests, but this is not related with sex or age. I also found some level of stability in the roosting associations, even though some individuals moved between nests and roosting groups. Despite the limited data, I also found indication of a roosting group size limitation similar to the breeding group size limitation. Comparing the roosting and nestling provisioning social networks, suggested an important relationship between roosting associations and the helping behaviour of nestling provisioning, indicating that a "pay-to-stay" might be relevant in this species.

The number of nests visited per individual ranged from 1 to 10 nests, with most birds using 2-4 nests. Sociable weavers are organized in a stable hierarchical structure, showing different ranks of dominance (Margaux et al. 2015). Having access to a roosting nest and a roosting group is essential to this weaver species, as it buffers them from the drop in outside temperatures at night (White et al. 1975). In addition, these benefits are more important when roosting with a larger group (Paquet et al. 2016). It's possible that nest access is achieve through dominance, with the most dominant individuals having access to a better nest and a larger roosting group. This would make the more dominant individuals sticking to their familiar nests and roosting group. On the other hand, if less dominant individuals have a lower chance of having access to a good nest or roosting group, they would have to sleep in any nest they could find, justifying the individuals with a higher number of nests visited. This means that in spite of some stability in roosting associations, I also found that for some individuals the roosting connections can be complex and hard to track

For the analyses of the roosting social network, I started by evaluating the proportion of days seen for each individual. Considering the total sample size of 70 individuals, only 15 individuals (21.4%) were seen in all 10 days of recording. This is likely to arise in part from the difficulty in detecting the colour rings under low light conditions of all individuals and not from a real turnover of individuals at the studied colonies. Nevertheless, I was still able to identify more than 89% of the birds in most days, which was enough to further infer about roosting consistency and the correlation between nestling provisioning and roosting.

This is, however, important to consider when looking at the roosting connection stability. Our results indicated that the correlation values when comparing daily networks were positive, and these positive values indicate that the roosting connections obtained between the different days are not random. A correlation value of 0.4 (for example) is high considering all the noise that the data can have, such as missing colour rings and miss identifications (Bell et al. 2009). My results also show that individuals probably associate with larger groups than the ones they sleep with on a single day. Considering another cooperative breeding bird (the carrion crow), some individuals can be group members but are not always seen feeding the chicks or only appear when other helpers are missing (de la Cruz et al. 2019). A similar case can happen with the sociable weaver, where individuals might change their roosting associations between days, but probably only change them between a selective number of individuals. A social bet-hedging strategy can also be present, considering that the individuals may try to create roosting connections in order to guarantee access to a roosting group by having a wider network

(Carter et al. 2017). My network analysis shows the existence of roosting groups as expected, but this hypothesis needs further investigation.

The difference in correlation values between days might have arisen from the sample sizes, since our network comparisons are based on the individuals that are identified on both days of recording. For example, we can identify 25 individuals but might have only identified 20 individuals that appear in both days, which will lead to a final sample size of 20 individuals for the network comparisons. This can have an impact on the correlation values obtained, since we obtained a very variable sample size between days (see supplementary materials). Nevertheless, the positive correlations obtained, which reached high values in some cases (for example, for colony 20 we obtained some correlation values reaching almost 0.8), are a good indicator of no-random association for roosting behaviour in this species. These roosting connections stability may indicate that the sociable weaver's roosting access does not bring temporary benefits, but rather an access to an important stable benefit. It's possible that these connections are maintained in a similar way as the cichlids (Bergmüller and Taborsky. 2005), with the individuals that engage in more helping behaviours, being tolerated in the dominant individual nest and roosting group, with this helping behaviour being constant rather than ephemeral, in order to maintain this benefit (pay-to-stay).

When comparing the roosting and nestling provisioning networks I obtained a correlation value of approximately 0.36. This indicates a non-random relation between both networks and indicates that the nestling provision behaviour can be connected to the roosting behaviour. It is important to mention that this result is based on a sample size of 16 individuals, because the sample size only comprises the individuals that appear in the roosting network and in the nestling provision network. Nevertheless, I found a possible connection between a costly helping behaviour (nestling provisioning) and a directly beneficial behaviour (roosting in group), which is consistent with a role for "the pay-to-stay" hypothesis as a mechanism underlying this cost-benefit trade off.

The results obtained here indicate that the roosting protocol created during this project and the criteria used to build the networks are adequate to study roosting associations in this species. This protocol is now being implemented. Running this protocol in the long-term will help, firstly, obtaining a higher sample size as more colonies can be analysed, for a longer period of time. Instead of comparing daily networks, there will be the possibility of comparing, for example, a network build from 10 days of recording in September, with another network build from 10 days of recording in October. This will increase the probability of having recorded all individuals from the colony and will allow to make comparisons between networks with much robust data and a higher sample

size. Besides that, roosting network stability can be tested for longer time periods and can be compared between the breeding season and the non-breeding season, as some differences are expected to be found between both seasons. With the genetic information and the relatedness information, it will also be possible to assess the importance of relatedness for social associations and understand if unrelated birds or immigrants are integrated into the new colony.

Moreover, comparing social networks from different cooperative behaviours will finally give the possibility of testing the "pay-to-stay" hypothesis. Testing this hypothesis will give important information regarding the cost-benefit relationship underlying cooperative behaviours. Direct benefits can be obtained by kin and non-kin individuals, so it is of major importance to understand if the "pay-to-stay" hypothesis applies to kin and non-kin, and if so, whether non-kin helpers have to help more in order to gain the same benefits as related helper.

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Supplementary material

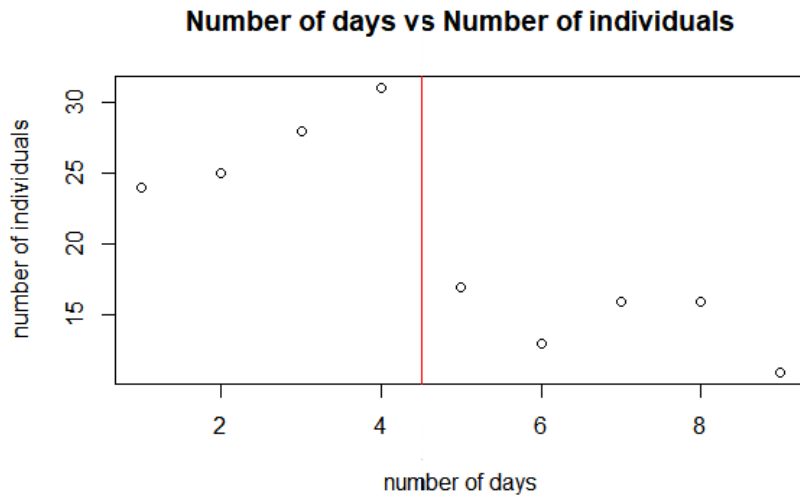**Number of days vs Number of individuals**

Figure 1S. Sample size for the comparison of networks between consecutive days of recording for colony 20. The red line divides the values obtained for the first round of recordings and for the second round of recordings.
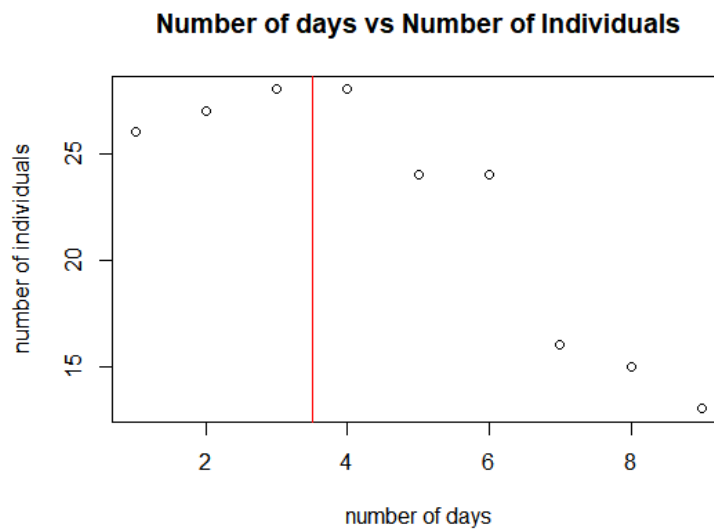
Number of days vs Number of Individuals

Figure 2S. Sample size for the comparison of networks between consecutive days of recording for colony 41. The red line divides the values obtained for the first round of recordings and for the second round of recordings.