UNIVERSITY OF CAPE TOWN

Dominance, social organisation and cooperation in the sociable weaver (*Philetairus socius*)

PhD Thesis

Margaux Rat
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Percy FitzPatrick Institute of African Ornithology

Department of Biological Sciences

University of Cape Town

Supervised by Prof Peter Ryan

Co-supervised by Dr Rita Covas, Dr Claire Doutrelant and Dr René E. van Dijk

‘If we knew what it was we were doing, it would not be called

research, would it’

Albert Einstein

Abstract

Sociality and cooperation are universal features of life, yet cooperative societies are highly vulnerable to conflicts-of-interests which may lead to societal collapse. Dominance may function as a central mechanism behind the maintenance of cooperative societies, because it may reduce conflict by the establishment of hierarchies, and may act in concert with kin-selection, enforcement or signalling mechanisms to promote cooperation. Yet, the significance of dominance in the evolutionary routes that maintain cooperation remains poorly understood (Chapter 1). Sociable weavers *Philetairus socius* are highly social, cooperative passerines. The species is particularly prone to conflicts because of their year-round coloniality and thus year-round sharing of resources. Using extensive field-data on individual behaviour, I examine in this thesis whether dominance may mitigate conflict and maintain cooperation, and how it may inform our understanding of the evolutionary mechanisms underlying cooperation. In Chapter 2, I investigate whether hierarchies and phenotypic traits allowing the assessment of social status may have evolved to mediate conflicts. I show that weavers establish ordered hierarchies within colonies and that the size of a melanin-based plumage trait, the black bib, is correlated to social status. In Chapter 3, experimental manipulation supports my proposition of a status-signalling function of the bib. In Chapter 4, I investigate the benefits of achieving high social status and whether these are shared with relatives through nepotism. Both dominants and their offspring gain enhanced access to resources. Dominants had more access to breeding positions, although this was not reflected by increased reproductive success. In Chapter 5, I explore how dominance and kinship predict individual cooperativeness to three tasks, nestling provisioning, nest construction and predator mobbing. I find that both explain variation in cooperativeness, yet some results follow opposite directions, revealing multiple routes to cooperation. Finally, in Chapter 6, I examine how dominance and kinship structure weavers' social network and whether network position are linked to cooperativeness. Social network analyses reveal that more central birds are more, related, dominant and cooperative. Chapter 7 concludes that dominance acts in concert with kinship to promote the societal lifestyle of sociable weavers highlighting the potential significance of dominance in the evolution of cooperation.

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PAPER ARISING FROM THIS THESIS:

The following manuscript has been accepted for publication prior to the submission of this Thesis and is included in this PhD thesis as Chapter 2. This manuscript has multiple authors, each of which contributed in some way to its production. I designed methods for data collection in consultation with my supervisors, Dr. Covas, Dr. Doutrelant and Dr. van Dijk. Data collection and analyses were entirely performed by myself. I redacted alone the first version of the manuscript which I subsequently revised several time, according to the modifications advised by the co-authors and by the reviewers, until publication.

Contributions: Rat 70%, van Dijk 12%, Covas 8%, Doutrelant 12%

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DECLARATION

This thesis describes original research undertaken towards a Ph.D. degree at the Percy FitzPatrick Institute, University of Cape Town, which has not been submitted in any form towards a degree at any other university. I declare that this thesis is the result of my own research, and except where indicated by a specific reference in the text, contains no work in collaboration with others. The text does not exceed 80 000 words. I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes. Any views expressed in this thesis are those of the author.

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Abstract

Chapter 1

General introduction

‘Surely the mitochondrion that first entered another cell was not thinking about the future benefits of cooperation and integration; it was merely trying to make its own living in a tough Darwinian world’

Stephen Jay Gould

Sociality is widespread and diverse in nature. Birds gather for migration or in winter flocks, the salmon or sardine runs regroup thousands of individuals over great distances. Social insects communally build their nest and live in colonies of hundreds of individuals. Giant herds in search of water can be constituted by hundreds of ungulates such as blue wildebeests (*Connochaetes taurinus*) or caribous (*Rangifer tarandus*). Sociality is also diverse because it integrates a wide range of interactions. A monkey grooming its conspecific, a bee dancing for its sisters, or a marmot calling to warn its relatives about a predator are all social behaviour. Furthermore, sociality can be found in less intuitive forms such as genes or cells involving less suspected interactions. Indeed, sociality occurs at any level of life, from the most primitive unicellular forms, such as bacterial populations (West et al. 2006b), to highly complex and cognitively developed organisms such as primates, including humans (Clutton-Brock et al. 2009). But what are the benefits and indeed the costs of such aggregations.

1.1 Benefits of sociality – emphasis on cooperation

The benefits of gathering in large groups are multiple and have some obvious advantages, such as enhanced defense against predators as a result of greater vigilance, because of a confusion effect caused by high density of individuals (Bertram 1980; Elgar 1989; McNamara and Houston 1992), or because of a dilution of predation risk (Foster and Treherne 1981). Large groups may also perform better at locating food, which is a potential evolutionary pathway to the evolution of colonialism in seabirds (Ward and Zahavi 1973; Buckley 1997) as locating a school of fish in vast oceans is finding a needle in a haystack. Saving energy is also a benefit of sociality. Japanese macaques (*Macaca fuscata*), for example, cooperate to form communal huddles to keep warm during the winter, and the more severe the ambient temperature is, the more individuals join the huddle (Wada 2007). Hence, one major advantage of sociality is that individuals in a group can cooperate to achieve higher benefits than solitary individuals or less cooperative groups.

But what is cooperation? Cooperation occurs when an individual performs a behaviour beneficial for other individuals that has been selected for its beneficial effect on the recipient, despite the potential relative costs to the cooperator (West et al. 2007a). The communal hunting behaviour of lions (*Panthera leo*) is a classic example of cooperation (Packer and Ruttan 1988; Stander 1992b). Pride members cooperate to catch a prey and hunting success increases with the number of cooperators (Caraco and Wolf 1975; Stander 1992a) and hence, larger groups get more prey. But does it imply that all individuals feed more in larger groups than in smaller groups? In other words, is the prey shared evenly between the group members? It is unlikely to be the case as food intake per group members decreases with the size of the pride as a result of competition between individuals to access their share of the meal (Caraco and Wolf 1975). Indeed, when a lion participates to communal hunting, it is largely with the purpose to get its own food, its participation is cooperative but at a selfish interest. Thus, cooperation is often explain as a by-product mutualism where the cooperative act of an individual is beneficial to both the recipient and the cooperators (Russell and Wright 2009). Such selfish interests are likely to result in competition and conflicts-of-interests between group members. Sociality thus leads to an evolutionary dilemma, that is whether to cooperate or to compete over resources (Innocent and West 2006).

1.2 Costs of sociality –emphasis on competition and conflict

The evolutionary dilemma of whether to cooperate or to compete underlies many conflicts-of-interest that are faced by any social animals and especially those living in groups (Trivers 1974; Parker 1979; Innocent and West 2006; Ratnieks et al. 2006; Rubenstein and Shen 2009). These conflicts-of-interest are common in group-living animals because groups are often constituted of different age and sex classes (i.e. different phenotypes) for which the balance between costs and benefits of sociality can be ruled by different strategies (Innocent and West 2006; Ratnieks et al. 2006; Rubenstein and Shen 2009). In the above-mentioned example of group-hunting in lions, not all individuals participate in the hunt, but especially females do (Schaller 1972; Scheel and Packer 1991). However, because males have higher competitive abilities than lionesses, they get prioritized access to the prey (Schaller 1972; Packer and Ruttan 1988). Males that do not bear the costs of the hunt while sharing the benefits are recognized as cheaters (Maynard-Smith 1982; Ghoul et al. 2014). Indeed, an individual is expected to perform best (i.e. obtaining the highest fitness pay-off) by following its own, selfish interest (Maynard-Smith 1982; West et al. 2007b). According to this Darwinian view, waiting for others to hunt the prey that an individual will consume is the most beneficial strategy. Such selfish behaviour is expected to evolve and selfish individuals to outcompete cooperative ones. Yet, the benefits obtained by cooperative hunting by the group outcompete those obtained when individuals hunt solitary so that cooperative groups outcompete less cooperative ones (Stander 1992b). This phenomenon is known as the tragedy of the commons (Hardin 1968) or the Prisoner's Dilemma: defectors (i.e. cheaters or 'free-riders') aim to get the communal benefits of cooperation, often termed "the public good" without bearing the costs (Axelrod and Hamilton 1981) but if all individuals in the group adopt this strategy, cooperation is no longer beneficial and the group is expected to collapse (Hardin 1968; Axelrod and Hamilton 1981). Hence, animals living in groups constantly face multiple social dilemmas (i.e. conflicts-of-interest) reviving the evolutionary conundrum around why do animals cooperate (Clutton-Brock et al. 2009) ? Central to this question is how are the costs and benefits of sociality trade-off and successful groups maintained?

1.3 Social trade-off and dominance

As we have seen above, the trade-off between the costs and benefits of sociality may be influenced by an individual's phenotype, such as the sex of an individual in the case of lions. In lions, males are larger and therefore of better competitive ability and thus dominating females, enabling them priority access to prey (Schaller 1972). The higher dominance status of males allows them to work less. Dominance relationships are considered one evolutionary solution to deal with the potentially deleterious effects of conflict in social groups (Wrangham 1980; Vehrencamp 1983; Lamprecht 1986; Isbell and Young 2002). In meerkats, *Suricatta suricata*, sexually mature individuals, the helpers, assist breeders in raising their offspring (Clutton-Brock et al. 1998). Breeders that reproduce are typically males and females that are dominant over the helpers (Clutton-Brock et al. 1998). These two examples show that dominance relationships can predict cooperative roles: subordinates meerkats are helpers as opposed to dominants who breed while female lions contribute more to the communal hunting than dominant males. Thus, dominance relationships among group members mediate the benefits and costs of sociality, but what are the mechanisms involved in this mediation?

1.4 Dominance: a mechanism to mediate the costs and benefits of sociality

The next sections emphasise how dominance may reduce the costs of sociality by mediating conflicts and thus promote cooperation.

There are many definitions of dominance in the literature (Drews 1993). The following definition of dominance by Drew (1993) is adopted throughout the thesis: *“Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate”*. It is important to acknowledge that agonistic interactions involve threats, submissive and aggressive behaviour so that it is expected that subtle cues such as avoidances may be used in dominance relationships.

1.4.1. Dominance mediating conflict

Dominance relationships are widespread in social groups as a result of increased competition (Wrangham 1980; Vehrencamp 1983; Isbell and Young 2002). Such relationships are diverse, since they can be actively displayed, such as aggression or displacement, but also more cryptically, such as submission or threat (Drews 1993; Cant 2011), and can shape different dominance structures (Chase 1980; Chase 1982; Vehrencamp 1983; Senar et al. 1997). For instance, when individuals can be ranked consistently, so that an individual clearly dominates all the individuals with lower ranks (van Doorn et al. 2003a), dominance relationships are established according to an ordered hierarchy (Landau 1951; Appleby 1983; Dugatkin 1997). Ordered hierarchies are expected to favour group stability and cohesion (van Doorn et al. 2003b). On the contrary, when ranking is not consistent (i.e. reversals in dominance role occur), hierarchies may be shallow and individuals more egalitarian. Such unsettled dominance relationships may favour conflict (Chiarati et al. 2010).

Ordered hierarchies are theoretically expected when resources are scarce and competition intense. In an intense competitive context, it may payoff for an individual to accept a subordinate rank as it reduces the frequency of escalated fights. By contrast, when resources are abundant, this payoff is diminished and individuals should be less willing to accept subordination leading to the establishment of more egalitarian societies (Wrangham 1980; Vehrencamp 1983). Thus, dominance may have different structures according to the availability of resources which shape the asymmetry between individuals.

Dominance relationships arise from the asymmetry in fighting ability or aggressiveness between individuals (Chapter 2). In juveniles crayfish (*Procambarus clarkii*), for instance, dominance hierarchies are based on difference in aggressiveness (Herberholz et al. 2007). Therefore, dominance hierarchies help individuals to predict the outcome of agonistic encounters and prevent escalated fights resulting in physical contacts and potential associated costs such as waste of energy, risk of injuries or death (Chase 1980; Chase 1982; Drews 1993; Senar 2006). As a result, dominance is expected to reduce the occurrence of conflicts in competitive contexts experienced by group-living species, such as fights over food (Aureli and de Waal 2000). For instance, when unfamiliar crayfish are brought together, a hierarchy is formed rapidly and once settled, conflicts over resources appear to be less pronounced as violent interactions decreased in frequency (Edwards and Herberholz 2005). Consequently, dominance relationships are often crucial components in conflict resolution (Aureli and de Waal 2000; Fraser and Aureli 2008), which may explain why dominance hierarchies have been found in a wide range of group-living animals, from insects (Cant et al. 2006a; Ratnieks et al. 2006; Wenseleers and Ratnieks 2006) to vertebrates, including mammals (Rowell 1974; Vervaecke et al. 1999; Albers and De Vries 2001; Archie et al. 2006) and birds (Pryke et al. 2002; Cornwallis and Birkhead 2008).

To be efficient in limiting conflict and escalated fights, dominance status needs to be predictable by individuals, implying that some phenotypic traits correlate with social status (Chapter 2; Senar 1999). These phenotypic traits may confer a direct advantages in fighting ability such as larger body size or horn size (Bergeron et al. 2010) or may signal social status without enhancing fighting ability such as badges-of-status (Chapter 3; Rohwer 1975; Rohwer 1977). In crayfish for instance, it is a chemical signal that informs individuals about one's dominance rank (Herberholz et al. 2007). In many bird species, plumage coloration indicates social status. For instance in the golden-crowned sparrow (*Zonotrichia atricapilla*), both the golden and black patches of the crown are used to signal social status (Chaine et al. 2011; Chaine et al. 2013) of individuals aggregating in winter flocks. While the existence of such signals has been well document in species forming winter flocks (Jarvi and Bakken 1984; Senar et al. 1993; Nakagawa et al. 2007) and extended to other taxa than birds (Anderholm et al. 2004; Thompson et al. 2014), little is known about their use in cooperative species (Chapters 2&3). Indeed, the expression of badges-of-status is expected to be more common in species where individuals are unfamiliar with each other, which may not be the case in cooperative groups (Senar 1999). However, when groups are large or migration frequent, badges-of-status may help to get an update on the social status of conspecifics.

Both dominance and its associated signalling are therefore predicted to evolve in group-living species in order to diminish the occurrence of conflicts and maintain group stability (Chapter 2; Aureli and de Waal 2000). Hence, dominance is crucial at both the individual level and at the group level. For individuals, dominance reduces energy expenditure by preventing conflicts over the access to resources (Aureli and de Waal 2000; Preuscholt and van Schaik 2000). In addition, it may also confer other advantages to dominants (Chapter 4). Indeed, dominants typically get enhanced reproductive success (Côté and Festa-Bianchet 2001; Dubuc et al. 2011; Majolo et al. 2012) and survival (Ang and Manica 2010) with potential consequences on the group or population dynamics and composition. These group- or population-level consequences can be reinforced by the fact that dominance has been shown to influence dispersal (Gauthreaux and Sidney 1978) and the decision to breed or to help (Woolfenden and Fitzpatrick 1977). Hence, the dominance structure has important potential impacts on social organisation and several fundamental life-history decision. Stevens and collaborators (2005) showed that variation in steepness of the hierarchy (i.e. steep and ordered as opposed to shallow and egalitarian) of captive bonobos (*Pan paniscus*) was involved in the distribution of grooming behaviour. In egalitarian groups, grooming was reciprocal, whereas in groups exhibiting steep hierarchy, grooming was directed toward high-ranking individuals following the biological market models, where individuals trade commodities (Noë et al. 1991; Stevens et al. 2005). In the bonobos example, the authors suggest that subordinates trade grooming against protection, reduced aggression, or facilitated access of resources by the dominant females (2005). Thus, in cooperative group, dominance has key influences on how much an individual should contribute to cooperative tasks (Cant and Field 2001).

1.4.2. Dominance and cooperation in social groups

At the mechanistic level, we have seen that dominance has the potential to reduce conflict between individuals, and thereby, the potential to promote the emergence of cooperation (West et al. 2006a; Burton-Chellew et al. 2010; Kummerli et al. 2010). Furthermore, dominance relationships may directly influence cooperative decisions, such as to cooperate or to defect (Clutton-Brock et al. 1998; Cant and Field 2001) or, in cooperative breeders, whether to breed or to help and how much (Woolfenden and Fitzpatrick 1977; Cant et al. 2006b). For instance, in paper wasps (*Polistes spp.*), high-ranking helpers contribute less to helping their relatives as they have a higher probability to inherit a breeding position, and thus helping may increase their energy expenditure or risk of being predated and reduce their future direct benefits (Cant and Field 2001; Field et al. 2006). Hence, dominance relationships can predict individual contribution to cooperation and may be involved in the maintenance of cooperation. Although such role has not been fully addressed yet (Bergmüller et al. 2007), yet the investigation of the links between dominance and cooperative contribution may add to our understanding of cooperation as these links are expected to vary, depending on the evolutionary routes driving cooperation.

Kin selection (Chapters 4&5 and Chapter 6) has been shown to be a major avenue leading to the evolution and maintenance of cooperation (Hamilton 1964; Hatchwell and Komdeur 2000; Griffin and West 2003; West et al. 2007b; Cornwallis et al. 2009). One particularly well-studied example is that of cooperative breeding (Hatchwell 1999; Cornwallis et al. 2009). Cooperative breeding implies that some reproductively mature individuals forgo their own reproduction, the helpers, and instead, assist other individuals to breed (Cockburn 1998). Under a kin-selection mechanism (Chapter 5), individuals help their kin to enhance their survival and/or reproduction and therefore gain indirect benefits via inclusive fitness (Hamilton 1964; West et al. 2007b). For instance, 96% of long-tailed tits helpers-at-the-nest (*Aegithalos* *caudatus*) prefer to provision chicks that are relatives (Russell and Hatchwell 2001). Although kin selection does not make predictions about a link between dominance and cooperative contribution, it gives a central place to dominance. When cooperation is kin-directed, as explained above, the establishment of dominance hierarchies may facilitate cooperation by limiting conflicts among kin (West et al. 2002). Additionally, dominance may enhance the benefits of nepotism for the relatives of dominants which may provide additional benefits of remaining at home and may contribute to delayed dispersal (Chapters 2&4 and Chapter 6), a pre-requisite for the formation of kin-based groups and potential for kin-selection. Nepotism occurs when individuals get privileges thanks to their relatives (Chapter 4). Such privileges may occur in the form of preferred affiliations (Wey and Blumstein 2010) or pacified aggressions among kin (Ensminger and Meikle 2005) so that associations and dominance relationships between individuals are expected to further reflect the relatedness structure of the groups (Chapter 6; Madden et al. 2012). Thus, kin typically get a facilitated access to resources (Chiarati et al. 2011) and a better protection such as an improved predator defense (Griesser 2003; Griesser and Ekman 2004; Griesser and Ekman 2005). This way, remaining in the territory to help may not be the mere result of a best-of-a-bad-job but could also confer direct fitness benefits to the philopatric offspring (Chapters 2&4; Griesser 2003; Griesser and Ekman 2004; Griesser and Ekman 2005; Covas and Griesser 2007). Dominance may improve nepotism as offspring from dominants may inherit and/or benefit from their parents' dominance status and gain better access to competitive resources than offspring from subordinates. For instance, as observed in many primate species (Wrangham 1980; Schino and Aureli 2010; Sueur et al. 2011) or in African elephants (*Loxodonta africana*; Wittemyer and Getz 2007), being the offspring of a dominant promotes the offspring's social status, as daughters obtain ranks adjacent to that of their mothers.

Direct benefits may also explain the evolution of cooperative behaviour, especially when cooperation among distantly related or unrelated individuals is common (Balshine-Earn et al. 1998; Dickinson 2004; Sumner et al. 2010; Riehl 2011; Dobson et al. 2012; Riehl 2013). It is important to mention that cooperation by kin-selection does not preclude direct benefits of cooperation (Blumstein et al. 1997). Such benefits might arise from cooperating when increasing the size of the group (i.e. group augmentation hypothesis; Kokko et al. 2001) may provide better defense against predator or higher hunting success. Cooperation may also involve the gain of direct benefits when, for instance, being a helper-at-the-nest may help individuals to accumulate parental care skills for their future own reproduction (i.e. 'the skills hypothesis'; Selander 1964; Komdeur 1996). Cooperation may also increase the chance to be chosen as a future mate (Zahavi 1995) or may enhance reciprocity (Milinski 1987; Heinsohn and Legge 1999; Schino and Aureli 2010). In this case, cooperative contribution can have signalling properties. The ‘social prestige’ hypothesis (Zahavi 1995) can be seen as a quality-based (i.e. handicap), non-human version of ‘image scoring’(Wedekind and Milinski 2000) or ‘reputation’(Milinski et al. 2002) and proposes that individual cooperators improve their social image through the advertisement of cooperation, thereby this behaviour is signalled (Zahavi 1995). Throughout the thesis, I adopt a definition *sensu largo* of social prestige which encompasses ‘image scoring’ and ‘reputation’ based on the fact that sexual selection is a form of social selection (Lyon and Montgomerie 2012; Roughgarden 2012). Thereby, cooperation by social prestige *sensu largo* may be sexually signalled to enhance future reproduction of individuals (Zahavi 1995) or socially signalled to enhance reciprocity, the prediction remain the same: individuals should compete to advertise their cooperative contributions and obtain benefits from third parties (Bergmüller et al. 2007). Thereby, under this hypothesis, dominant individuals may invest more in signalling their cooperative contributions as a result of their better competitive abilities (Chapters 5&6). Thus, integrating dominance asymmetry between individuals could add to our understanding on the evolution of cooperation by social prestige (Chapters 5&6).

Alternatively, individuals may help others in order to be authorized to stay in the territory and avoid the risk of eviction by others leading to dispersal costs (Chapters 5&6; Gaston 1978; Kokko et al. 2002; Koenig et al. 2009), a hypothesis termed “pay-to-stay” (Gaston 1978). A pay-to-stay driven cooperation is expected to occur when survival is high, ecological constraint tight and when the presence of non-helping subordinates imposes a costs to the dominants (Kokko et al. 2002). Under these circumstances, subordinates are expected to help dominants in order to be tolerated in the groups. Unrelated helpers are predicted to work more than more related helpers (Zöttl et al. 2013) as their presence is likely to be more detrimental to the dominants than the presence of related helpers (Kokko et al. 2002). The presence of dominant helpers may also imposes a higher costs to the dominant breeders as opposed to subordinate helpers because they may represent a higher competitive threat (Bergmüller and Taborsky 2005). On the other hand, the prospect of territory inheritance and future opportunity of own reproduction is expected to decrease helping effort (Kokko et al. 2002) and such prospect may be higher for more dominant helpers (Cant and Field 2001; Field et al. 2006). Furthermore, those individuals failing to contribute to cooperative tasks (i.e. cheaters) are expected to be punished and thus, to suffer from aggressions by dominants (Mulder and Langmore 1993; Henrich and Boyd 2001; Bruintjes and Taborsky 2008; Raihani et al. 2012; Roberts 2013). Thereby, dominance is also crucial for the evolution of a pay-to-stay-driven cooperation as (i) the dominance status of the breeders and (ii) the dominance status of helpers predict cooperative contributions. Additionally, (iii) dominant individuals are expected to prevent cheating by punishment or social enforcement (Mulder and Langmore 1993; Raihani et al. 2012). Alternative forms of social control may also occur such has threat (Cant 2011) or reinforcement of subordination (Bergmüller and Taborsky 2005). Yet, these hypotheses are currently lacking from empirical evidence. Support for the social prestige hypothesis or for image scoring resides mainly in humans (Wedekind and Milinski 2000; Tognetti et al. 2012; Kurzban et al. 2015) and the pay-to-stay hypothesis received strong support from mainly one species, the cooperatively breeding African cichlid *(Neolamprologus pulcher*; Balshine-Earn et al. 1998; Bergmüller and Taborsky 2005; Zöttl et al. 2013; but see Mulder and Langmore 1993 for an example in superb fairy wrens *Malurus cyaneus*).

The conundrum to explain cooperation and the maintenance of complex societies persists, while the proposed evolutionary routes for cooperation may not be mutually exclusive (Dickinson 2004; Sumner et al. 2010; Dobson et al. 2012).

Thus, dominance appears central in the evolution of cooperation: it can enhances kin-selection potential through nepotism or conflicts prevention, gives an advantage in the competition for cooperation (i.e. prestige hypothesis), or is involved in tolerance or punishment mechanisms to promote cooperation. Thereby, the study of the relationships between dominance status and cooperative contributions could help to shed light on the potential pathways promoting cooperation in group-living species. This is the aim of this thesis and the biological model used to investigate these relationships is the sociable weaver (*Philetairus socius*).

1.5 The biological model

The sociable weaver (*Philetairus socius*) is a passerine endemic to the semi-arid savannahs of southern Africa (Maclean 1973d). Sociable weavers are small (26-32g; Covas 2002), long-lived (max. 16yrs; Covas 2012) and sexually monomorphic so that both sexes display similar melanin-based plumage, including the black bib and black feathers in the shape of scales expressed on both sides of their body (Maclean 1973d; Acker et al. 2015).

The species is probably most famous for its massive colonial nest, the largest of any bird (Fig. 1.1). The weavers cooperatively build their nest through generations (Fig. 1.2B), by adding straw and other materials to the thatch (Collias and Collias 1978). The nest is used year-round by the colony comprising between two to hundreds of individuals (Maclean 1973b). They breed but also roost in individualized nest chambers that are embedded underneath the thatch (Maclean 1973b; Collias and Collias 1978). The communal nest have important insulation properties (Maclean 1973b) and the deeper a nest chamber is embedded in the thatch, the higher are its thermoregulatory benefits (van Dijk et al. 2013).

Figure 1.1 Sociable weavers are mostly famous for their massive communal nest, as illustrated here. In this photo I am checking each independent nest chambers to monitor the reproduction. Credit: F Théron

Sociable weavers are facultative cooperative breeders (Maclean 1973c) so that a pair can be assisted by up to five helpers-at-the-nests (Fig. 1.2A; Covas et al. 2006) but recent observation raised this number to seven helpers-at-the-nest (R. Covas, *pers. comm.*). These helpers contribute to feed the nestlings but can also be involved in other activities such as maintaining the nest cavity or snake mobbing. Snakes are a major threat to clutches and broods as they are responsible for about 70% of nest losses (Covas et al. 2008). Hence, the evolution of mechanism to diminish predation rate such as predator defense behaviour are expected. Alarm calling and snake mobbing have been observed (Fig 1.2C; Maclean 1973e) yet, to date not study have investigated these behaviours.

Helpers-at-the-nest are mainly philopatric (i.e. offspring of previous reproductive events). Covas and collaborators (2006) reported that helpers are typically related to at least one of the parents (93 %) and related to both parents in 43 % of cases. 50% of helpers were direct offspring of either the male breeder or the female breeder.

Figure 1.2 The three cooperative behaviours of sociable weavers examined in this thesis
A. Nestling provisioning – a helper-at-the-nest delivering a prey to the nestlings (credit M. Loubon)
B. Thatch building – an individual is picking a twig from the ground in order to add it to the communal thatch (credit M. Loubon)
C. Snake mobbing – snakes are the most important predators of sociable weavers, here the four individuals are calling after a Cape cobra *Naja nivea* and may perform attacks to the snake (credit C. van Rooyen)

The average relatedness between members at the colony is low, yet significant (Covas et al. 2006; van Dijk et al. 2014). The kin structure within colony is largely explained by a higher relatedness between males (Covas et al. 2006; van Dijk et al. 2014), the most philopatric sex as dispersal is female-biased in this species (Brown et al. 2003).

Given the recurrent relatedness between helpers and breeders and among colony members of sociable weavers, indirect benefits are likely to be important in the evolution of sociable weavers cooperative behaviour. Previous work reported that thatch building behaviour is directed toward an individual’s own and its kin’s nest chamber and predicted by the local relatedness of individuals occupying the nest chambers near where the thatch is constructed (van Dijk et al. 2014). As deeper, more embedded nest chambers in the thatch have superior insulation properties, they may offer better thermoregulatory advantages (van Dijk et al. 2013) likely to enhance indirect benefits when thatch building is kin-directed (van Dijk et al. 2014). In the cooperative breeding context, the alloparental care provided by helpers may be beneficial as their presence enhances reproductive success under adverse conditions (e.g. low rainfall or large brood size; Covas and du Plessis 2005; Covas et al. 2008), reduces maternal investment in eggs (Paquet et al. 2013) and favours female survival (Paquet et al. 2015). Yet, under non-adverse conditions, the presence of helpers has no or detrimental effects on the fledglings (Covas et al. 2011; Paquet et al. 2013) and reduces male survival (Paquet et al. 2015).

Hence, the beneficial presence of helpers classically expected in a cooperative context appears equivocal in sociable weavers and may mitigate the potential benefits gain through kin-directed help. This puzzle paired with the great levels of sociality and the multiple cooperative acts exhibited by sociable weavers, make this species an excellent study system to investigate the role of dominance in conflict mediation and to give insight on the potential underlying mechanisms explaining cooperation.

1.6 Aims and outline of the thesis

In this thesis, dominance relationships between group members of sociable weavers at feeders were investigated, quantified and qualified. The challenging purpose of this investigation was framed to assess the significance of dominance behaviour in mitigating conflict and promoting cooperation in order to unravel its role on the potential pathways to the evolution of cooperation and the maintenance of complex societies in general.

Chapter 1: Introduces the central role of dominance in complex cooperative societies.

Keyword: sociality, group-living, conflicts, cooperation

Chapter 2: explores whether dominant hierarchies are established and whether social status is predictable. As resources are likely to be limited in sociable weavers, groups may not be egalitarian, this chapter explores whether the access to resources is established by a hierarchies to prevent costly conflicts and whether phenotypic traits were correlated with dominance to predict the outcome of a potential fight.

Keywords: conflicts, hierarchies, orderliness, badge-of-status

Chapter 3: tests experimentally that black patches may represent badge-of-status by manipulating the badge size of mounted decoys and examining whether colony members had a preference to associate with the enlarged or reduced bib decoy in relation to their own badge size.

Keywords: conflicts, melanin, badge-of-status

Chapter 4: investigates the benefits of achieving a high social status in terms of access to resources and reproduction. This is analysed from the perspective of the dominant individual itself and its offspring. This provides a preliminary test for the existence of nepotism as one of the additional mechanisms to maintain family living in this system.

Keywords: resources access, benefits, nepotism, reproductive success

Chapter 5: tests the links between dominance and individual contribution to cooperation over three different tasks: nestling provisioning, communal thatch building and predator mobbing. This chapter examines whether dominants individuals contribute more or less to cooperative tasks and taking into account relatedness, to shed light on the potential mechanisms that may drive cooperation, specifically kin-selection, pay-to-stay or social prestige.

Keywords: cooperative effort, kin-selection, pay-to-stay, social prestige

Chapter 6: examines the overall effect of dominance and kinship on the social organisation of the whole colony. Social network analyses were performed to explore the links between kinship, dominance and associations networks and to test whether central network positions were occupied by most dominant, related and/or cooperative individuals.

Keywords: cooperation, kinship, competition, association, social network centrality

Chapter 7: summarises the main results and discusses the possible implications of dominance in the broad, general framework of conflict resolution and evolution of cooperation in complex societies. This chapter also points potential key lines of future research based on the questions raised by this thesis yet, not addressed or which are offering further challenges.

Keywords: conflicts, cooperation, direct and indirect benefits, group size, costs of dominance

Chapter 2

Dominance hierarchies and associated signalling

'Without agreement on rank and a certain respect for authority there can be no great sensitivity to social rules, as anyone who has tried to teach simple house rules to a cat will agree'

Robert Frost

2.1 Abstract

In animal societies, individuals face the dilemma of whether to cooperate or to compete over a shared resource. Two intertwined mechanisms may help to resolve this enduring evolutionary dilemma by preventing conflicts and thereby mediating the costs of living in groups: the establishment of dominance hierarchies and the use of 'badge-of-status' for signalling dominance. I investigated these two mechanisms in the sociable weaver (*Philetairus socius*), a colonial and social passerine which cooperates over multiple tasks. I examined the sociable weavers' dominance structure in two years by recording 2563 agonistic interactions between 152 individuals observed at a feeder at eight colonies. I tested which individual traits, including sex, age, relatedness, and two melanin-based plumage traits, predicted variation in social status. Firstly, using social network analysis, I found that colonies were structured by strongly ordered hierarchies which were stable between years. Secondly, medium-ranked birds engaged more in aggressive interactions than highly ranking individuals, suggesting that competition over food is most pronounced among birds of intermediate social status. Third, I found that colony size and kinship influenced agonistic interactions, so that aggression was less pronounced in smaller colonies and among relatives. Finally, within- and between-individual variation in social status and presence of an individual at the feeder were associated with variation in bib size, as predicted by the badge-of-status hypothesis. These results suggest that dominance hierarchies and bib size mediate conflicts in sociable weaver societies.

2.2 Introduction

Sociality involves conflicts of interests around vital resources such as mates, or access to food or nesting sites (Trivers 1974; Huntingford and Turner 1987). Yet, individuals in a group often also cooperate and share such resources. Social species thus face the enduring dilemma to compete and cooperate over resources, both of which have profound implications on individual fitness (Székely et al. 2010). An understanding of how individual conflicts within a given social environment are resolved is of crucial importance to explain social evolution (Aureli and de Waal 2000). Although social characteristics of the environment, such as group composition (e.g. sex ratio), group size, relatedness or connectivity among individuals, are key parameters influencing the outcome of conflicts (Stearns 2000; Ratnieks et al. 2006; Wolf et al. 2007b; Liker et al. 2013), behavioural mechanisms might also play a key role.

Two intertwined mechanisms may mitigate conflicts and hence reduce their associated costs: the establishment of dominance hierarchies (Rowell 1974) and the evolution of phenotypic traits that signal social status (Maynard-Smith and Harper 2003). Typically, hierarchies and status-signalling traits define access to resources in relation to an individual's dominance status and may help individuals to adjust their own behaviour accordingly. Additionally, individuals of high social status may get better access to or monopolise limited resources (Herberholz et al. 2007) enhancing fitness components such as survival and reproductive success (Nelson-Flower et al. 2011; Majolo et al. 2012).

Dominance hierarchies are found in many taxa ranging from insects to primates, including humans (Chase 1980; Izawa and Watanabe 2008), and are crucial for group stability and cohesion (Poisbleau et al. 2005). Hierarchies can also be affected by the social environment, including group size and composition, or environmental factors influencing resource distribution and availability (Isbell and Young 2002). Hierarchies are marked by strong directional asymmetry (i.e. one of the opponents wins more than 50% of the conflicts) within a dyad. Asymmetry is often linked to phenotypic differences between the opponents (Parker 1974). Such phenotypic traits are associated with an individual's resource holding potential (i.e. fighting ability) or aggressiveness (Parker 1974) and hence signal dominance status. In birds, dominance has been reported to be linked to size (Laubach et al. 2013), sex (Barkan et al. 1986), age (Poston 1997), relatedness (Archie et al. 2006), or ornamentation (Senar 1999). Determining the phenotypic correlates of dominance is of prime importance because these traits can help to make predictions about the social organisation of a group and ultimately about which individuals are likely to obtain the highest fitness.

When phenotypic correlates of dominance are traits that have evolved to signal social status they are often termed "badge-of-status" (Rohwer 1975). This status-signalling system is based on the finding that individuals with larger badges are dominant over the ones displaying smaller badges (Senar 1999; Maynard-Smith and Harper 2003). Only dominants are able to grow large badges as honesty of the signal is maintained either by costs of displaying a badge of dominance, so that subordinates displaying a large patch are intensively aggressed by members of the group (Rohwer 1977; Tibbetts and Safran 2009; Laubach et al. 2013) and/or specific costs in production of the dominance signal. For instance, in house sparrows (*Passer domesticus*), the dominance signal (a melanin-based bib) is testosterone-dependent (Laucht and Dale 2012) and high levels of circulating androgens typically involve costs of high metabolic rates or immunosuppression (Ketterson and Nolan 1992; Muehlenbein and Bribiescas 2005). Badges-of-status have been found in many taxa (reptiles: Anderholm et al. 2004; insects: Tibbetts and Dale 2004; birds: Senar 2006; fishes: Dijkstra et al. 2009; mammals: Bergeron et al. 2010). In birds, they often correspond to melanin-based plumage patches (Tibbetts and Safran 2009). Melanin-based plumage has, for example, been shown to be linked to social status (status-signalling hypothesis) in house sparrows (*Passer domesticus*: Nakagawa et al.

2007), Eurasian siskins (*Carduelis spinus*: Senar et al. 1993) and great tits (*Parus major*: Jarvi and Bakken 1984).

Group-living species with complex social systems, such as cooperative breeders where helpers may assist parents in raising the offspring, provide a particularly interesting case to examine how the costs of sociality are averted. In this context, group members are strongly dependent on each other owing to the benefits they gain from cooperative behaviour (Roberts 2005). As a result group-living animals are particularly expected to invest into conflict management strategies (Baan et al. 2014) such as the establishment of stable dominance relationships (Preuscholt and van Schaik 2000). Additionally, in cooperative species quantifying and qualifying the structure of social dominance is a crucial first step to test predictions about which group members are likely to get the highest fitness benefits. Cooperative breeding systems are characterized by significant reproductive skew, but detailed assessment of social dominance structure will also help to understand how individual investment into cooperative tasks is distributed among group members (Richner 1989; Tiddi et al. 2012). In many cooperative species, the level of help provided by individuals within a group is often influenced by individual variation in degree of kinship toward the receiver, age, body condition, (Clutton-Brock et al. 2000), and dominance status (Roulin et al. 2012; Tiddi et al. 2012).

Here I investigate dominance hierarchies and phenotypic correlates of dominance in a highly social and colonial passerine, the sociable weaver (*Philetairus socius*). Sociable weavers are cooperative breeders that roost throughout the year in a communal nest and cooperate over several tasks, including provisioning of young, defense against predators and nest construction (Maclean 1973c; Covas et al. 2006; Covas et al. 2008; van Dijk et al. 2014).

I used an artificial food source to investigate whether access to food in sociable weavers is egalitarian or is organized according to a hierarchy. I examine the number of asymmetrical dyads, the amount of reversals (i.e. the number of encounters won by the individual of a dyad who has won less than 50% of encounters). I also quantify the orderliness index of each colony. Orderliness (or "linearity") occurs when the dominance relationships between three individuals, for instance A, B and C, are transitive (A is dominant to B, and B to C, so that A dominates C) as opposed to cyclic (A dominates B, B dominates C but C dominates A; Landau 1951; Kendall 1962). Orderliness is an important feature of the hierarchal structure, because ordered hierarchies tend to remain stable over time when the composition of the group does not change drastically (Senar et al. 1990). It is therefore a cue of group stability and cohesion. While ordered hierarchies have been well documented in small groups of various taxa (e.g. Cant et al. 2006a), in cooperatively breeding birds and mammals their existence and structure have hitherto been poorly investigated (Cockburn 1998; but see Chiarati et al. 2010), especially in contexts other than reproductive skew (Johnston 2000; Cant and Field 2001).

Sociable weavers inhabit semi-arid savannahs, an environment where the availability of food is unpredictable (Maclean 1973c; Covas et al. 2008) and hence competition for food is likely to be common (Wrangham 1980; Isbell and Young 2002). I therefore predicted that sociable weavers should not have egalitarian access to food resources. Instead, I expected dominance relationships to mitigate conflicts and predict access to food. As a result, I predicted to find structured dominance hierarchies in this species exhibiting a high level of orderliness. On the other hand, since multiple pairs breed in the same communal nests as opposed to a single pair monopolizing reproduction, the system may be egalitarian, typically described by shallow, non-ordered hierarchies (Vehrencamp 1983; de Vries et al. 2006). I also expected relatedness among individuals, colony size and sex to influence the dominance structure as these factors may affect the levels of competition between individuals. In particular, because colonies of sociable weavers are composed of many related individuals (Covas et al. 2006), kinship plays an important role in the social and spatial organisation of individuals within the communal nest (van Dijk et al. 2014), and parents are often helped by relatives, I predicted related individuals to interact less aggressively than unrelated individuals (Hamilton 1964). Based on theoretical models on the evolution of fighting behaviour, I further expected more aggressive interactions between individuals of similar strength as both have a chance to win the fight (Parker 1974; Arnott and Elwood 2009). I also expected more frequent conflict at larger colonies, because at these colonies competition over resources, such as occupancy of breeding chambers, and an increased probability to encounter individuals with a similar resource-holding-potential may be expected. Although I acknowledge that the reverse, i.e. increased competition and higher chance of encountering similarly ranked individuals at smaller colonies, is also conceivable. Lastly, because sociable weavers are sexually monomorphic with biparental care and are not territorial, I had no a priori prediction about dominance relationship between sexes although in many passerines, males dominate females (e.g. better competitive ability due to intra-sexual competition; Jarvi and Bakken 1984).

I further investigated whether phenotypic traits have the potential to signal social status while accounting for relatedness among individuals within a group. Specifically, I investigated the function of two melanin-based plumage patches displayed by both sexes: the size of the black bib and the number of black feathers located on both flanks. Under the badge-of-status hypothesis, I predicted that unequal access to food would be associated with phenotypic variation between individuals in the size of the melanin-based bib, so that individuals with larger patches and/or with more black, flank feathers are expected to be dominant.

2.3 Material and methods

2.3.1. Species and study area

Sociable weavers are facultative cooperative breeders that build large, communal thatched nests within which several independent nest chambers are embedded (van Dijk et al. 2013). The chambers are used throughout the year for roosting and for breeding. These communal nests are usually built on *Vachellia erioloba* trees (although other trees or human-built structures may be used) and colonies may vary in size from less than ten to hundreds of individuals (Maclean 1973d).

The study was conducted at Benfontein Nature Reserve (28˚52’S, 24˚50’E) near Kimberley, Northern Cape province, South Africa (Fig. 2.1), between September 2011 and February 2013, which encompassed two breeding seasons. The area consists of about 15 km^2 of Kalahari sandveld covered by *Stipagrostis* grasses and *Vachellia spp.* Trees (Fig. 2.1). It contains approximately 30 active colonies comprising between 5–80 individuals. As part of the long-term research on this study population, these colonies have been captured, using mist nets, every year since 1993 (see Covas et al. 2002 for more details on the captures). These annual captures allow us to accurately assess the age of individuals banded as nestlings or to estimate the minimum age of individuals based on the date of first capture when not banded as a chick. During capture, birds are individually banded, using a uniquely numbered metal band and three color bands to allow visual individual identification in the field. I took blood samples (*c.* 10µl) by puncturing of the brachial vein using a sterile needle and a heparinized capillary tube. I weighed individuals to the nearest 0.1g, measured tarsus length to the nearest 0.1mm and wing length to the nearest 0.5mm.

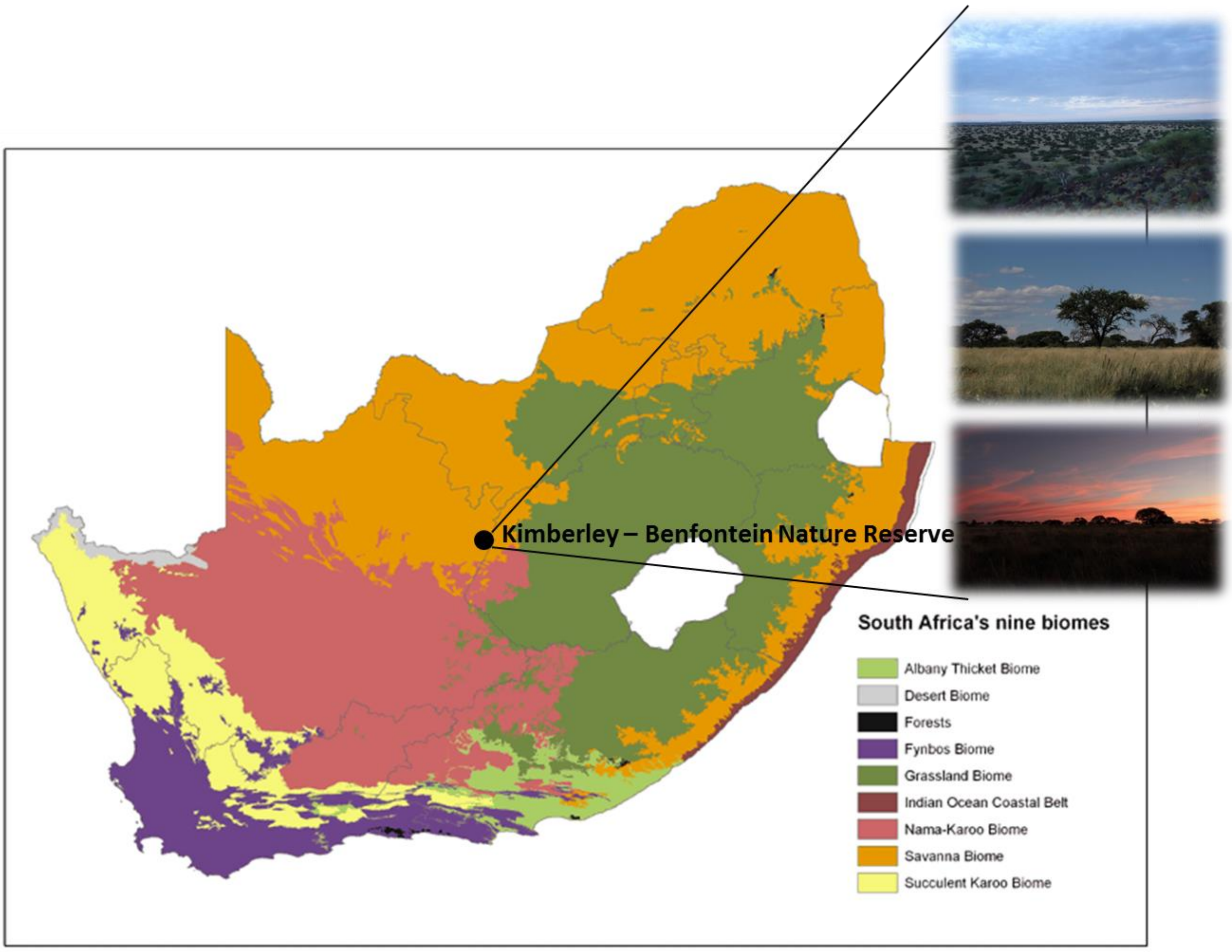

Figure 2.1 Benfontein Nature Reserve, the study site is located in South Africa and is representative of semi-arid savannas of southern Africa (map adapted from the South African National Biodiversity Institute)

Adults display two distinct types of melanin-based plumage traits: a black throat patch (the 'bib'; Fig. 2.1) and black feathers in the shape of scales located on both flanks ('scaly feathers'; Fig. 2.2). I distinguished between fully grown and dark (counted as 1) and not fully grown, smaller and light scaly feathers (counted as 0.5). I used the average number of scaly feathers on each flank in the analyses. To estimate the size of the black bib, I photographed each individual three times using a Canon EOS D500 digital camera. Digital photographs were taken perpendicular to the head with each individual positioned against a neutral grey background (a Kodak 18% Gray Card) and aligned with a ruler (Fig. 2.1). I used Photoshop CS5.1 (Version 12.1) to select the black pixels of the bib and calculate its size (in cm^2). The mean bib size as measured from three pictures was used in the analyses. Within-individual repeatability of bib-size measurements was 0.782 ± 0.028 (mean ± SE; $P < 0.001$, $N = 116$) as calculated using the package "*rptR*" in R (Nakagawa and Schielzeth 2010).

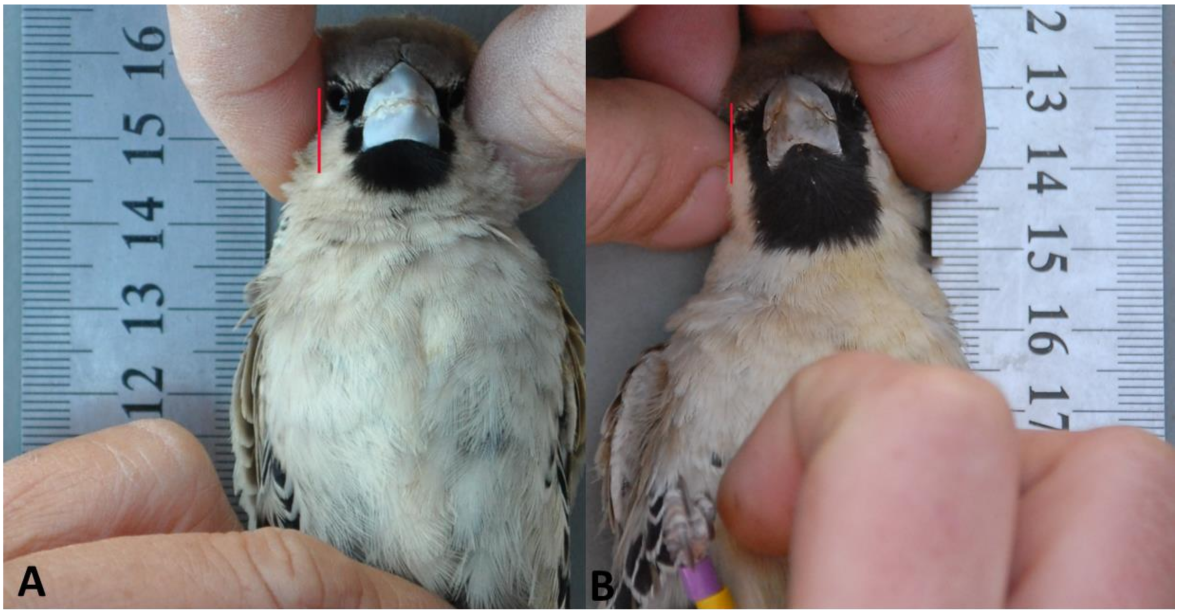

Figure 2.2 Photographs of the black bib for two different individuals. (A) illustrates an individual displaying a small bib (0.853 cm^2), (B) an individual displaying a large bib (1.804 cm^2). The red line represents the scale of 1 cm

One observer (MR) counted the scaly feathers, took the photos and analysed the photographs in both seasons. Males and females did not differ significantly in any morphometric measurements (wing length, tarsus length, body mass, bib size, average number

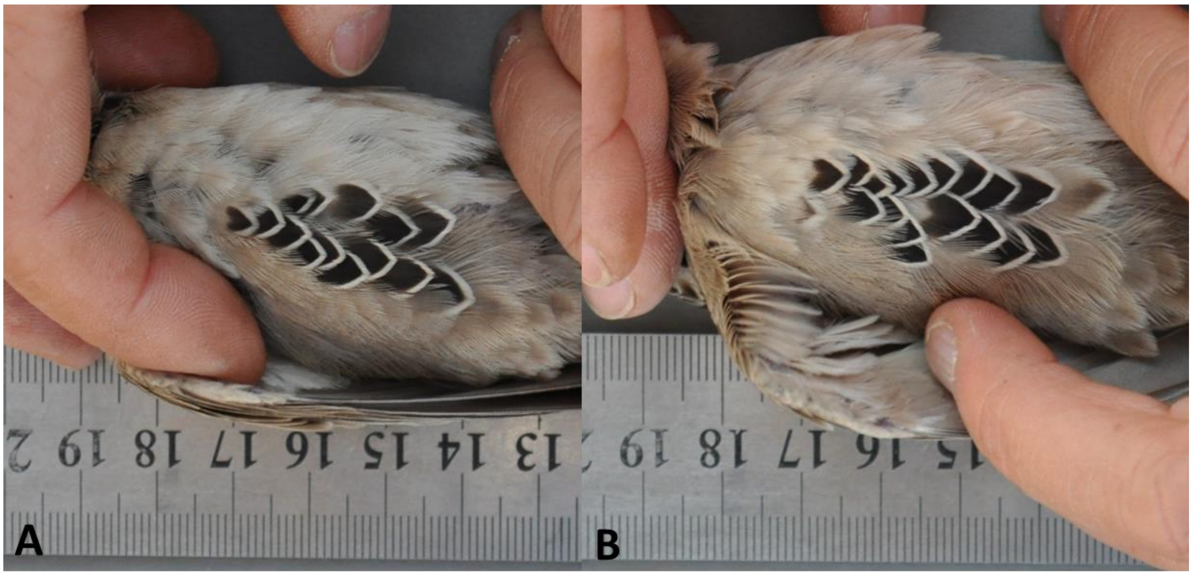

Figure 2.3 Photographs of the "scaly feather" patch for two different individuals. (A) illustrates an individual displaying 14 scaly feathers on the right side), (B) illustrates an individual displaying18 scaly feathers, including two feathers counted as 0.5

of scaly feathers; all $p > 0.05$, all $n > 136$). There was no significant variation in morphological traits between the two seasons except for the average number of scaly feathers. The average number of scaly feathers traits was higher for Season 2 (15.01 ± 1.68) compared to Season 1 (14.03 ± 1.78, $N = 142$, $T = -3.104$, $P = 0.002$).

2.3.2. Genetic analyses and estimates of relatedness

Blood samples taken at capture were preserved in 1mL of absolute ethanol. I extracted genomic DNA using a precipitation of ammoniate acetate (Richardson et al. 2001) in preparation for polymerase chain reaction amplification. The sex of all individuals using *P2–P8* sex-typing primers (Griffiths et al. 1998) was molecularly determined. Seventeen autosomal polymorphic microsatellite markers were used to genotype each individual. Pairwise relatedness was estimated using Queller and Goodnight's genetic estimate of relatedness using KINGROUP v. 2_090501 (Konovalov et al. 2004), with reference to genotypes from the entire population across all colonies ($N = 1138$). For more details on genotyping procedure and analyses, see van Dijk et al. (2014).

2.3.3. Behavioural observations and dominance

I recorded agonistic interactions (pecking, kicking, chasing, displacing, avoiding; table 1) at a feeder (a plastic red-brown plate, ∅ 20cm) containing a mixture of bird seeds. The study was conducted in two breeding seasons. Five colonies were observed between September 2011 and March 2012 (Season 1; colony size at capture: 27.5 ± 10.1 individuals, range: 9-38). Three of these five colonies plus an additional two colonies were also observed between September 2012 and February 2013 (Season 2; colony size at capture: 21.3 ± 8.8 individuals, range: 9-32). The feeder was placed at a fixed location on the ground underneath the centre of the colony. To habituate the birds, a tripod and the feeder were positioned underneath each colony with an *ad libitum* supply of a seed mixture until the first individual was observed to feed from it (3.3 ± 2.1 days) and before dominance observations started. Once the birds were habituated to the feeder, it was removed between observations to increase the occurrence of agonistic interactions for access to food. Two hours of observation were conducted twice a day, between 8:30-10:30 and between 16:00 and 18:00. Observations were made from underneath a hide, located approximately five metres from the nest and/or using a video-camera (Sony Handycam HD) on a tripod 2-3m from the feeder, which filmed all interactions within a 1m radius around the feeder. The presence (and arrival) of the observer did not affect the number of individuals present at the feeder (GLMM estimate = 0.059, $N = 24$, $P = 0.651$; analyses performed on a subsample including a total of 12 sessions with observer and 12 sessions without at 4 different colonies). Observations were carried out each day until no new dyadic interactions were observed (total observation time per colony: 40.1 ± 10.9 hours).

The number of agonistic interactions within dyads, the direction of the interactions and the identity of the birds involved (i.e. identities of the 'winner' and the 'loser' for each interaction) were scored. In order to avoid the inclusion of prospecting birds (i.e. individuals which do not roost in the colony and are not considered as colony members), only individuals seen interacting at the feeder during at least three different observations were included in the analyses. For three colonies in Season 2, the observer additionally recorded the identity of all individuals present at the colony and not only at the feeder. Those individuals, which were also seen during three different observations but did not approach the feeder, were considered as members of the colony and qualified as 'non-feeding' individuals (as opposed to the 'feeding' individuals). For Season 2, I also qualified the type of agonistic interactions between individuals. I defined a passive dominance interaction as an interaction where the focal individual approaching the feeder was avoided by another individual then leaving the feeder without direct interaction between these two individuals, and an active dominance interaction as an interaction where the focal individual actively displaced or aggressed its opponent (table 1).

Agonistic interactions were distributed as follows: a total of 629 agonistic interactions were observed during Season 1 for 91 individuals (30 females, 56 males and 5 of unknown sex) and a total of 1915 agonistic interactions were collected during Season 2 (61 individuals: 21 females, 38 males and 2 of unknown sex) so that I had 152 individuals for which I calculated dominance scores. These 1915 interactions included a total of 835 avoidances and 1080 acts of aggression. Twenty-eight individuals were assigned in matrices for both seasons. 'Feeding' and 'non-feeding' categories were qualified for 44 individuals (30 'feeding' individuals and 14 'non-feeding').

I used the David's score (David 1987) to describe the dominance score of the 152 individuals. David's Score is calculated by the sum of proportions of wins minus the sum of proportions of losses of an individual weighted by the relative strength of its opponents (Gammell et al. 2003). I scaled dominance scores within colonies ($\frac{DS_i - DS_{min}}{DS_{max} - DS_{min}}$; *i* representing an individual within its colony, DS_{min} the lowest dominance score in that colony and DS_{max} the highest dominance score in that colony), so that all scores ranged from 0 (most subordinate individual) to 1 (most dominant individual) for each colony, thereby allowing comparison of dominance scores obtained from colonies of different sizes.

2.3.4. Structure of hierarchy

I used an orderliness index to assess how transitive and consistent dominance relationships are within a colony. The orderliness index was calculated based on Triangle Transitivity (T_{tri}), a recently described technique (Shizuka and McDonald 2012) which is based on social network analyses but is similar to classic linearity tests (Landau 1951; Kendall 1962; de Vries 1995; de Vries 1998). T_{tri} is the relative proportion of transitive triads observed among all possible triad configurations within the empirical matrix. Compared to previously developed linearity tests, it offers the advantages to be less biased when dyads of individuals fail to interact. T_{tri} was calculated using the R package *"statnet"* (Handcock et al. 2003) and the p-value of orderliness was obtained using randomisation tests with 1000 permutations (Shizuka and McDonald 2012). Orderliness indices between 0 to 0.5 reflect egalitarian systems, 0.5 to 0.8 moderate hierarchies and 0.8 to 1 strong ordered hierarchies (Bergstrom and Fedigan 2010).

I tested between-year stability of dominance scores for 28 individuals observed at three colonies in both seasons by fitting a linear mixed model with dominance score from Season 2 as response variable. Dominance score from Season 1, sex and colony size were set as covariates. Colony identity was included as a random factor.

2.3.5. Correlates of dominance

I investigated whether the number of aggressions given by an individual was predicted by its sex, dominance score, colony size and its average relatedness to the colony. I fitted a generalized linear mixed model with a Poisson distribution and colony identity as a random factor to account for potential correlated behaviour between colony members. I then used dyadic relatedness to test for the effect of kinship on the likelihood of engaging in agonistic interactions and on their frequency between two individuals. I fitted Generalized Linear Mixed models with colony size, the type of the dyad (i.e. male-male dyad, male-female dyad or female-female) as covariates. Individual, colony and season identities were set up as random factor to control for repeated measures.

I then examined which traits explained the variance in dominance scores by fitting a linear mixed model. Covariates included in the full model were sex, minimum age (individuals older than 8 years were grouped together to improve homoscedasticity), bib size, average number of scaly feathers, colony size and average relatedness to the colony. Body mass and tarsus were included together as an estimate of body condition (Green 2001; Cotton et al. 2004). None of the covariates in this model were strongly correlated (maximum significant correlation coefficient r between all covariates of 0.27; range: 0.016–0.27). I also included the most relevant interaction terms (the two way interactions of age and sex, the size of the bib and the number of scaly feathers, sex and the size of the bib, sex and the number of scaly feathers, and the interaction between colony size and the size of the bib). The size of the bib was centred to enable a better estimation of the intercept. Season, colony identity and individual identity were fitted as random factors. This model was performed on a subsample of 116 individuals (out of 152 in total) consisting of sexed and genotyped birds for which morphological measurements were available for the season of observation. I repeated this model removing from the sample individuals which interacted less than once (N = 110) and individuals which interacted less than twice (N = 101). I also conducted separate analyses of interactions among males only (N = 84) and between males and females only (N = 102) to test for sex-specific signalling function of melanin-based plumage traits. Because only 7% of dyads observed at all colonies were among females, I am unable to meaningfully assess the relationship between bib size and dominance within females.

I also investigated if the difference in dominance scores between both seasons was predicted by a difference in the size of the bib by fitting a linear model with within-individual difference in dominance scores between Season 1 and Season 2 regressed against within-individual difference in the size of the bib. Differences in body mass, wing length and average number of scaly feathers were also included as covariates. Age and tarsus length were excluded from this model (all individuals became one year older and tarsus length is a fixed trait). Finally, I tested whether the size of the bib predicted the presence or absence of an individual at the feeder using a two-tailed unpaired Student's T-test.

All statistical analyses were conducted in R version 2.15.0 (R Development Core Team 2012). For all models, I used the Generalized Linear Model approach with an identity link for the Gaussian family and a log link for the Poisson family. I used the Maximum Likelihood criterion for models containing only fixed effects (LM) and the Restricted Maximum

Likelihood criterion with the package "*lme4*" (Bates and Maechler 2009) for mixed effect models (LMM for the Gaussian family GLMM for the Poisson family). Model selection was achieved following a backwards stepwise procedure. I selected the set of best fit models based on the corrected Akaike Information Criterion (AICc) using the function *"dredge"* from the *"MuMin"* package (Barton 2013). Only models with a ΔAICc < 2 were kept. P-values and confidence intervals were estimated using the *"lmerTest"* package (Kuznetsova et al. 2014). I used model averaging estimation of effects, p-values and confidence intervals when the set of best-fit models contained more than one model.

2.4 Results

Based on the dominance scores there was a higher proportion of medium-ranked individuals (60%; dominance scores 0.333-0.667) than subordinates (10%; dominance scores 0-0.333) or dominants (30%; dominance scores 0.667-1.000) at the study colonies (Chi-square test for contingency table: $\chi_{22} = 68.30$, $P < 0.001$).

Dominance scores were significantly positively associated with the number of aggression interactions (Spearman's rank test $R_s = 0.56$, $N = 152$, $P < 0.001$) and with avoidance behaviour (Spearman's rank test $R_s = 0.70$, $N = 152$, $P < 0.001$). The number of aggressive interactions was significantly higher than avoidance behaviours among medium-ranked individuals (ratio: 1.097). Among dominant ones the reverse was true (ratio: 0.886; Chi-square test for contingency table: $\chi_{22} = 3.074$, $P = 0.040$), so that high-ranked individuals were avoided while medium-ranked ones were actively and aggressively approached.

I found that the proportion of dyads engaging in agonistic interactions depended on the sex of the two opponents (Chi-square test for contingency table: $\chi_{22} = 16.5838$, $P < 0.001$), so that the proportions of male-male dyads (43%) or male-female dyads (50%) engaging in agonistic interactions were higher than expected by chance, while this proportion was significantly lower than expected by chance for female-female dyads (7%). This can be

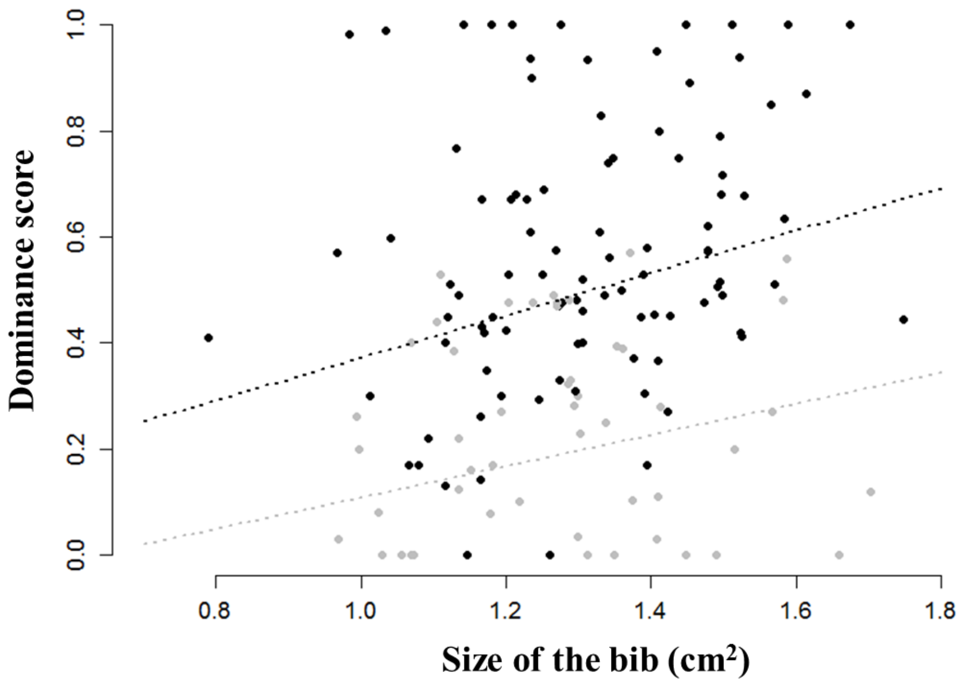

Figure 2.4 The relationship between the size of the bib and inter-individual variation in dominance score for each sex group is shown for 116 individuals from 7 colonies. Higher dominance scores indicate more dominant individuals. Males are in black and females in grey. The dash lines represent the estimated effect of the bib on dominance scores for each sex

explained by the fact that males were more often involved in aggressive interactions than females (GLMM estimate = -2.778 ± 0.734, *N* = 52, *f* = 203.45, *P* = 0.0002), an effect that was stronger in large colonies than in smaller ones (GLMM estimate = 0.176 ± 0.042, N=52, *f* = 17.07, *P* < 0.001) and resulting in males having higher scores than females (LMM: 0.334 ± 0.043, *N* = 116, *T* = 7.838, *P* < 0.001, Fig. 2.3).

I also found that kinship played an important role in shaping the occurrence of agonistic interactions. First, my results revealed that the likelihood of individuals to interaction agonistically decreased with relatedness (GLMM estimate: -2.574 ± 1.054, N= 900, p=0.014). Additionally, the number of aggressive interactions between two individuals decreased with their level of relatedness (GLMM estimate: - 0.436 ± 0.212, *N* = 284, *P* = 0.040).

2.4.1. Structure of hierarchies

In both seasons, 97.9% of dyadic relationships were asymmetric and the percentage of reversals was low (2.1%). I obtained an index of orderliness varying from 0.61 to 1 when considering all agonistic interactions. The index was not significant for three colonies in Season 1 (all p-values > 0.27; 0.43 ± 0.26), which is likely due to the high presence of missing dyads. For Season 2, I differentiated between types of agonistic interactions (avoidance and aggression). When considering only avoidance relationships, the mean orderliness index and the percentage of asymmetric relationships appeared slightly higher (avoidance relationships: orderliness = 0.885 ± 0.147; percentage of asymmetric relationships = 96.4%) compared to when accounting for aggressions only (orderliness = 0.781 ± 0.295, asymmetric relationships = 94.4%). In line with these results, there were fewer reversals when accounting for avoidances only than for aggressions only (3.6% vs. 5.6%).

The dominance score of individuals in Season 2 was predicted by their dominance score in Season 1 (LMM estimate = 0.631 ± 0.177, *N* = 28, *T* = 3.568, *P* = 0.002, Fig. 2.4). Males tended to maintain more stable dominance scores than females, but this effect was not significant (LMM estimate for the effect of sex: 0.160 ± 0.093, *N* = 28, *T* = 1.729, *P* = 0.097) and colony size did not play a role in the stability of dominance (LMM estimate: 0.004 ± 0.006, *N* = 28, *T* = 0.607, *P* = 0.592).

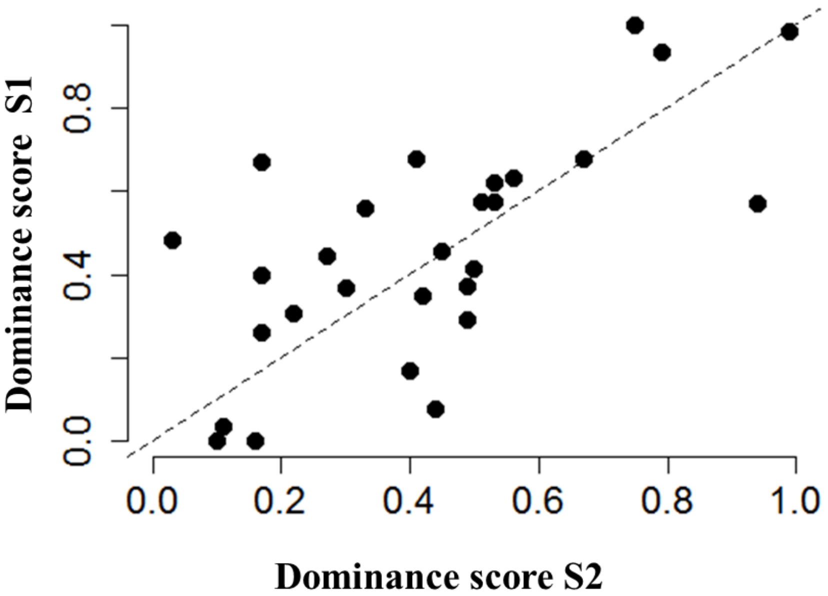

Figure 2.5 The relationships between the dominance scores of an individual in Season 1 (S1) and in Season 2 (S2) illustrating stability (N = 28). The dash line represents perfect stability

2.4.2. Correlates of dominance

On the whole data set, dominance scores were significantly positively associated with the size of the bib (LMM estimate = 0.295 ± 0.097, *N* = 116, *T* = 4.606, *P* = 0.003; Table 2.2 & Fig. 2.3). The size of the bib also predicted the inter-individual variation in dominance scores when removing individuals that interacted only once (LMM estimate = 0.338 ± 0.109, *N* = 110, *z* = 3.052, *P* = 0.002), or when removing individuals that interacted only twice (LMM estimate = 0.332 ± 0.105, *N* = 101, *T* = 3.152, *P* = 0.002). Dominance scores were significantly positively associated with the size of the bib when the dominance scores were calculated based only on interactions among males (LMM estimate: 0.410 ± 0.035, *N* = 84, *T* = 1.324, *P* = 0.019) but not when based on interactions between males and females only (LMM estimate: 0.138 ± 0.117, *N* = 102, *T* = 1.167, *P* = 0.243). This result suggests that interactions between males and females are not mediated by bib size. In addition, 'non-feeding' individuals had significantly smaller bibs (1.252 ± 0.131 cm^2) than those birds that did access the feeder (1.359 ± 0.173 cm^2, Student's *T*-test: *N* = 44, *T* = 2.276, *P* = 0.029).

Table 2.1 Estimates and standard errors of model parameters for the single best-fit model explaining the variations in dominance scores for 116 individuals

Variable	**Estimate (± SE)**	**95% CI**	**T**	**p**
Intercept	0.196 (± 0.042)	-0.403 – 0.8457	4.606	<0.0001
Bib size	0.295 (± 0.097)	-0.0005 – 0.4730	3.042	0.0031
Sex	0.401 (± 0.045)	0.2386 – 0.4047	8.908	<0.0001

Finally, the within-individual variation in dominance status between the two seasons was predicted by variation in the size of the black bib (LM estimate = 0.275 ± 0.188, *N* = 28, $F_{1,21}$ = 5.778, *P* = 0.027, Fig. 2.6; this effect remained significant when the outlier, with a difference in dominance scores between the two years > 0.6, was removed). The scaly feather patch (mean number of scaly feathers) and body mass did not account for inter- and intra-individual variation in dominance score (*P* > 0.22 for all these variables in both models). Average relatedness of an individual with its opponents, tarsus length, colony size, colony identity and minimum age did not explain the inter-individual variation in dominance scores (all *P* > 0.102) in any of the models.

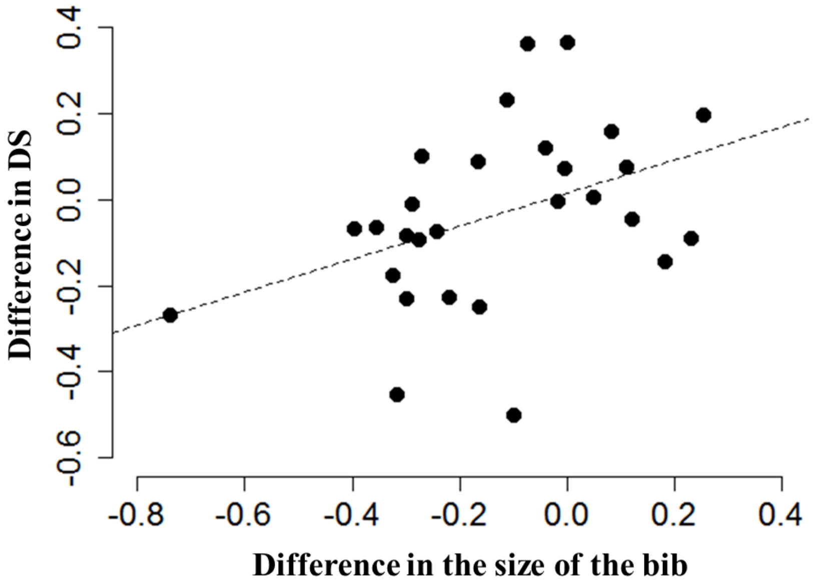

Figure 2.6 Within-individual change in dominance score between seasons is predicted by a change in the size of the bib (N = 28). The dash line represents the association, estimated by the model fit, between the dominance scores of the previous year and the following one. Exclusion of the outlier which does not qualitatively alter the relationship illustrated here

2.5 Discussion

I found that sociable weavers were not egalitarian over access to a food resource. Instead, their social system was characterized by ordered hierarchies where individuals competed over food by engaging in agonistic interactions that were highly asymmetric with a low degree of reversal. These results are consistent with the theoretical prediction that when resources are patchily distributed or scarce, social species establish hierarchies to mediate conflict (Wrangham 1980; Isbell and Young 2002). Bib size was correlated to both between- and within-individual variation in dominance status suggesting that it could be a badge-of-status. However, bib size did not predict dominance scores when calculated only for interactions between sexes, suggesting that this plumage trait may thus have a sex-specific signalling function of dominance. Sex, colony size and relatedness also had a strong influence on the occurrence and type of dyad interactions at the colony. I conclude that both stable, ordered hierarchies and badges-of-status may help to mediate conflicts and are likely to be important for the stability of the cooperative societies of sociable weavers.

Males were dominant over females, a pattern observed in many passerines (e.g. Barkan et al. 1986; Izawa and Watanabe 2008; Chiarati et al. 2010) and suggests that males initiate interactions (Tarvin and Woolfenden 1997). Males also exhibited more aggressive interactions than females, an effect which was more pronounced at larger colonies. The proportions of male-to-female agonistic dyads were higher than expected by chance while female-female dyads represented only 7% of agonistic interactions. The latter is surprising since in cooperative societies, female-female competition for access to reproduction can be strong (Rubenstein and Shen 2009; Nelson-Flower et al. 2013). My results, however, suggest that such reproductive competition may not be reflected in competition over food.

Conflicts therefore appear to be more pronounced among males, because they interact more aggressively than females, particularly medium-ranked males. This can explain why I found that males were more involved in aggressive interactions at larger colonies as they are expected to contain higher proportions of medium-ranked males (which I show engage more in aggressive interactions). Furthermore, as expected under theoretical predictions of fighting behaviours (i.e. aggressions are predicted to occur when dominance relationships are unsettled; Kaufmann 1983), I found that all measures of dominance were less pronounced when based on aggressive interactions only than when they were calculated based on avoidance interaction only: lower average values of dyad’s asymmetry, lower average values of orderliness and lower correlation coefficients of the number of agonistic interactions with dominance score.

Conflicts among medium-ranked individuals are expected to be more frequent than among either high- or low-ranking individuals for several reasons: Medium-ranked individuals are more numerous and hence, have more chance to encounter an opponent with similar resource-holding potential (Parker 1974; Maynard-Smith and Parker 1976; Arnott and Elwood

2009), especially in larger colonies. Additionally, medium-ranked individuals may engage more in aggressive interactions to raise their hierarchal position. Indeed, victory of escalated fights could lead to important benefits such as obtaining a breeding position (Thompson et al. 2014), while dominant individuals have a higher probability to breed (M. Rat, R. E. van Dijk, C. Doutrelant & R. Covas, *unpublished data*).

High-ranking individuals were mainly avoided by subordinates. Such conflict-avoidance between familiar high-ranking and low-ranking individuals is common in social species (Senar et al. 1990; Cant et al. 2006b). Both dominants and subordinates may mutually benefit from each other and are therefore expected to invest into conflict management strategies. For instance, in cooperative species subordinates may provide help to high ranking individuals so that they diminish their risks of being evicted from the group by dominants (Zöttl et al. 2013).

Conflict management strategies to facilitate communal lifestyle are predicted to take the form of well-structured, stable dominance hierarchies (Preuscholt and van Schaik 2000). For instance, orderliness is expected to promote group cohesion and stability (Poisbleau et al. 2005) and stable interactions (affiliations or agonistic encounters) between group members which are important parameters to foster cooperation (Aureli and de Waal 2000). In line with this expectation and as observed in other cooperative species across taxa (Insects: Cant et al. 2006a; Primates: Bergstrom and Fedigan 2010; Corvids: Chiarati et al. 2010), year-round colonies of sociable weavers exhibit, overall, strictly ordered hierarchies (orderliness indices obtained at each colony: 0.875 ± 0.136). Additionally, dominance hierarchies among group members were stable between the two years of study. In contrast, in non-cooperative species, group members are not as interdependent of each other (e.g. for raising young or for hunting preys; Roberts 2005). Consequently, they may not need to invest in conflict management strategy to facilitate communal lifestyle such as ordered and stable dominance relationships

(Preuscholt and van Schaik 2000). Mexican jays (*Aphelocoma wollweberi*) and Florida scrub jays (*Aphelocoma coerulescens*), for example, both cooperative species, establish ordered dominance hierarchies (Woolfenden and Fitzpatrick 1977; Barkan et al. 1986), while this is not the case for the closely related, non-cooperative blue jay (*Cyanocitta cristata*; Barkan et al. 1986).

In structured dominance systems, one or several phenotypic traits are expected to signal individual differences in dominance scores so that the asymmetry in resource holding potential between two opponents can be assessed and escalated fights avoided. Because such phenotypic traits are often linked to fighting ability, body size and condition are traits often correlated to dominance status (but see Nakagawa et al. 2007). Yet, in my study I did not find that rank position was signalled by body size or condition. I also did not detect an effect of age on dominance scores, although I acknowledge that my estimation of age using a minimum age proxy may not have been accurate. However, I did find evidence that inter-individual variation and within-male variation in dominance status is signalled by a melanin-based plumage trait, i.e. the size of an individual's bib: individuals displaying larger bibs ranked higher in the hierarchy and had better access to the feeder than individuals with a small bib. These results suggest that the size of the melanin-based black bib has the potential to be a badge-of-status.

Yet, the size of the bib did not significantly account for variation in dominance scores when those scores were based only on interactions between males and females. This implies that my result of bib size signalling dominance may have been driven by interactions among males and that bib size may be less involved in the signalling of dominance status between sexes. I cannot exclude the possibility that bib size has a similar function within females, yet this appears less pronounced than in males (Fig. 2.3). Although I found that the interaction between the size of the bib and sex was not significant, the sample size of females being involved in interaction was smaller than that for males, while there was a greater spread of data around the predicted relationship between bib size and dominance score in females than in males (figure 3), so that firm conclusions on the signalling function of bib size in females cannot be drawn.

At the mechanistic level, previous studies pointed out that individuals with larger melanin-based patches are usually more aggressive and have higher circulating testosterone levels than less-pigmented individuals (Ducrest et al. 2008). This relationship typically emanates from pleiotropic effects of genes regulating melanin synthesis which are closely linked to physiological pathways affecting behaviour (Ducrest et al. 2008). In sociable weavers, individuals with higher expression of melanism may also exhibit higher level of androgens and aggressiveness, which may explain why they obtain higher dominance status (Bókony et al. 2008; Ducrest et al. 2008). The link between social status and flexible traits, such as condition and/or levels of circulating androgens, implies that status-signalling traits are often dynamic rather than static. Dynamic traits are sensitive to short-term condition and provide information about the current state of an individual. On the contrary, static traits (e.g. body size) usually inform about past condition or genetic quality (Kodric-Brown and Nicoletto 2001; Suk and Choe 2008). I found that even minor within-individual differences in dominance status were predicted by a difference in the size of the bib over the study period. These results suggest that there may be a dynamic feedback between the social environment and a plumage-based status signal which corroborate the insights of recent studies where social interactions drive rapid changes in status-signalling ornamentation (Karubian et al. 2011; Rhodes and Schlupp 2012; Dey et al. 2014).

The expression of badges to signal dominance status is expected to evolve mainly in groups of unfamiliar individuals who have to compete for food. Examples of such groups include wintering flocking species (Senar 2006). Groups that remain together year round and thus are more likely to consist of familiar individuals, signals of recognition, and not badges of status, are expected to evolve. My finding that a badge-of-status is correlated with dominance in sociable weavers may be explained by the fact that sociable weavers may live in large groups (sometimes hundreds of individuals) and may not have the cognitive capacity to recognize and memorize the competitive ability of each member of their colony. Also, as the size of the melanin-based bib appears to be a dynamic trait in this system, its expression may help individuals to get an updated dominance status on the members of a colony, including recent immigrants. Last, in groups exhibiting high levels of relatedness, such as cooperatively breeding groups, individuals may share interests of clear dominance signals to avoid unnecessary conflicts over reproduction and instead communally share associated benefits of dominance. In these groups, clear hierarchies, mediated by badge size, may be a mechanism to minimize costs while sharing benefits of group living.

While my results suggested that kinship did not remove the potential signalling function of the black bib, it did appear to play an important role in the social organisation of this species. The degree of kinship between two individuals influenced the occurrence of agonistic interactions between two individuals: relatedness was negatively associated with the likelihood of aggressions between two individuals and with the number of interactions within a dyad (Hamilton 1964; Ensminger and Meikle 2005). In sociable weavers, genetic relatedness plays an important role in social organisation (van Dijk et al. 2014) and cooperation (Covas et al. 2006). Nepotism could have major consequences in the distribution of direct and indirect benefits of individuals according to the social status of their relatives (Blumstein et al. 1997; Dobson et al. 2012). For instance, relatives of highly dominant individuals could get enhanced access to food resources or to chambers conferring better thermoregulatory benefits (van Dijk et al. 2013). Related helpers-at-the-nest provisioning offspring from highly dominant breeders may also get higher inclusive fitness if those dominants have higher reproductive output than subordinates. My results on the influence of kinship on dominance interactions add to the understanding of how relatedness plays a role in shaping and maintaining the social organisation of the complex cooperative societies of sociable weavers.

In sum, sociable weavers exhibit a strongly ordered hierarchy within colonies which appears to be stable across years. Additionally, I found that the size of the bib predicts success in social competition indicating the trait’s potential as a badge-of-status in the cooperative sociable weavers. Hence, both stable, ordered dominance hierarchies and a melanin-based badge-of-status might be used as a conflict resolution strategy of this highly social species. One important future avenue of research would be to explore the consequences of dominance hierarchies and status-signalling traits on cooperative behaviour, thus linking dominance, melanin-based colouration and investment in cooperation.

Chapter 3

Experimental evidence that bib size has a status-signalling function

> *‘The strongest and most effective force in guaranteeing the long-term maintenance of power is not violence in all the forms deployed by the dominant to control the dominated, but consent in all the forms in which the dominated acquiesce in their own domination.’*
>
> *Robert Frost*

3.1 Abstract

Badges-of-status are traits that have evolved to signal the social status of individuals, mediating potentially costly agonistic interactions. Theory predicts they should evolve as signals between unfamiliar individuals. They are assumed to be less important in group-living species such as cooperative breeders, and their role in these species has been seldom investigated. I tested experimentally whether the size of a coloured plumage patch, the black bib, signals social status in sociable weavers *Philetairus socius*, a year-round colonial, cooperatively breeding passerine exhibiting ordered dominance hierarchies. Two feeders were presented underneath their communal nest, giving individuals the choice to feed from either feeder. I assessed whether individuals fed preferentially at one feeder to control for a feeder preference. I then positioned two male decoys at each feeder, one with its bib experimentally reduced, the other with its bib enlarged. During the control phase (i.e. feeders without decoys), individuals showed a preference for a particular feeder, suggesting that the social environment played a role in foraging associations. However, I found support for a status-signalling function of the size of the melanin-based bib. First, individuals were more submissive toward the enlarged-bib decoy as opposed to the reduced-bib decoy, an effect that was stronger for individuals with smaller bibs. Second, individuals arrived faster at the feeder with the reduced bib decoy compared to the enlarged bib decoy. These responses were impacted by complex interactions between the decoy's bib size, an individual's sex and its bib size. I conclude that, despite the role played by the social environment in mediating access to a feeder, the response of sociable weavers to the presentation of an experimental black bib is consistent with a social status signalling function of the bib size in this cooperatively breeding, group-living passerine.

3.2 Introduction

Group-living species often exhibit dominance hierarchies to mediate the conflicts over access to resources (Drews 1993). Dominance hierarchies are particularly relevant when resources are scarce or clumped (Vehrencamp 1983) as they establish a priority order to access resources according to an individual's rank. The position within the dominance hierarchy is typically based on competitive ability such as fighting capacity or aggressiveness. Hierarchies enable individuals to avoid escalated fights, saving energy and avoiding injuries (Aureli and de Waal 2000). However, one obvious assumption for such hierarchies to successfully mediate conflicts is that individuals must be able to assess the rank of their opponents. Phenotypic cues about individual's competitive ability are thus required and, consequently, selection is expected to act upon the evolution of mechanisms allowing individuals to assess their probability to win over conflicts (Rutte et al. 2006).

Typically, an individual assesses its chance to win a contest over its opponent by examining one or several phenotypic traits that are related to competitive ability or aggressiveness. This way, when resources are not highly valuable, an individual should engage in escalated fights if they are likely to win only. On the contrary, they should avoid the encounter when loosing is the more probable outcome, thus saving energy (Maynard-Smith and Harper 2003). Different kinds of phenotypic cues may exist. Traits that have evolved under intra-sexual competition (i.e. armaments), for example, may give information regarding the outcome of conflicts when they directly confer an advantage in terms of fighting ability. In many ungulates, like the Alpine ibex (*Capra ibex*), horn size is correlated with dominance status and increases mating success through increased performance in male-male competition (Bergeron et al. 2010). Similarly, in many fish, like the cooperative cichlid, *Neolamprologus pulcher*, body size is highly correlated with dominance rank within groups and smaller fish avoid costly fights with larger fish (Balshine-Earn et al. 1998).

Colouration is another widespread signal of dominance (Senar 1999). Across taxa, black colouration has often evolved to signal competitive ability and hence, the social status of an individual (Tibbetts and Safran 2009). One reason for this is that pigmentation of the colour patch signalling social status is melanin-based. The production of melanin is linked to physiological pathways controlling also the production of testosterone and corticosterone, two hormones known to be tightly linked with behaviour. Testosterone is typically associated with high level of aggressiveness (Ducrest et al. 2008; McGraw 2008) and corticosterone with stress behaviour (Ducrest et al. 2008). Other studies have found supports for the use of carotenoid-based colouration (Pryke and Andersson 2003) or UV reflectance (Remy et al. 2010) to settle agonistic encounters. Phenotypic traits that have evolved to signal dominance status have been termed “badge-of-status” (Rohwer 1975; Rohwer 1977). The honesty of such signals is expected to be, at least partly, maintained by social mechanisms, such as the punishment of cheaters (i.e. subordinate individuals displaying large badges) by dominants (Møller 1987; Tibbetts and Dale 2004). Another social mechanism to maintain signal honesty is that individuals with similar badges are expected to intensively challenge each other so that cheaters would be harassed by opponents with similar badges without the requisite competitive abilities (Rohwer 1977). However there also is evidence that badges-of-status are costly to produce and submitted to the handicap principle so that only individuals in good conditions are able to express large badges (Evans et al. 2000; Buchanan et al. 2003; Laubach et al. 2013).

Badges-of-status occur in a wide range of taxa, including reptiles (Anderholm et al. 2004), insects (Tibbetts and Dale 2004), fish (Dijkstra et al. 2009), crustaceans (Aquiloni et al. 2012), mammals (Bergeron et al. 2010), and birds. They have been particularly well studied in birds, where they often take the form of coloured plumage patches (Senar 2006; Nakagawa et al. 2008), and are particularly relevant in species forming winter groups where unfamiliar individuals have to compete for scarce resources in winter (Senar 2006; Tibbetts and Safran

2009; Chaine et al. 2013). Correlative studies have found a positive association between the size of a coloured plumage patch and dominance status in many sparrows species, for example in Harris sparrows (*Zonotrichia querula*; Rohwer 1977), house sparrows (*Passer domesticus*; Nakagawa et al. 2007), white-crowned sparrows (*Zonotrichia leucophrys*; Laubach et al. 2013) or golden-crowned sparrows (*Zonotrichia atricapilla;* Chaine et al. 2011) but also in other families such as Eurasian siskins or great tits *(Parus major;* Jarvi and Bakken 1984; *Cardualis spinus*; Senar et al. 1993) for instance.

In order to demonstrate that a trait has evolved to signal dominance status and is not simply correlated to another trait used in such signalling function, it is necessary to experimentally manipulate it. Studies that have performed experimental manipulations of a coloured trait to explore its status-signalling function have used laboratory-controlled experiments (i.e. aviary; Pryke and Andersson 2003; Chaine et al. 2013) and field experiments (Pryke and Andersson 2003; Midamegbe et al. 2011). In both cases, the treatment is either applied directly to the individuals (enlargement or reduction of the patch; Pryke and Andersson 2003) or using mounted models with different patch sizes (Préault et al. 2002; Vergara et al. 2007; Laubach et al. 2013). Manipulated individuals then can be either tested against each other in groups (Bókony et al. 2006) or in pairwise contests (Senar and Camerino 1998; Remy et al. 2010; Chaine et al. 2013).

While experimental evidence supporting the use of badge-of-status in species wintering together or in territorial species has accumulated in the literature (Senar 1999; Senar 2006; Nakagawa et al. 2007; Tibbetts and Safran 2009), support that badges-of-status have evolved in birds that live in groups year-round are less common. Furthermore, there have been very few experiments conducted with highly social species, such as cooperative breeders. To my knowledge, the only study that experimentally manipulated a status-signalling plumage trait in a non-territorial, cooperatively breeding bird, was performed by manipulating UV reflectance of Florida scrub jays' plumage (*Aphelocoma coerulescens*; Tringali and Bowman 2012), where the experimental manipulation altered the number of wins and losses obtained by an individual.

The evolution of badge-of-status is especially interesting to test in cooperatively breeding species as dominance is likely to play a key role in the social organisation and cooperation (Cant 2011; Zöttl et al. 2013). In family-based groups, accurately signalling one's dominance status may have multiple benefits. For instance, in such groups, conflicts may occur over the access to a breeding position. A clear signal of dominance may prevent these conflicts, which may be highly beneficial for family groups as the costs of conflicts will be shared among relatives and could potentially reduce indirect fitness benefits given by cooperation. However, badges-of-status are typically predicted to evolve in group of individuals that do not know each other and is expected to mainly play a role in meditating interaction between unfamiliar individuals (Senar 1999; Vedder et al. 2008; Remy et al. 2010; Quesada et al. 2013). By contrast, cooperatively breeding groups usually consist of individuals familiar with each other. Experimental studies are thus needed to test the role badges-of-status within social groups of cooperative breeders.

I test whether the expression of a melanin-based plumage trait has evolved to signal social status in sociable weavers, *Philetarius socius*. Sociable weavers are long-lived, cooperatively breeding passerines (Maclean 1973d). Adults of both sexes display a melanin-based black bib (Maclean 1973d) and plumage maturation is reached during the first year after fledging (Maclean 1973a). My previous work showed that adult variation in the size of the black bib is strongly affected by year and moderately by age, body condition and colony size, and that bib size does not differ between sexes (Acker et al. 2015). Each colony exhibits strongly ordered hierarchies and that the size of an individual's bib is positively associated with its dominance status, suggesting that it could be a badge-of-status (Rat et al. 2015). To test this hypothesis, I experimentally presented two male decoys, one with its bib reduced and one with the bib enlarged in size. The two decoys were positioned next to two feeders, 48 cm apart, and located underneath the sociable weavers' communal nest. In this way, I offered a binary choice for each members of the colony to feed near either of the decoys (Senar and Camerino 1998). I tested whether the treatment applied to the decoys (enlarged or reduced bib size) predicted (i) the number of agonistic interactions the individuals directed towards a decoy, (ii) the first feeder from which each individual chose to feed, (iii) the latency each individual took to feed from a feeder, and (iv), the time each individual spent at a feeder.

If the black bib is a badge-of-status, I have the following predictions: (i) because mid- and low-ranked individuals are expected to be more numerous than highly dominant individuals with large badges, I predict that the reduced bib decoy should receive more agonistic interactions than the enlarged one and fewer submissive behaviours; (ii) more individuals should feed first, take less time to start feeding, and feed for longer at the feeder with the reduced bib decoy because individuals should avoid feeding close to dominants (Ekman 1989; Senar and Camerino 1998); and (iii) differences between treatments should be less pronounced for females than for males (as they are dominated by males; Rat et al. 2015) and for individuals with small bibs than individuals with large bibs (i.e. individuals with larger bib should clearly avoid risking to fight another large badged individual). I thus anticipated that the sex of an individual and its bib size should interact with the treatment to predict the first feeder chosen, the latency to feed from a feeder and the time spent at a feeder.

3.3 Materials and methods

3.3.1. Study species and site

Sociable weavers are social passerines endemic to the semi-arid savannahs of southern Africa. They are facultative cooperative breeders that also cooperate to build their massive, communal nests over generations (Maclean 1973b). The thatched nest is typically built on *Vachellia erioloba* trees (although other trees or human-built structures may be used) and can host less than ten to hundreds of individuals (Maclean 1973d). The colonies roost year round in independent nest chambers embedded within the communal thatch. These chambers are also used for breeding (Maclean 1973b; van Dijk et al. 2013).

My study site was located at Benfontein Nature Reserve (28˚52'S, 24˚50'E) near Kimberley, Northern Cape Province, South Africa. The area consists of about 15 km^2 of Kalahari sandveld covered mainly by *Stipagrostis* grasses and *Vachellia spp.* trees (Covas et al. 2006). It contains approximately 30 active colonies comprising between 5–80 individuals each. As part of the long-term research on this study population, these colonies have been captured annually using mist-nets since 1993 (see Covas et al. 2002 for more details on the captures). The annual captures occur prior to the breeding season and allow us to estimate the minimum age of individuals based on the date of the first capture event when not ringed as a nestling. During capture, birds are ringed with a uniquely numbered metal ring and three colour rings to allow individual identification in the field. Birds are weighed (to the nearest 0.1 g) and their tarsus length measured (to the nearest 0.1 mm).

3.3.2. Bib measurements

Measurements of the black throat patch ('bib') of each adult, was photographed three times at capture using a Canon EOS D500 digital camera (Rat et al. 2015). I positioned each bird on their back over a grey background (Kodak Gray Card) aligned with a ruler. The bib was smoothed between each photograph. I then used ©Photoshop CS5.1 (Version 12.1) to select the black pixels of the bib and calculate its size (in cm^2). The mean bib size from the three pictures was used in the analyses. Within-individual repeatability of bib-size measurements was high (0.894 ± 0.016, $P < 0.001$, $N = 107$) as calculated using the package "*rptR*" in R (Nakagawa and Schielzeth 2010).

3.3.3. Manipulation of decoys

The use of decoys ensures that the manipulation was applied to unfamiliar individuals (Senar 2006; Edler and Friedl 2010; Remy et al. 2010). The decoys were made using two males found dead in this population at colonies distant from the experimental sites. The size of the bib was manipulated to be either reduced or enlarged by three standard deviations from the mean of the natural population (1.48 ± 0.22 cm^2, N = 662). The manipulated bibs remained within the natural range of bib sizes (min: 0.35 cm^2; max: 2.45 cm^2). I have chosen to reduce the bib from the male with the original larger size (before manipulation: 1.359 cm^2; after manipulation: 0.825 cm^2) by plucking feathers from inner layers of feathers so that the patch remained homogenous. I used a permanent black Sharpie marker to enlarge the bib of the male with the original smaller bib (before manipulation: 1.179 cm^2; after manipulation: 2.142 cm^2). I checked with a spectrophotometer (USB2000 OceanOptics spectrophotometer) that the colouration of the painted feathers was similar to the natural black feathers of the bib. This procedure, paired with the use of decoys, enhances the likelihood that only the manipulated trait provided information about social status.

3.3.4. Experimental design

Between October and November 2013, I set up the following experiment under each colonial trees. I used two identical 10-cm diameter circular feeding trays with an *ad libitum* mixture of seeds. Each feeder was sunk into the ground so that its edge was level with the ground and enclosed in a green 48-cm diameter ring to delimit the feeding area (seeds tend to be spread around the feeder by the group when feeding). The experimental area was marked with a dark green rope forming a rectangle (108 x 156 cm) within which the two feeders were placed in the centre (Fig. 3.1). A neutral zone was defined as the remaining area of the whole experimental area excluding the two feeding area (Fig. 3.1). Two camcorders set up on tripods 10 m from the experimental area each recorded 50% of the experimental area for two hours

(Fig. 1). For each colony, my experimental procedure consisted of two phases, a control phase at day 1 and an experimental phase at day 2, both performed in the morning between 1 to 2 hours after sunrise.

During the control phase, the two feeders were set up without the decoys to allow individuals to habituate to the feeders (feeder A and feeder B) but also to assess whether a preference existed for one of the feeders. Feeders A and B were randomly allocated to the right or the left side of the experimental design. At the end of the experiment, I left the design (i.e. rings and delimitation) on the ground but removed the feeders. At day 2, I re-positioned the feeders, added an *ad libitum* supply of the seed mixture. Feeders were re-positioned at the

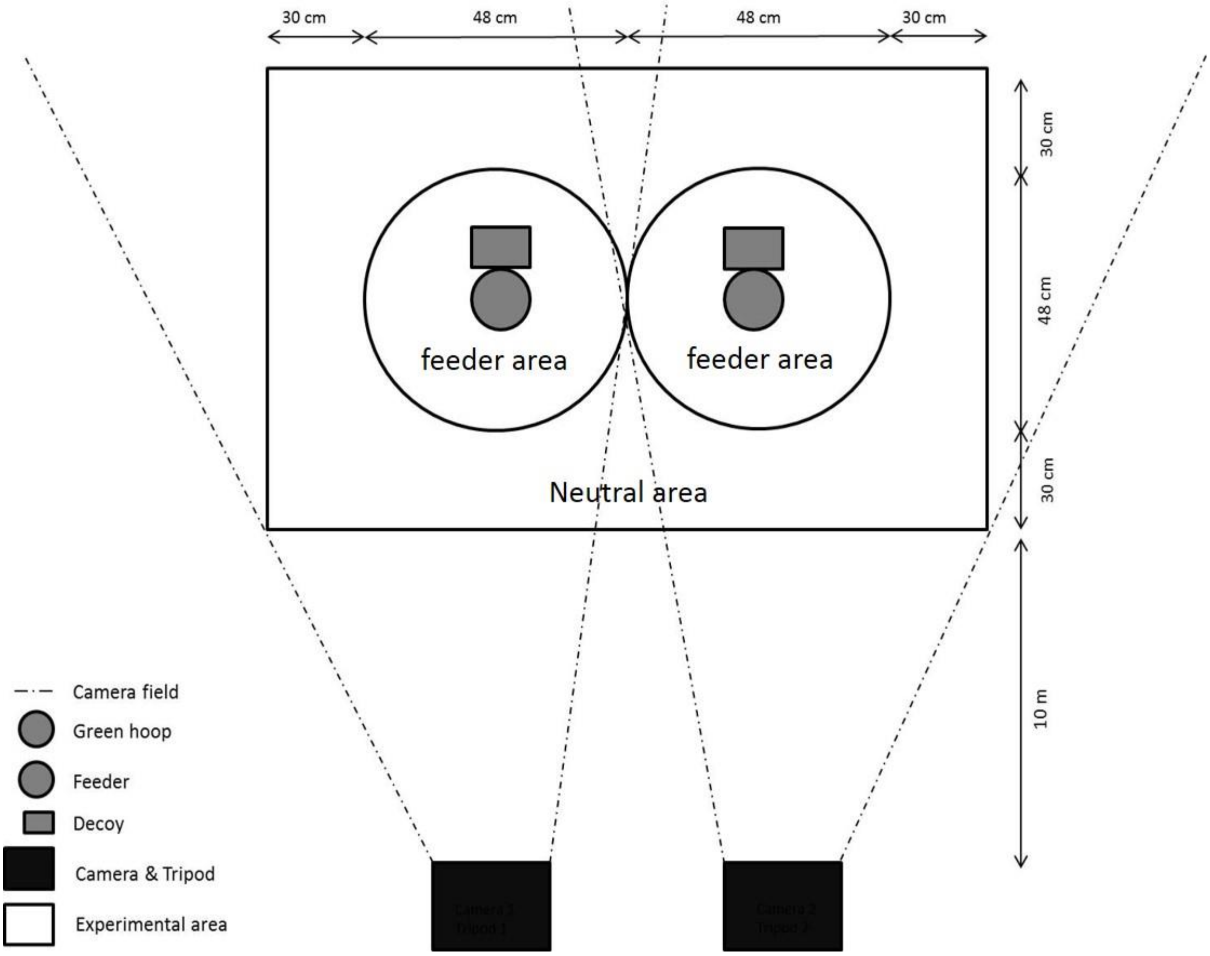

Figure 3.1 Scheme of the experimental design set up to test for a status-signalling function of the bib. The control phase is at day 1 where the feeders A and B are randomly assigned to a side of the design, filled with a mixture of seeds and left without decoy for 45 minutes while a camera records the behaviour of the weavers. At the end of the control phase, the seeds are removed. The experimental phase is at day 2 where the feeders are filled with a mixture of seeds, the reduced bib decoy is assigned to feeder A and the enlarged one to feeder B. A camera records the behaviour of the weavers for 45 min

location randomly assigned during the control phase. Feeder A was associated with the reduced bib decoy and feeder B with the enlarged bib decoy (Fig. 3.1). This procedure was conducted once per colony.

A camera recorded the feeding area for both phases. For both phases, I then analysed the video-recordings for 5 minutes after the first individual was seen entering the neutral area. I analysed only five minutes of the recording as individuals may get habituated to the decoys and stop being deceived.

From the videos, I collected first the number of ‘submissive’, ‘dominant’ and ‘assessment’ interactions an individual showed against the enlarged bib decoy and/or the reduced bib decoy for the experimental phase only (Table 3.1). Then, for both control and experimental phases, I determined (i) which decoy was chosen first by most individuals, (ii) measured the latency for each individual to feed from each feeder, and (iii) recorded the time an individual spent in each feeding area.

Table 3.1 Types and number of interactions with each decoy collected during the experimental phase

Interaction	**Description**	**Reduced bib**	**Enlarged bib**
Dominant	Individual pecks a decoy	2	2
Submissive	Individual lowers its head and body and moves away from the decoy	9	18
Assessment	Individual extends its body and raises its head while looking at and approaching the decoy	3	6

Comparison of control and experimental phases show that decoys were likely perceived as conspecifics because their presence impacted the behaviour of the individuals. On average, individuals fed less in the experimental phase (40 ± 53 s) as opposed to the control phase (60 ± 68 s; $N = 59$, $T = -2.552$, $P = 0.011$). They also took longer to feed from the feeders during the experimental phase (147 ± 143 s) than the control phase (102 ± 137 s, $N = 59$, $T = -2.561$, $P = 0.011$). However, presence of decoys did not prevent individuals from visiting the feeders. More individuals visited the feeding area when the decoys were present ($N = 107$) than during the control phase ($N = 72$) so that neophobia was unlikely to explain the increased latency to approach the feeder. Furthermore, I did not observe a difference in bib size distribution between the two phases (control: 1.383 ± 0.225 cm^2; experimental: 1.415± 0.213 cm^2; $N = 59$; $P = 0.434$) suggesting that there was the potential for comparable (i.e. similar) social status to be represented at both phases.

3.3.5. Statistical analyses

All statistical analyses were conducted in R version 3.1.1 (R Development Core Team 2012). I used the Generalized Linear Model approach, with the Restricted Maximum Likelihood criterion using the package '*lme4*' (Bates and Maechler 2009) for mixed effect models of the Gaussian family (LMM) and of the Poisson or Binomial family (GLMM). I then selected the set of best fit models based on the corrected Akaike Information Criterion (AICc) using the function '*dredge'* from the '*MuMin'* package (Barton 2013). Only models with a ΔAICc < 2 were kept. I used the package '*lmerTest'* to infer *P*-values and estimate confidence intervals for fixed effects (Kuznetsova et al. 2014). Colony identity was set as a random factor in the mixed models to account for repeated measures of individuals within colonies.

Feeder preference during the control phase

I tested for a feeder preference (A or B) during the control phase (i.e. without decoys). There was no difference in the time individuals took to approach each of feeder ($P = 0.149$), but at the six colonies tested, more individuals fed first from feeder A than feeder B (Chi-square test: $\chi_{2,2} = 64$; $N = 107$; $P < 0.001$; Fig. 2). Furthermore, individuals fed longer at feeder A (LMM estimate: 26.88 ± 15.11; $T = 1.779$; $N = 76$; $P = 0.080$). Therefore, I controlled for a feeder preference when examining the first feeder chosen and the time spent at the feeder during the experimental phase. I had convergence problems when analysing the latency to approach a feeder due to the small and unbalanced sample size for females (N= 47 for males, $N = 13$ for females) between the two feeders, so I only analysed this behaviour for males

Badge-of-status experiment

I used a chi-square contingency table to test whether there was a difference between treatments in the number of submissive and assessment interactions with the decoy (N = 36 interactions exhibited by 13 individuals; Table 3.1). I then fitted a GLMM with a Poisson error distribution to investigate whether the treatment applied to the decoy, an individual's bib size and the interaction between these two explanatory variables affected the number of submissive interactions exhibited toward each decoys.

To examine which traits predicted the decision to feed first from one of the two feeders, I fitted a GLMM with a binomial error distribution. To test whether the latency to approach a feeder and the time spent at a feeder differ according to the treatment applied to the decoys, I fitted a LMM of the Gaussian family (Table 3.2). Covariates in these three models included the treatment applied to a decoy during the experimental phase, sex, minimum age, tarsus length, body mass (Green 2001), and bib size. I included the two-way interactions between the treatment and sex, treatment and bib size, treatment and minimum age, and sex and bib size. I also tested for an effect of two three-way interactions: treatment, bib size and sex, and treatment, sex and minimum age. I also controlled for a feeder preference in the first feeder chosen and the time spent at the feeder by including, respectively, the first feeder chosen during control part and the time spent at a feeder.

Table 3.2 Samples sizes obtained for the control and the experimental phases to conduct our analyses

	Sample size	
	Control	**Experimental**
Individuals that were seen in the feeding area	72	107
Individuals that fed from the feeder (latency and first feeder)	60	76
Individuals that were seem during both phases	59	59

3.4 Results

In line with my predictions, I found that the plumage manipulation of the decoys was associated with observed agonistic interactions and access to the feeder. There were significantly more submissive interactions directed toward the large bib decoy than toward the small bib decoy ($\chi^2 = 6$; *df* = 1; *N* = 27; *P* = 0.014; Table 3.1), although assessment behaviour did not differ significantly between the two decoys ($\chi^2 = 3$; *df* = 1; *N* = 9; *P* = 0.083; Table 3.1). Also as expected, individuals that were more submissive toward the large bib decoy tended to have smaller bibs (GLMM estimate: -8.643 ± 4.419; *T* = -1.956; *N* = 13; *P* = 0.051).

More individuals chose to feed first from the feeder associated with small bib decoy than the large bib decoy ($\chi^2 = 9.026$; *N* = 76; *P* = 0.011; Fig. 3.2). However, the size of a male's bib did not appear to affect its choice to feed first from either feeder (*P* = 0.443). During the control phase, minimum age and body size contributed to the model fit and remained in the minimal model but were non-significant (all *P* > 0.192).

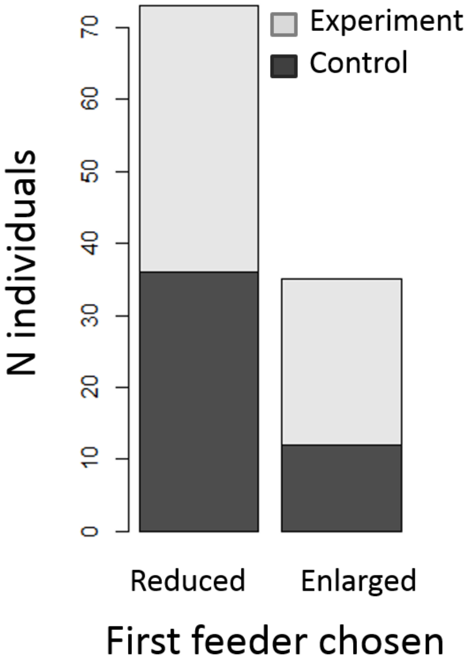

Figure 3.2 First feeder chosen by each individual. For both the control and the experimental phases, feeder A was preferred for both phases so also when it was associated with reduced bib decoy

The interaction between treatment applied to the decoys and sex predicted an individual's latency to visit the feeder (Table 3.3). Males arrived faster at the feeder with the small bib decoy than the feeder with the large bib decoy, whereas the effect for females was less pronounced (GLMM estimate: -456 ± 220s; T = -2.074; N = 76; P = 0.044; Table 3.3). The latency to approach one feeder also was influenced to some extent by an individual's bib size (i.e. interaction between sex, treatment and bib size): males and females with larger bibs tended to arrive faster at the enlarged bib decoy, and this effect tended to be reversed for males - but not females - with smaller bibs at the feeder with the small bib decoy (GLMM estimate: 318 ± 161s; T = 1.979; N = 76; P = 0.054; Table 3.3, Fig.3.3). All other variables (i.e. minimum age, tarsus length and body mass) contributed to improve the goodness-of-fit (i.e. ΔAICc < 2), but were not significant (P > 0.281).

Table 3.3 Model estimates and standard errors (SE) for the single minimal model explaining the variation in the latency to arrive to the feeder. For discrete variables, the level estimated is stipulated in brackets. The reduced bib treatment is indicated by a negative sign '-', males are indicated by 'M'. The asterisks represent an interaction. Significant effects are in bold and marginal effects in italic

Effect	**Estimate±SE**	**T**	**P**
Intercept	128±133	0.963	0.340
Sex (M)	-31.±142	-0.215	0.831
Bib	-77±100	-0.765	0.448
Weight	4±5	0.824	0.414
Tarsus	-13±14	-0.962	0.341
Minimum age	-5±17	-0.304	0.763
Treatment (-)	245±224	1.091	0.281
Treatment (-) * Sex (M)	**-456**±220	**-2.074**	**0.044**
Bib * Treatment (-)	-157±163	-0.964	0.340
Bib * Sex (M)	20±104	0.195	0.846
*Bib * Treatment (-) * Sex (M)*	*318*±161	*1.979*	*0.054*

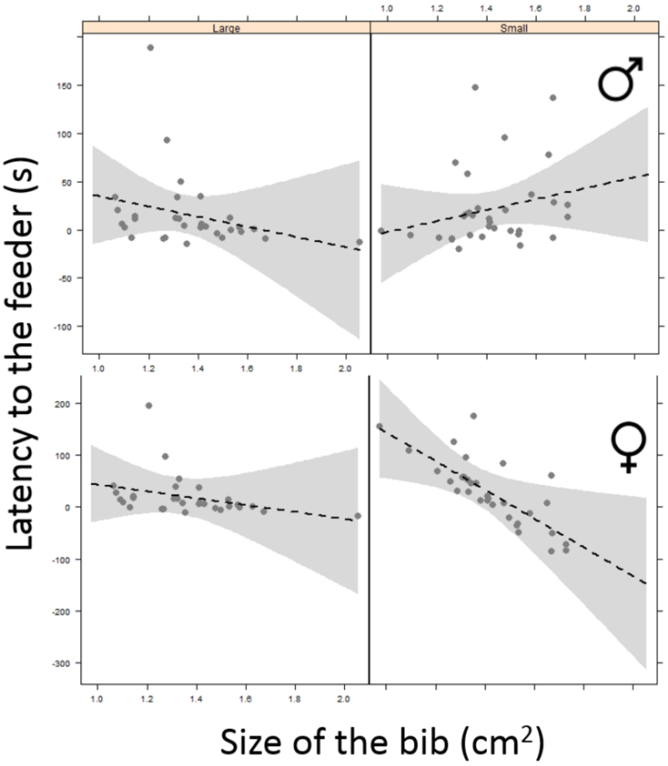

Figure 3.3 Latency each individual took to visit to a feeder. Model estimates are represented in relation to the size of the bib, the sex and the treatment applied to the decoys. The dash lines represent the main effect of the size of the bib and the grey shades the 95% confidence interval

The treatment did not predict the time an individual spent feeding (Table 3.4). Overall, males with a larger bib fed for longer from either feeder than males with smaller bibs, independent of the decoy present (LMM estimate: 241 ± 100s; $T = 2.338$; $N = 59$; $P = 0.019$;Table 3.4, Fig. 3.4). All other variables (i.e. minimum age, tarsus length and body mass) contributed to improve the goodness-of-fit (i.e. ΔAICc < 2), but were not significant ($P > 0.281$).

Table 3.4 Effects affecting the time spent at the feeder during the experimental phase. Estimates and standard errors (SE) are indicated when the effects are retained in the set of best fit models and are based on models averaging. For discrete variables, the level estimated is stipulated in brackets. The small bib treatment is indicated by a negative sign '-', males are indicated by 'M'. The asterisks represent an interaction. Significant effects are in bold and marginal effects in italic

Effect	**Estimate±SE**	**Z**	**P**
Intercept	-129±363	0.346	0.729
Time spent during control			
Bib size	**-236**±94	**2.455**	**0.014**
Treatment(-)	*-319±180*	*1.728*	*0.084*
Minimum Age	2±3	0.764	0.445
Sex (M)	**-376±147**	**2.496**	**0.012**
Tarsus length	12±16	0.711	0.477
Weight	9±7	1.236	0.217
Bib size * Treatment	184±123	1.457	0.145
Bib x Sex (M)	**241±100**	**2.338**	**0.019**
Treatment (-) x Sex (M)	*390±204*	*1.859*	*0.063*
Bib * Treatment (-) x Sex (M)	-229±140	1.594	0.111

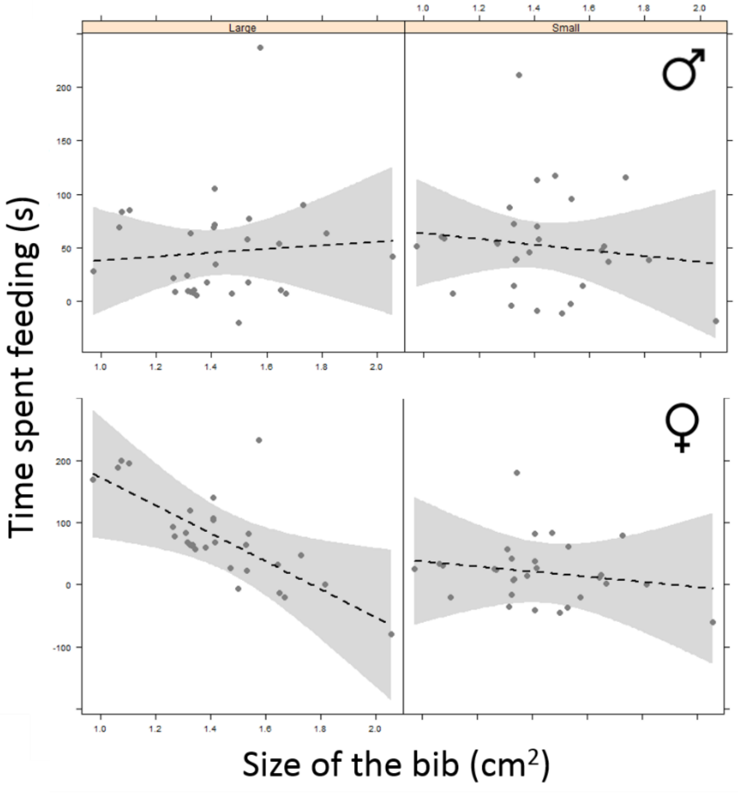

Figure 3.4 Time an individual spent at the feeder after controlling for the bias observed during the control phase. Model estimates are represented in relation of the size of the bib, the sex and the treatment applied to the decoys. The dash lines represent the main effects of the size of the bib and the grey shades the 95% confidence interval

3.5 Discussion

Badges-of-status have evolved to settle conflicts without escalated fights, saving energy expenditure and risk of injuries in groups of unfamiliar individuals (Maynard-Smith and Harper 2003; Senar 2006). However, their evolution in year-round social species, such as cooperative breeders, is less clear (Senar 1999; Quesada et al. 2013). In this study, I experimentally tested whether the size of the black bib has status-signalling function in a highly social, colonial and cooperatively breeding passerine, the sociable weaver. Sociable weavers live in colonies structured by ordered hierarchies (Rat et al. 2015). I offered weavers a choice to feed either nearby an enlarged bib decoy or a reduced bib decoy. I found that, both, the decoy's and an individual's size of the bib influenced the feeding behaviour of the birds: More individuals chose to feed near to the reduced bib decoy and visited that feeder faster as opposed to the feeder with the enlarged bib decoy. Yet, the latter was visited faster by individuals with larger bibs compared to individuals exhibiting smaller bibs. Last, I observed submissive interactions, which occurred more frequently when directed toward the enlarged bib decoy than toward the reduced bib decoy. My results suggested that the sociable weaver's bib has a status-signalling function and that this plumage trait is involved in the regulation of food access.

For the control phase, individuals fed longer and more often chose to feed first from feeder A, which was subsequently associated with the small bib decoy. As individuals did not know which decoy would be assigned to a feeder and as the feeders were randomly positioned, my results suggest that colonies had a preference for a feeder, independently of the side. Such bias may be due to a preference to associate with individuals already present at the feeder. For instance, Robert et al. (2013) offered tunas *Thunnus spp.* the choice to aggregate beneath two identical floaters (a frequently observed behaviour in these fishes). Instead of aggregating in a symmetrical way around the two floaters, social interactions shaped the aggregation patterns so that one floater was preferred. A similar role of social interactions may have occurred in this experiment. The influence of social effects on foraging decision is common for species visiting food patches in groups. For instance, group size influences foraging rates in impalas (*Aepyceros melampus*; Fritz and Garine-Wichatitsky 1996). Furthermore, social species use social information to influence their foraging decision, which can be further linked to the social position of individuals within their group's network. For instance, in tits (*Paridae*), social associations between individuals strongly predicted the arrival of tits at a new food patch because the diffusion of social information is strongly influenced by social positions (Aplin et al. 2012). The social status of individuals already present at the food patch (Foerster et al. 2011; Marshall et al. 2012) or the degree of relatedness (Rossiter et al. 2002; Tóth et al. 2009) with those individuals may also influence the decisions about where and when to feed. That could have been the case in sociable weavers, because previous work demonstrated that social status is linked to the access to food while relatedness structures the relationships between individuals (van Dijk et al. 2014; Rat et al. 2015). My results suggest that the social environment may have influenced feeder choice and aggregation patterns. Indeed, interactions with familiar members of a colony may play an important role in foraging decisions and may regulate the access to food (Vedder et al. 2008).

Despite the possible confounding effects of the social environment, I found support for a status-signalling function of bib size. The decoy's bib size was associated with the distribution of agonistic behaviour and the latency to approach a feeder exhibited by sociable weavers. Theories on the evolution of aggressive behaviour and status-signalling predict that, when the asymmetry between opponents is high, individuals should settle conflicts without physical contact (Maynard-Smith et al. 1988; Maynard-Smith and Harper 2003). If plumage patch signals competitive ability or aggressiveness, both individuals will benefit by saving energy, time and reducing the risk of injuries (Rohwer 1982). Accordingly, small-badged individuals are expected to avoid large-badged individuals, as shown in my results. For individuals with small bibs, exhibiting submissive behaviour may be extremely beneficial are they are the less likely to win an encounter.

In species where status is signalled by a plumage traits, individuals often prefer to associate with individuals/decoys of lesser rank (Senar and Camerino 1998). I therefore expected to observe individuals to reach quicker and feed longer at the feeder with the small bib decoy. I did not find any difference in the time spent feeding between the two feeders associated with the decoys. However, males visited the feeder associated with the small bib decoy faster and more individuals chose to feed first from this feeder. In females, their feeding behaviour in relation to the decoys' bib appeared more complex as they took longer than males to visit the small bib decoy. Two non-mutually exclusive hypotheses may explain this pattern. First, as females are subordinate to males, they may seek protection from dominant (Smuts and Smuts 1993; Clutton-Brock and Parker 1995), larger-badged males that are unlikely to perceive them as competitors. Second, females could be attracted to males with larger badges as signals used in male-male contests are often used in mate choice (Kodric-Brown and Brown 1984; Berglund et al. 1996; Griggio et al. 2007; Tobias et al. 2011).

As predicted, an individual's bib size affected access to food as well as the decoy's bib size. Overall, males with large bibs fed longer than males with small bibs, independent of the decoy's bib size. Furthermore, even though the effect was marginal, my study indicates that complex interactions between an individual's sex, bib size and the decoy's bib size regulated access to the feeders. Males and females with larger bibs approached the feeder with the large bib decoy more rapidly, but this effect was reversed for males (but not females) with small bibs at the feeder with the reduced bib decoy. Such interactive patterns are expected under a status-signalling function of the bib because the trait asymmetry between opponents is a crucial determinant of whether to escalate a conflict (Maynard-Smith 1982; Maynard-Smith and Harper 2003) and because sex plays an important role in determining dominance status in this system (Rat et al. 2015). For instance, in blue tits (*Cyanistes caeruleus*), individuals preferred to feed with males that had similar plumage signals to themselves (Remy et al. 2010), a pattern that has been observed in other species such as *Parus spp*. and Eurasian siskins (Ekman 1989; Senar and Camerino 1998). Only individuals with large bibs may risk feeding near the large bib decoy, benefiting from reduced competition with conspecifics. On the other hand, individuals with small bibs may have to share the small bib decoy feeder with individuals displaying larger badges than themselves, increasing the risk of conflict, and potentially explaining why the latency of feeding at this feeder was high for this category of individuals.

The evolution of traits that signal social status is predicted to occur mainly when individuals are unfamiliar with their conspecifics and compete over relatively low-value resources (Senar 1999; Maynard-Smith and Harper 2003; Senar 2006). Accurate status signalling has the potential to reduce the costs of interacting with relatives. Despite the fact that sociable weavers live together within their colony all year and are cooperative breeders (Maclean 1973d; Maclean 1973a), I found that the size of the sociable weaver's black bib shows properties that are in agreement of a status-signalling function. I propose that, because sociable weavers can potentially live in large groups (hundreds of individuals; Maclean 1973b), they may not have the possibility to recognize and/or memorize the social status of all colony members. Status badges may also be useful when encountering members from neighbouring colonies while foraging, or, when prospecting birds visit a colony. The melanin-based bib also may be dynamic, with a size adjustment according to a change in social status (Rat et al. 2015). Such adjustment may help individuals to gain updated information regarding the social status of group members. Therefore, badges-of-status may be relevant in this system as large groups are common (Maclean 1973d; Maclean 1973b) and as conflicts over competition and cooperation are likely to occur frequently (van Dijk et al. 2014). More studies are needed to assess whether the evolution of badges-of-status in cooperatively breeding species may be more common than previously thought.

In synthesis, I found support for a status-signalling function of the melanin-based bib in the sociable weaver. My study suggests that badges-of-status may be relevant in colonial, cooperative species where individuals are likely to be familiar with other group members. However, I observed control biases that were likely to be due to confounding effects of the social environment. Such biases would need to be better controlled in future experiments. For instance, the size of the bib from unfamiliar individuals (i.e. from different colonies) in an aviary could be manipulated to assess dominance status in pair-wise contests. The design of a laboratory-controlled experiment to validate the status-signalling function could be paired with a physiological approach in order to explore how signal honesty is maintained in this system.

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Chapter 4

Multiple benefits associated with social status

‘The greatest leader is not necessarily the one who does the greatest things. He is the one that gets the people to do the greatest things’

Ronald Reagan

4.1 Abstract

The establishment of dominance hierarchies is expected to create a bias in individual access to resources reflecting the competitive asymmetry between individuals. Dominants are expected to gain better access to resources and, as a result, higher fitness benefits than subordinates. Sociable weavers are year-round colonial and cooperatively breeding passerines that establish ordered dominance hierarchies. Here, I tested whether dominance status of sociable weavers was associated with enhanced access to food, high quality nests, mates and helpers-at-the-nest. I further tested whether dominance status was associated with increased reproductive success. Additionally, I investigated if dominance confers benefits via nepotistic access to food provided to subordinate group members. I obtained dominance scores for 86 individuals based on 3625 agonistic interactions observed at a feeder. My results suggest that most dominant individuals get priority access to food and occupy nest chambers conferring better thermoregulatory benefits. Dominants were also more likely to breed and tended to be assisted by helpers more frequently. However, among the birds that reproduced, dominance was not reflected in higher fledging success. Finally, I found evidence in favour of nepotism as the time spent by helpers (mainly philopatric offspring) at the feeder was positively associated with the time the group's dominant male spent at the feeder. This study shows that dominance is associated with several direct benefits and also with indirect benefits via nepotism.

4.2 Introduction

Many animals live in groups, where both cooperation and conflict occur over access to resources or other decisions such as predator defense and foraging. Conflicts are often settled without physical interactions as a result of dominance hierarchies, which reflect the competitive asymmetry between individuals of a group. The establishment of hierarchies enables individuals to predict the outcome of potential fights and prevent the occurrence of costly, escalated conflicts (Drews 1993). Dominance hierarchies are thus expected to promote group stability and cohesion (Chiarati et al. 2010) and, as a result, facilitate a communal lifestyle.

Dominant individuals rank higher in the hierarchy as a consequence of their higher competitive ability (Parker 1974) or aggressiveness (Hsu et al. 2006). Such asymmetry between individuals implies that resources are not distributed uniformly among group members (Senar and Camerino 1998). Because dominant individuals have better competitive ability, they are expected to monopolize or get a privileged access to a range of valuable resources such as food, mates or territories (Dubuc et al. 2011). For example, high-ranking female Japanese Macaques (*Macaca fuscata*) occur at higher frequency in patches containing their favourite winter seeds compared to lower ranking ones, which are constrained to patches with poor quality seeds (Saito 1996). Additionally, social status can also account for the monopolization of social resources. In captive bonobos (*Pan panicus*), high-ranking females received more grooming than lower-ranking ones (Stevens et al. 2005). In another species, the cooperatively breeding long-tailed tit (*Aegithalos caudatus*), the central position within a roost, which provides better thermoregulatory benefits than a position on the periphery, was predicted by dominance status (Napper et al. 2013).

However, dominance is not only beneficial (Ang and Manica 2010), it also involves important short- and long-term costs (Muehlenbein and Watts 2010; Acker et al. 2015). For example, individuals with high social status often have high testosterone levels (Wingfield et al. 1990; Muller and Wrangham 2004; Desjardins et al. 2008) which may potentially result in higher aggression rates (Wingfield et al. 1990; Muller and Wrangham 2004), energy expenditure (Muller and Wrangham 2004) or higher oxidative stress (Muehlenbein and Bribiescas 2005; Muehlenbein and Watts 2010; Dijkstra et al. 2011). Furthermore, rank maintenance may be traded off against, for example, foraging (Ang and Manica 2010). Such costs explain why not all individuals achieve high social status so that only the most competitive individuals may be able to endure them.

In cooperatively breeding species, where a pair is assisted in rearing young by one or more helpers (Cockburn 1998), dominance may offer additional benefits such as recruiting and/or keeping more helpers. The presence of helpers is expected to be beneficial as helpers may allow parents to reduce parental investment (e.g. work load: Hatchwell 1999; maternal investment in eggs: Russell and Lummaa 2009; Paquet et al. 2013) and may increase reproductive success (Mumme 1992; Hatchwell et al. 2004; Williams et al. 2006; but see: Covas et al. 2011). On the other hand, the presence of helpers may also increase within-group competition and conflicts. Increased competition with the presence of helpers may explain why some studies have found that short-term productivity was not enhanced by the presence of helpers (Hatchwell et al. 2004; Covas et al. 2011).

Additionally, individuals associating with dominants may also share some of the benefits of dominance. For instance, dominant individuals may facilitate access to resources to their kin. This behaviour, termed nepotism, occurs when individuals obtain favoured access to resources (direct benefits) provided by their relatives (Sherman 1980). Nepotism has been reported for primates (Chapai 1992; Silk 2009) and some social species of birds, including carrion crows (*Corvus corone*; Chiarati et al. 2011) and Siberian jays (*Perisoreus infaustus*; Ekman et al. 2001; Griesser 2003). In these studies, offspring of dominant individuals benefited from reduced aggression by group members (Chiarati et al. 2011), enhanced access to food, favoured predator protection (Griesser and Ekman 2004; Griesser and Ekman 2005) and higher dominance rank (Lea et al. 2014). Hence, the benefits of dominance can extend to relatives of dominant individuals, providing them additional indirect fitness benefits arising from dominant status that have been poorly explored.

Here, I investigated whether social status is associated with multiple potential benefits in the sociable weaver (*Philetairus socius*), a colonial, highly social and relatively long-lived passerine (Maclean 1973d; Covas et al. 2002). Sociable weavers are facultative cooperative breeders with breeding pairs being helped by 0 to 6 helpers. Helpers are mainly males and usually offspring from previous breeding attempts (93% of helpers are related to at least one parent; Doutrelant et al. 2004; Covas et al. 2006). Sociable weavers exhibit ordered, linear hierarchies with males being dominant over females (Rat et al. 2015). Multiple breeding pairs co-occur in the same colony and hence reproductive skew is expected to be low at the colony level. Consequently, the benefits of achieving a high social status in this species are not as clear-cut as in a cooperative species with highly despotic system, such as naked-mole rats (*Heterocephalus glaber*; Jarvis 1981; Faulkes et al. 1990) where subordinates suffer reproductive suppression. The presence of multiple breeding pairs in each colonial nest makes sociable weavers a suitable study system to investigate the potential benefits of dominance as it is possible to compare variation in these benefits not only between individuals of the same breeding group, but also between members of different breeding groups within a given communal nest.

I examined whether social status conferred advantages in terms of access to food (i.e. time spent at the feeder), the quality of the breeding chambers used (i.e. depth to which the nest chamber is embedded within the communal nest mass; van Dijk et al. 2013), and in terms of access to reproduction (i.e. the probability of becoming a breeder and of receiving assistance from helpers). I predicted that more dominant individuals are able to feed for a longer time at the feeder, occupy the nest chambers that confer the highest thermoregulatory benefits, have a higher probability to breed and are more likely to receive help to raise their offspring than subordinate individuals. Additionally, I investigated whether dominance in sociable weavers confers benefits through nepotism. I tested whether access to food by helpers was predicted by the status of their group's dominant male and whether their dominance status was related to the dominance status of the group's dominant male. I then examined whether enhanced access to resources was reflected in reproductive output. Because dominant individuals are expected to enjoy enhanced access to resources, and because dominants may be of better parental quality than subordinates (Bisazza et al. 1989; van Oort et al. 2007), I expected to find a positive association between dominance rank and fledging success.

4.3 Material and methods

4.3.1. Study species and study site

Sociable weavers are highly social passerines endemic to the semi-arid savannahs of southern Africa. They communally construct a large, thatched nest that is typically built on *Vachellia erioloba* trees (although other trees or human-built structures may be used). Colonies may vary in size from less than ten to hundreds of individuals that often forage in groups (Maclean 1973d). The nests contain several, independent nest chambers embedded within the communal thatch. Individuals use these chambers for roosting throughout the year and for breeding (Maclean 1973b; van Dijk et al. 2013). Sociable weavers are facultative cooperative breeders. Each breeding units usually consist of either a breeding pair alone or may contain up to seven helpers (Covas et al. 2006; Covas et al. 2008). Helpers are mainly the philopatric male offspring of one or both breeders (Doutrelant et al. 2004; Covas et al. 2006), although females also help. Extra-pair paternity appears to be absent in this species (Covas et al. 2006).

The study was conducted at Benfontein Nature Reserve (28˚52'S, 24˚50'E) near Kimberley, Northern Cape province, South Africa, between September 2013 and June 2014.

The area consists of about 15 km^2 of Kalahari sandveld covered mainly by *Stipagrostis* grasses and *Vachellia spp.* trees (Covas et al. 2006). It contains approximately 30 active colonies that comprised between 5–80 individuals over the period when this study was conducted. As part of the long-term research on this study population, most of these colonies have been captured annually using mist-nets since 1993 (see Covas et al. 2002 for more details on the captures). At 13 of these colonies reproduction was monitored since 2008 and all chicks are ringed in the nest before fledging; hence age is known for most birds born in the study colonies during this period. When not ringed as nestling, the minimum age of individuals can be estimated based on the date of the first capture event. All nestlings and immigrants caught during the annual captures, were individually ringed using a uniquely numbered metal ring and three colour rings to allow visual individual identification in the field. Individuals were also weighed (to the nearest 0.1g) and tarsus length (to the nearest 0.1mm) measured.

4.3.2. Access to the food and dominance

Between September and December 2013, I positioned a feeder (a plastic red-brown plate, ∅ 20cm) containing a mixture of bird seeds at 6 colonies (colony size at capture: 24.5 ± 10.5 individuals, range: 9-40). The feeder was situated at a fixed location on the ground underneath the nest. To habituate the birds, a tripod and the feeder were positioned underneath each colony with an *ad libitum* supply of a seed mixture until the first individual was observed to feed from it ($\mu = 8.7 \pm 9.2$ days). Once the birds were habituated to the feeder and tripod, the feeder was removed between observation bouts in order to increase competition for the access to the food. Two hours of observation were conducted twice a day, between 6:30-8:30 and between 16:00-18:00 using a video-camera (Sony Handycam HD) on a tripod 2-3 m away from the feeder which filmed all individuals within a 1 m radius around the feeder (mean total observation time per colony: 40.1 ± 10.9 hours).

All videos were viewed to extract the number of agonistic interactions within dyads, the direction of the interactions and the identity of the birds involved (i.e. identities of the ‘winner’ and the ‘loser’ for each interaction). The matrices describing agonistic interactions were based on 86 individuals involved in 3625 interactions. I determined the dominance score of these 86 individuals using David’s score (David 1987). I scaled dominance scores within colonies, so that all scores ranged from 0 (the most subordinate individual) to 1 (the most dominant individual) for each colony, thereby allowing comparison of dominance scores obtained from colonies of different sizes (see Rat et al. 2015 for details).

Additionally, for 10 randomly selected videos (out of the 20 made at each colony) I determined the time each individual spent inside the feeder or inside the 1 m radius around the feeder during the first 30 minutes after the first individual was observed at the feeder. I used the first 30 minutes and not the full two hours since I expected the effect of competition to be stronger during the first 30 minutes of feeding. This was confirmed by the observation of reduced activity at the feeder after 30 min (MR, personal observations), which may be a consequence of satiation (Bonter et al. 2013).

4.3.3. Breeding data collection

Breeding data were collected from four colonies between September 2013 and June 2014. Sociable weavers suffer from high snake predation rate on eggs and chicks (70% ; Covas et al. 2008). To ensure collection of sufficient breeding data, these four colonies have been protected against snake predation by covering the trunk from the base to a height of two metres with industrial plastic wrap. Each breeding chamber was uniquely identified by a numbered tag. All chambers in the study colonies were checked for the presence/absence of eggs and chicks every three days. These regular nest checks enable us to accurately assess laying date, clutch size, the number of clutches laid, and to follow the fate of eggs and chicks until fledging. Chicks were ringed (metal ring and colour rings) at seventeen days after the first chick hatched.

Fledging usually occurs after 20 days, but chicks disturbed after day 17 may fledge prematurely. Hence, nestlings present at day 17 were considered to have fledged.

The identities of breeders were assessed by direct observation. Parents were determined during incubation and qualified as parents when they entered the focal chamber to incubate at least three times in three different observations during the incubation phase. Observations were made from underneath a hide, located approximately five metres from the nest.

Sociable weavers lay multiple clutches within a single breeding season and breeding group composition tends to remain stable across multiple clutches within a breeding season (Covas et al. 2006), I obtained the breeding group size and composition for all broods from clutches laid before the 20th of November 2013. Breeding group was determined after the chicks were 6 days old, when nestling provisioning activity is high (Paquet et al. 2013). Group membership was confirmed when an individual was seen entering the focal nest chamber with food at least three times during three different observations of about 1-2 hours.

Based on the subset of individuals for which dominance scores were collected, I obtained the following samples per breeding categories: 16 female breeders, 26 male breeders, 21 helpers (17 males and 4 females) and 15 individuals that were never observed helping or breeding (9 females, 2 males and 4 individuals with unknown sex). Ten pairs bred without helpers and 16 pairs were assisted by at least one helper.

Among the 21 helpers and 15 individuals who were not seen incubating nor helping at the beginning of the season, 11 males, 1 female and 4 individuals with unknown sex, were seen breeding later in the breeding season. I examined whether their change in breeding status, a binary variable, was associated with their dominance scores.

My sample with breeding categories is biased toward males because females are subordinated to males in this species. Consequently, they approached the feeder less frequently and tended to interact less with other individuals. Thereby, I could not calculate a dominance score based on the number of interactions won and lost for several females present at the colonies.

4.3.4. Nest chamber quality

I estimated nest chamber quality by measuring the depth to which a nest chamber is embedded within the thatch shortly before the breeding season started. This depth corresponds to the length of the short tunnel that leads to the nest chamber and is positively associated with the chamber's function as a thermoregulatory buffer and the stability of the temperature inside the nest chamber increases with the depth to which it is embedded within the thatch (van Dijk et al. 2013). I measured depth to the nearest 0.5cm as a straight line using a ruler. When breeders used more than one breeding chamber (average number of breeding chambers used per breeder: 1.3 ± 0.7) I used the average depth from all the chambers a breeder used in my analyses.

4.3.5. Statistical analyses

My aim was first to investigate whether dominance predicts access to resources. I then examined the association between dominance score and reproduction. Third, I explored the potential of nepotistic benefits of dominance. I used Linear Mixed Models with Restricted Maximum Likelihood using the package "*lme4*" (Bates and Maechler 2009) for mixed effect models of the Gaussian family (LMM) and of the Poisson or Binomial family (Generalized Linear Mixed Models; GLMM). For all models I selected the set of best fit models based on the corrected Akaike Information Criterion (AICc) using the function *"dredge"* from the *"MuMin"* package (Barton 2013). Only models with a ΔAICc < 2 were kept. I used the package "*lmerTest*" to compute *P*-values and to estimate confidence intervals for fixed effects (Kuznetsova et al. 2014). Colony identity was set as a random factor in the mixed models to account for the non-independence of data originating from a given colony. Breeding group identity was nested within colony identity when the members of a pair, helpers or chicks were the unit of the analysis. In addition to dominance I included the following covariates: minimum age, tarsus length and body mass. Sex was also accounted for when sexes were pooled together in the models and an interaction term between sex and dominance scores was included as a covariate. I found no collinearity of the terms included in my models (mean correlation coefficient ± SD: 0.210 ± 0.128; max = 0.518; (Tabachnick and Fidell 1996).

Dominance and access to resources

I used two separate LMMs to investigate whether individual variation in the time spent at the feeder and the physical properties of a breeding nest chamber were predicted by individual variation in dominance scores. In the model predicting nest chamber depth, I focused on male breeders only because dispersal is female biased in this species so that I expected males only to compete over the access of high quality nest chambers (Doutrelant et al. 2004; Covas et al. 2006). Males are expected to compete for breeding chambers within the communal nest as deeper breeding chambers buffer environmental temperature variation (van Dijk et al. 2013). The time spent at the feeder and nest chamber depth were available for 86 individuals, 26 of which were male breeders.

Dominance and reproduction

I used GLMMs from the binomial family to test whether dominance status predicted the likelihood of obtaining a breeding position early in the season and to investigate the likelihood to change from helper to breeder status within a breeding season. For the former response variable, I analysed the probability of breeding separately for males and females. Additionally, I investigated whether the number of nestlings that successfully fledged during the breeding season was related to dominance status by fitting a GLMM with a Poisson error distribution and a log-link function. I included colony size in this model as results from a previous study indicated that colony size negatively affects some breeding parameters (Covas et al. 2008).

I investigated whether there was a relationship between dominance status of breeders and their probability of being assisted by helpers by fitting a GLMM with a binomial error distribution and using a logit-link function.

Social effects of dominance:

To test whether the dominance score of a male helper was related to that of the male breeders it helped, I used a general linear model (GLM) with the male breeder's dominance score as the predictor variable. Females were not included in this analysis as I collected dominance scores for only 4 female helpers. To examine whether the time spent at the feeder by a helper was related to the time spent at the feeder by the male breeder in its breeding group I fitted a GLM and included the time spent at the feeder by the male breeder, the sex of the helper and the interaction term between these two factors as predictor variables. All statistical analyses were conducted in R version 3.1.1 (R Development Core Team 2012).

4.4 Results

Dominance and access to resources

I found that the time individuals spent at the feeder was associated with dominance status in both sexes. Only one best-fit model, containing dominance score only as a predictor variable, was retained to explain between-individual variation in the time spent inside the central zone of the feeder (LMM estimate: 0.063 ± 0.019; $T = 3.430$; $N = 86$; $P < 0.001$; Fig. 4.1). Minimum age, body condition, sex or the interaction between sex and dominance did not significantly explain the time spent at the feeder (all $P > 0.309$).

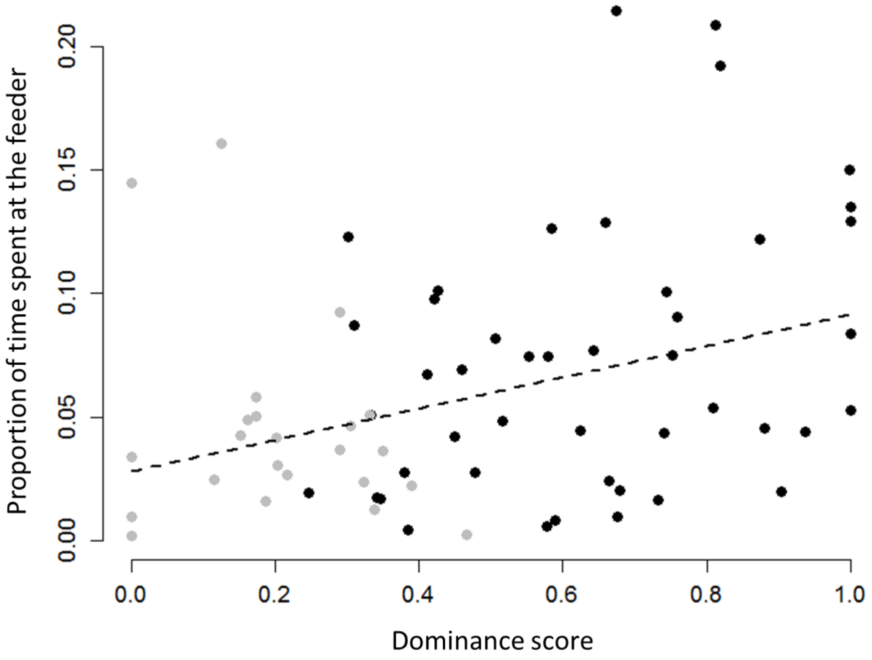

Figure 4.1 Time spent at the feeder in relation to dominance status. Males are represented by black dots and females by grey dots (*N* = 86). The dash line represents the estimated effect of dominance scores on the time an individual spent feeding.

I also found a positive, but non-significant, relationship between male dominance and the depth of the breeding chamber occupied by male breeders (LMM estimate: 3.573 ± 1.988; *T* = 1.798; *N* = 26; *P* = 0.086; Table 4.1). The quality of breeding nest chambers was also positively predicted by tarsus length (LMM estimate: 2.187 ± 0.824; *T* = 2.656; *N* = 26; *P* = 0.015; Table 4.1). Minimum age and body mass did not significantly explain variation in the depth of the breeding nest chamber used (all *P* > 0.342).

Table 4.1 Estimates of model parameters for the single best-fit model investigating the role of dominance on the depth to which the breeding chamber occupied by a given individual is embedded within the thatch (*N* = 26)

Variable	**Estimate**	**T**	**P**
Intercept	-36.5±19.99	-1.823	0.083
Dominance score	3.573±1.988	1.798	0.086
Tarsus length	2.187±0.824	2.656	0.015

Dominance and reproduction

The probability of obtaining a breeding position was associated with dominance status (GLMM estimate: 6.008 ± 0.203; *T* = 2.679; *N* = 78; *P* = 0.007; Fig. 4.2) and with minimum age (GLMM estimate: 0.392 ± 0.176; *T* = 2.192; *N* = 78; *P* = 0.028). Body condition, tarsus, sex or the interaction between sex and dominance did not significantly explain the probability of obtaining a breeding position (all *P* > 0.127).

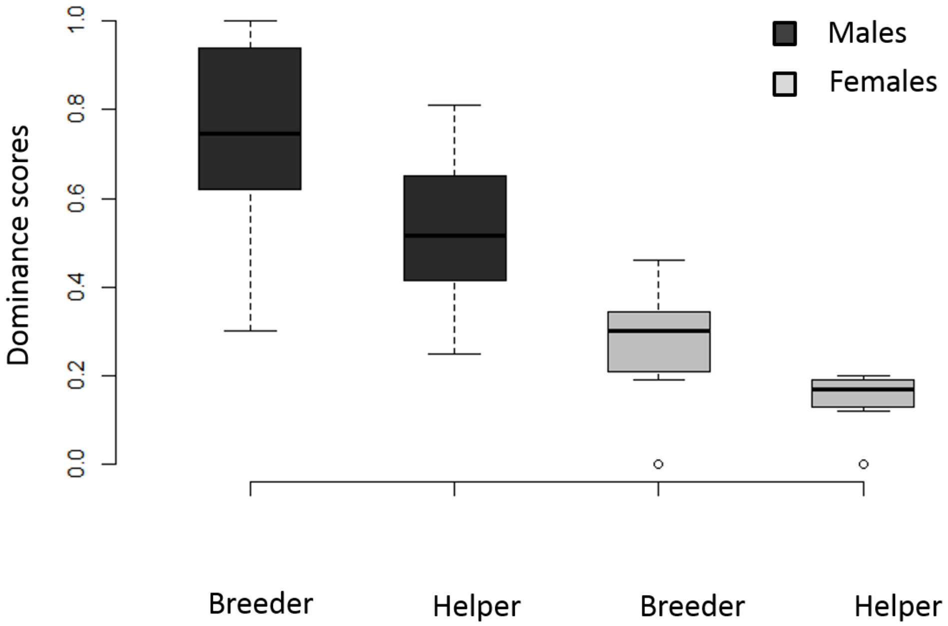

Figure 4.2: Access to breeding position in relation of dominance status (N=78). Male breeders are typically the most dominants while female helpers are the most subordinated category.

The probability to change breeding status from non-breeder to breeder within a breeding season was positively, but non-significantly, associated with the dominance of an individual (GLMM estimate: 5.170 ± 2.958; *T* = 1.748; *N* = 36; *P* = 0.081). Minimum age, body condition, tarsus or sex alone or in interaction with dominance did not significantly explain the probability of changing breeding status throughout the breeding season (all *P* > 0.127).

The total number of fledglings was not predicted by the dominance status of the male or female breeder (GLMM estimate: 0.036 ± 0.385; *T* = 0.094; *N* = 42; *P* = 0.925) nor by any of the other variables (all *P* > 0.397).

Social effects of dominance

The dominance status of breeders was positively but not significantly associated with the probability of receiving help at the nest (GLMM estimate: 16.025 ± 8.075; *T* = 1.940; *N* = 42; *P* = 0.052, Fig. 4.3). Minimum age improved model fit but was not significant (*P* = 0.595). Body condition and sex, alone or in interaction with dominance, did not significantly contribute to this model and were not retained by model selection (all *P* > 0.571).

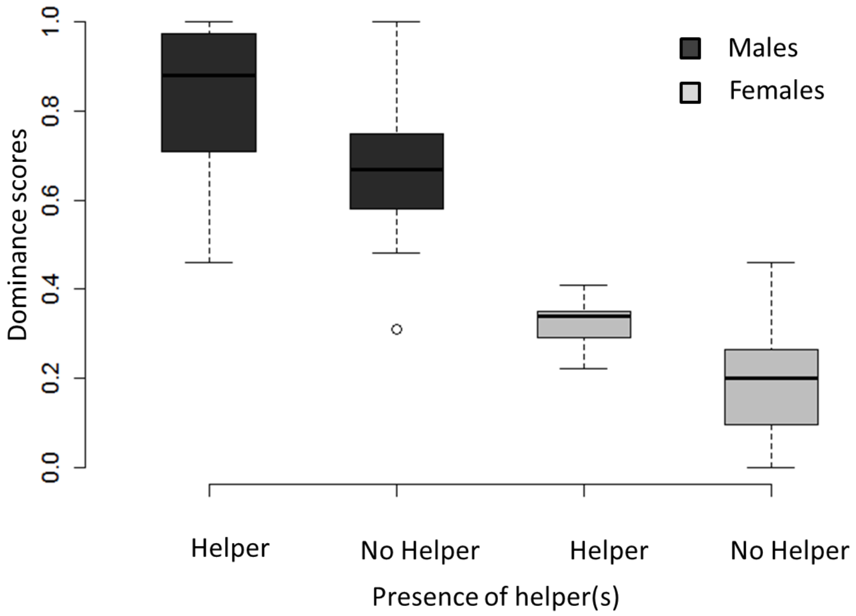

Figure 4.3 Probability of being assisted by helpers in relation to dominance status (*N* = 42). Dominants tend to have higher probability of being helped but this effect was only marginal *P* = 0.081)

The dominance score of the male breeder was the best predictor of the dominance scores of its helpers (LMM estimate: 0.958 ± 0.363; *T* = 2.644; *N* = 17; *P* = 0.020, Fig. 4.4). This effect could only be shown for male helpers, because the sample size for female helpers was too small (*N* = 4).

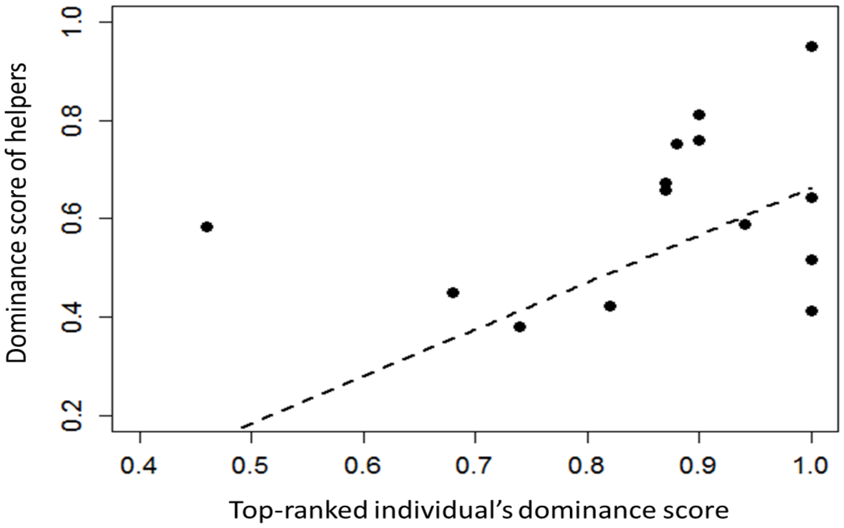

Figure 4.4 Relationship between the dominance scores of a male breeder and the dominance scores of its male helpers (*N* = 17). The estimated relationship is represented by the dash line

The time spent at the feeder by the male breeder predicted the time spent at the feeder by its helpers (LMM estimate: 0.534 ± 0.222; *T* = 2.409; *N* = 24; *P* = 0.035; Table 4.2, Fig. 4.5), independent of the sex of the helper (*P* = 0.600).

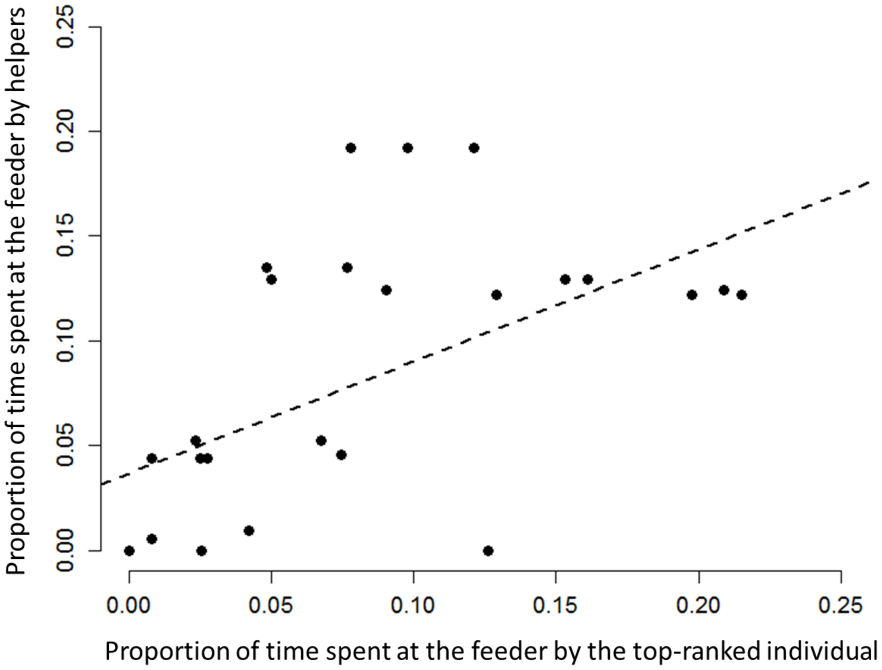

Figure 4.5 Association between the presence of a male breeder at the feeder and that of its helpers (*N* = 21). The dash line represents the estimated effect of the presence of a male breeder on the presence of its helpers at a feeding station

Table 4.2 Estimates and standard errors (SE) of model parameters for the single best-fit model investigating the association between the presence at the feeder by a male breeder and its helpers (*N* = 24)

Variable	**Estimate ± SE**	**T**	**P (>T)**
Intercept	0.118±0.002	1.664	0.118
Sex of the helpers	0.084±0.112	0.751	0.466
Time spent by male breeder	0.534±0.222	2.409	0.035
Interaction	-0.558±1.038	-0.538	0.600

4.5 Discussion

I found that dominance status of sociable weavers confers multiple benefits. Dominance scores were positively associated with an enhanced access to resources, i.e. the time spent feeding at the artificial food sources increased with dominance and there was a tendency for dominants to roost and breed in deeper nest chambers. Dominant birds also had higher probability of reproducing and the dominance status of breeders was positively, but non-significantly associated with the number of helpers they had. However, among breeders, I did not find a relationship between dominance and reproductive success. Finally, my results indicated that nepotism might play a role in generating access to resources in sociable weavers. The presence of breeder males at the feeder was positively correlated with the presence of their helpers (usually the breeders’ offspring). Furthermore, helpers of dominant males were more likely to have higher a social status. Taken together, these results suggest that dominance confers both direct and indirect benefits in sociable weavers.

In many species, dominant individuals monopolized resources because they have higher competitive ability (Dubuc et al. 2011). In line with this expectation, I found that dominant birds fed longer than subordinates. Privileged access to the food (i.e. quality or duration) favours energy intake and is known to be associated with survival (Thomas et al. 2003), particularly over winter (Kikkawa 1980; Piper and Wiley 1990). Sociable weavers live in semi-arid savannahs, where daily variation in temperature can be substantial (average lowest temperature of each month in winter = -6.4 ˚C; average highest temperature of each month in summer = 38.4˚C; South African Weather Service 2011-2014). Hence, maximizing energy intake may help sociable weavers to go through the colder months of winter and may enhance their lifetime survival. Under such circumstances, competition for mechanisms that allow to reduce energy expenditure is also expected. Nest quality is often a crucial resource as nest site or design is expected (Mainwaring et al. 2014) to be selected to provide good insulation against the environment (Reid et al. 2002) saving energy expenditure and favouring offspring development (Dawson et al. 2011; but see Lambrechts et al. 2012; Mainwaring et al. 2014). Consequently, competition for such thermoregulatory benefits is expected. Accordingly, I found that dominance scores were associated with the probability for breeding males to occupy more deeply embedded nest chambers within the thatch and to be more frequently assisted by helpers. Indeed, deeper nest chambers act as thermoregulatory buffers (van Dijk et al. 2013) and the number of birds roosting in a cavity increases cavity's temperature in this species (White et al. 1975; Bartholomew et al. 1976; Paquet M. *unpublished data*) as for other species (Plessis and Williams 1994; Willis and Brigham 2007). Hence, by favouring energy taking, the prolonged access to the food, and by reducing energy expenditure, the occupation of better quality chambers coupled with the presence of additional helpers in those nest chambers may enhance survival.

Furthermore, dominant males were found to be more likely to breed and tended to do so with the assistance of helpers. Such individuals of high social status are expected to be more successful in terms of intra-sexual competition (Eason and Sherman 1995). I also found that older individuals were more likely to obtain a breeding position later in the season if they had started the breeding season as helpers. These older individuals also tended to have higher dominance scores, although this effect was only marginal. These results again indicate some reproductive skew at the level of the colony, so that younger and/or more subordinated individuals may have to wait longer to access a breeding position. In many species, reproductive success is reduced for younger individuals. This maybe because young individuals may not be competitive enough in both intra- and inter-sexual selection (Lozano et al. 1996), are not experienced enough to successfully complete a reproductive event (Wooller et al. 1990) or wait for optimal environmental conditions to increase their chance of success (Forslund and Pärt 1995).

Because dominant birds are likely to be of higher quality, more experienced, assisted by helpers and gained better access to food and high quality chambers, these advantages were predicted to be reflected in a higher reproductive success for dominant breeders as opposed to more subordinate breeders. However, I did not find a link between dominance scores and the number of chicks fledged within the breeding season. Similar results have been found in other species (Festa-Bianchet 1991; Packer et al. 1995), while the reason of this lack of relationship between dominance and reproductive success remains unclear. One possibility is that high dominance status does not translate in better parental care (Qvarnström and Forsgren 1998). For instance, in the sand goby (*Pomatoschistus minutus*), the winners of male-male contests did not provide better parental care than the losers (Forsgren 1997). Dominant individuals may neglect their offspring and provide less parental care because they allocate more time to interact with their conspecifics in order to maintain their rank. A trade-off between the time allocated to parental care or to contests has been observed in the collared flycatcher (*Ficedula albicollis*; Qvarnström 1997) and three-spined sticklebacks (*Gasterosteus aculeatus*; Sargent 1995). However, it is important to point out this study was conducted during an exceptionally good breeding season, and under such favorable conditions most individuals are likely to experience good reproductive output. Positive effect of dominance on reproduction may be particularly important in years where conditions are adverse, competition intense (van Oort et al. 2007) and only top-ranked individuals may obtain access to sufficient resources (Koenig et al. 2009).

Dominance status in sociable weavers also appears to confer indirect benefits, as the feeding time of helpers as well as the dominance scores of male helpers were positively associated with the time the male breeder spent at the feeder. Hence, sociable weavers appear to favour family members. Nepotistic access to resources provides a net benefit for subordinates of associating with higher ranking kin. In addition, when subordinates are offspring or close relatives of the dominant, nepotism is likely to provide indirect fitness benefits to the dominant by increasing its subordinates' survival prospects (e.g. enhanced access to food or protection) and thus enhanced recruitment and prolonged their association with the group. Nepotism is thought to be a major route to the formation of kin groups (Ekman et al. 2001), since the benefits obtained by offspring from the high social status of their parents may be partly responsible for delayed dispersal and recruitment of helpers (Chiarati et al. 2011), and hence it is a crucial step for kin cooperation to occur (Emlen 1982; Covas and Griesser 2007).

While this study showed that nepotism confers some advantages to the group subordinates which may explain their delayed dispersal, the advantages for the dominant males of subordinated helpers' presence remain obscure. The presence of helpers is typically expected to increase reproductive success or survival (offspring and/or breeders; Cockburn 1998; Hatchwell 1999). Yet, previous findings in the same study population showed weak positive effects of the number of helpers on reproductive success (under adverse conditions; Covas and du Plessis 2005; Covas et al. 2008) and unexpectedly, negative effects on both fledglings' (Covas et al. 2011) and breeding males' survival (Paquet et al. 2015) . So far, in this system, the benefits of being assisted by more helpers appear to be directed mainly toward female survival, particularly in their first reproductive attempts (Paquet et al. 2013; Paquet et al. 2015).

In conclusion, while sociable weavers show an original social system with multiple breeding pairs occurring within one communal nest, I did not find that access to resources was egalitarian. I expected reduced skew in the access to resources as opposed to highly despotic system where the top-rank individuals in a group are the dominant pair, the only pair to breed and to monopolize resources (*Lycaon pictus*; Vehrencamp 1983; *Suricata suricata*; Clutton-Brock et al. 2000; *N. pulcher*; Bruintjes and Taborsky 2008; *Plocepasser mahali*; Harrison et al. 2013). However, I found that dominance in sociable weavers is also associated with multiple benefits favouring energy intake while reducing expenditure which is likely to favour survival. Some of the benefits obtained by dominant male breeders were extended to their helpers so that helpers gained facilitated access to food which suggests that nepotism enhances access to resources. This result implies that dominance, via nepotistic mechanisms, may favour delayed dispersal and hence, may operate in concert with kin-selection to maintain cooperation in this highly social species. Dominance and nepotism may act together to reduce conflicts, promote social cohesion and hence, facilitate the evolution of cooperation in this highly social passerine.

Chapter 5

Dominance, kinship and cooperativeness

‘The only thing that will redeem mankind is cooperation’

Bertrand Russell

Chapter 5 – Dominance, kinship and cooperativeness

5.1 Abstract

Cooperation is universal, yet why individuals help at a cost to themselves leads to an apparent evolutionary paradox. Helping may be kin-directed so that helpers gain indirect benefits ('kin selection' hypothesis). Alternatively, cooperation may confer direct benefits such as remaining in the natal territories and avoiding dispersal costs ('pay-to-stay' hypothesis where helpers are subordinate to breeders) or by increasing future chances of reciprocity or mating ('social prestige' hypothesis). Under this scenario competition to cooperate is expected and more dominant individuals might cooperate more. Hence both kinship and dominance may drive individual contribution to cooperation, thus my aim was to examine their relative importance in predicting cooperativeness. Sociable weavers (*Philetairus socius*) live year-round in a communal nest, establish dominance hierarchies and cooperate over multiple tasks. Specifically, I investigated individuals' cooperative contributions to nestling provisioning, communal thatch building and predator mobbing according to their level of kinship, dominance status, breeding category, sex, body condition and age. Provisioning was positively predicted by the relatedness to the father and mobbing positively by the relatedness to the mother supporting kin-selected cooperation. In addition, in agreement with both the pay-to-stay and the social prestige hypotheses helpers more distantly related to the female breeder provisioned nestlings at a higher rate, suggesting also potential direct benefits of cooperation. Furthermore, also in agreement with the pay to stay hypothesis, helpers contributed more than breeders to snake mobbing and among helpers, more subordinates males mobbed more frequently while it was the reverse for females. Finally, helpers contributed more than breeders to thatch building but there was no link to dominance or relatedness among helpers. Taken together, results suggest that cooperation in sociable weavers may have evolved and be maintained by multiple mechanisms involving both direct and indirect benefits.

5.2 Introduction

Cooperative behaviour can be observed at any level of biological organisation ranging from microbes to species with highly developed cognitive abilities including humans. Despite being widespread, the evolution of cooperative behaviour continues to puzzle scientists. One of the reasons behind this conundrum is that cooperative individuals typically help others at a cost to themselves (Axelrod and Hamilton 1981). Hence, cooperative systems are vulnerable to cheating as selfish individuals may exploit the cooperative resources without incurring the costs (Axelrod and Hamilton 1981; Huntingford and Turner 1987). For these reasons, cooperation leads to an apparent evolutionary paradox (Axelrod and Hamilton 1981; Huntingford and Turner 1987).

Hamilton (1964) proposed that helping can be beneficial and evolutionarily stable if the benefits of helping are shared among relatives and, as such, larger than the costs of helping, promoting indirect benefits of cooperation. Under a kin-selected cooperation, cheating is limited as kin members of a group share both the benefits and the costs of cooperation. For example, kin-selection has provided an explanation for extreme behaviour such as complete reproductive skew in some insect societies where only the queen reproduces while subordinates help (Foster et al. 2006). In birds and mammals, it is seen as a major evolutionary route for cooperative breeding based on the accumulation of empirical evidences where helpers preferentially choose to provide care or provide more care to their close kin as opposed to non-kin offspring (e.g. brown hyenas *Hyaena brunnea*: Owens and Owens 1984; Seychelles warblers *Acrocephalus sechellensis*: Komdeur 1994; house mice *Mus domesticus*: König 1994; long-tailed tits *Aegithalos caudatus*: Russell and Hatchwell 2001; carrion crows *Corvus corone corone*: Baglione et al. 2003).

However, individuals of a cooperative groups may have similar levels of relatedness toward the breeders, and yet they may not contribute equally to their cooperative tasks (Arnold et al. 2005). Furthermore, cooperation among poorly related individuals or unrelated individuals has also been observed (Reyer 1984; Chapais et al. 1991; Riehl 2011; Riehl 2013). Although this does not preclude kin selection (apart from cases of absence of kinship), it suggests that direct benefits of cooperation may also be gained where cooperative acts involve selfish benefits (Clutton-Brock 2002; Stiver et al. 2005; Riehl 2013). Mechanisms of cooperation involving direct, selfish benefits include mainly, the pay-to-stay hypothesis (Gaston 1978), signalling cooperation to improve an individual's social prestige (Zahavi 1995) similarly to one's social image in humans (Wedekind and Milinski 2000) or advertising parental skills (Selander 1965; Komdeur 1996) and enhance future chances of reproduction (Zahavi 1995) or reciprocation (Milinski 1987). Yet, this is a non-exhaustive list and other hypotheses have been proposed (e.g. 'group augmentation hypothesis'; Kokko et al. 2001).

Theoretically, a pay-to-stay cooperation (Gaston 1978; Kokko et al. 2002) is expected to evolve mainly in (i) long-lived species (ii) experiencing moderately tight environmental constraints and where (iii) the level of relatedness between the helpers and the breeders can be low (Kokko et al. 2002). Additionally, the presence of non-helping individuals is expected to generate a cost to the breeder due to increased competition (Kokko et al. 2002). Under the pay-to-stay hypothesis, individuals may help in order to be allowed to remain in their natal territories and compensate for the costs their presence inflicts to the breeders (Gaston 1978; Kokko et al. 2002). By remaining in their natal territories, individuals may benefit from a prolonged parental protection, a better chance of inheriting a territory or a breeding position (Emlen 1994; Ekman et al. 2000; Ekman et al. 2001; Bruintjes and Taborsky 2008). Additionally, remaining in the natal territory suppresses the costs associated with dispersal such as increased predation risks and competition (Selander 1964; Emlen 1994). There is therefore an exchange of commodities between individuals. Subordinates trade helping commodities for group acceptance by the dominants (Gaston 1978; Noë et al. 1991; Bergmüller and Taborsky 2005). Less related helpers are expected to provide more help because their presence is likely to increase competition and may generate greater costs to the breeders (Kokko et al. 2002). For instance, in cooperative African cichlids *Neolamprologus pulcher*, the group is structured by a size-based hierarchy where the largest fish is usually the dominant breeder while the other members are subordinates, the helpers, that cooperate in order to be allowed to stay (Hamilton et al. 2005). Both less related (Stiver et al. 2005; Zöttl et al. 2013) and larger, more dominant (Bruintjes and Taborsky 2008) helpers work harder in some cooperative tasks than more related and smaller, highly subordinated helpers because they are likely to represent a more important competitive threat and thus, face higher risks of eviction (Bruintjes and Taborsky 2008). Thereby, a pay-to-stay mechanism is expected to act only in species exhibiting dominance relationships (Clutton-Brock and Parker 1995) and has been proposed to be maintained by social enforcement where dominant individuals of the cooperative groups punish cheaters, i.e. individuals who failed to help (Mulder and Langmore 1993; Kokko et al. 2002; Bruintjes and Taborsky 2008; Raihani et al. 2012; Roberts 2013). Punishing can occur in the form of active aggressions (Raihani et al. 2012) but can also be more cryptic when threats without physical contact are used (Cant 2011; Raihani et al. 2012) or when an individual anticipates punishment and exhibits submissive behaviour as a 'pre-emptive appeasement' (Bergmüller and Taborsky 2005; Hamilton et al. 2005). Thus, dominance relationships are essential to investigate the pay-to-stay hypothesis.

Similarly dominance relationships are also likely to be central for social prestige hypothesis. According to this hypothesis, by investing in cooperation, individuals advertise their efforts not only to remain in a group but to improve their social image (i.e. 'social prestige'; Zahavi 1995). For instance, by contributing to nestling provisioning, an individual may signal to the nearby conspecifics its parental quality, which may increase its chances of mating in the current or following years (Komdeur 1996). In the sociable weaver (*Philetairus socius*), individuals adjust their feeding behaviour in relation to the number of conspecifics at the colony, which could maximize their chances of being seen helping (Doutrelant and Covas 2007). Similarly, men in a rural population of Senegal showed more cooperativeness when observed by women rather than men (Tognetti et al. 2012). Hence, cooperation may have signalling properties that can be sexually and/or socially selected (Zahavi 1995; Wedekind and Milinski 2000). In this context, competition over cooperation is expected as being cooperative is supposed to be beneficial in terms of social and/or sexual selection (Zahavi 1995). Thus, individuals with high competitive ability (e.g. high social status) are predicted to contribute more to cooperative tasks (Zahavi 1995) and dominants are expected to invest more in cooperation when cooperating enhances their social prestige.

Hence, the study of dominance, relatedness and cooperative contributions enable to establish an evolutionary framework to test which routes to cooperation are likely to be involved in the evolution and maintenance of cooperation. (Clutton-Brock and Parker 1995; Cant and Field 2001; Bergmüller and Taborsky 2005; Clutton-Brock 2009). It is important to keep in mind that these hypotheses may not be mutually exclusive so that multiple mechanisms may drive cooperation (West et al. 2007b). This is expected in particular when cooperation is performed for different tasks as the costs and benefits of cooperation may depend on the phenotype of the cooperator, the nature of the task (e.g. predator sentinel, babysitting, nestling provisioning) and the recipient of the help so that different tasks may be driven by different mechanisms (Keller and Reeve 1994; Cant et al. 2006b; Field et al. 2006; Komdeur 2006). Consequently, in order to understand the evolution of cooperative societies it is of crucial importance to allow the test of multiple evolutionary mechanisms by exploring individual variation in helping effort across multiple tasks and considering dominance asymmetries between individuals.

I investigated how kinship and dominance explained individual contributions to three different cooperative tasks, in order to assess their potential roles in the evolution of cooperative behaviour in sociable weavers. No study have previously investigated the links between dominance and cooperative contributions in this species while this exploration could reveal whether additional mechanisms to kin-selection, namely the pay-to-stay hypothesis and the social prestige hypothesis, may be involved in the evolution of cooperative behaviour.

Sociable weavers (*Philetairus socius*) are long-lived colonial passerines (Maclean 1973d; Covas 2012) that inhabit in semi-arid savannahs where environmental conditions are largely unpredictable (Covas et al. 2004; Covas et al. 2008). They live in complex cooperative societies structured by ordered hierarchies within colonies (Rat et al. 2015) where male breeders dominate helpers and males dominate females (Chapter 2). The level of relatedness within colonies remains generally low but significant (Covas et al. 2006; van Dijk et al. 2014). Sociable weavers are cooperative breeders and the degree of relatedness within breeding groups can be high as helpers-at-the-nest are mainly philopatric offspring (i.e. 93% are directly related to at least one of the parents) but unrelated helpers to both parents have also been observed (Covas et al. 2006; Doutrelant et al. 2011). Hence, the cooperative societies of sociable weavers exhibit the pre-requisites for kin-selected, pay-to-stay and social prestige cooperation (as suggested above) which may rule both at the scale of the breeding group or at the colony level. In this study, I specifically investigated (i) nestling provisioning (i.e. helping-at-the-nest); (ii) communal thatch building - these weavers build communally a large nest mass that is used year-round to roost and breed, and is built continuously through generations (Maclean 1973a; Maclean 1973b) and (iii) predator mobbing - sociable weavers may also engage in communal mobbing against snakes, their main nest predators. Snakes are responsible for ca. 70% losses of eggs and chicks (Covas et al. 2008), although snake mobbing has not been previously studied in this species. Kin-selection has already been suggested to be an important evolutionary route for cooperation in this species and notably for helping-at-the-nest (Covas et al. 2006; Covas et al. 2008; Paquet et al. 2015) and communal thatch building (van Dijk et al. 2014).

I recorded individual feeding rates, thatch-building contributions and mobbing. Then, I examined the influence of relatedness, dominance scores, sex, breeding category, body condition and minimum age on each of these behaviours. First, I explored how breeders and helpers contributions differed in these three tasks. According to the pay-to-stay hypothesis, helpers are expected to work as much as breeders or harder when their presence has important detrimental effects to the breeders (e.g. unrelated helpers; Kokko et al. 2002). Second, I excluded breeders (nestling or provisioning for breeders can relate to parental care) and focused on helpers only to examine the role of relatedness and dominance behind helper's cooperation. If cooperation is kin-selected, the degree of relatedness is expected to co-vary positively with cooperative contribution (Hamilton 1964) but not specifically with dominance. However, if cooperation also conveys direct benefits (i.e. pay-to-stay or social prestige), I expected that more dominant or less related helpers should be more cooperative than subordinated or more closely related helpers.

5.3 Material and methods

5.3.1. Study species and Study site

Sociable weavers are highly social passerines endemic to the semi-arid savannahs of southern Africa. Their communal nest is typically built on *Vachellia erioloba* trees (although other trees or human-built structures may be used). Colonies may vary in size from less than ten to hundreds of individuals (Maclean 1973d) that often forage in groups (Flower and Gribble 2012). The nests contain several, independent nest chambers embedded within the communal thatch (Maclean 1973b; van Dijk et al. 2013). Sociable weavers are facultative cooperative breeders. Each breeding unit usually consists of either a breeding pair alone or may contain up to seven helpers (R. Covas, *pers. comm.*). Helpers increase breeding success but mostly under adverse conditions (Covas et al. 2006; Covas et al. 2008). The presence of helpers allows females to save energy through reduced maternal investment in reproduction and thereby, their presence is also associated with increased female survival (Paquet et al. 2013, 2015). Males are more often helpers-at-the-nest than females (Doutrelant et al. 2004). Extra-pair paternity appears to be absent in this species (Covas et al. 2006; van Dijk et al. 2014).

Snakes are responsible for most of the predation events on eggs and chicks. The two main snake predator species at this study site are boomslangs (*Dispholidus typus*) and Cape cobras (*Naja nivea*). Mobbing may be efficient on small-sized boomslangs (i.e. body length ca. 50cm) as attacks resulting in the snake falling off the nest have been observed multiply (M. Rat, *unpublished data*). Furthermore, mobbing a poisonous snake is a risky behaviour and when weavers physically attack snakes (i.e. bite), they seem to avoid actively the head and typically target their attacks to the tip of the tail (M. Rat, *unpublished data*).

The study was conducted at Benfontein Nature Reserve (28˚52’S, 24˚50’E) near Kimberley, Northern Cape province, South Africa. Data were collected during two consecutive breeding seasons, between the 1st September 2012 and 18th February 2013 and between the 2nd September 2013 and the 3rd February 2014.

The area consists of about 15 km^2 of Kalahari sandveld covered mainly by *Stipagrostis* grasses and *Vachellia spp.* trees (Covas et al. 2006). It contains approximately 30 active colonies comprising between 5–80 individuals. As part of the long-term research on this study population, these colonies have been captured annually using mist-nets since 1993 (see Covas et al. 2002 for more details on the captures). The annual captures take part prior to the breeding season and allow the estimation of the individual minimum age based on the date of the first capture event when not ringed as nestling (Altwegg et al. 2014). During the captures, birds are individually ringed using a uniquely numbered metal ring and three colour rings to allow visual individual identification in the field. Each individual was weighed (to the nearest 0.1g) and tarsus length (to the nearest 0.1mm) measured.

5.3.2. Behavioural observations

All observations were made from underneath a hide, located underneath the colony and/or using a video camcorder for dominance interactions.

Contribution to nestling provisioning

I determine individual feeding rate for 35 groups (Table 5.1) with confirmed group size and composition at 2 colonies in 2012-13 and at 4 colonies during in 2013-14. The feeding rate was calculated by dividing the number of time a member of group was seen entering its breeding group chamber by the duration of the observation. Only observations of at least 45 minutes containing less than 15% of missing identities (i.e. when the individuals did not perch before or after entering the chamber) were included in the analyses (291 +/- 102 minutes of feeding rate per colony).

Contribution to thatch building

I collected data on communal thatch building behaviour at 3 colonies in 2012-13 and at 5 colonies in 2013-14 (Table 5.1). Thatch building activity is highly variable (Maclean 1973b) and building events unevenly distributed among individuals (van Dijk et al. 2014). Furthermore, information on individual thatch building rate is difficult to obtain, because multiple individuals may be building simultaneously on different sides of the nest. Therefore, I restricted the analysis to a binary categorisation of individuals qualified as thatch builder when an individual has been seen building the thatch, or as non-thatch builder when it has not (van Dijk et al. 2014). Individuals contributing to the communal thatch more than once were qualified as thatch builders (33.03% of individuals; mean observation time at each colony 23hr22 min ± 9hr57min).

Contribution to snake mobbing

I use a plastic toy snake to simulate a snake predation threat toward a focal nest chamber (Fig. 5.1A) and collect an individual likelihood to mob (1 = yes; 0 = no) and the number of attacks (i.e. when a weaver flies in the direction of the predator while producing alarm calls) exhibited by an individual within the duration of the experiment. The snake was 46cm long and Ø2cm which is similar to the size of a small juvenile boomslang (*Dispholidus typus*). The head of the snake decoy was positioned inside the tunnel leading to the focal nest chamber with the rest of its body attached to the surrounding nest structure. The position of a focal chamber was qualified either as "central" (radius based on the difference between the maximum distance to the edge minus and one third of this distance), "semi-peripheral" (radius based on the difference between the two third and one third of the maximum distance to the edge) or "peripheral" (radius based on the difference between one third of the maximum distance to the edge and the edge of the nest).

The experiment was conducted over two consecutive seasons at 12 colonies for 16 focal chambers containing eggs and for 23 focal chambers containing chicks aged between 7 and 14 days (Table 5.2). The decoy was left at the nest chamber for 45 min. In order to maximize the number of birds visiting the colonial nest during the experiment, it was replicated the following day at each chamber (i.e. replicate 1 and replicate 2 per focal nest chamber). To avoid decoy habituation, a maximum of three chambers per colonies were tested within a season and I lapsed a minimum of two weeks to test another chamber from the same colony. Using a handheld recorder, the same observer (MR) recorded all the IDs of the individuals visiting the colony during the experiment and noted whether they mobbed the snake and at what frequency.

To assess whether the weavers perceived the decoy as real snake, I compared their reaction to an unfamiliar object, a black and white soft football of Ø8cm (Fig. 5.1B). On a subset of 10 nest chambers, I positioned the football below the entrance of the focal nest chamber for 45 min. This control was performed randomly, before or after, the snake decoy experiment. The same variables as for the experimental part were recorded by the observer.

Figure 5.1 Illustration of the method used to collect mobbing data. On the left hand side (A), the snake decoy (plain arrow) is positioned in a focal chamber (circled). The dash arrow indicates an individual initiating a mobbing. On the right hand side (B), illustration of the control used, the focal nest chamber is circled and the unfamiliar object, a small football, is indicated by a plain arrow

236 individuals visited the colonies when the football was positioned and only 11.11% of them mobbed the ball. In contrast, 256 individuals visited the colony when the snake decoy was positioned and 77.78% of them mobbed the decoy. Additionally, weavers exhibited the same behaviour and gave the same alarm call than when real snakes are sighted in the surroundings of their colony supporting that the decoy was perceived as a snake.

I conducted preliminary analyses to determine, first, which parameters of the social environment, and of the focal nest chamber’s reproductive status and position, influenced mobbing behaviour (i.e. the probability of mobbing and the number of attacks) and should be controlled for in the analyses. To achieve this goal, I investigated whether a set of explanatory variables predicted (i) the probability to observe mobbing attack and (ii) how frequently (number of attacks within 45 min). These two response variables were fitted using Generalized Linear Mixed Models (GLMM) with respectively a binomial error and a Poisson error. The explanatory variables were the position of a focal nest chamber, the number of birds visiting the colony during the experiment (as a proxy of potential observers and/or mobbers), the number of mobbers, the number of reproductively active nests as well as the reproductive status of the focal chamber (i.e. egg or chicks and clutch/brood size). Models were repeated focusing on nest chambers that contained chicks only in order to assess whether mobbing behaviour was affected by the age of the chicks thereby the investment in reproduction. Only the total number of individuals that got involved in mobbing behaviour within the 45 minutes of the experiment predicted both whether an individual were likely to mob (GLMM estimate: 0.343± 0.035, N = 1057, T = 9.718, $P < 0.001$) and the number of attacks it exhibited (GLMM estimate: 0.343± 0.035, N = 1057, T = 9.718, $P < 0.001$). This result suggests that an individual was more likely to exhibit this behaviour and to exhibit it several times when other individuals were also involved in mobbing behaviour. In addition, the number of individuals visiting the colony during the experiment predicted the probability of mobbing (GLMM estimate: -0.064± 0.016, N = 1057, T = -3.883, $P < 0.001$), but not the number of attacks (P = 0.134). Therefore, both the number of mobbers and the number of individuals visiting the colony were controlled for in further analyses on the probability of mobbing whereas only the number of mobbers was controlled for when analysing the number of attacks. The position of the nest chamber, the number of nests reproductively active, the status of the reproductive chambers (i.e. eggs or chicks), the clutch or brood size and the age of the chicks did not have a significant effect on the probability of mobbing (all $P > 0.102$) and were therefore not included in further analyses.

5.3.3. Breeding status: helpers versus breeders

The identities of breeders were assessed by observations. Parents were determined when they were seen entering the focal nest chamber for incubation (i.e. remained in the nest) at least three times during three different observations at the incubation phase. Helpers-at-the-nest were identified as non-breeding individual entering the focal chamber with food at least three times on two different days after the chicks were 6 days old (when nestling provisioning activity is high; Doutrelant and Covas 2007; Paquet et al. 2013), during three different observations of about 1-2 hours.

5.3.4. Dominance status

I obtained individual's dominance scores for 35 individuals in 2012-2013 (based on 1915 interactions between 152 individuals collected between September and November) and for 86 individuals at a total of 7 colonies in 2013-2014 (based on 3625 interactions between 112 individuals collected between September and October). Dominance scores were based on agonistic interactions observed at a feeder and recorded by a video camera. I used these agonistic interactions to calculate David's score (David 1987) and determine individual's dominance scores (Rat et al. 2015). I scaled dominance scores within colonies, so that all scores ranged from 0 (the most subordinate individual) to 1 (the most dominant individual) for each colony, thereby allowing comparison of dominance scores obtained from colonies of different sizes (Rat et al. 2015).

5.3.5. Genetic analyses and estimates of relatedness

Blood samples taken at capture were preserved in 1mL of absolute ethanol. Genomic DNA was extracted using a precipitation of ammoniate acetate (Richardson et al. 2001) in preparation for polymerase chain reaction amplification. The sex of all individuals was molecularly determined using *P2–P8* sex-typing primers (Griffiths et al. 1998). Sixteen autosomal polymorphic microsatellite markers were used to genotype each individual. Pairwise relatedness was estimated using Queller and Goodnight's genetic estimate of relatedness using ML-RELATE (Kalinowski et al. 2006), with reference to genotypes from the entire population across all colonies (N = 2714). For more details on genotyping procedure and analyses, see van Dijk et al. (2014).

Four helpers were not genotyped, although estimated relatedness to the breeding parents was deduced through pedigree data. Two of these helpers were offspring of the same female breeder but unrelated to the male breeder and two helpers were offspring of the male breeder but unrelated to the female breeder. Thereby I defined three categories of relatedness (i.e. 1^{st} order relatives, 2^{nd} order relatives and unrelated helpers) that were used to analyse helper contribution to nestling provisioning in order to increase the sample size.

5.3.6. Breeding data collection:

In order to collect information about the reproductive stage of a nest chamber, each nest chamber was uniquely identified by a numbered yellow tag. Every nest chambers from every colonies was checked for the presence/absence of eggs and chicks every three days during the full duration of the breeding season. These regular nest checks enable us to accurately assess the laying date of a clutch, clutch size and to follow the fate of eggs and chicks until fledging at every nest chambers of the colonies.

5.3.7. Statistical analyses

All statistical analyses were conducted in R version 2.15.0 (R Development Core Team 2012). For all models, I used the Generalized Linear Model approach and used an identity link for the Gaussian family (i.e. feeding rate), a log link for the Poisson family (i.e. number of attacks) and a logit link for the Binomial family (i.e. probability of mobbing, building and cooperating). I used the Maximum Likelihood criterion for models containing only fixed effects (LM) and the Restricted Maximum Likelihood criterion with the package “*lme4*” (Bates and Maechler 2009) for mixed effect models (LMM for the Gaussian family, GLMM for the Poisson & Binomial families).

The set of best fit models was selected based on the corrected Akaike Information Criterion (AICc) using the function *“dredge”* from the *“MuMin”* package (Barton 2013). Only models with a ΔAICc < 2 were kept. *P*-values and confidence intervals were estimated using the *“lmerTest”* package (Kuznetsova et al. 2014). I used model averaging estimation of effects, *P*-values and confidence intervals when the set of best-fit models contained more than one model.

As nestling provisioning and snake mobbing relate to parental care for the breeder of the focal nest chambers, I analysed cooperative contributions in two steps for these tasks. First, I included both breeders and helpers in the analyses in order to compare contributions according to one's breeding status. Second, I focused on true cooperative acts and included helpers only in the analyses.

Contribution to nestling provisioning

I explored whether nestling provisioning was influenced by breeding status (helpers or breeders; Table 5.1), dominance score ,sex, minimum age and body condition, Brood size, the age of the chicks and the breeding group size were also included as fixed factors to control for differences in the reproductive stage of a chamber. I also included in this Linear Mixed Model (LMM) two-way interactions between breeding categories, sex, dominance score and minimum age. Nest ID nested within colony ID were included as a random factor to account for repeated measurements.

Then, I repeated this analysis focusing on helpers only (N = 21; Table 5.1). In the models concerning helpers only, minimum age was not taken into account as 76.20% of the helpers in this sample were one year old (and the results were qualitatively similar when age was included). Covariates also included relatedness between the helper and the male and female breeder, the two-way interactions between relatedness to the female or to the male breeder (i.e. pedigree) and dominance scores. I could not test for the interaction between the relatedness to the female breeder and the relatedness to the male helpers or for the interactions between the relatedness to the parents and the sex of the helpers because of a lack of power inherent to the small sample size.

Contribution to communal thatch building

I tested whether individual contribution to the communal thatch building (1 = yes, 0 = no) was associated with breeding status (breeder or helper; Table 5.1), average relatedness to all the colony members and with dominance score, sex, minimum age and body condition. I also included two-way interactions between sex, dominance score and minimum age. Colony ID was included as a random factor to account for repeated measurements.

Table 5.1 Sample sizes obtained for nestling provisioning, communal thatch building and overall contribution to cooperation as used in the analyses. Thereby presenting the sample size when both breeders and helpers (B&H) were included in the analyses and when only helpers were. The samples size illustrated here exclude individual with missing data for one of the covariates used in the analyses, with the exception of unknown sex

		Males		**Females**		**Unknown**		**Total**
		B	**H**	**B**	**H**	**B**	**H**	
Nestling provisioning	B&H	23	16	13	5	0	3	60
	H with pedigree	.	16	.	5	.	3	24
Thatch building	B&H	40	23	29	7	0	3	102
	H genotyped	38	23	25	7	0	0	93
All tasks	B&H	25	17	20	6	0	3	71

Contribution to snake mobbing

All analyses on individual contribution to mobbing behaviour included the replicate ID nested in the focal nest chamber ID nested in the colony ID as well as the individual ID and the year of the experiment included as random factors in the Generalized Linear Mixed Models (GLMMs) to account for repeated measurements.

First, I investigated which type of individuals (Table 5.2) were more likely to mob (i) and (ii) to mob more frequently (i.e. number of attacks). The explanatory variables were breeding categories (6 defined categories as defined below), sex, minimum age, body condition. I also included two-way interactions between breeding category, sex and minimum age and I controlled for the number of individuals mobbing (refer to the section on data collection). In the analyses to explain the number of attacks (ii), I additionally controlled for the number of individuals visiting the colony during the experiment (refer to the section on data collection). The six breeding categories were defined according to whether an individual was the breeder or helper of focal threatened nest chamber (‘B’ or ‘H’), whether it was a breeder or a helper from an active (‘BA’ or ‘HA’, respectively) or inactive chamber (‘BI’ or ‘HI’) for the duration of the experiment. In these analyses, I excluded dominance scores and because breeders dominate helpers and exclusion of dominance scores allows to increase sample size

As one of my aims was to investigate the precise links between dominance, relatedness and cooperation, I repeated models (i) and (ii) focusing on helpers only (i.e. helper’s category H, HA and HI; Table 5.2) and additionally included dominance scores, the relatedness between the helpers and the male breeder, the relatedness between the helpers and the female breeder and the interactions between a helper’s relatedness to the male breeder and to the female breeder. Here again, I could not test for interactions between the relatedness to the parents and the sex of the helper because of a lack of power inherent to the small sample size.

Table 5.2 Sample sizes obtained for the snake mobbing experiment according to whether the analyses were conducted on helpers and breeders (B&H) or on helpers only (H). The sample sizes are reported according to the breeding category: respectively B and H for breeders and helpers of the threatened nest chambers, respectively BA and HA for breeders and helpers occupying reproductively active nest chamber at the moment of the experiment or inactive for BI and HI. For helpers (H), the sample sizes reported here illustrate only individuals with dominance scores, the limiting covariate.

		Males		**Females**	
		B&H	**H**	**B&H**	**H**
Breeding category	B	43	.	38	.
	BA	112	.	82	.
	BI	112	.	51	.
	H	17	9	6	5
	HA	37	30	15	8
	HI	25	6	15	1
	TOTAL	346	45	207	14

Overall contribution to cooperation

I investigated whether there was a consistent profile in individual contribution to cooperation over the different cooperative tasks observed (*N* = 71; Table 5.2). The increase in the sample size by contrast with the one I used for nestling provisioning is explained by the fact that this analysis excludes phenotypic covariates (e.g. relatedness, dominance scores, body mass). Regarding feeding rate, to account for several variables that are known to influence provisioning effort, I use the residuals of a linear model with feeding rate fitted as a response variable against breeding group size, brood size and age of the chicks. Individual consistency was estimated by using Shrout and Fleiss's Intra-Class Correlation coefficient (2, *k*) ('ICC'; Shrout and Fleiss 1979) between cooperative tasks two by two and also across the three cooperative tasks all together (i.e. feeding, building, mobbing).

5.4 Results

5.4.1. Contribution to nestling provisioning

Sample with breeders and helpers

In the analyses that included both helpers and breeders, I found that the two ways interactions between breeding category and both sex (N =57, $F_{5,56}$= 13.54, $P < 0.003$; Table 5.3) and dominance (N =57, $F_{2,56}$ = 5.406, $P = 0.027$; Table 5.3) predicted variation in nestling provisioning. Effect sizes showed that male breeders fed nestlings at the highest rate (LMM estimate: 0.100 ± 0.011, $N = 23$, $T = 8.920$, $P < 0.001$; Table 5.3) by contrast with female breeders and helpers. Effects sizes also showed that dominance status had a strong negative impact on feeding rates among breeders (LMM estimate: -0.162 ± 0.048, $N = 36$, $T = -3.422$, $P = 0.002$; Table 5.3) as opposed to helpers for which dominance had a positive effect on nestling provisioning (LMM estimate: 0.127 ± 0.054, $N = 21$, $T = 2.325$, $P = 0.027$; Table 5.3. The influence of dominance on feeding rates was also age-dependent so that older dominants contributed more to this task than younger subordinates (LMM estimate: 0.019 ± 0.008, $N = 57$, $T = 2.247$, $P = 0.032$; Table 5.3). Individual contribution to nestling provisioning increased with body mass (LMM estimate: 0.009 ± 0.004, $N = 57$, $T = 2.200$, $P = 0.035$; Table 5.3) and decreased with breeding group size (LMM estimate: -0.014 ± 0.006, $N = 57$, $T = -2.300$, $P =$

0.030; Table 3). Brood size and the age of the chicks did not significantly predict variation in individual nestling provisioning (all *P* > 0.315).

Table 5.3 Estimates and standard errors (SE) of model parameters for the best-fit model explaining variation in both breeders' and helpers' contribution to nestling provisioning. N = 57. Females and breeders are the reference levels for the sex and for the breeding category, respectively. 'DS' is abbreviated for 'dominance scores', 'Min Age' for 'minimum age' and 'B. status' for 'breeding status'. F-statistics are additionally given to assess the significance of the overall effect the two-way interactions include a factor.

Covariates		**F**	**Estimate ± SE**	**T**	**P**
Intercept			-0.062±0.093	-0.663	0.051
DSs			-0.162±0.047	-3.422	0.002
Sex (M)			0.087±0.023	3.854	<0.001
Min. age			-0.003±0.004	-0.891	0.381
Weight			0.008±0.004	2.268	0.030
Group size			-0.014±0.006	-2.434	0.022
BS			-0.036±0.023	-1.603	0.120
Sex x BS		13.54			0.003
	Female breeder (*N* =13)		0.044±0.011	3.98	<0.001
	Male breeder (*N* = 23)		0.099±0.009	9.99	<0.001
	Female helper (*N* = 5)		0.075±0.021	3.55	0.001
	Male helper (*N* = 16)		0.036±0.009	4.12	0.002
Sex x Min Age		4.16	-0.011±0.005	-2.04	0.05
DS x BS		5.406	0.127±0.055	2.325	0.027
DS x Min. age			0.019±0.009	2.247	0.032

Sample with helpers only

When focusing only on helpers, sex and dominance did not predict variation in nestling provisioning (both *P* > 0. 177). Only relatedness to the breeders (male: *N* =21, $F_{2,20}$ = 4.643, *P* = 0.006; female *N* =21, $F_{2,20}$ = 7.348, *P* = 0.032; Fig. 5.2) predicted nestling provisioning by helpers. Inspection of effect sizes revealed opposite, sex-dependent effects of the relatedness to the breeder on the provisioning efforts performed by helpers. The provisioning effort of helpers decreased with relatedness to the breeding female so that 2nd order relatives and unrelated individuals fed more than 1st order relatives (Fig.5.2). Yet, 2nd order relatives fed more than unrelated helpers (Fig. 5.2). By contrast, helpers' provisioning effort increased linearly with relatedness to the breeding male (Fig 5.2). All the other variables, including breeding group size, were not significant (All $P > 0.215$).

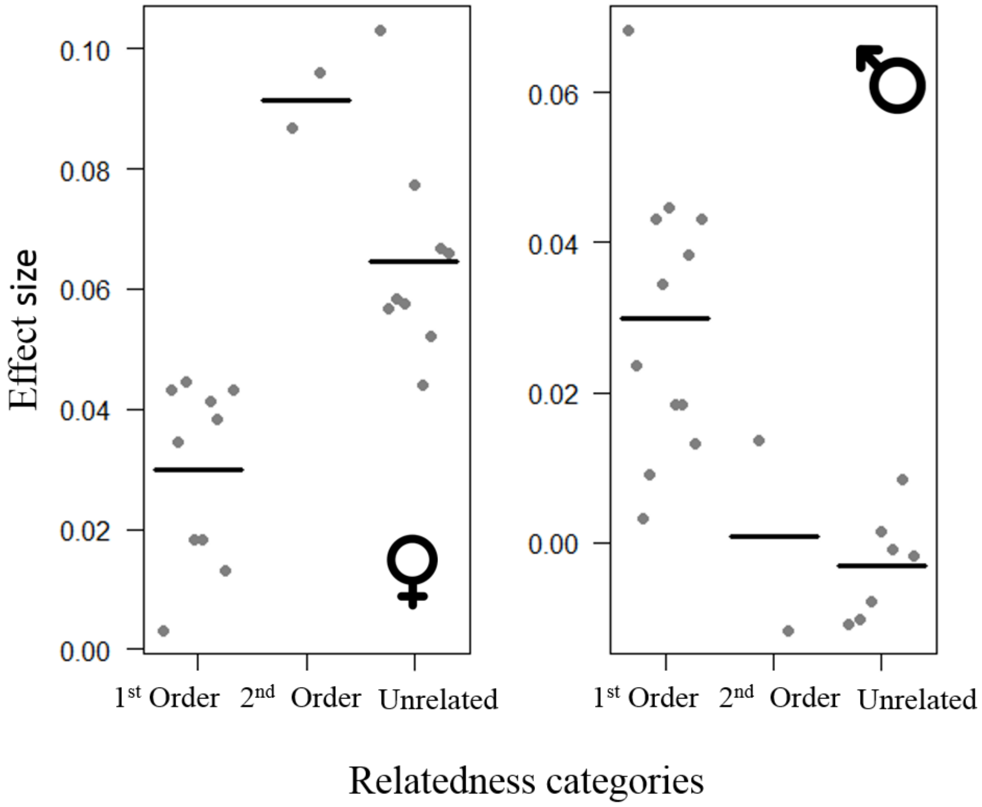

Figure 5.2 Helpers' nestling provisioning rate in relation of their relatedness to the female breeder (left hand side) and to the male breeder (right hand side). The solid bars represent the mean effects of the relatedness categories controlling for the other variables included in the model

5.4.2. Contribution to communal thatch building

Working here on the whole sample I found that the breeding category and sex predicted variation in communal thatch building (Table 5.4). Among breeders, 23 males and 4 females were seen contributing to the thatch out of, respectively, 40 male and 29 female breeders. Among helpers, 19 males but no females were observed contributing to the thatch out of 23 males and 7 female helpers. Inspection of effect sizes showed that helpers are more likely to be seen building than breeders (GLMM estimate: 1.462 ± 0.689, $N = 99$, $T = 2.101$, $P = 0.037$; Table 5.4) and males are more likely to be seen building than females (GLMM estimate: 3.381

± 0.895, $N = 99$, $T = 3.730$, $P < 0.001$; Table 5.4). Although dominance scores contributed to improve the model fit and were retained in model selection, the positive effect of dominance scores on the likelihood to build was non-significant (GLMM estimate: 1.324 ± 1.489, $N = 99$, $T = 0.877$, $P = 0.381$; Table 5.4). The average degree of relatedness between the individual that build and the colony did not explain variation in communal thatch building ($P = 0.645$). Minimum age and the two-ways interactions between breeding status and sex, breeding status and dominance, sex and dominance did not explain variation in thatch building behaviour (all $P > 0.410$).

Table 5.4 Estimates and standard errors (SE) of model-averaged parameters for the set of best-fit models explaining variation in both breeders and helpers contribution to communal thatch building ($N = 99$). Females and breeders are the reference levels for the sex for the breeding category respectively. 'DS' is abbreviated for 'dominance scores' and 'BS' for breeding status

Covariates	**Estimate ± SE**	**T**	**P**
Intercept	-0.354±0.911	0.364	<0.001
DS	1.324±1.450	0.877	0.380
Sex (M)	3.381±0.895	3.730	<0.001
BS	1.462±0.686	2.101	0.040
Weight	0.233±0.265	0.867	0.386
Tarsus	-1.648±0.681	2.386	0.017

5.4.3. Contribution to snake mobbing

Sample with breeders and helpers

When the analyses included both helpers and breeders, I found that the probability of mobbing and the number of attacks were qualitatively affected by the same variables. Both were predicted by the breeding categories alone (probability of mobbing: $N = 553$, $\chi^2 = 42.05$, $P < 0.001$; Fig. 5.3; number of attacks: $N = 553$, $\chi^2 = 39.85$, $P < 0.001$; Tables 5.5 and 5.6) and the sex of an individual (probability of mobbing: $N = 553$, $\chi^2 = 42.51$, $P < 0.001$; number of attacks: $N = 553$, $\chi^2 = 80.043$, $P < 0.001$; Tables 5.5 and 5.6). Males were more likely to mob and performed higher number of attacks than females (GLMM estimate: 1.009 ± 0.460, $N = 553$, $T = 2.192$, $P = 0.028$; Tables 5.5 and 5.6). Inspections of effect sizes showed that breeders from other chambers, independently of the reproductive stage of their nest chambers, were less likely to mob (*N* = 357; both *P* < 0.001; Table 5.5) and mobbed less frequently (*N* = 196; both *P* < 0.020; Table 5.6) while helpers (all categories) and the breeders to the threatened chambers did not significantly differ in both their likelihood of mobbing (all *P* > 0.144; Table 5.5) and their frequency of attacks (all *P* > 0.210; Table 5.6). Minimum age, body condition, and the interactions between breeding status and sex, sex and minimum age, breeding status and minimum age were not significant (all *P* > 0.229).

Table 5.5 Estimates and standard errors (SE) of the best fit model predicting the likelihood to mob when both helpers and breeders are included in the dataset (N = 553). Females and breeders (B) to the threatened chambers are the reference levels for the sex for the breeding category respectively. 'BS' is abbreviated for breeding status. B and H indicate breeders and helpers of the threatened nest chambers respectively; BA and HA breeders and helpers occupying reproductively active nest chamber at the moment of the experiment or inactive for BI and HI. I further included the statistics of a Wald test and the corresponding *P*-value in order to assess the overall significance of categorical covariates

Covariate	**Wald test**	**P Wald**	**Effect**	**Estimate ± SE**	**T**	**P**
Intercept				-1.891±0.414	-4.569	<0.001
Sex (M)	42.51	<0.001		0.071±0.328	2.175	0.030
BS	42.05	<0.001	BA	-2.256±0.441	-5.111	<0.001
			BE	-2.08±0.455	-4.573	<0.001
			H	-1.077±0.737	-1.461	0.144
			HA	-0.076±0.518	-1.471	0.141
			HI	-0.471±0.555	-0.85	0.395
N ind mob			.	0.281±0.049	5.71	<0.001

Table 5.6 Estimates and standard errors (SE) of the best fit model predicting the number of mobbing attacks when both helpers and breeders are included in the dataset (N = 553). Females and breeders (B) to the threatened chambers are the reference levels for the sex for the breeding category respectively. 'BS' is abbreviated for breeding status. B and H indicates breeders and helpers of the threatened nest chambers, respectively; BA and HA breeders and helpers occupying reproductively active nest chamber at the moment of the experiment or inactive for BI and HI. I further included the statistics of a Wald test and the corresponding *P*-value in order to assess the overall significance of categorical covariates

Covariate	**Wald test**	**P Wald**	**Effect**	**Estimate±SE**	**T**	**P**
Intercept				-2.540±0.430	-5.913	<0.001
Sex (M)	80.04	<0.001	M	1.009±0.460	2.192	0.028
BS	39.85	<0.001	BA	-1.23±0.559	-2.326	0.020
			BE	-1.532±0.632	-2.423	0.015
			H	1.065±0.850	1.254	0.210
			HA	-0.502±0.842	-0.597	0.551
			HI	0.271±0.704	0.385	0.700
N ind. mob	.	.	.	0.242±0.037	6.637	<0.001

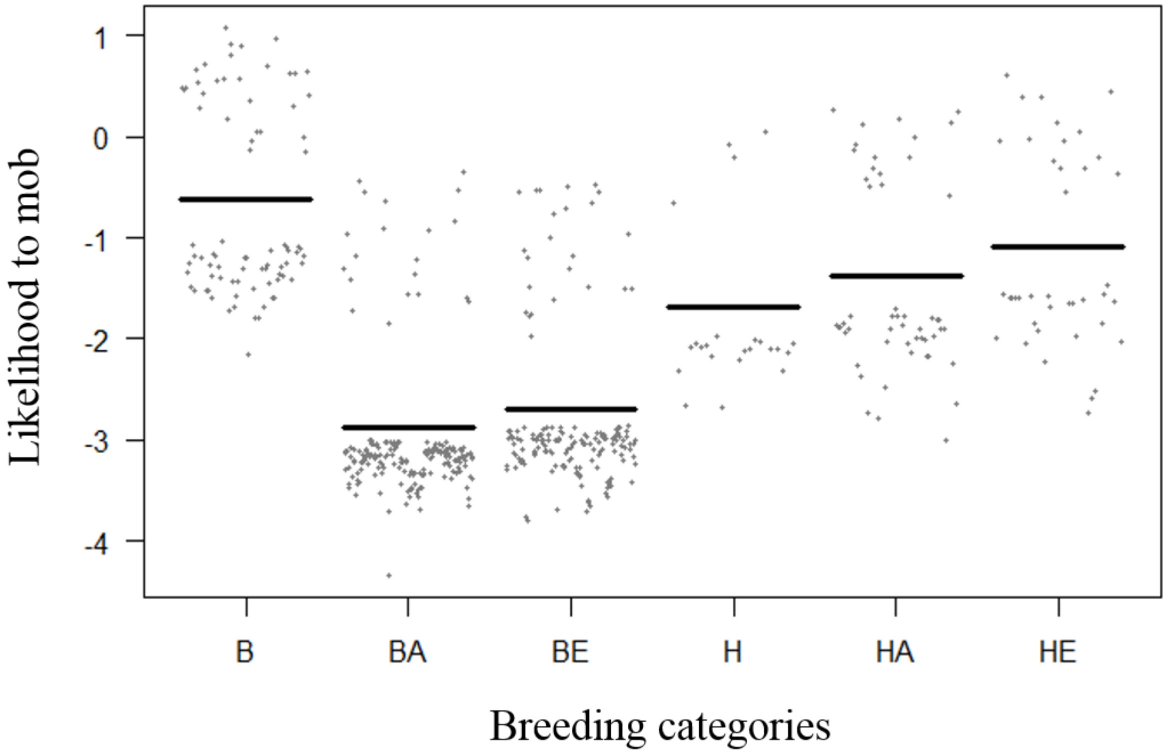

Figure 5.3 Effects of the breeding categories on the likelihood of mobbing the snake. For each breeding categories, the solid black bars represent the mean effect estimates and the dots, the response observed, controlling for the other variables included in the model: Individuals with unknown breeding status (0), breeders (B) or helpers (H) of the threatened nest chamber, breeders (BA) or helpers (HA) of other reproductively active nest chambers, breeders (BI) or helpers (HI) of nest chambers that were not reproductively active during the experiment

Sample with helpers only

When focusing on helpers only (*N*=59 with dominance scores; Table 2), the likelihood of mobbing was neither predicted by the helper's category (i.e. membership to the threatened chamber, to a reproductively active or inactive nest chamber during the experiment), nor sex and nor dominance (all *P* > 0.381). Hence, the effect size of predictors were estimated for a larger sample size incorporating 29 additional helpers in the data set which did not have dominance scores (*N* = 88). With this sample size, helpers' probability to mob was predicted by the degree of relatedness to the female breeder so that helpers were more likely to mob when more relate to the breeding female (GLMM estimate: 1.194 ± 0.549, *N* = 88, *T* = 2.175, *P* = 0.030). By contrast, helpers tended to be more likely to mob when less related to the male breeder of the focal chamber but that effect was marginal (GLMM estimate: -12.65 ± 6.756, *N* = 88, *T* = -1.873, *P* = 0.061).

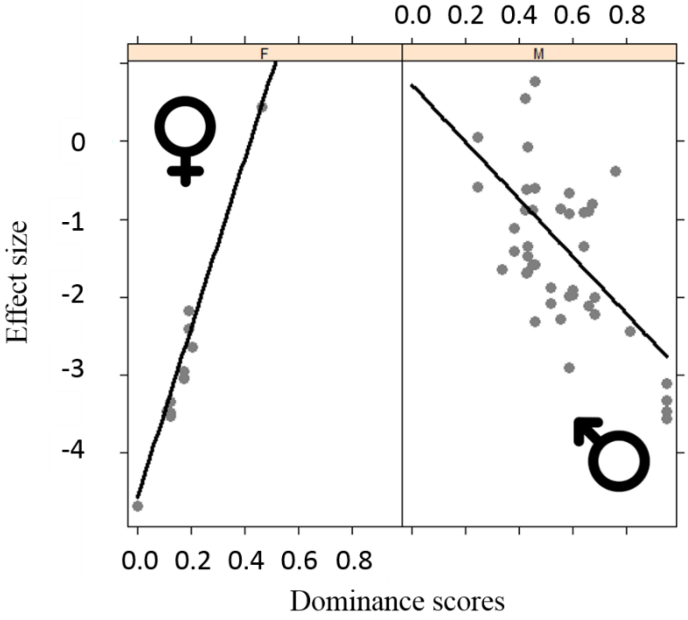

Figure 5.4 Effect of dominance scores on the number of mobbing attacks conducted by female (left hand side) or male helpers (right hand side). The lines represent the LMM effect estimates controlling for the variables included in the model

On the other hand, the number of mobbing attack conducted by a helper, was predicted by both the helper' sex and the helper's sex in interactions with its dominance status. Overall, males conducted more attacks than females (GLMM estimate: 5.307 ± 0.1.759, *N* = 59, *T* = 2.175, *P* = 0.003). Dominance had an antagonistic effect on the two sexes. For females helpers, dominant status positively predicted the number of attacks (GLMM estimate: 10.87 ± 3.405, *N*

= 59, *T* = 3.193, *P* = 0.001, Fig. 5.4). By contrast, dominance status negatively predicted the number of attacks for male helpers (GLMM estimate: -14.55 ± 3.872, *N* = 59, *T* = -3.757, *P* < 0.001, Fig. 5.4). Age did not contribute to explain variation in neither the probability of mobbing nor the number of attacks (both *P* > 0.488).

Last, a helpers number of attacks was predicted by the degree of relatedness to the female breeder so that helpers mobbed more frequently (GLMM estimate: 2.418 ± 1.126, *N* = 59, *T* = 2.143, *P* = 0.038) when more related to the female breeder of the focal chamber. The relatedness to the male breeder of the focal chamber did not significantly predict mobbing frequency (*P* = 0.281).

Body condition did not explain the probability to mob nor the number of attack (all *P* > 0.104). None of the two-way interactions between breeding categories, dominance, minimum age and the degree of relatedness to the male or female breeder were significantly predicting the likelihood to mob and mobbing frequency (all *P* > 0.258).

5.4.4. Overall contribution to cooperation

Individuals which were more likely to mob were also more likely to build (ICC coefficient= 0.32, *N* = 71, *F* = 1.50, *P* = 0.047). There was no correlation between nestling provisioning neither with the likelihood of mobbing nor with the likelihood to build the communal thatch (both *P* > 0.51) resulting in a non-significant consistency in the overall contribution across these three cooperative tasks (ICC coefficient= 0.17, *N* = 71, *F* = 1.28, *P* = 0.109).

5.5 Discussion

Whether and how kin selection and alternative non kin-based mechanisms drive the evolution and maintenance of complex cooperative societies is still poorly understood. In this study, I tested whether kinship and dominance predicted individual cooperative contribution in nestling provisioning, communal thatch building and snake mobbing. I found that kinship appears to influence the evolution of cooperation as the level of relatedness to the breeder partly predicted nestling and mobbing behaviour, both being positively related to male and female relatedness respectively. However, for the three studied cooperative behaviours, I also found results predicted under hypotheses suggesting that cooperation may confer direct benefits, namely the pay-to-stay and social prestige hypotheses. I found that helpers fed more when less related to the breeding females. In addition helpers, which are typically subordinate to breeders, contributed more to communal thatch building and to snake mobbing, an effect that was additionally influenced by dominance status for the latter. More dominant female helpers performed more attacks against the experimental snake while it was the reverse for males. Hence, exploring the relation between helping effort and kinship or dominance status suggested that individuals may partition helping efforts in cooperative tasks according to their degree of kinship, dominance, sex and breeding category and that more than one mechanisms promote cooperation in this species. Cooperation may therefore provide direct and indirect benefits.

In cooperatively breeding passerine, individuals providing alloparental care, the helpers, often direct their help to related offspring suggesting this behaviour is kin-selected (Komdeur 1994; Russell and Hatchwell 2001; Browning et al. 2012). This way, helpers may gain indirect fitness benefits through improved reproductive success and offspring survival (Dickinson et al. 1996; Cockburn 1998; Dickinson and Hatchwell 2004; Hatchwell et al. 2004; Browning et al. 2012). Additionally, the presence of helpers-at-the-nest may also improve the parents' survival as they may be able to reduce their investment in the offspring, decreasing their work load and/or their maternal investment in eggs for females which may contribute to further indirect benefits (Hatchwell 1999; Russell et al. 2007; Russell and Lummaa 2009). In this study, I found that the degree of relatedness between the helper and the male breeder positively predicted helpers' provisioning effort thereby supporting the expectation of a kin-selected helping behaviour in regard to nestling provisioning. By contrast, helpers related to the female breeders provisioned at lower rate as opposed to more distantly related helpers, in line with previous reports on nestling provisioning in this population (Doutrelant et al. 2011). In addition, dominant helpers fed more. However this result was found in the global analyses containing both helpers and breeders and not when comparing only among helpers. This may have been an effect of reduced sample size, and thus needs to be confirmed. These results may be explained by two potential hypotheses involving direct benefits of cooperation. First, less related and more dominant helpers could contribute more in order to pay their rent (Gaston 1978; Kokko et al. 2002) because they may face greater risk of eviction as seen in the cooperatively breeding cichlids (*Neolamprologus pulche*r; Zöttl et al. 2013). Yet, this first possibility is unlikely as I would also have expected less related helpers to the male breeder to also work harder than more related helper, particularly because male breeders are dominant so they are the ones with potential to coerce helpers contribution (Chapter 4). Second, these more distantly and dominant related helpers could signal their cooperative efforts in order to improve their social image and to enhance future direct benefits (Zahavi 1995; Wedekind and Milinski 2000). Previous correlative results showed that helpers often wait at the colonies with prey in their beak before feeding, spending longer than parents to go into the nest to feed and, additionally, helpers fed more in the presence of a larger audience (Doutrelant and Covas 2007). Thereby, the presence of an audience, and hence more potential sexual or social partners, appears to influence feeding behaviour in this species (Danchin et al. 2004). Nonetheless, these results have still to be demonstrated experimentally and have not been found in other species where audience effects were examined (McDonald et al. 2008; Nomano et al. 2013). It is however possible that showing-off cooperative behaviour might increase an individual's chances of being chosen by a mate when a breeder lose its partner (sociable weavers are genetically monogamous and pairs typically stay together for several years) or with other helpers of the nest and/or colony (Putland 2001; Covas et al. 2007). Additionally, as a result of enhanced prestige, cooperative individual may associate more closely and/or with more social partners which may improve predator vigilance, stronger support via coalition (Kokko et al. 2001), or more opportunities to get reciprocated cooperation (i.e. tit-for-tat; Milinski 1987; Croft et al. 2006). A result found with social network analyses (Chapter 6). Taken together, my findings coupled with the work of Doutrelant and collaborators (2007; 2011), suggest that helper's contribution to nestling provisioning is partly kin-directed and partly driven by other mechanisms providing direct benefits.

Direct and indirect benefits are also likely to contribute to the evolution thatch building behaviour in this species. I did not find that the average relatedness to the colony predicted the likelihood to build the thatch. This suggests that the degree of relatedness at the colony level may be too low to explain individual cooperative contribution to the communal thatch and that a more precise estimate of relatedness might have been used. Indeed, a previous study on the same population reported that individuals built preferentially in areas of the nest above their own nest chamber(s) and above the nest chambers that were occupied by close-kin. Thereby, local relatedness where the building effort was targeted predicted building behaviour and not the average relatedness to the colony (van Dijk et al. 2014). The communal nest of sociable weavers acts as a thermal buffer with the most embedded, deepest nest chambers having the highest thermoregulatory advantages (van Dijk et al. 2013). Nests that provide thermoregulatory advantages typically favour offspring development and enable individuals to save energy expenditure (Dawson et al. 2011; Mainwaring et al. 2014). Thus, accumulating thatch material preferentially above one's nest chamber(s) and nest chambers that are occupied by relatives may provide direct and indirect benefits. Kin-directed thatch building may also contribute to maintain honesty in the system (Rankin et al. 2007) as the nest of sociable weavers is built communally and such communal goods are highly sensitive to cheating and hence, to the tragedy of the commons (Hardin 1968).

Cheating may further be prevented if cheaters are socially controlled (e.g. punishment; Raihani et al. 2012), as predicted under the pay-to-stay hypothesis, at the colony level and / or if participating to the common good is also socially or sexually selected and individuals competed for it (i.e. social prestige; Milinski et al. 2002). I found that helpers were more often thatch builders as opposed to breeders. Hence, dominance indirectly influenced thatch construction: helpers, which are typically subordinated to male breeders (Chapter 4), contributed the most to the communal thatch building. However among helpers, effort in thatch building was not influenced directly by dominance status. If confirmed by further study, the fact that helpers build more than breeders but that dominance is not linked to building behaviour in helpers could suggest that competition in order to advertise building effort is unlikely (and thus that cooperating to thatch building would not be a signalled). Under this scenario, subordinate helpers may contribute to thatch building in order to be tolerated in the colony (Bergmüller and Taborsky 2005; Heg and Taborsky 2010) so that a pay-to-stay mechanism may act in concert with kin selection to prevent cheating. In agreement with this suggestion, results established in Chapter 6 show that individuals that do not build are more aggressed. However, van Dijk and collaborators (van Dijk et al. 2014) found that older individuals build more than young ones, a result that contrasts with what was found in this study, as helpers are also typically younger than breeders being their offspring (Covas et al. 2006), and call for more study of this cooperative behaviour.

In cooperative species, contribution to predator defense is regularly observed as a form of vigilance (Griesser 2003), alarm calls (Griesser and Ekman 2004) or direct attack to the predator (Heg and Taborsky 2010) such as mobbing behaviour (Maklakov 2002). However, this contribution is often kin-directed as seen in Arabian babblers (*Turdoides squamiceps*; Maklakov 2002) and Siberian jays (*Perisoreus infaustus*; Griesser and Ekman 2005) where the presence of relatives initiates contribution to predator defense. In sociable weavers, when a nest chamber was under a simulated threat of predation by a snake, not only the helpers provisioning at that nest chamber but also other helpers mobbed. Nonetheless, as expected by kin selection helpers mobbing behaviour (i.e. likelihood and frequency) was predicted by the relatedness to the female breeder of the threatened nest chamber so that mobbing is likely to confer indirect benefits. Surprisingly, the level of relatedness to the male breeder did not impact the likelihood of a helper to mob. A result that still need to be understood but which may suggest that helpers mob also at nests of unrelated individuals to be accepted by male breeders.

The fact that helpers in general mob more than breeders could have several explanations. First, younger individuals are often less bold and more prone to take risks (Fairbanks 1993; Zuckerman and Kuhlman 2000). Helpers are typically younger than breeders (Covas et al. 2006) in this system, and hence they may have higher propensity to mob. Second, subordinate helpers may contribute to mobbing in order to be tolerated in the group and avoid dispersal costs (Bergmüller and Taborsky 2005; Heg and Taborsky 2010). Here, the group can be considered at two levels, the breeding group and the colony. Respectively, helpers from the threatened nest chamber mob to pay their rent to their breeders and helpers from other nest chambers may mob to reduce their risk of being evicted from the colony. Indeed, harassing a snake from one nest chamber may be beneficial to the whole colony. Finally, helpers may signal their cooperativeness to increase their social prestige which could explain why helpers from other nest chamber also engaged in mobbing behaviour.

The relationship found between mobbing and dominance does not allow to disentangle these two hypotheses. These relationships were in opposite directions for male and female helpers in a sense that was not particularly predicted by the prestige hypothesis or the pay-to-stay at the scale of the breeding group. Both hypotheses predict that dominants helpers are expected to work harder than subordinates In the pay-to-stay, the presence of dominant is expected to inflict a larger cost on breeders as they represent more competition, a cost compensated by a more intense helping effort (Kokko et al. 2002; Bruintjes and Taborsky 2008). Under the prestige hypothesis (Zahavi 1995), dominants are expected to work more because of their better competitive abilities. It is unlikely that dominant female helpers work more because they represent a better threat to the breeders as this category of individuals is typically the most subordinate within a colony (Chapter 4). Thereby, this result needs to be verified with a larger sample size before drawing conclusions (analysis based on 14 females only). Subordinated males, by contrast, may have incentives to work more and to invest more in mobbing. Indeed, they may face greater risks of eviction and at higher dispersal costs (i.e. phenotype-dependent dispersal; Lawrence 1987; Clobert et al. 2009) if they have reduced chances to get accepted at a new colony due to their lower competitive ability. Alternatively, in cooperatively breeding paper wasps (*Polistes dominulus*), more dominant helpers provide less help because they are at the top of the queue to access a breeding position and are thus likely to save energy for their own future position (Cant and Field 2001). A similar pattern may hold for sociable weavers as more dominant individuals have higher probability to access a breeding position (Chapter 4).

Furthermore, female breeders were contributing the less in the three different tasks by contrasts with male breeders and female and male helpers. Hence, female breeders appear to benefit from a reduced work which could improve their survival (Hatchwell 1999). Sociable weaver females are expected to suffer the highest costs from predation because, in addition of losing their offspring, they have to cope with the costs of laying a replacement clutch (Monaghan et al. 1998; Visser and Lessells 2001) which may reduce their survival (Monaghan and Nager 1997), particularly as they are long-lived passerines (Bergerud and Gratson 1988). Therefore, helpers that are highly related to the breeder female may mob more in order to prevent both direct predation on the nestling and/or saving energy to the female breeders, hence maximizing their indirect fitness benefits (Griesser and Ekman 2005). Accordingly, in sociable weavers, the presence of helpers seems to be mainly beneficial to females and their survival (Paquet et al. 2013; Paquet et al. 2015). Yet, this explanation comes at odds with the results that the feeding rate of helpers is positively linked to their relatedness to the breeding male and negatively to their relatedness to the breeding female.

Individuals contributing to build the thatch consistently invested more in predator defense but not in nestling provisioning. Hence, in addition to the variability in cooperativeness between individuals revealed by this study, variability in cooperativeness within individuals is also likely to occur. In the noisy minor (*Manorina melanocephala*) for instance, individual contribution to nestling provisioning is negatively correlated with predator mobbing (Arnold et al. 2005). As suggested above, less bold individuals may be more prone to take risks and to mob (Zuckerman and Kuhlman 2000) .Indeed, between- and within-individuals variation or consistency in cooperativeness may further reflect different behavioural profiles (i.e. personalities; Dingemanse and Réale 2005; Bergmüller et al. 2010). This preliminary result offers exciting research perspectives, particularly because different behavioural profiles may be associated with different social strategies (Sih et al. 2004; Krause et al. 2010). I stress that more works adopting the methodologic framework developed by the study of animal personalities (e.g. incorporating within-individual repeatability for each tasks and standardised personality tests) are required (Carter et al. 2013) to investigate whether different cooperativeness strategies occur in sociable weavers, what are their causes and their fitness consequences.

In conclusion, I explored whether kinship and/or dominance predicted cooperative efforts over multiple tasks in order to highlight the evolutionary processes that are likely to be involved in the evolution and maintenance of cooperation in sociable weavers. This species exhibits a very complex cooperative system where cooperative acts are performed over multiple tasks for which the benefits can be gained by different social units (i.e. individual, breeding group, colony) so that cooperative acts may be under different selective pressures. Kinship appeared to be a key driver of individual cooperative contribution for all three cooperative tasks examined (i.e. nestling provisioning, thatch building, snake mobbing; although, this study failed to capture its complex effect on thatch building). Although the examination of the relationships between dominance and cooperativeness failed to give the clear answers, I found that overall, helpers, usually dominated by male breeders (Rat et al. 1015) contributed more than breeders in building the thatch and mobbing predators suggesting that cooperation may also be used as currency to 'pay the rent' in order to be accept in the group or colony or can be used to advertise an individual's prestige. Similarly, variation in nestling provisioning revealed some potential to be socially and/or sexually selected as helpers fed more the nestling of unrelated females and dominant helpers appeared to feed more. Therefore, both direct and indirect benefits may promote the evolution of cooperation in sociable weavers reinforcing the idea that kin-selection alone is often not sufficient to explain the evolution cooperation.

Chapter 6

The roles of dominance, kinship and relatedness on social network structure and position

> ‘*Man is by nature a social animal; an individual who is unsocial naturally and not accidentally is either beneath our notice or more than human. Society is something that precedes the individual. Anyone who either cannot lead the common life or is so self-sufficient as not to need to, and therefore does not partake of society, is either a beast or a god.*’
>
> *Aristotle*

6.1 Abstract

Identifying the main factors shaping social interactions is of prime importance to understand the evolution of group-living as they may reflect the distribution of benefits and conflicts. Both kin selection and non kin-based mechanisms often shape the social organisation of groups but how they regulate large complex societies remain poorly understood. I used social network analyses to test for the structuring role of kinship on association and dominance interactions in the cooperative societies of a colonial passerine, the sociable weaver (*Philetairus socius*). I tested whether relatedness among colony members (N=134) predicts associations and whether it pacified dominance interactions as predicted by kin facilitation. I then explored the role of kinship and dominance in predicting social network position of breeders and helpers, assuming that being well-connected and central is beneficial. If group-living is kin-selected, I predicted that more related individuals should occupy central network position. Alternatively, the occupation of these central positions by dominants suggests that direct benefits may further help to maintain group-living. Finally, I tested whether helpers that contributed more to cooperative tasks (i.e. snake mobbing, nestling provisioning and thatch building) were more central, in relation to their dominance status, and whether helpers that cooperated less received more aggressions. In support of kin-facilitation, I found that relatives bond more frequently than non-kin, aggressions are pacified among male relatives and network centrality of helpers increases with relatedness. In addition, dominance enhanced network centrality for both breeders and helpers suggesting that dominants may occupy key social position with enhanced benefits. Finally, helpers which contributed more to mobbing and nestling provisioning exhibited greater network centrality, while helpers with reduced contribution to communal thatch building received more aggression. We conclude that kinship and dominance shape social organisation of sociable weavers, while the position within the colony social network appears closely linked to individual cooperative behaviour.

6.2 Introduction

Group-living animals are typically vulnerable to conflicts-of-interest as individuals often face the dilemma of whether to cooperate for or to compete over the access to resources (Parker 1979; Huntingford and Turner 1987; Parker and Mock 1987; Parker and Partridge 1998). These conflicts arise because an individual is expected to gain the highest payoff by exploiting the common good without bearing the costs (Axelrod and Hamilton 1981; Huntingford and Turner 1987). This dilemma may be reflected in the social structure of group-living species where individuals frequently interact with each other in multiple ways (Croft et al. 2008). Indeed, conflict or cooperation may underlie the nature of these interactions as they can be positive, such as grooming to remove parasites (Tiddi et al. 2012) or huddling to enhance thermoregulation (Napper et al. 2013). Alternatively, they may be negative, such as aggressive interactions over access to resources, potentially resulting in injuries or death (Senar et al. 1990; Chiarati et al. 2010). Hence, interactions among group members shape groups' social organisation, which is essential to study as it has profound implications on, among others, the spread of information and levels of cooperation (Sih et al. 2009; Croft et al. 2011). Examining why and how individuals interact within groups is thus essential to understand the evolution of complex cooperative societies.

The study of interactions between individuals is often focused on pairwise interactions. Such a simplistic approach may fail to capture the social complexity of a group (Wey et al. 2008; Croft et al. 2011) which may have unique properties but with potential consequences on the individual (e.g. collective movement). By capturing interactions among all individuals across a whole group, recently developed social network analyses, have helped to understand the factors shaping the complexity of social groups (Whitehead 2008; Sueur 2015). Social networks analyses have been used to describe social structures in a wide range of taxa (e.g. bottlenose dolphins, *Tursiops* spp.: Lusseau 2003; Wolf et al. 2007a; house finches, *Carpodacus mexicanus*: Oh and Badyaev 2010; Primates: Bret et al. 2013; Ants, *Leptothorax spp.*: Shimoji et al. 2014). They have helped to determine the impacts of the social structure on a large panel of biological processes, including population dynamics – e.g. impact of juveniles sociability on dispersal strategies (Blumstein et al. 2009); survival and conservation – e.g. implication on group cohesion of removing key individuals (Williams and Lusseau 2006) and information processing and decision making – e.g. diffusion of information and foraging decisions within a guild of tits (Aplin et al. 2012). As such, social network analyses have drastically changed our perception and study of social systems. They are essential to complete our understanding of the evolutionary forces that maintain group-living and cooperation (Sih et al. 2009; Croft et al. 2011; Micheletta et al. 2012). Indeed, exploring similarities and differences in the structure of different networks is a powerful way to give insight on the mechanisms that shape the social organisation such as kin selection, kin competition or other non-kin-based mechanisms. To date the structuring roles of these different mechanisms in the social organisation of complex cooperative groups and in contexts other than reproduction, are still poorly understood.

Kin-selection is one of the major forces driving the evolution of group-living and cooperation (Hamilton 1964; Axelrod and Hamilton 1981; Cockburn 1998; Hatchwell 2009) and it is also likely to play an important role in different contexts such as shaping aggregation or affiliative interactions between individuals (Baglione et al. 2003; Wolf and Trillmich 2008; van Dijk et al. 2014). Patterns of affiliation may be especially important in a context of competition over food as individuals may choose to associate preferably with kin in order to reduce the costs of foraging in groups (King et al. 2011). Indeed, kin associations are expected to decrease the occurrence of conflicts so that kin groups often experience reduced level of aggression compared to groups consisting of unrelated individuals (Chiarati et al. 2011). This is likely to result from nepotism, where individuals get privileged protection or access to resources by their relatives (Griesser 2003; Griesser and Ekman 2004; Griesser and Ekman 2005). Kinship is thus expected to structure social organisation of a group and to influence patterns of interactions between group members (Hinde 1976). Both positive (as above) and negative interactions between kin may occur. In racoons (*Procyon lotor*) for instance, although co-occurrence of individuals at foraging stations was not predicted by kinship, levels of aggression were higher among related individuals, suggesting that kin competition may influence social associations in this species (Hauver et al. 2013).

However, kinship alone may not always be sufficient to explain neither the structure of interactions between individuals (Braun and Bugnyar 2012; Shizuka et al. 2014) or the maintenance of cooperation between group members (Clutton-Brock 2002; Roberts 2005; Riehl 2011). Groups are often composed of both related and unrelated individuals and cooperation between distantly related or unrelated individuals has been shown to be more common than previously assumed (Schino and Aureli 2010; Riehl 2013). In such cooperative societies, both indirect (i.e. kin-selected) and direct benefits may be important (Sumner et al. 2010; Dobson et al. 2012).

Dominance is likely to have major consequences on the distribution of direct benefits among the individuals of a group, and it is thus crucial to study and to integrate the role of dominance, in addition to relatedness, on the social organisation of group-living species (Cant 2000; Cant and Field 2001; Bergmüller et al. 2007; Majolo et al. 2012). Dominants may compete to help if cooperation is expected to raise an individual's image scoring or social prestige and to enhance the likelihood to obtain future direct benefits in return (Milinski 1987; Wedekind and Milinski 2000). Thus, individuals with high prestige are expected to be well integrated in their network (e.g. more social partners). Alternatively, subordinates may accept not to reproduce and help dominant breeders in order to be tolerated in the territory as suggested by the pay-to-stay hypothesis (Balshine-Earn et al. 1998; Kokko et al. 2002). Defecting individuals are expected to be punished in order to maintain honesty in the system (Cant 2011; Thompson et al. 2014). In the cooperatively breeding African cichlid *Neolamprologus pulcher*, for instance, helping contributions were predicted both by the degree of relatedness and by the dominance status of helpers (Zöttl et al. 2013) and followed the predictions of a pay-to-stay driven cooperation. Indeed, subordinates *N. pulcher* have been shown to provide help in order to be tolerated by dominants and allowed to remain in the group (Balshine-Earn et al. 1998), a tolerance for which, unrelated subordinates have to work harder (Stiver et al. 2005; Zöttl et al. 2013). Hence, both direct and indirect benefits may drive the evolution of cooperation in this species where dominance acts in concert with kinship on the social interactions between individuals and on predicting individual contribution to cooperation.

In structured social systems, the position within a social network may greatly influence individual behaviour and in turn, the fitness benefits obtained by this position (Croft et al. 2008; Krause et al. 2010; Croft et al. 2011; Wilson et al. 2013). Central network positions characterize individuals that are well connected to other individuals and/or that are important to allow the connections of other individuals in the network. As a result, central individuals have more chances to get information or to receive reciprocal cooperative behaviour (Croft et al. 2006; Micheletta et al. 2012). For example, in the long-tailed manakins (*Chiroxiphia linearis*), a long-term studies of male-male and male-female interactions observed during the breeding season revealed that juveniles occupying central position within social networks were more likely to form successful coalitions as adults, a pattern associated with higher reproductive success (McDonald 2007). Consequently, individuals that are socially well integrated, i.e. occupying central positions in a network, may cooperate more, have increased survival and/or enhanced reproductive success (Silk et al. 2003; Silk et al. 2010; Barocas et al. 2011; Stanton and Mann 2012). Because of these benefits, phenotypic attributes, such as age or sex and social status, through its role on the distributions of benefits and cooperation, are likely to be linked with the social position an individual occupies within its network (Lusseau and Newman 2004).

Here, I used social network analyses to characterize the social structure within colonies of sociable weavers (*Philetairus socius*). Sociable weavers are long-lived, cooperatively breeding passerines. They live throughout the year in a colony that can contain hundreds of individuals (Maclean 1973d), roosting and breeding in their massive communal nest. Males are mainly philopatric (dispersal is female-biased) which favours the existence of a kin structure between colonies (particularly among males) and within breeding groups (Covas et al. 2006; van Dijk et al. 2014). The colony is sub-structured in breeding groups that are constituted by a pair that can be assisted by helpers (up to 7; R. Covas *unpublished data*). The sociable weaver's communal lifestyle makes this species an excellent study system to investigate the role of kinship and dominance on the network structure and the impact of these factors on cooperation.

I examined associations and aggressive interactions at a feeder. First, I explored the influence of kinship in structuring the association and dominance networks by examining the correlation between the interaction matrices (association or dominance) and the kinship matrix, among males and females and among males only. I predicted that if associations at the feeders are kin-directed, i.e. facilitating access to food by relatives, relatives will be more closely connected than non-relatives and birds living in the same family group should be more associated. The reverse is expected for dominance interactions between individuals so that related individuals are expected to engage less in agonistic interactions than unrelated individuals.

Second, I investigated whether network centrality was associated with dominance, kinship, the breeding status of an individual and its sex. I expected dominant males to be more central in their network as they typically get better access to resources. Additionally, I further expected kinship to influence network centrality as kin-selection was found to be an important route behind the evolution of cooperation in this species (Covas 2002; Covas and du Plessis 2005; Covas et al. 2006; Covas et al. 2008; Paquet et al. 2013; van Dijk et al. 2014; Paquet et al. 2015).

I further tested whether social network position (i.e. central or not) was associated with helper's contribution to three specific cooperative tasks (i.e. mobbing, nestling provisioning, and communal thatch building) in order to preliminary explore if cooperativeness may impact the position of an individual in the social group. I predicted that a positive relationship between network centrality and cooperative behaviour offers the possibility that cooperation confers direct benefits and may be used as a signal of individual quality (i.e. social prestige hypothesis) to other members of the colony or alternatively a rent payment (i.e. pay-to-stay hypothesis). Also, under the prestige hypothesis, I expected a positive link between dominance and centrality (individuals compete for cooperation so that dominants are more central) while the reverse can be expected for a pay-to-stay driven cooperation (subordinates cooperate to stay and reduce their chance of eviction, hence subordinates are more central). Furthermore, according to the pay-to-stay hypothesis, helpers who did not help or helped less are expected to be punished for their defection and to receive more aggressions. Hence, to support this hypothesis, I predicted that helper's dominance *indegree* (i.e. a network metric representative of the number of individuals that aggressed an individual taking into account the frequency of such interactions when the network is weighted) will be negatively associated with their cooperative contributions.

6.3 Material and methods

6.3.1. Study species and study site

Sociable weavers are highly social passerines endemic to the semi-arid savannahs of southern Africa. They communally construct a large, thatched nest that is typically built on *Vachellia erioloba* trees (although other trees or human-built structures may be used). Colonies may vary in size from less than ten to hundreds of individuals (Maclean 1973d) that often forage in groups (Flower and Gribble 2012). The nests contain several, independent nest chambers embedded within the communal thatch. Individuals use these chambers for roosting throughout the year and for breeding (Maclean 1973b; van Dijk et al. 2013). Sociable weavers are facultative cooperative breeders. Each breeding units usually consist of either a breeding pair alone or may contain up to seven helpers (R. Covas, *unpublished data*). Helpers are mainly philopatric male offspring of one or both breeders (93% of helpers are related to at least one parent; Doutrelant et al. 2004; Covas et al. 2006). Extra-pair paternity appears to be absent in this species (Covas et al. 2006; Paquet et al. 2015).

The study was conducted at Benfontein Nature Reserve (28˚52’S, 24˚50’E) near Kimberley, Northern Cape province, South Africa, between September 2013 and June 2014. The area consists of about 15 km^2 of Kalahari sandveld covered mainly by *Stipagrostis* grasses and *Vachellia spp.* trees (Covas et al. 2006). It contains approximately 30 active colonies comprising between 5–80 individuals. As part of the long-term research on this study population, these colonies have been captured annually using mist-nets since 1993 (see Covas et al. 2002 for more details on the captures). The annual captures take part prior to the breeding season and allow us to estimate the minimum age of individuals based on the date of the first capture event when not ringed as nestling. During the captures, birds are individually ringed using a uniquely numbered metal ring and three colour rings to allow visual individual identification in the field. Each individual was weighed (to the nearest 0.1g) and tarsus length (to the nearest 0.1mm) measured.

6.3.2. Collection of behavioural data: interactions and dominance scores

In order to establish the association and agonistic interaction networks, I collected associations (i.e. contact, *N* = 2046; Table 6.1) and agonistic interactions (i.e. active displacement and aggressions, *N* = 2286; Table 6.1) from observations at a feeder between

September 2012 and November 2012 and between September 2013 and December 2013 at 8 colonies (Colony size: 16.88 ± 7.38; Number of hours: 40.3 ± 0.52) for 134 individuals. I excluded 7 fledglings and prospective individuals, which were observed less than three times). One observer recorded the ID of the individuals involved in a dyadic interaction as well as the frequency of each type of interactions within a dyad. Interactions were collated in association and dominance matrices for each colony.

Table 6.1 Interactions collected to construct the dominance and the association networks respectively. The dominance network only included active dominance relationships so that threats and avoidances were excluded

Type		**Description**	**N**
Associations	Contact 1	Individual A feeds side by side with individual B peacefully (i.e. no agonistic interactions involved)	2046
	Contact 2	Individual A is side-by-side with individual B within 1m radius around the feeder	
Agonistic interactions	Fight	Individual A actively attacks individual B using bill, feet, and/or wings.	2286
	Active displacement	Individual A moves toward individual B until individual B retreats from the feeder.	

David's score was then used to calculate the dominance scores of each individual within its colony (*N* = 86). To compare dominance scores between colonies, I scaled David's scores between 0 and 1 within each colony so that the most dominant individual obtained a score of 1 and the most subordinate, a score of 0. David's scores were based on agonistic interactions matrices that further included avoidances as agonistic interactions. For more details on the calculation of dominance scores, see Rat et al (2015).

Observations were carried out from a hide and/or by video analyses. The hide was located within five metres from the colonial tree and did not alter the weaver's behaviour (Rat et al. 2015).

6.3.3. Measures of centrality

Based on the association network, I calculated three measures of individual network centrality, *degree, betweenness* and *closeness.* In network semantics, an individual is represented by a 'node' and its relationship with another individuals (or nodes) is an 'edge'. *(i) Degree* indicates the number of social partners so that it quantifies the number of edges connected to a node (i.e. the number of individuals the focal individual was seen interacting with). (ii) B*etweenness* is a measure of centrality that indicates the relative connectivity contribution of a node (Whitehead 2008) and is quantified as the number of shortest paths between other nodes that pass through the focal node (i.e. how important is an individual to connect other individuals in the network). (iii) *Closeness* is the number of edges separating one node and its most distant node (i.e. whether an individual is more or less peripheral in its social network). In a weighted network, these metrics are weighted by the number of times the same edge is observed between two nodes (Whitehead 2008).

Based on the dominance network, as relationships are directed (i.e. the relationship 'individual A aggresses individual B' is not symmetric), *degree* can be further refined as *indegree,* which is the sum of the number of edges reaching a node (by contrast the *outdegree,* is the number of edges departing from a node, so that *degree* is the total of both *indegree* and *outdegree*).

6.3.4. Breeding status and cooperative contributions

Breeding status

I determined the breeding status of 87 individuals observed in 2013-2014 as breeder, i.e. observed incubating during at least three separate observations, or as helpers, i.e. allo-parent observed feeding chicks during at least three separate observations.

Nestling provisioning

I collected individual feeding rate for 72 individuals by dividing the number of time an individual came feeding at a breeding chamber against the number of hours spent observing. Feeding rates were determined between the 7th and 14th day of the first hatched chick (9.62 ± 0.92 days). In some feeding events, it was not possible to identify the individual provisioning, I excluded all bouts that have more than 15% of missing ID and only calculated feeding rates on observation bouts of at least 60min with less than 15% of missing ID. The age of the chicks, the number of individuals contributing to nestling provisioning and the number of chicks to feed are likely to influence feeding rate. To control for those effects, I used the residuals of a generalized linear model where individual feeding rate was regressed against the age of the chick, the number of individuals in the breeding group and the number of chicks in the brood, as individual feeding rates in my analyses.

Communal thatch building

For these 87 individuals, I qualified as non-builder individuals which were never seen bringing material to or constructing the communal thatch, while they were qualified as builder when they were seen contributing to the communal thatch at least once (33.03% of individuals, hours of observation for thatch building: 20.2 ± 11.12).

Snake mobbing

I use a plastic toy snake to simulate a predation event at a focal nest chamber in order to collect mobbing rate for 117 individuals. The snake was 46cm long and Ø2cm which is similar to the size of a juvenile boomslang (*Dispholidus typus*), one of two common snake predator species encountered at this study site (the other being the Cape cobra, *Naja nivea*). The head of the snake decoy was positioned inside the tunnel leading to the focal nest chamber with the rest of its body hanging off the communal thatch. The focal nest chamber was in a reproductively active stage containing either eggs or chicks. Whether the nest chamber contained eggs or chicks does not affect mobbing behaviour (Chapter 5). The experiment was conducted over two consecutive seasons at eight colonies and was performed at two different focal nest chambers per colony. The decoy was left at the focal nest chamber for 45 min. In order to maximize the number of birds visiting the communal nest during the experiment, it was replicated the following day for each focal nest chamber (i.e. replicate 1 and replicate 2 per focal chamber). Refer to Chapter 5 for more details on the contribution to mobbing behaviour. The sum of the total number of mobbing attacks observed during the two replicates for each of the two focal nest chambers was used in my analyses (32.5% of individuals mobbed; mean number of attacks per chamber 1.30, range = 0-6).

6.3.5. Genetic analyses to establish the kinship network

Blood samples taken at capture were preserved in 1mL of absolute ethanol. Genomic DNA was extracted using a precipitation of ammoniate acetate (Richardson et al. 2001) in preparation for polymerase chain reaction amplification. The sex of all individuals was molecularly determined by using *P2–P8* sex-typing primers (Griffiths et al. 1998). Sixteen autosomal polymorphic microsatellite markers were used to genotype each individuals. Pairwise relatedness was estimated using Queller and Goodnight's genetic estimate of relatedness in ML-RELATE (Kalinowski et al. 2006), with reference to genotypes from the entire population across all colonies (*N* = 2714). For more details on genotyping procedure and analyses, see van Dijk et al. (2014). Relatedness matrices were obtained for 3 colonies in 2012-2013 and 5 colonies in 2013-2014.

6.3.6. Social network analyses

All statistical and social network analyses were performed using R (R Development Core Team 2012). Social network analyses were conducted using the suite of packages developed in *'statnet'* (Handcock et al. 2003): '*sna'*(Butts 2006), *'network'* (Butts 2008) and *'ergm'* (Hunter et al. 2008). I worked on four networks: (i) undirected and weighted for the association and kinship networks, (ii) directed and weighted for the dominance network and (iii) undirected un-weighted for the breeding group membership network. In a weighted network, the edges are associated with the frequency of associations or interactions between nodes. All networks were computed using the package '*statnet*'.

Correlations between networks

I tested whether relatedness and breeding group membership structured the associations and the agonistic interactions observed at the feeder for each of the eight colonies monitored in this study. Each colonial group included the same individuals across the different networks (i.e. kinship, membership, association and agonistic interaction networks). I ran Multiple Regression Quadratic Assignment Procedure (MRQAP) with 5000 permutations to assess correlations between the association or the dominance networks with kinship and breeding group membership networks in two ways (Dekker et al. 2007): First, I included all individuals for which behavioural data were available. Second, I tested males only, because the kin structure is stronger between males than between females within colonies while males dominate females. Consequently the correlations between kinship and association or between kinship and dominance are likely to be less pronounced when including both females and males. QAP regression is a type of Mantel test allowing the regression of a single matrix against multiple explanatory matrices. When parameterizing a continuous dependent matrix, the MRQAP regression examines and controls for all multiple predictors, so that the results can be interpreted similarly to those of standard regression procedure (Dekker et al. 2007; Mann et al. 2012). I combined probabilities from QAP analyses of eight colonies using a Fisher’s omnibus test to assess the overall significance of both predictor networks (kinship and group membership) together and their individual effects, on the association network or on the dominance network (Madden and Clutton-Brock 2009; Madden et al. 2012). When I had different directions of relationship between groups for the networks correlation, I used the procedure developed by Madden et al. (2009; 2012) to assess the mean correlation coefficient and the overall p-values.

Centrality, phenotypic attributes and cooperative contribution

I obtained centrality metrics for 134 individuals (52 females, 76 males and 6 individuals of unknown sex). Based on the undirected, weighted association networks, I calculated the following centrality metrics for each individual within their colony: *degree*, *betweenness* and *closeness*. Based on the directed, weighted networks of dominance, I calculated an individual's *indegree* within its colony. Centrality metrics were normalized to allow comparison between colonies (Croft et al. 2006).

I used a Bayesian mixed model approach (package '*MCMCglmm*'; Hadfield 2010) to evaluate inter-individual variation in centrality metrics in all the models because network data are intrinsically not independent so that classic least squares regression procedure cannot be performed. Parameter estimates, 95% confidence intervals and p-values were estimated using Markov-Chain-Monte-Carlo randomization method as follows: 100000 iterations, a thinning of 100 and a burn-in of 1000 to ensure convergence. The minimal models were obtained by removing non-significant predictors according to a stepwise downward model selection procedure. In all models, colony identity nested in the year of observation was included as the random factor.

For 87 breeders and helpers, I first tested whether dominance, the average relatedness to the colony, sex, breeding status (i.e. breeder or helper) and minimum age predicted central positions (*betweenness*, *degree* and *closeness*) within the association network while controlling for body size (tarsus length) and body mass (i.e. body condition). I also included the interactions between dominance and breeding status, dominance and sex, and between breeding status and sex as well as the interactions between the average degree of relatedness and dominance, sex or breeding status.

I then focus on helpers only to assess whether centrality in the network is predicted by cooperative contributions as contributions in mobbing, nestling provisioning and communal thatch building are all true cooperative acts for helpers but may not be for breeders (i.e. nestling provisioning is an act of parental care for breeders). I did not include relatedness in this analysis for two reasons. First, I had helpers not genotyped yet so the inclusion of relatedness would decrease drastically a sample size already limited (exclusion of 8 helpers). Furthermore, as seen in Chapter 5, cooperative contributions may depend on different levels of relatedness depending on the task considered (e.g. both high level of relatedness to the father and low level to the mother predict high provisioning). For instance, thatch building is not influenced by average relatedness to the colony (Chapter 5) but by local relatedness to the members occupying the nest chambers embedded in the preferred area of building (van Dijk et al. 2014). Therefore, I focused here on whether dominance, sex, minimum age and contributions in mobbing, feeding and communal thatch building predicted helpers' network centrality (N = 27). As males are dominant over females, I also included the interaction between sex and dominance. I controlled for body size and body mass and included colony identity as a random factor.

In order to test whether helpers that contributed less to cooperative tasks suffered from higher level of aggressions, I examined whether an helper's *indegree* (based on the dominance network, N = 27) was predicted by its cooperative contributions (i.e. mobbing, nestling provisioning and communal thatch building) while controlling for dominance, sex, minimum age and body size and the interactions between dominance and the cooperative contribution for each task and the interaction between dominance and sex. The average relatedness to the colony was not included for the same reasons mentioned above.

6.4 Results

6.4.1. Correlation between networks

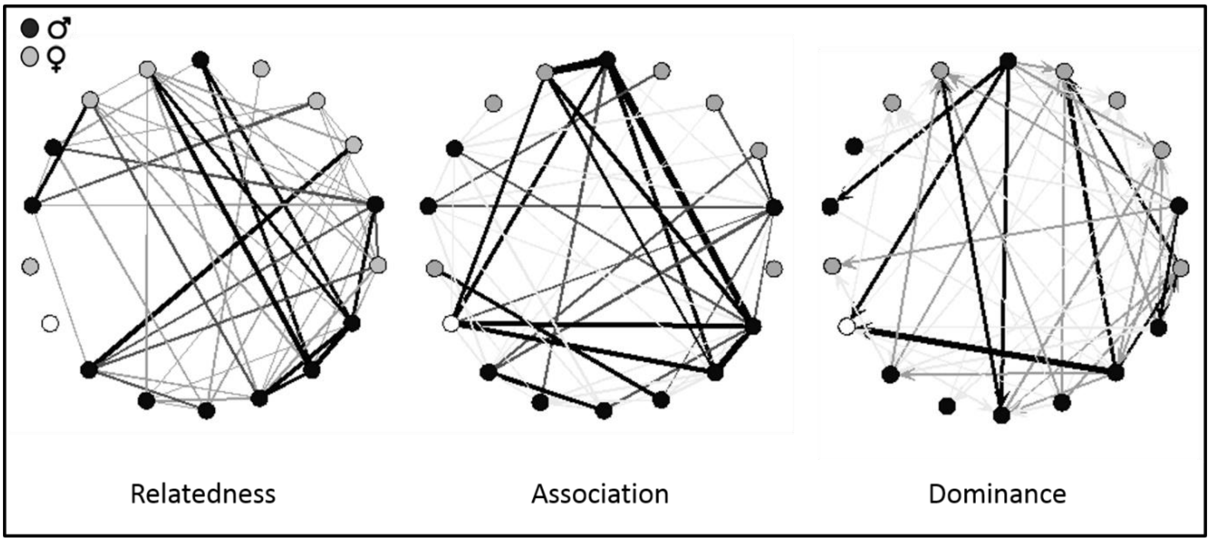

Figure 6.1 Examples of kinship, association and dominance networks of a colony based on 18 individuals. The nodes represent individuals, females in grey, males in black and an individual with unknown sex in blank. The width of the edges represents the strength of the relationships between the nodes. For visual enhancement, networks have been filtered so that edges between individuals that associated or interacted agonistically less than twice have not been displayed. In order to facilitate networks comparison of similarities and differences, the colour of edges varies according to the strength of the relationship with lighter colours for weaker relationships and darker for stronger relationships

Association network

I found that the both kinship and breeding group membership networks structured the network of associations observed at the feeder so that related individuals (coefficient: 1.972, $\chi^2 = 49.86$, *overall P* < 0.001; Table 6.2; Fig. 6.1) and members of a group (coefficient: 0.685, $\chi^2 = 158.3$, *overall P* < 0.001; Table 6.2) associated significantly more with each other than with the rest of the colony at the feeder. The overall effect of kinship (Table 6.2) and breeding group membership (Table 6.2) on the association patterns observed at the feeder was even stronger when the networks included males only.

Dominance network

The overall effect of both kinship and breeding group membership in predicting the dominance network observed at the feeder across the eight colonies was not significant ($R^2 = -0.011$, $\chi^2 = 14.11$, *overall P* = 0.591; Table 6.2; Fig 6.1). However, the effect of breeding group membership alone significantly contributed to explain the structure of the dominance networks of males and females, where the effect was negative (coefficient – 0.771, χ^2 = 31.81, *overall P* = 0.011; Table 6.2), while kinship was not significant. When networks were based on males only, the overall effect of both kinship and breeding group membership in structuring the dominance network was also non-significant (R^2 = -0.074, χ^2 = 23.51, *overall P* = 0.101; Table 6.2, Fig. 6.1), while the effect of group membership was only marginal (P > 0.063). However, kinship negatively predicted the occurrence of dominance interactions between males (coefficient: -1.438, χ^2 = 27.34, *overall P* = 0.037; Table 2).

Table 6.2 Summary statistics of MRQAP analyses to estimate the correlations between the association or dominance networks with the kinship and membership networks. MRQAPs have been performed for males and females and for males only. The average estimates across the eight colonies and their associated p-value are given for each predictor and for the overall correlation coefficient (R^2). In brackets, the X^2 statistic of the Fisher's omnibus test to assess the overall p-values across the 8 colonies

		Kinship		**Co-membership**		**Correlation**	
		Estimate	*P* (*X*^{2})	Estimate	*P* (*X*)^2	R^2	*P* (*X*^{2})
ASSOCIATION	Males and Females	1.972	<0.001 (49.86)	0.685	<0.001 (58.31)	0.221	<0.001 (123.6)
	Males only	8.514	<0.001 (45.95)	0.489	<0.001 (56.58)	0.301	<0.001 (94.96)
DOMINANCE	Males and Females	-0.527	0.119 (22.80)	-0.771	0.011 (31.81)	-0.012	0.591 (14.11)
	Males only	-1.438	0.037 (27.34)	-0.191	0.063 (17.27)	-0.074	0.101 (23.51)

6.4.2. Centrality, phenotypic attributes and cooperative contribution

The centrality metrics based on the association networks ranged from 0 to 1 (0.374 ± 0.247) for the normalized weighted *degree*, from 0 to 0.714 (0.084 ± 0.127) for the normalized weighted *betweenness* and from 0 to 0.654 (0.254 ± 0.110; Fig. 6.2) for normalized weighted *closeness* showing a clear variation in the centrality metrics between individuals.

Sample with breeders and helpers

When I worked on the sample containing breeders and helpers, *degree* and *closeness* centrality metrics were significantly predicted by individual dominance and breeding status

(Table 3). Dominance positively predicted the *degree* (MCMC estimate: 0.244 ± 0.212, *N* = 87, *P* = 0.034; Table 6.3) and the *closeness* (MCMC estimate: 0.066 ± 0.034, *N* = 87, *P* < 0.001; Table 6.3) of individuals (but not the *betweenness*, *P* = 0.384). In addition, the average degree of relatedness influenced marginally the degree of an individual when in interaction with its breeding status so that helpers more related to the colony had higher degree, i.e. more social partners and stronger relations with these social partners than helpers less related to the colony and breeders (MCMC estimate: 1.571 ± 0.186, *N* = 87, *P* =0.051; Table 6.3). The sex of an individual predicted marginally the variation in degree centrality so that males tended to have higher *degrees* than females (MCMC estimate: 0.126 ± 0.129, *N* = 87, *P* = 0.071; Table 6.3). Last, breeding status but not relatedness influenced *closeness* so that helpers had higher *closeness* (MCMC estimate: 0.027 ± 0.0235, *N* = 87, *P* = 0.016; Table 6.3; Fig. 6.2) than breeders. Variation in *betweenness* centrality between breeders and helpers was not predicted by any explanatory terms include in the model (all *P* > 0. 345).

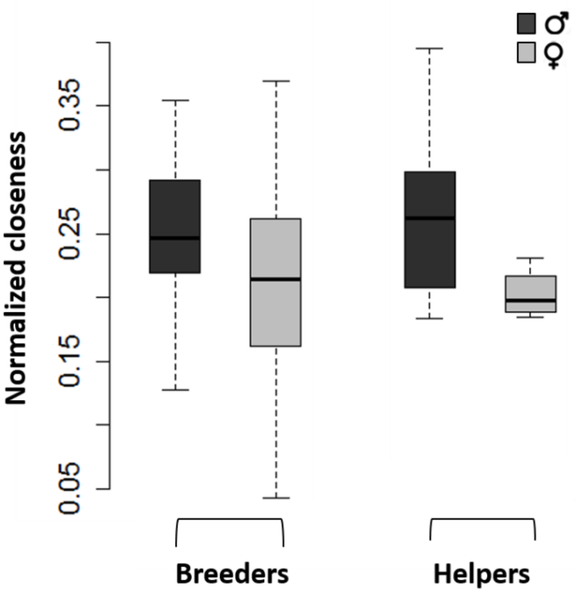

Figure 6.2 Distribution of *closeness* centrality according to an individual breeding status and sex. Female breeders tend to have lower *closeness* than other individuals, yet, as seen graphically, there is an important variation in *closeness* within sex and breeding status

Minimum age, body condition and the interactions between dominance, sex and breeding status did not account for differences in centrality metrics when both breeders and helpers were included in the analyses (all $P > 0.172$).

Sample with helpers only

When focusing on helpers only, dominance positively predicted an individual's *degree* (MCMC estimate: 0.433 ± 0.344, $N = 27$, $P = 0.016$; Table 6.3; Fig. 6.3) but not variation in *betweenness* and *closeness* (Table 3).

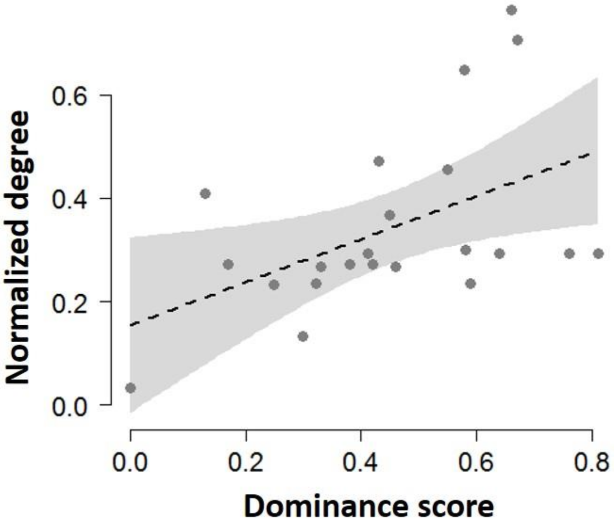

Figure 6.3: More dominant helpers interact with more social partners as they exhibit higher *degree*. The dash line represents model estimates of the effect of an helper's dominance score on *degree* centrality while controlling for other significant predictors in the models. The grey shade indicates 95% confidence interval

Cooperative contributions, in mobbing and nestling provisioning, further predicted a central position: individuals that feed more tended to have highest values of *betweenness* (MCMC estimate: 0.577 ± 0.664, $N = 27$, $P = 0.070$; Table 6.3) and had higher values of *closeness* (MCMC estimate: 0.072 ± 0.038, $N = 27$, $P < 0.001$; Table 3). *Closeness* was further positively predicted by the number of attacks to the snake given by an individual (MCMC estimate: 0.009 ± 0.008, $N = 27$, $P < 0.0485$; Table 6.3), although the effect was minimal. By contrast, contribution to the communal thatch building was not related to any of the three centrality variables (all $P > 0.119$). Sex, minimum age, body condition and the interaction between sex and dominance did not account for variation in any centrality metrics (All $P > 0.119$).

Variation in a helper's *indegree* was negatively predicted by its dominance status, helper's contribution in the communal thatch building and helper's minimum age so that less dominant (MCMC estimate: -0.399 ± 0.295, $N = 27$, $P = 0.024$; Table 6.3), and helpers that were not contributing to the communal thatch building (MCMC estimate: -0.152 ± 0.112, $N = 27$, $P = 0.018$; Table 6.3; Fig. 6.4) received more agonistic interactions from more members of their colony. Furthermore a helper's *indegree* was positively but marginally affected by its age: older helpers tended to receive more aggression (MCMC estimate: 0.030 ± 0.032, $N = 27$, $P = 0.062$; Table 6.3). Sex, body condition and the interaction between sex and dominance did not account for variation in any centrality metrics (All $P > 0.160$).

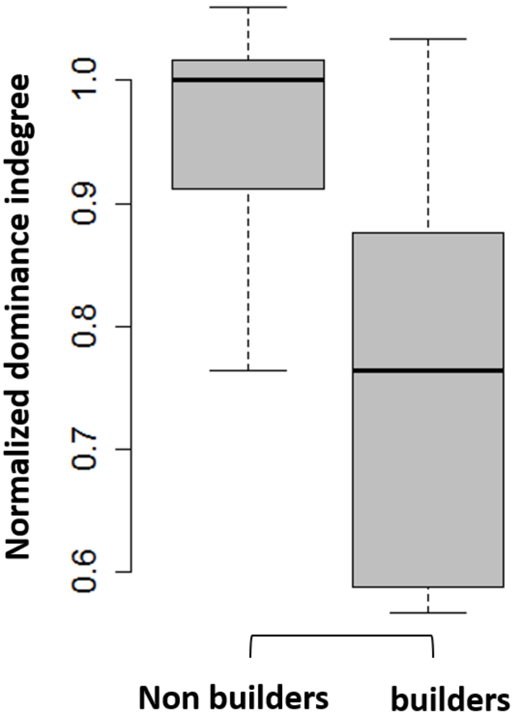

Figure 6.4 Differences in dominance *indegree* according to whether a helper contributed or not to build the communal thatch. Non-builders have higher dominance *indegree* so that they received more aggressions from more conspecifics than builders

Table 6.3 Summary statistics of the best fit models that predict individual variation in four network centrality metrics (i.e. *degree*, *betweenness*, *closeness*, dominance *indegree*) between breeders and helpers (B&H; *N* = 87) and among helpers only (H; *N* = 27) in relation of dominance (DS), breeding status (BS), sex, average degree of relatedness to the colony (Kin), minimum age and body condition. The separated analyses for helpers included cooperative contributions in snake mobbing, nestling provisioning (‘Provis.’) and communal thatch building. Estimates (Est.), their standard error (SE) and their associated P-value (P) of significant or marginal effects from the minimal models are reported in the table (with an exception for single effects that are significant or marginal when in interaction) so that non-significance is further indicated by shaded cells. Body size and body mass are not displayed as the remained non-significant in all our analyses

		Degree		**Betweenness**		**Closeness**		**Indegree**	
		Est.±SD	**P**	**Est.±SE**	**P**	**Est.±SE**	**P**	**Est.±SE**	
B&H	Intercept	0.227±0.150	0.008			0.204±0.006	0.006	Non available	
	DS	0.244±0.212	0.034			0.066±0.033	<0.001		
	BS	-0.079±0.138	0.240			0.027±0.022	0.016		
	Sex	0.126±0.067	0.071			.			
	Kin	-0.083±0.622	0.845			.			
	Kin:BS	1.571±1.385	0.051						
H	Intercept	0.321±0.246	0.026	0.067±0.025	<0.001	0.283±0.270	0.0121	1.054±0.140	<0.001
	DS	0.434±0.344	0.016					-0.399±0.295	0.024
	Mobbing					0.009±0.008	0.046		
	Provis.			0.577±0.664	0.071	0.072±0.038	<0.001		
	Building							-0.152±0.112	0.018
	Age							0.030±.032	0.06

6.5 Discussion

I used social network analyses to determine whether and how kin selection, kin competition or other non-kin-based mechanisms shape the social organisation of cooperative groups. First, I analysed whether kinship and group membership structure the associations and dominance interactions observed at a feeder. I expected a positive effect of kinship on associations and a negative effect of kinship on dominance interactions if kin-selection influences the evolution of sociable weavers’ cooperative societies. I obtained support for these predictions. I found that the associations observed at the feeder were positively linked with both kinship and breeding group membership. Furthermore, the distribution of dominance interactions between males and females were pacified when individuals belonged to the same breeding group while kinship pacified such interactions between males only. Second, I explored whether dominance and kinship influence the position of individuals in the social network. For both breeders and helpers, dominance positively predicted central positions (i.e. *degree* and *closeness* centrality) in the association network. Being closely related to the other colony members favoured high number of social partners, but for helpers this was only to the extent that kinship appears to predict central position mainly within this category. Also helpers were closer to their most distant social partners (i.e. high *closeness*) than breeders suggesting they are more integrated in their network than male and female breeders. Contributions to nestling provisioning, thatch building and mobbing were positively associated with central positions in helpers. Finally, examining the relationship between a helper's dominance *indegree* and its contribution to cooperation revealed that helpers who did not contribute to build the communal thatch received more aggression and from more individuals as opposed to helpers who participated in this cooperative task. Such relationship was not observed for nestling provisioning and snake mobbing. Together these results suggest that kinship and dominance play a crucial role in the social organisation of this social passerine, predicting central social network position and being linked to cooperative behaviour.

More related weavers appear to forage more often together as opposed to distantly related individuals. Furthermore, males were less aggressive when foraging with male kin suggesting that kinship reduces competition and conflicts, particularly among males as it has been found in other species (Belisle and Chapais 2001; Chiarati et al. 2011). Thus, kin affiliation as opposed to kin competition seems to predict the access to resources in sociable weavers. Additionally, helpers more related to the other members of the colony had more and stronger relationships with their social partners (i.e. higher *degree*) as opposed to breeders for which the degree of relatedness to the colony did not improve their social network centrality. These results suggest that nepotism occurs in this species. Nepotism might thus play an important role in the cooperative lives of sociable weavers, with individuals benefiting from the protection of, or the tolerance from their relatives at the feeder and more generally, at colony (van Dijk et al. 2014; Rat et al. 2015). Nepotism can drastically reduce the cost of living in groups (Wolf and Trillmich 2008) and can explain why offspring delay or avoid dispersal leading to the formation of family groups (Griesser 2003; Dickinson and Hatchwell 2004; Griesser and Ekman 2004; Griesser and Ekman 2005; Hatchwell 2009). It is often considered as a first step toward cooperating breeding (Ekman et al. 2001; Covas and Griesser 2007). These results strongly suggest that the social organisation of this colonial passerine is largely influenced by kinship which may help to promote kin-selected cooperation.

Other mechanisms than kinship, such as friendship or group membership, may further influence individual decision to bond with conspecifics (Belisle and Chapais 2001; Silk et al. 2006; Braun and Bugnyar 2012). Group membership positively predicted associations within and between sexes at the feeder: members of a breeding group were more frequently observed feeding together than members of mixed breeding groups. Furthermore, it also predicted a reduction of aggressive interactions between males and females but not among males. Thus, membership seems to favour the presence of male and female group members at feeders which may be particularly relevant for females in this species as they are dominated by males (Rat et al. 2015). Indeed, such bonds between males and females may enhance females access to the feeder as the presence of their breeding group members may improve their protection (e.g. coalition effects ; Perry 1997; Sterck et al. 1997; van Schaik et al. 2004) or their tolerance from dominant members of other breeding groups (Sterck et al. 1997; Silk et al. 2003; Silk et al. 2006). Taken together, these results suggest that foraging activity is strongly articulated by family bonding to limit conflicts over food between males and/or by breeding group membership as it may enhance group member protection and may promote the integration of subordinate females. Thereby, both kinship and breeding group membership appear to structure the social organisation of sociable weavers.

In group-living species, associations and conflicts between individuals are often further articulated by dominance relationships, a central mechanism to the study of social organisation as it often helps to maintain a communal lifestyle (Cant 2000; Cant 2011). Indeed, once established, dominance hierarchies prevent individuals to engage into constant costly conflicts over resources, sparing them energy expenditure or risk of injuries (Senar 1999; Maynard-Smith and Harper 2003). In many cooperative species, dominant individuals occupy key position within their social network which may be beneficial (Modlmeier et al. 2014). For instance, as suggested above, dominants may structure the access to resources by favouring access to their kin as a result of nepotism (Chiarati et al. 2010; Chiarati et al. 2011) or by limiting access to less related subordinates (Cant 2000). Additionally, decisions made by dominant individuals often influence the group behaviour for coordinated activities such as collective movements (e.g. foraging activities, migration) because dominants are often associated with leadership position (Addison and Simmel 1980; Peterson et al. 2002; Krueger et al. 2014). I found that dominance positively predicted central positions within a network of sociable weavers for both breeders and helpers. Individuals associating more, i.e. associating with more individuals (high weighted *degree*) and associating more closely to other members of their colony (high weighted *closeness*), were more dominant. Sex only marginally predicted higher *degree* for males in contrast to females, despite of a consistent tendency that persisted for *closeness* and *betweenness* centrality. Males were predicted to have higher centrality values because they exhibit a stronger kin-structure at the level of the colony, of social groups within colony (Covas et al. 2006; van Dijk et al. 2014), are more dominant (Rat et al. 2015) and contribute more to cooperative behaviours than females (Doutrelant et al. 2011; van Dijk et al.

2014). The minimal effect of sex in predicting central position may be due to a great male variability in these metrics (Fig. 6.2). A lack of effect was also observed for age (in agreement with the results found by van Dijk et al. 2014) and for body condition, independently of the breeding status considered (i.e. breeders and/or helpers). Consequently, dominant individuals, independently of their sex, age or body condition, are therefore likely to play a central role in the social organisation of sociable weavers. Furthermore, in cooperative societies, sociality has been shown to enhance fitness (Silk et al. 2003) so that more socially integrated individuals with high centrality metrics often benefit from better survival or enhanced reproduction (Stanton and Mann 2012). In sociable weavers, more dominant males have multiple benefits such as privileged access to resources in terms of food, nest chambers or the number of helpers-at-the-nest (Chapter 4), and as shown here, these males are more central. Centrality could be involved in how these benefits are obtained (Modlmeier et al. 2014) as both dominance and strong social bonds may enhance fitness (Silk et al. 2010).

Additionally, helpers had higher values of centrality for the *closeness* metric suggesting that they are more closely integrated in the social network of associations than breeders (mainly females, but also maybe males). By contrast to breeders, helpers may allocate more time to actively maximise their interactions with other members of the colony seeking protection and other nepotistic advantages but also to shape and to assess the quality of their social environment. Indeed, the social environment of a helper can have crucial impacts on major lifetime decisions such as whether to stay or to disperse and whether to breed or to help (Taborsky et al. 2012).

Individuals may have different important social roles or social tactics according to both their dominance and breeding status. This difference in social roles and tactics may be reflected in an individual’s contribution to different communal tasks. For instance, an individual may contribute more to communal tasks in order to improve its social image (i.e. social prestige hypothesis) and to enhance chances of future reproduction or reciprocation (Milinski 1987; Zahavi 1995; Wedekind and Milinski 2000). Under this hypothesis, cooperation is expected to increase the number of social or sexual partners which is expected to be reflected in the social network by a more central position. Here, I found that helpers that contributed more to predator mobbing and to feed the nestling were more closely associated to their network than individuals who fed less and mobbed less. Such pattern is expected when provisioning generates direct social benefits like those predicted by the social prestige hypothesis or the pay-to-stay hypothesis. Under a pay-to-stay driven cooperation, subordinate helpers are expected to invest in cooperation in order to be tolerated in the colony by dominant breeders (Gaston 1978; Kokko et al. 2002). Such mechanism has the potential to drive (at least partly) cooperation in sociable weavers as helpers who are subordinated to breeders, contributed more to the communal nest building than breeders (Chapter 5). A further step in the test of a pay-to-stay driven cooperation for communal nest building is to assess whether helpers that failed to contribute to this cooperative task received more aggressions (i.e. were punished for defecting). Indeed, under a pay-to-stay cooperation, dominant breeders are predicted to punish cheaters in order to maintain honesty in the system (Bergmüller and Taborsky 2005; Bruintjes and Taborsky 2008; Thompson et al. 2014). According to this prediction, I found that helpers who contributed less to the communal thatch building were more physically aggressed and actively displaced by more individuals (i.e. higher weighted dominance *indegree*) than helpers that contributed to these tasks. Consequently, nest building behaviour which is known to be kin-directed in this species (van Dijk et al. 2014) may be further driven, at least for helpers, by a pay-to-stay mechanism. However this result would need to be confirmed by a larger sample size and integrating relatedness in the analyses. Also, whether a helper contributed to build the communal thatch or not was independent of centrality metrics despite that both a kin-selection (van Dijk et al. 2014) and a pay-to-stay mechanisms (Chapter 5). would predict thatch builders to be more central, (kin selection because more related helpers are more central van Dijk et al 2014 and pay-to-stay if individuals construct to be accepted in the colony). The lack of relationships between centrality and building behaviour may be affected by the limited sample size.

In conclusion, I found that kinship and breeding group membership structured associations between males and dominance interactions observed at a feeder reducing competition over food. Also I found that dominance was strongly associated with central network position for both breeders and helpers suggesting that dominant individuals occupy crucial social positions within their social network. Kinship however, appears to explain network centrality primarily for helpers and should be controlled for in future, detailed analyses about network properties and cooperation. In addition, helpers that contributed more to nestling provisioning and predator mobbing were more socially integrated within their network. This result invites to determine whether it is helpers' cooperation that brings this centrality and thus whether they may get direct social benefits by cooperating (i.e. pay to stay, social prestige). Also helpers who failed to build the communal thatch were more aggressed and displaced than helpers who built suggesting that helpers may contribute to communal nest building in order to be tolerated in the colony as expected under a pay-to-stay hypothesis. Taken together, these results indicate that kin-selection and dominance shape the social structure of a cooperatively breeding passerine where social positions are linked with contribution to communal tasks.

Chapter 7

General discussion

'Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning'

Albert Einstein

7.1 Overview

Conflicts-of-interest, where individuals act selfishly to increase their own benefits at the costs of others, are frequent in cooperative groups and may lead to the collapse of such cooperative societies, a phenomenon known as the tragedy of common. Yet, cooperation among individuals can be observed across the tree of life. How do individuals mediate conflicts and maintain successful cooperative groups? Dominance may play a major role in mediating conflicts as it regulates access to resources and often predicts individual investment in cooperative tasks. In my thesis, I investigated whether and how dominance shapes the social organisation of sociable weavers. I aimed to test whether dominance may be at work to mediate conflicts (Chapters 2&3 and Chapter 6) and promote cooperation over three tasks (nestling provisioning, communal nest building and snake mobbing) in societies of sociable weavers (Chapters 4&5 and Chapter 6). I found the following main results:

- Colonies are organised according to ordered hierarchies, which were stable between years (Chapter 2).
- A melanin-based bib has status-signalling function (Chapters 2&3).
- Dominants have better access to resources and facilitated access to resources to their offspring (Chapter 4).
- Dominance pacifies interactions among male relatives (Chapters 2&6).
- Affiliations are more pronounced among kin and members of the same breeding group (Chapters 6)
- Helpers contributed more to nestling provisioning when related to male breeders but the opposite result was found in regard to the degree of relatedness to the female (Chapter 5).
- Helpers contributed more to snake mobbing when related to the female breeders (Chapter 5) but the relatedness to the male breeders did not impact mobbing behaviour.

  - Subordinate males/helpers contributed more than dominant males/breeders in snake mobbing and thatch building (Chapter 5).
  - Helpers who did not contribute to thatch building also received more aggressions (Chapter 6).
- More related, dominant individuals are more central in their social network and a central position is associated with higher cooperativeness (Chapter 6).

In this final chapter, I highlight the main findings of my thesis and emphasize their significance and their limitations. I focus on how dominance may mitigate conflicts, how it interacts with kin-selection and why the links (or the lack of such links) between dominance, kinship and cooperative contribution indicate that additional routes to the evolution of cooperation are likely to be involved. I also make recommendations on future research that may help to further our understanding of the evolution of cooperative societies.

7.2 Dominance mediates the costs of living in groups

7.2.1. Evolution of hierarchies

Group-living species that have limited resources are expected to establish hierarchies in order to regulate the access to resources and prevent conflicts such as escalated fights (Wrangham 1980; Vehrencamp 1983). This prediction was met in sociable weavers. In Chapter 2, I found that individuals were not egalitarian, instead, ordered hierarchies regulated the access to the food (*orderliness* index varied from 0.61 to 1) where males dominated females. Avoidances were more frequently observed than aggressions suggesting that the establishment of hierarchies help to prevent escalated fight. Ordered hierarchies where each individual is ranked consistently limit conflicts (Poisbleau et al. 2005) as they typically imply that no or little reversals in dominance relationships occur between individuals (Chase 1982; Appleby 1983; Shizuka and McDonald 2012). This type of hierarchy is expected to be more stable than shallow ones and to enhance group stability and cohesion (Aureli and de Waal 2000). In agreement with this prediction, I find that individual ranks were stable between years indicating a certain level of hierarchy stability (Chapter 2). However, whether my results clearly suggest that the evolution of hierarchies mediate conflicts in sociable weavers, requires experimental manipulation to test for a reduction in conflicts upon the formation of a hierarchy. I suggest that a group of unfamiliar individuals should be brought together in an aviary and the agonistic interactions observed until individuals can be ranked consistently. The distribution of aggressions is expected to be frequent when birds are released in the aviary and diminishes once the hierarchy is established (Chase 1982; Herberholz et al. 2007).

7.2.2. Evolution of badge-of-status

In stable groups, individuals are familiar with each other. Individuals may not need to express signals that accurately inform about their social status in these stable groups and are instead predicted to express signals that facilitate individual recognition (Whitfield 1986; Whitfield 1987; Senar and Camerino 1998; Senar 1999; Senar 2006). Indeed, badges-of-status have been found to evolve in many avian species forming winter flocks (Rohwer 1975; Rohwer 1977; Senar et al. 1993; Nakagawa et al. 2007; Chaine et al. 2013; Laubach et al. 2013) but appear less common in cooperatively breeding species (but see Dey et al. 2014). I found that the size of the black bib has a status-signalling function in sociable weavers: it was correlated with an individual’s social status and was reflecting minor changes in social status (Chapter 2). Such changes in the size of the bib between years imply that melanin-based pigmentation may be more plastic than commonly accepted (Griffith et al. 2006), despite the strong genetic control acting upon melanin-based colouration (Ducrest et al. 2008; Roulin 2015; Roulin and Jensen 2015). It would be highly relevant to carry on investigating the link between bib size and social status in order to verify this pattern over several years with a larger sample size (this study: $N = 28$) and including environmental variations. This way, change in bib size could be related to the intensity of the competitive contexts as environmental conditions are likely to influence resource availability and thus, competition (Acker et al. 2015).

In order to disentangle the function of the size of the bib from other potential confounding factors, such as beak size or beak colouration, I experimentally enlarged and reduced the size of the bib using mounted decoys and offered to sociable weavers a choice to feed between two feeders, each assigned to a decoy with either an enlarged or a reduced bib (Chapter 3). More individuals exhibited submission toward the enlarged-bib decoy as opposed to the reduced-bib decoy. Furthermore, individuals chose first and took less time to feed from the feeder associated with the reduced-bib decoy by contrast with feeder associated to the enlarged-bib decoy (Chapter 3). This experiment could be improved by controlling for the social environment at the feeder. I have shown that the access to the feeder was regulated by one’s dominance status and by kinship (Chapters 4&6). Hence, it should be taken into consideration that the social environment may also be involved in explaining some aggregation behaviour (Fritz and Garine-Wichatitsky 1996; Durisko et al. 2014) and thus the preference for a feeder (Robert et al. 2013).

Sociable weavers can live in very large groups (Maclean 1973d) and they have been frequently seen interacting with members of other nearby colonies (M. Rat, *unpublished data*). Hence, the evolution of badge-of-status may help individuals to keep track of their conspecifics’ social status, particularly when cognitive abilities may limit individual recognition as in such large groups (Senar and Camerino 1998; Wiley 2013). Furthermore, the expression of badge-of-status may be highly relevant for the interactions that occur between colonies and when dispersing. My results add to the understanding of the evolution of a badge-of-status in a cooperatively breeding species where individuals are familiar. The evolution of such badges-of-status may help to reduce escalated fights between kin (Chapter 2&6). Such reduction of competition and conflicts among relatives is highly relevant to promote kin-selection as competition limits the extent of cooperation between individuals (West et al. 2002).

7.3 Dominance, nepotism and kin-selected cooperation

7.3.1. Dominance mitigates conflicts within groups

The establishment of ordered and stable dominance hierarchies, coupled with the evolution of badge-of-status, has the potential to mediate and to limit conflicts between group members regardless of relatedness. In addition, I found that pairs of individuals engaging in aggressive interactions were less related than pairs which did not, or engage less frequently (Chapter 2). In Chapter 6, I confirmed that kinship may further pacify relationships by examining its effect upon the whole dominance networks, as opposed to the more simplistic approach used in Chapter 2 where such relationships were examined only pairwise. This more detailed exploration revealed that the reduction of conflicts in dominance interactions was observed only among males but not between males and females (Chapter 6). Males are more aggressive by contrast with females and they establish a stronger kin structure (Covas et al. 2006; van Dijk et al. 2014) as dispersal is female-biased in this species (Doutrelant et al. 2004). Thereby, such pacification of dominance relationships is more likely and more relevant among males. My work highlights that dominance acts in concert with kinship to mitigate conflicts and competition. Thus, dominance may decrease the costs of living in groups which may facilitate the evolution and maintenance of family groups (Fig. 7.1).

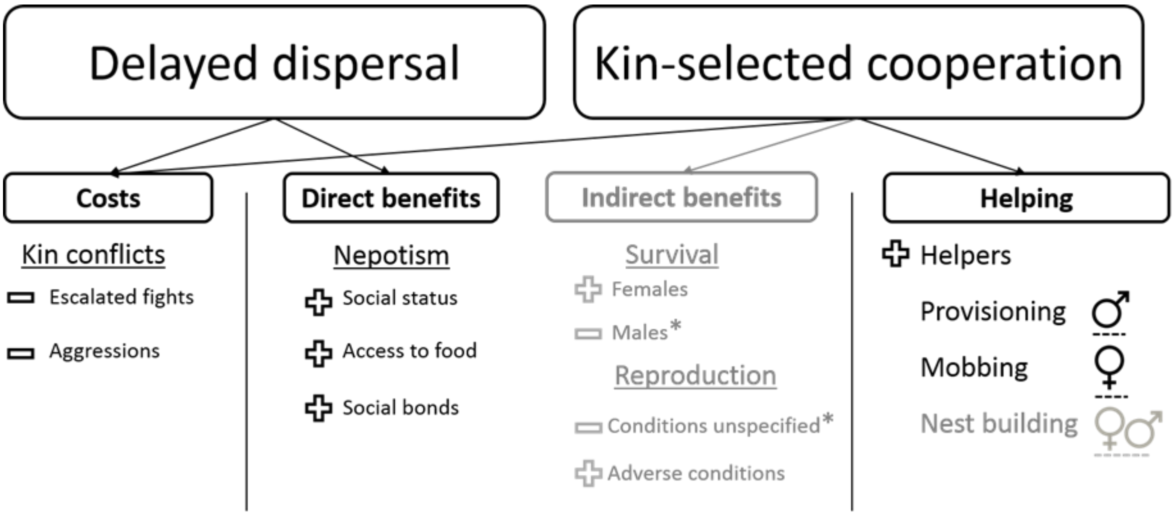

Figure 7.1 Dominance and kin selection. In black, summary of the results obtained in my thesis, which are in agreement with kin-directed cooperation in sociable weavers and the significance of dominance in promoting kin-selection. The direction of the effect of dominance is indicated by a negative or a positive sign. Kin-directed help according to the tasks and the sex of the related parents are reported. In grey, the signs indicate positive or negative effects of ehlpers according to previous findings on the same study population and cited elsewhere in this section. Asterisks indicate the effects where the potential benefits of kin-directed cooperation remain obscure.

7.3.2. Dominance enhances the benefits of nepotism

Not only dominance had a role in meditating conflicts and the costs of living with relatives, but my results suggest that it is also likely to enhance nepotism and thus the benefits of living with relatives (Fig. 7.1; Chapter 4). I found that helpers' ranks were correlated to the rank of the male breeder in their breeding group (Chapter 4). Helpers are typically philopatric offspring (93% of helpers are related to at least one parents; Covas et al. 2004). Thus, being the offspring of a dominant male may raise the offspring's social status in the hierarchy and may be an additional benefit of dominance for offspring and parents (Chapter 4). Moreover, dominant individuals enjoyed multiple benefits according to my findings. They had prolonged access to food and occupied chambers that may confer a thermoregulatory advantage (Chapter 4). Offspring from dominants ranked higher and gained enhanced access to resources, both from their own social status but also from the presence of their breeding group's male breeder at the feeder (in a feeding context; Chapter 4). Similar parental facilitation has been observed in another cooperatively breeding species establishing ordered hierarchies (Chiarati et al. 2010), the carrion crow *(Corvus corone*) where male breeders also associate preferentially with and reduce aggressions toward their offspring (Chiarati et al. 2011). Yet, nepotism also occurs in species living in family groups but are not cooperative breeders. For instance, when exposed to an artificial predator threat, Siberian jays (*Perisoreus infaustus;* which live in family groups but are not cooperative breeders) were more likely to engage in predator defense behaviour (vigilance, alarm call and mobbing) when relatives were present in the experimental area as opposed to when there were only distantly related individuals (Griesser 2003; Griesser and Ekman 2004; Griesser and Ekman 2005). Hence, being the offspring of a dominant clearly offers advantages in terms of direct benefits (Fig. 7.1) and may contribute to explain why offspring remain in their territory instead of dispersing (Griesser 2003), a first step toward kin-selected cooperation (Ekman et al. 2001). However nepotism and delayed dispersal do not automatically lead to the evolution of cooperative breeding. Why do some species exhibit alloparental care in addition then?

7.3.3. Cooperation is kin-directed

I have shown that dominance improves nepotism efficiency so that it may be particularly relevant for the offspring of a dominant to stay at home (Emlen 1994). Should these offspring help their parents raise subsequent broods? According to Hamilton's rule (1964) helping evolves if the benefits gained by helping a relative outweigh the costs. The helper is expected to be related to the recipient and the help beneficial to the recipient in order to increase indirect benefits of fitness. I found support for the first part of this statement so that individuals that were more related to their father fed chicks more often and those more related to the breeding female mobbed an experimental predator more (Fig. 7.1; Chapter 5). This is in agreement with a previous study on the same population where helpers were found to preferentially provision related over unrelated nestlings (Covas et al. 2006). Furthermore, I did not find support for the average relatedness to the colony predicting contribution to the communal thatch (Chapter 5). This results is also consistent with an earlier study which revealed that thatch-building behaviour is predicted by the local relatedness of individuals occupying the nest chambers near where the thatch is constructed rather than the average relatedness to the colony (van Dijk et al. 2014). Thus, kin selection seems also a major selective pressure to explain thatch-building behaviour. Taken together these results coupled with the work of collaborators suggest that cooperation is kin-directed and thereby likely to be kin-selected in sociable weavers (Fig. 7.1). However, precise quantifications of the indirect benefits gained by helping a kin remains necessary in order to fulfil the predictions of Hamilton's rule.

7.3.4. Perspectives on kin-selected cooperation

In this thesis, I did not aim to quantify the indirect benefits of helping in order to explain the evolution of kin-selected cooperation. Previous studies have documented indirect benefits of helping and it is relevant to report and confront them with my findings in order to improve our understandings of cooperation in this system.

The presence of helpers in sociable weavers has been reported to be beneficial to females, as it was found that the presence of helpers enable mothers to reduce their work load, investment in eggs (Paquet et al. 2013) and increase their survival (Fig. 7.1; Paquet et al. 2015). However, the presence of helpers has been found to either have no effect on fledgling condition (Paquet et al. 2013) or to enhance condition only when environmental conditions are unfavourable (Covas and du Plessis 2005; Covas et al. 2008). Furthermore helpers have been reported to have also a negative impact on yearling survival (Covas et al. 2011) and survival of males (Paquet et al. 2015). Such negative effects raise further evolutionary puzzles when confronted with some of the results I obtained in my thesis. Indeed, I showed that dominant male breeders were more likely to be assisted by helpers, but why tolerating helpers if it decreases their survival? Particularly when dominants should be able to evict other members of their group as a result of their higher competitive abilities? Furthermore, helpers fed nestlings more often when they were highly related to the father (Chapter 5) underlining the puzzle that represents the negative effect of helper presence on the breeding male survival, i.e. why helping male relatives if this does not translate in gaining indirect benefits for the helpers? Hence, here again further studies focusing on the potential costs and benefits of helping behaviour in sociable weavers are needed to understand the ramifications of why helping and why tolerating helpers.

7.4 Alternatives to kin-selected cooperation

Throughout the thesis, I found indication that additional routes to kin-selection cannot be neglected in the evolution of cooperation (Chapters 5&6). My work tested two hypotheses and found correlative indications of both a pay-to-stay (Gaston 1978; Kokko et al. 2002) and social prestige (sensu largo –i.e. enhanced future chance of reproduction or reciprocity; Zahavi 1995) mechanisms. Yet, based on my findings, it was not possible to firmly disentangle between these two hypotheses. They may be non-mutually exclusive and some of their predictions are similar. Both hypotheses predict that (i) dominant breeders are unlikely to invest as much in cooperation as helpers. (ii) Dominant or unrelated helpers are predicted to work harder than subordinates or related helpers, yet for different reasons – i.e. to be tolerated by breeders and remain in the group (pay-to-stay; Gaston 1978) or to enhance future direct benefits (social prestige; Zahavi 1995; Wedekind and Milinski 2000). In this section I discuss the main findings supporting these hypotheses and speculate on why they are more likely to involve a pay-to-stay or a prestige mechanism.

Under a pay-to-stay mechanism, helpers are expected to work as much as breeders or more when their presence is likely to inflict a costs on the dominant breeder survival (Kokko et al. 2002). For instance, in cases where helpers are dominants (Bruintjes and Taborsky 2008) or unrelated (Stiver et al. 2005; Zöttl et al. 2013). This prediction was met for the contribution to snake mobbing where helpers from the whole colony and not only from the threatened nest chamber mobbed as much as the male breeder of the threatened nest chamber (Chapter 5).

Furthermore, the variation of mobbing effort within helpers was linked to dominance. Most subordinate male helpers attacked the snake most while it was the reverse for females (Chapter 5). Because male helpers mobbing effort was not positively linked to dominance, mobbing in order to increase prestige is unlikely. Yet such pattern also contradicts the expectations of a pay-to-stay hypothesis as reported above where subordinate males where expected to attack the snake more. However, most dominant helpers are also more likely to access a breeding position earlier than less dominant helpers as dominance is positively linked with breeding probability for males (Chapter 4), which may explain why, in sociable weavers, subordinates male contributed more to mobbing (Cant and Field 2001).

The fact that on the contrary, more dominant females attacked the snake more than subordinate females is puzzling and doubtfully supports to pay-to-stay and prestige hypotheses. No link between female dominance and access to breeding position is known. In addition the costs imposed on the male breeder is unlikely to increase when female helper are more dominant because they are highly subordinate to males (Chapter 2). On the other hand, their presence could increase the costs on the female breeder. Although, previous study have shown that the presence of helpers is beneficial to the female so this hypothesis is also unlikely (Paquet et al. 2013; Paquet et al. 2015). Female helpers are rarer than male helpers (14 out of 59 helpers in the sample size used to examine helpers contributions to snake mobbing; see also Doutrelant et al. 2011), so that this result could also be an artefact of the small sample size and I stress that further data are required before concluding on whether dominant female helpers that attack the snake more may signal their prestige.

I also found that helpers contributed more to build the thatch than breeders a behaviour that is better explain under the pay-to-stay than a signalled cooperation, particularly because there was not link between dominance status and contribution to thatch building among helpers (Chapter 5). Furthermore, social network analyses revealed that non-builder helpers had a higher dominance *indegree* indicating that these helpers were more frequently aggressed and by more individuals (Chapter 6). This result supports further a pay-to-stay mechanism as defectors are predicted to be punished (Mulder and Langmore 1993; Raihani et al. 2012; Roberts 2013; Fischer et al. 2014). Yet, this result is correlative and the fact that not contributing to build the thatch caused an increased in aggression remains to be demonstrated experimentally and to be controlled for relatedness.

Unrelated helpers to the female breeder provisioned more the chicks than more related helper, as expected under a pay-to-stay mechanism (Chapter 5). Yet, females are dominated by males and the presence of helpers is most detrimental for males (Paquet et al. 2015) while beneficial for females (Paquet et al. 2013; Paquet et al. 2015) so compensatory effects are expected to be targeted to males and not to females as found here. These results thus contradict the expectation of a pay-to-stay for nestling provisioning (Kokko et al. 2002). Contribution to nestling provisioning by helpers that are distant relatives or unrelated to the female breeder may instead serves as a signal. However, the sample size of helpers unrelated to the mother was small (only 9 helpers totally unrelated; Chapter 5). Nonetheless, a previous study conducted on the same population by Doutrelant and collaborators (Doutrelant et al. (2011) also found that older helpers unrelated to the breeding females fed most, providing additional confidence to the pattern observed here. Furthermore, I also found that dominant individuals fed more. Finally, signalling through provisioning appears to be important in sociable weavers as helpers hold their prey for longer than parents before delivering them to the chicks and fed more when in the presence of a wider audience (Doutrelant and Covas 2007). Hence cooperation for nestling provisioning may be signalled so that cooperation may be socially selected or sexually selected. With a larger sample size, it would be important to incorporate the helper's sex in the analyses and to investigate whether unrelated males to the female breeder contribute the most to provision the nestling as opposed to unrelated females as expected if cooperation is advertised to enhance future chance of reproduction.

Under both pay-to-stay and prestige hypotheses, helping should be translated in a better social integration (respectively due to acceptation in the group and higher prestige), thereby, I predicted helpers working hard to be more connected within their social network, a pattern that should be reflected in their network centrality metrics (Chapter 6). In support, I found that (i) helpers had higher *closeness* metric than breeders, (ii) helpers with higher provisioning rate had higher *betweenness* and *closeness* metrics and (iii) helpers with high *betweenness* also attacked the experimental predator more. However, relatedness remained to be controlled for in my analyses before firmly drawing conclusion on the links between cooperativeness and social centrality in sociable weavers. Furthermore, I predicted that both 'prestige' or 'pay-to-stay' cooperators should be more integrated, an effect which should be reflected by higher centrality metrics, yet to date (and to my knowledge) no theoretical nor empirical supports exist to validate this prediction as the study of social network is a young paradigm in animal behaviour. I stress that future research should aim to fill this gap.

In synthesis, when examining the relationship between social status, breeding status, sex and cooperative contributions, may findings suggest that additionally to the degree of relatedness, variation in helping effort over multiple tasks are best explained by both the pay-to-stay and the social prestige mechanisms. Hence, in addition to the indirect benefits of kin-selection, sociable weavers may also gain direct benefits via pay-to-stay (both defending and thatch building) or social prestige (nestling provisioning). Both indirect and direct benefits appear important in the evolution of their complex cooperative societies.

7.4.1. Proposition of an experimental design

Experimentally simulating defection in helping behaviour may help to shed light on whether cooperation may be signalled (i.e. social prestige), used as currency (pay-to-stay), or both. Such manipulation would also add to our understanding of how honesty may be maintained in a pay-to-stay and signalled cooperation, a persistent conundrum (Hauert et al. 2007; Raihani et al. 2012) as it questioned how individuals keep track of cooperative contributions (i.e. limited by cognitive abilities), who bears the costs of punishment, or which alternative to punishment may exist (e.g. pre-appeasement; Bergmüller and Taborsky 2005). I suggest to temporary remove specific individuals during the breeding season (i.e. a few hours within a day), according to their breeding status, their level of kinship and their dominance once the breeding groups are identified. Captures can be performed before dusk and be targeted to specific, single nest chambers in order to minimize stress to other individuals of the colony. Removing the male breeder may help to test for a sexually selected cooperation so that less related helpers are expected to intensify their provisioning rates under circumstances enhancing mating opportunities. Removing helpers varying in their degree of relatedness and dominance may help to test for a pay-to-stay hypotheses and get insights on which individuals bear the costs of punishment, if any (Henrich and Boyd 2001; Hauert et al. 2007). Under this hypothesis, the defecting individuals are expected to receive higher aggressions rate once released at their colony (Mulder and Langmore 1993; Balshine-Earn et al. 1998; Fischer et al. 2014). Furthermore aggression rate is expected to vary according to the degree of relatedness and the dominance status of the defector so that less related and most dominant individuals are predicted to be more aggressed (Bruintjes and Taborsky 2008). Repeating this experiment at colony of different size may further help to test for the effects of group size and of the social environment. For instance, I predict that an increase in aggressions after an experimentally induced defection is more likely to occur at smaller colonies as cognitive capacities may limit the efficiency of the pay-to-stay mechanism.

7.5 Additional future directions

7.5.1. The role of group size

In sociable weavers, colony size has a strong impact on survival (Brown et al. 2003; Spottiswoode 2009) and reproduction (Spottiswoode 2007; Covas et al. 2008; Spottiswoode 2009). Group size impacts on competition and cooperation (Kokko et al. 2001), but may also impact the efficiency of potential proximate and ultimate mechanisms that lead to the evolution and maintenance of group living. For instance, punishment is less likely to occur in large groups where cognitive abilities may limit to keep track on who contributed and how much to the public good (Raihani et al. 2012). In the cichlid *Neolamprologus pulcher*, punishment was initiated mainly when groups of individuals were experimentally small (Fischer et al. 2014). Similarly, the evolution of badges-of-status may be relevant in large groups where cognitive abilities limit individual recognition (Maynard-Smith and Harper 2003). By contrast, expression of badges of status may be less relevant in small groups where individuals are more likely to remember the social status of their conspecifics as a result of past experiences (Senar and Camerino 1998; Aquiloni et al. 2012). Hence, badges-of-status may be more closely tied to social status in large groups across different contexts and circumstances. In line with this possibility, Acker and collaborators (2015) found that within-individual variability in the size of the sociable weaver' bib was influenced by colony size so that an individual expresses a larger bib when observed at a large colony and a smaller bib when observed at a small colony. Individuals at larger colonies may therefore invest more in expressing a large bib as competition is likely to be more intense, conflicts frequent and individual recognition less likely. Furthermore, while a pay-to-stay and signal of individual recognition (as opposed to badge-of-status) may be particularly efficient at small sized colony, they may be obsolete at colonies of hundreds of sociable weavers. Future works should integrate the potential impacts of colony size in order to test for whether groups of different size may use different social strategies.

7.6 The costs of being dominant and the honesty of badge-of-status

Studies often focus on the benefits of being dominant while the costs, have been under-investigated (Ang and Manica 2010). Indeed, such costs often manifest over long term, such as an impact on survival for instance. These costs may be harder to track and to tackle than the benefits. Yet, investing the costs of dominance is of crucial importance to understand which individuals can afford to be dominants and how honesty about signalling one's social status is maintained. Honesty of badge-of-status may be maintain by the handicap principle when the status-signalling traits are condition-dependent (Zahavi 1975). However, when the status-signalling trait is apparently cheap to produce such as the melanin-based bib of sociable weavers, honesty may be maintained by social costs imposed on cheaters (Rohwer 1977; Tibbetts et al. 2011). In both type of signals, social costs may maintain honesty as individuals that express unreliable badges do not possess the competitive ability advertised by their signals (Maynard-Smith and Harper 2003; Tibbetts and Dale 2004; Thompson et al. 2014; Tibbetts 2014). In sociable weavers, individuals expressing smaller, more subordinates, and larger bib, more dominants, survive better than individuals exhibiting intermediate badges-of-status, thereby medium-ranked individuals (Acker et al. 2015). As this rank category suffers from a high aggression rates (Chapter 2), it is likely that social costs may maintain honesty about one's social status. These social costs may be linked with additional physiological costs as both aggressiveness and melanin-based colouration are known to be linked with both testosterone and corticosterone (Ducrest et al. 2008). Based on the recent works of Laubach (2013), Dey (2014) and their respective collaborators, I suggest the implementation of the following experiment to test whether social costs may be at work to maintain honesty in social status. Collecting agonistic interactions before (i.e. control) and after the manipulation (i.e. experiment) of individuals' bib size (i.e. enlargement and reduction) they experienced in their groups as well as a measure of their basal corticosterone level at the end of the experiment. If social costs maintain honesty in the system, individuals with enlarged badges are predicted to experience increased aggression rates in the experimental phase and to exhibit higher levels of stress at the end of the experiment by contrast with reduced-bib individuals.

7.7 Conclusive notes

I believe this thesis highlights the importance of dominance in the evolution and maintenance of complex cooperative societies. Dominance acts in concert with kin-selection as found across a wide panel of cooperative behaviour to mould social organisation and cooperation. However, the examination of the links between dominance and individual contribution to cooperative tasks did not allow to reject any of the three hypotheses tested to explain the evolution of cooperative behaviour (i.e. kin-selection, pay-to-stay, social prestige; Chapter 5&6). Thereby my results show that alternative routes to kin-selected cooperation cannot be excluded (i.e. social prestige or pay-to-stay). I stress that future works should experimentally manipulate individuals contribution to cooperation in order to unravel the potential roles of a signalled and/or pay-to-stay mechanisms in the evolution of cooperation.

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