



The impacts of out-group threats on within- and between-group behaviours in the cooperatively breeding white-browed sparrow-weaver

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Thesis Abstract

Groups face a variety of potential threats from out-group conspecifics. Individuals from outside the group may challenge the breeding position and success of group members and groups often defend against neighbouring or unfamiliar groups. These groups might attempt to acquire the group's resources or encroach into their territory. Together, these threats from out-group conspecifics may give rise to costs affecting group members, resulting in a greater incentive to cooperatively defend against rivals. Few studies have investigated the long-term effects of threats from out-group conspecifics on group dynamics, cooperation and spatial competition. This thesis aims to address the need to investigate, not only the long-term impacts of inter-group conflict for competition over space, but also the consequences of the breakdown in monogamy resulting from out-group breeder replacement in the cooperatively breeding white-browed sparrow weaver (*Plocepasser mahali*). Firstly, I investigated the effects of out-group breeder replacement on helper retention and reproductive success, finding that neither is markedly negatively impacted by out-group breeder replacement, even though breeder replacement was expected to destabilise cooperative groups due to reductions in relatedness. Secondly, I investigated the role of group size in between-group conflict over space and found that larger social groups dominate competition for space. To maintain a large group size relative to neighbouring groups, subordinate helpers may work to increase group size by improving the reproductive success of the dominant (known as group augmentation) in order to enjoy the benefits of living in a large group. As a result, there may be strong selection for cooperative territorial defence, especially if success in conflict relies on cohesion between group members, to overcome the threat from out-group conspecifics.

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Thesis Introduction

Cooperative breeding is a system in which individuals live in groups and provide care to young that are not their own (Hatchwell 2007; Sorato *et al.* 2012). In these systems, offspring (known as helpers) who have delayed dispersal and remained in their natal group, help their parents to raise subsequent broods, which results in the formation of nuclear families (Brown, 1987; Stacey & Koenig 1990; Hatchwell *et al.* 2002). Family formation can result from limited dispersal of individuals (Clutton-Brock 2002) due to a short supply of mates or territories (Pruett-Jones 1990; Walters *et al.* 1992) or high dispersal costs (Emlen 1982, 1997). Delayed dispersal is therefore often associated with lost reproductive opportunities, with dominant members often securing a higher share of breeding opportunities, causing a reproductive skew (Young 2009).

As offspring are expected to stay at home only if their fitness payoff by remaining in the natal group exceeds that of dispersing and seeking an independent breeding position, there must be fitness benefits to delayed dispersal (Koenig *et al.* 1992; Young 2003). By remaining in the natal group and contributing to cooperative activities, offspring may receive direct fitness benefits such as increases in survival (Kokko and Ekman 2002), chances of successful dispersal (Hannon *et al.* 1985; Ligon and Ligon 1990), mating success (Cockburn 1998; Grinnell *et al.* 1995), ability to rear offspring (Komdeur 1996), or likelihood of current or future reproduction (Dickinson and Hatchwell 2004; Chiarati *et al.* 2011). Additionally, families are comprised of close genetic relatives and individuals can thus gain indirect fitness benefits through cooperative behaviours that increase the reproductive success of relatives (Hamilton 1964; Emlen 1997).

While explanations for the evolution of group living and cooperative behaviour in unrelated individuals focus on the role of direct fitness benefits, in societies of close kin they are most likely complemented by indirect fitness effects (Griffin and West 2002). Kin selection theory predicts that cooperation is more prevalent in family groups and is highest between genetically close relatives (Hamilton 1964; Brown 1978; Emlen 1997). For example, long-tailed tits (*Aegithalos caudatus*) that are failed

breeders preferentially help at the nests of kin and improve the condition and reproductive success of the recipients they help (Russell & Hatchwell 2001). Non-breeding individuals can gain indirect fitness benefits by lightening the workload of related breeders, which may improve their survival and/or fecundity (Khan and Walters 2002; Russell *et al.* 2003), or by improving the survival and downstream fitness of offspring of a related breeder (Brown *et al.* 1982; Emlen and Wrege 1991; Clutton-Brock *et al.* 2001). In addition to indirect fitness benefits, non-breeding subordinates may gain direct fitness benefits from helping to raise offspring, such as potential survival benefits of group augmentation (Rood 1978; Woolfenden & Fitzpatrick 1984; Kingma *et al.* 2014). Individuals may stand to gain direct fitness benefits via group augmentation when their actions increase group size (e.g. by improving reproductive success of dominant breeders or engaging in antipredator vigilance to reduce losses to predation), and living in a larger group yields direct benefits, such as improved survival and/or future reproductive success (Woolfenden and Fitzpatrick 1978; Clutton-Brock *et al.* 1999; Kingma *et al.* 2014).

Recent studies have highlighted the importance of monogamy in the evolution of cooperatively breeding societies of insects, birds and mammals (Hughes *et al.* 2008; Cornwallis *et al.* 2010; Boomsama 2012; Lukas & Clutton-Brock 2012). When dominant individuals are monogamous (and diploid), relatedness between successive generations of offspring is equal to relatedness between any individual and their own young (Bourke 2014). There may be marked indirect benefits of forgoing reproduction and remaining in the group as a helper in monogamous systems. Monogamy may, however, periodically break down following replacement of one of the breeders (Emlen 1997). Such a breakdown is predicted to destabilise cooperative family groups by intensifying reproductive conflict and eroding the benefits of cooperation. However, few studies to date have investigated the consequences of the breakdown in long-term monogamy that occurs on breeder replacement for the stability and persistence of cooperative groups, despite the potential for marked impacts on helper retention and reproductive success.

To test evolutionary theories of cooperation, cooperatively breeding species have received a great deal of attention due to their conspicuous cooperative alloparental

behaviours (Emlen, 1991; Cant, 2012; Koenig & Dickinson, 2016). However, other forms of cooperation are more widespread but comparatively understudied, including the cooperative territorial defence widely observed across animal societies regardless of whether they breed cooperatively (Stacey & Koenig 1990; Taborsky 1994; Wilson & Wrangham 2003; Mosser & Packer 2009). Groups face a variety of potential threats from out-group conspecifics (Radford *et al.* 2016). Firstly, individuals from outside the group may challenge the breeding position and success of group members (Raihani *et al.* 2010; Mares *et al.* 2011; Lowney *et al.* 2017), and the presence of out-group individuals may suggest the rest of the intruding group is close by and may attack imminently (Herbinger *et al.* 2009; Radford *et al.* 2016). Secondly, groups often defend against neighbouring or unfamiliar groups who might attempt to acquire the group's resources or encroach on their territory (Radford 2003; Wilson & Wrangham 2003; Mosser & Packer 2009). Together these threats from out-group conspecifics may give rise to costs affecting all or most group members, resulting in a greater incentive to cooperatively defend against rivals (Radford *et al.* 2016). Interactions between groups may be 'neutral' which involves visual or auditory signalling to gather information about group composition and breeding opportunities (Lewis 1981; Lewis 1982b; Lazaro-Perea 2001; Golabeck *et al.* 2012) or interactions may escalate to physical fights which have the potential to result in injuries or fatalities (Boydston *et al.* 2001; Cant *et al.* 2002; Batchelor & Briffa 2011; Wrangham *et al.* 2012).

Cooperation should increase when between-group conflict occurs at a higher rate relative to within-group conflict, for both groups of relatives (West *et al.* 2002) and non-relatives (West *et al.* 2006), especially if success in conflict relies on cohesion between group members (Reeve & Hölldobler 2007; Radford 2008). A number of studies using a range of taxa have explored the immediate defensive behavioural responses elicited by rival groups, the factors determining the outcome (winning or losing) of interactions with outsiders (Wilson & Wrangham 2003; Radford & du Plessis 2004b; Mosser & Packer 2009) and the characteristics of interactions such as duration, intensity and outcome (Radford & du Plessis 2004b; Wich & Sterck 2007). Additionally, few between-group conflict studies have focused on post-conflict aggression and affiliation in the short-term (Radford 2008; Polizzi di

Sorrentino *et al.* 2012; Radford & Fawcett 2014). However, to date, no study has investigated the long-term effects of threats from out-group conspecifics on group dynamics and cooperation. This thesis aims to address the need to investigate, not only the long-term impacts of inter-group conflict for competition over space, but also the consequences of the breakdown in monogamy resulting from out-group breeder replacement.

This thesis investigates the impacts of conspecific out-group threats on within- and between-group conflict in a wild population of cooperatively breeding white-browed sparrow-weavers (*Plocepasser mahali*). All research for this thesis was conducted using a habituated population of white-browed sparrow-weavers which has been studied since 2007. The study population is comprised of 40 cooperatively breeding groups that defend small contiguous territories. The 2km² study site lies just west of the Korranaberg hills in the Kalahari desert in Tswalu Kalahari Game Reserve, Northern Cape, South Africa (27°16'S, 22°25'E). The white-browed sparrow-weaver is a sparrow-sized passerine of the family Ploceidae and is common in acacia savanna where it nests in small colonies in trees throughout the central plateau of southern Africa (Sinclair *et al.* 2011). Groups contain 2-14 individuals and comprise a dominant male and female and subordinates of both sexes. Only the dominant pair breed and helpers participate in cooperative behaviours including territorial defence, sentinelling, weaving and offspring provisioning (Collias and Collias 1978; Lewis 1982a, b; Walker *et al.* 2016). All individuals in the study population are uniquely marked using a metal ring and 3 colour rings (SAFRING license 1444) (Cram *et al.* 2015).

In this thesis, I use a long-term field study of cooperatively breeding white-browed sparrow-weaver (*Plocepasser mahali*) societies to examine the impacts of extra-group threats to within-group reproductive monogamy (Chapter 1) and territory size (Chapter 2) in a wild social vertebrate. Specifically, the aims of this thesis are to investigate: (i) the effects of breeder replacement, and the consequent breakdown of within-group reproductive monogamy, on helper retention and reproductive success, and (ii) the role of group size and relative group size in inter-group conflict over space.

Chapter 1 (pg. 13) investigates the effects of “out-group breeder replacement” (i.e. the immigration of a new breeder from outside the group) on helper retention and reproductive success. Breeder replacement is expected to destabilise cooperative groups impacting negatively on helper retention and reproductive success, therefore, I use group composition and reproduction as behavioural responses to breeder replacement.

Chapter 2 (pg. 46) investigates the effect of group size on between-group conflict over space. I utilise a within-group centering statistical approach (Van de Pol and Wright 2009) to investigate the relationship between within-group variation in group size (and relative group size) over time and within-group variation over time in a number of territorial traits including, territory size, boundary location and *per capita* territorial space.

Finally, the Thesis Discussion provides a general discussion and synthesis of the findings in this thesis.

Chapter One: Cooperative families are robust to the breakdown of monogamy: impacts of breeder replacement in a social bird

1.1. ABSTRACT

Recent studies have highlighted the importance of monogamy in the evolution of cooperatively breeding societies of insects, birds and mammals. When dominant individuals are monogamous (and diploid), relatedness between successive generations of offspring is equal to relatedness between any individual and their own young. There may be marked indirect benefits of forgoing reproduction and remaining in the group as a helper in monogamous systems. Monogamy may, however, periodically break down following replacement of one of the breeders. Such a breakdown is predicted to destabilise cooperative family groups by intensifying reproductive conflict and eroding the benefits of cooperation. This study investigates whether breeder replacement destabilises family groups by reducing the retention of helpers and reproductive success in a cooperatively breeding species, the white-browed sparrow weaver (*Plocepasser mahali*). Our findings reveal that while breeder replacement affected helper retention, the effect was not markedly negative. Female subordinates were significantly more likely to stay after male breeder replacement and there was a non-significant trend for male subordinates to be more likely to disappear after female breeder replacement. There was no difference in the probability of natal subordinate disappearance if the parent of the same-sex was replaced. Reproduction was also impacted by breeder replacement, though again, not in a markedly negative manner: while the number of eggs laid after breeder replacement was significantly lower than when no breeder replacement occurred and there was a significant increase in the probability of chicks fledging after male breeder replacement, there was no effect on when eggs were laid, the hatchability of eggs and the number of fledglings produced. Together, our findings suggest that after breeder replacement there may be increases in within-group conflict, specifically reproductive conflict. Finally, the delayed dispersal of subordinates despite breeder replacement suggests there are fitness benefits of

remaining and cooperating in the natal group that cannot be explained solely by relatedness.

1.2. INTRODUCTION

Recent studies have shown that monogamy is important in the evolution of cooperative breeding in societies of insects, birds and mammals (Hughes *et al.* 2008; Cornwallis *et al.* 2010; Boomsama 2012; Lukas & Clutton-Brock 2012). In societies in which a monogamous dominant pair continuously monopolise reproduction and their offspring delay dispersal and help to rear future generations of young (hereafter termed 'nuclear family cooperative breeders'), successive generations of offspring are equally related to each other as they would be to their own offspring (Bourke 2014). The resulting high levels of relatedness within a group are predicted to reduce reproductive competition and favour the evolution of helping behaviour (Boomsama 2012; Lukas & Clutton-Brock 2012). In some eusocial insect societies, lifetime monogamy is guaranteed because queens mate just once prior to the founding of a colony and utilise the resulting sperm to produce offspring throughout the lifespan of the colony. However, it is important to note that while monogamy and delayed dispersal does ensure high relatedness, it can also increase local competition which may cancel out selection for helping in cooperatively breeding populations (Taylor 1992; West *et al.* 2002). In cooperatively breeding vertebrates, by contrast, the continuity of monogamous reproductive pairings periodically breaks down, when one of the breeding individuals is replaced following their death, departure or displacement (Emlen 1997). Such 'breeder replacement' might therefore be predicted to destabilise nuclear family cooperative groups, by i) eroding the indirect fitness benefits of cooperation and ii) intensifying within-group conflict over resources or reproduction. Both processes could lead to the breakdown of the nuclear family by triggering the dispersal of natal subordinates and conceivably the collapse of the social group (Emlen 1997). However, few studies to date have investigated the consequences of the breakdown in long-term monogamy that occurs after breeder replacement for the stability and persistence of cooperative groups, despite the potential for marked impacts on helper retention and reproductive success. A handful of studies of cooperatively breeding birds suggest that subordinates are indeed more likely to disperse in the presence of unrelated dominants (Goldstein *et al.* 1998; Ekman and Griesser 2002; Eikenaar *et al.* 2007; Dickinson *et al.* 2009; Nelson-Flowers and Ridley 2016). While

studies of Damaraland mole-rats (*Fukomys damarensis*), an archetypal nuclear family cooperative breeder, highlight the potential for a more extreme outcome. In this species entire social groups typically disband on the death of the breeding female (Bennett and Faulkes 2000).

Breeder replacement might be predicted to increase the probability that subordinates in nuclear family cooperative breeders disperse for several reasons. First, in nuclear family cooperative breeders, breeder replacement would be expected to reduce the relatedness of subordinate group members to the next generation of offspring that they could help to rear, thereby reducing the indirect fitness benefits to be accrued from doing so (Emlen 1997). As it has been suggested that the indirect fitness benefits available from helping within the natal group may be a key factor in rendering the delayed dispersal of subordinates adaptive (Dickinson and Hatchwell 2004), reductions in the magnitude of these benefits following breeder replacement might well be expected to trigger subordinate dispersal (Emlen 1997).

Second, breeder replacement could also increase the tendency for natal offspring to disperse because the associated reduction in breeder-offspring relatedness may increase within-group conflict over resources (Cockburn 1996; Russell 2004; Eikenaar *et al.* 2007). Offspring may enjoy direct benefits of delaying dispersal if parents give their offspring preferential access to food, as shown in carrion crows (*Corvus corone corone*, Chiarati *et al.* 2011), Siberian jays (*Perisoreus infaustus*, Ekman *et al.* 1994) and western bluebirds (*Sialia mexicana*, Dickinson *et al.* 2009). Parents may also provide offspring with nepotistic assistance for future reproduction, whether via territory budding (Woolfenden and Fitzpatrick 1990) or competing for reproductive vacancies (Brown 1987). The lower relatedness of offspring to their step-parent following breeder replacement may therefore result in a decrease in the extent of nepotistic support and/or toleration that they receive from the resident breeders, potential triggering their voluntary or forced dispersal (Ekman *et al.* 1994; Ekman and Griesser 2002; Eikenaar *et al.* 2007). Consistent with this logic, Ekman and Griesser (2002) showed that Siberian jay offspring dispersed in response to the replacement of experimentally removed tolerant fathers by an unrelated male,

suggesting that parental nepotism is essential to offspring who delay dispersal; replacement males no longer provided benefits to philopatric offspring.

Third, breeder replacement could impact subordinate dispersal decisions because the associated reduction in within-group relatedness (both among intra-sexual reproductive competitors and among potential opposite-sex breeding partners) may markedly impact patterns of reproductive conflict within groups and the future reproductive prospects of resident subordinates. Replacement breeders may perceive unrelated subordinates of the same sex as competitors for mates and therefore may force them to disperse (Emlen 1991; Goldstein *et al.* 1998). Acorn woodpecker (*Melanerpes formicivorus*) offspring often left the natal territory or were evicted following reproductive competition between the replacement breeder and the remaining offspring (Hannon *et al.* 1985). Replacement of a parent may also create reproductive opportunities for resident subordinates by affording them access to unrelated mates. In nuclear family cooperative breeders, subordinate group members frequently lack access to unrelated breeding partners within their groups (Young 2009). As many such species show strong inbreeding avoidance, this acts as an effective block on subordinate reproduction (thereby mitigating reproductive conflict with their parents) and a key factor favouring subordinate dispersal (Young 2009). Breeder replacement could therefore conceivably either increase (Emlen 1997) or decrease the dispersal probability of resident natal subordinates of the opposite sex. These subordinates could be *more* likely to disperse following replacement of the opposite-sex breeder if any associated reproductive opportunities for subordinates now made it adaptive for their same-sex parent to subject them to aggression and/or evict them from the group. For example, in stripe backed wrens (*Campylorhynchus nuchalis*), matings between sons and immigrant step-mothers were met with increased aggression between fathers and sons (Piper and Slater 1993; see also Goldstein *et al.* 1998 for a similar finding in Florida scrub jays, *Aphelocoma coerulescens*). However, these subordinates might also be *less* likely to disperse following breeder replacement if the arrival of the opposite sex immigrant breeder increases the subordinates' current or future reproductive prospects within the group (e.g. the prospect of ultimately inheriting the breeding position alongside the immigrant breeder; Balcombe 1989).

Subordinate dispersal following parental replacement may give rise to costs to both the individual and the group. Firstly, parental replacement could negatively affect subordinate fitness, because individuals that disperse early may have reduced reproductive success (Ekman *et al.* 2000) and survival (Green and Cockburn 2001; Griesser *et al.* 2006) than individuals that delay dispersal (Eikenaar *et al.* 2007). Additionally, parental replacement may have negative consequences for the reproductive success of the dominants, and therefore the group, as retaining helpers can improve a dominant's reproductive success and some species require helpers to successfully raise young in cooperatively breeding species (Cornwallis *et al.* 2010). Costs arising from breeder replacement may be an under-appreciated mechanism that strengthens selection for traits, in both breeders and helpers, which prolong reproductive tenures (e.g. helping in territorial defence against potential usurpers, Sharp and Clutton-Brock 2011). Indeed, these traits may include helping to repel potential challengers for either breeding position, offspring showing restraint from challenging their parents, and helping to lighten the workloads of breeders (Sharp & Clutton-Brock 2011).

Here we investigate whether breeder replacement destabilises nuclear family groups, triggering helper dispersal and consequent reductions in reproductive success in a nuclear family, cooperatively breeding bird, the white-browed sparrow weaver (*Plocepasser mahali*). White-browed sparrow-weaver groups are composed of a dominant male and female and zero to 12 subordinates of both sexes, the vast majority of whom are offspring from previous breeding attempts that have delayed dispersal (Collias and Collias 1978; Lewis 1982a, b; Ferguson 1988; Harrison *et al.* 2013b, 2014). These natal subordinates contribute to the cooperative care of subsequent generations of offspring born to the dominant breeding pair, as well as a range of other cooperative activities, including cooperative weaving, vigilance and territorial defence (Collias and Collias 1978; Lewis 1982a, b; Harrison *et al.* 2014; Walker *et al.* 2016). Reproduction within the group is monopolised by the dominant pair, with no evidence to date of within-group subordinate reproduction (Harrison *et al.* 2013a, b). However, dominant males lose approximately 12-18% of paternity to extra-group males, principally dominant males in other groups (Harrison *et al.* 2013a, b; Cram *et al.* 2015). There is, therefore, high within-group relatedness, and

subordinate birds typically lack access to unrelated breeding partners within their groups (Harrison *et al.* 2013a). Following delayed dispersal, both subordinate males and females can emigrate to join existing groups or to establish new territories (Lewis 1982b; Harrison *et al.* 2013b, 2014). When 'breeder replacement' (replacement of one of the dominant breeding pair) occurs in this species the newly dominant bird is typically (in ~85% of cases in both sexes; Harrison *et al.* 2013a) an immigrant bird. As outlined above, therefore, breeder replacement in this species would therefore be expected to reduce any indirect fitness payoffs to natal subordinates of helping to rear future clutches of the dominant breeding pair, and may also enhance conflict between breeders and helpers over both resources and reproduction.

The aims of this study are to utilise a long-term field study of white-browed sparrow weaver societies to investigate the effects of breeder replacement on a) group composition (specifically the retention of natal subordinates) and b) the reproductive success of the dominant breeding pair. According to the logic outlined above, we predict that after breeder replacement (i) natal subordinates will be more likely to leave the group (because of reduced indirect fitness benefits available to subordinates via helping within the natal group and increased within-group conflict over resources and reproduction resulting from reduced within-group relatedness), (ii) group sizes will therefore decrease, and (iii) the reproductive success of the dominant breeding pair may also be negatively affected (given the time that may be required to re-establish dominance relationships following such a replacement, the expected reduction in the size of their helping workforce, and/or the scope for increased reproductive conflict between dominants and subordinates following such a replacement). Specifically, we analyse the effects of breeder replacement on multiple components of the reproductive success of dominants: the time lag to laying the first clutch, the number of eggs laid in the ensuing year, the hatching probability of those eggs, the fledging probability of the resulting offspring, and the combined result of these parameters, the total number of fledglings reared in the ensuing year.

1.3. METHODS

The study population comprises 40 white-browed sparrow-weaver groups, which have been monitored since 2007 and are located in an area of about 1.5 km² in the semi-arid Kalahari Desert at Tswalu Kalahari Game Reserve, South Africa (27°16'S, 22°25'E). Individual birds were fitted with a metal ring and 3 colour rings for identification (SAFRING licence 1444) (Cram *et al.* 2015). Males and females could be distinguished by beak colour (Leitner *et al.* 2009; Cram *et al.* 2015) and group compositions were recorded and maintained with weekly visits (Harrison *et al.* 2013b). Group size was determined by the number of birds consistently seen foraging and roosting together in territory's central trees (Cram *et al.* 2015) and was averaged for the season.

All stages of breeding attempts were monitored throughout the breeding season which coincides with the southern summer (October to April), and after heavy rainfall clutch initiation occurs (Harrison *et al.* 2013b). Nest checks were conducted every 1 to 2 days in the afternoon (eggs are laid in the morning; Young, personal communication), to determine lay date for all eggs and hatch date for all chicks. By monitoring key dominance-related behaviours, as described in previous studies (e.g. Collias and Collias 1978; Lewis 1981; Harrison *et al.* 2013b), on a weekly basis, the dominant bird of each sex could be determined (Harrison *et al.* 2013b). All dominant females were assumed to be the mother (Harrison *et al.* 2013b). The dominant male of the group was assumed to be the father (and acted as the social father) though extra-group paternity cannot be ruled out (Harrison *et al.* 2013b).

Analyses were conducted at two levels. Group level analyses explored the effects of breeder replacement on reproduction and helper retention, specifically, group size. Individual level analyses explored the effects of breeder replacement on helper retention, specifically, the disappearance of natal subordinates. Analyses at the group level were restricted to years when more than 70% of subordinates had their mother and social father present at the beginning of the year (from now known as a "nuclear family"). Analyses at the individual level investigated was restricted to birds that were born in that group (thus excluding unknown origin and immigrant birds),

defined as when at least one of the dominant birds were present when they were born and where replacement involves the loss of a "parent".

To allow for any order effects and seasonality, one calendar year was used as the time window from the day that the dominant was last seen. By using this "years" approach and by calculating aggregate measures for the group we avoided duplicating analyses. The 365 days following the date at which a dominant bird was last seen were classified as a "replacement year" for that group. Where further replacements occurred (of either sex) within a replacement year, the remaining days of the year following such replacements (that were not already labelled as replacement) were discarded from analysis. All "stable" full year windows (within which we know the dominant male and female are unchanged; non-replacement years) were determined by working back in time from i) the end of monitoring and then ii) the start of any replacement years. This method resulted in some time windows of less than a year, which were discarded from analysis.

Disappearances of natal subordinates were used to investigate the effects of breeder replacement on helper retention. Disappearance from a group could be the result of i) death while still in the natal group, ii) dispersing successfully beyond the boundaries and peripheral areas of the study site or iii) known emigrants seen in groups within the study site and peripheral areas which are frequently checked for ringed birds. Rainfall was calculated as the total over the time window and was averaged between data collected from two weather stations close to the study site (one to the east and one to the west) and was converted to meters due to disparities in scale with other variables. Maternal age was a minimum age in years and was factorised (<2, 2-3, 3-4, 4-5, 5+ years) due to uncertainty about the ages of the oldest birds as many dominants were already adults at the start of monitoring. The time elapsed between the start of the breeding season (September 1st) and the date of breeder replacement (hereafter called 'Time Elapsed'), was converted to months due to disparities in scale with other variables. Group sizes included adults and juveniles (young birds that had fledged but were less than one year) because juveniles had the potential to help during the time window.

Statistical Analysis

R version 3.3.0 (R Core Team, Vienna, Austria) was used for all statistical analyses. Generalised linear mixed effect models (GLMMs) and linear mixed effect models (LMMs) were used for the majority of analyses (lme4, Bates *et al.* 2014). Backwards stepwise model selection using P-values was used to obtain the minimum adequate model (Crawley 1993). All predictor terms of interest were initially entered to create a full model and then they were dropped sequentially, the least significant term first (significance was ascertained by comparing models using anova), until only the terms whose removal would have significantly weakened the explanatory power of the model remained: the final model. Significance of each term was obtained by comparing the final model with and without this term using anova. Only specific statistical interactions were fitted which were considered *a priori* to be plausible and of potential interest given the biology of study species and the aims of the investigation, and these included: sex, breeder replacement and start group size. Random terms were included to take into account repeated measures, e.g. group, and season. All full models were subjected to a visual inspection of their residual plots, which did not reveal any obvious deviations from homoscedasticity or normality. Conditional (total variance explained by the best-supported model, i.e. both fixed and random factors) and marginal (variance explained by fixed effects alone) R^2 formulations were calculated for all models to provide meaningful information with regard to the fixed and random factors (Nakagawa & Schielzeth 2013). In all tables, the 'average effect' refers to the model coefficient for a given independent variable.

1.3.1. Group Composition

i) Does the probability of natal subordinates disappearing increase when there is a replacement of the dominant female compared to years with no replacement?

A GLMM was used to investigate the effect of female breeder replacement on the probability of a natal subordinate disappearing. The probability of disappearance

from the group was calculated as a binomial response term where the presence of each individual at the end of the time window was either 1 (if they disappeared) or 0 (if they stayed in the group). The type of year (female replacement or no replacement) was determined as described above. In addition, the following predictor terms were also fitted to the model: group size (including both adults and juveniles) at the start of the time window, age of natal subordinate and its quadratic, sex of natal subordinate, rainfall (total over the window in question), time since last September 1st (Time Elapsed) and its quadratic (to control for variation during the breeding season when breeder replacements occurred). Group ID, Bird ID and Window (sequential order of years for each group, i.e. year 1, year 2, year 3 etc.) were included as random effects.

ii) Does the probability of natal subordinates disappearing increase when there is a replacement of the dominant male compared to years with no replacement?

A GLMM was used to investigate the effect of male breeder replacement on the probability of a natal subordinate disappearing. The same model as above (1.3.1) was fitted, with the exception that male rather than female replacement was used for type of year.

iii) Are group sizes smaller after a breeder replacement?

A GLMM was used to investigate the effect of breeder replacement on group size. For group size, the number of individuals present within a group at the end of the time window was used (henceforth referred to as end group size). Type of year had 3 levels: no replacement, female replacement, and male replacement. In addition to the type of year, the following predictor terms were included: group size at the start of the window, age of dominant female (a 5-level factor), rainfall, and "Time Elapsed" and its quadratic. Group ID was the only random effect.

1.3.2. Reproduction

i) Does breeder replacement increase the lag from the start of the replacement year to the laying of the first clutch compared to control years?

A GLMM was used to investigate the effect of breeder replacement on the lag to laying the first clutch of eggs in the ensuing year. The lag was calculated as the number of days between the start of the time window of interest (either “replacement” or “stable” years) and the date on which the first egg was laid in the first clutch. Type of year had 3 levels: no replacement, female replacement, and male replacement. In addition to type of year, the following predictor terms were fitted to the model: group size at the start of the window, age of dominant female in years (a 5-level factor), rainfall, and Time Elapsed (see above for definition) and its quadratic. Group ID was the only random effect.

ii) Does the dominant female lay fewer eggs in the year following breeder replacement events?

A GLMM was used to investigate the effect of breeder replacement on the number of eggs a dominant female laid during a time window. Predictor variables and random effects were as described for 1.3.2*i*. A likelihood-ratio test was used to show the statistical significance of the variable as a whole and any differences across levels were shown using a plot.

iii) Is the hatching probability of eggs lower in the year following breeder replacement events?

A GLMM was used to investigate the effect of breeder replacement on the probability of eggs hatching (calculated as the number of chicks that hatched divided by the number of eggs laid in the group by the end of the time window). Predictor variables and random effects were as described for 1.3.2*i*.

iv) Is the probability that nestlings fledge lower in the year following breeder replacement events?

A GLMM was used to investigate the effect of breeder replacement on the probability of chicks fledging, calculated as the number of chicks that fledged divided by the number of chicks that hatched for the group by the end of the time window. Predictor variables and random effects were as described for 1.3.2*i*. A likelihood-ratio test was used to show the statistical significance of the variable as a whole and any differences across levels were shown using a plot.

v) Do the dominant pair fledge fewer young in the year following breeder replacement events?

A GLMM was used to investigate the effect of breeder replacement on reproductive success, calculated as the number of chicks that fledged in the group by the end of the time window. Predictor variables and random effects were as described for 1.3.2*i*.

1.4. RESULTS

During this study, a total of 40 breeder losses were recorded, 23 of which were the loss of the dominant female, and 17 were the loss of the dominant male. The majority of breeder losses were of birds that were not seen on the study site again, so it was difficult to ascertain whether they emigrated to another group or died. Emigration of a breeder into a new group was confirmed in only three cases. The mean (\pm SE) time between the start of the breeding season (September 1st) and the date of breeder disappearance was 6.70 (\pm 0.23) months (range 0.33 - 10.2 months). The mean (\pm SE) yearly rainfall was 405.7 (\pm 10.2) mm (range 178.0 - 670.5 mm) per year. The mean (\pm SE) start group size was 4.82 (\pm 0.22) individuals (range 2 - 13 individuals) per group. The mean (\pm SE) minimum age of natal subordinates was 1.15 (\pm 0.05) years (range 0.05 - 5.09 years).

1.4.1. Group Composition

i) Does the probability of natal subordinates disappearing increase when there is a replacement of the dominant female compared to years with no replacement?

23 incidences of dominant female replacement were recorded in 18 groups. The mean (\pm SE) percentage of natal subordinate disappearances per group after a dominant female replacement was 51 (\pm 3) % (range 0 – 100%). There was no significant effect of the loss of the dominant female on the probability of natal subordinates disappearing from their natal group during the ensuing year, compared to control years (i.e. those where the dominant female remained; GLMM: $\chi^2_1 = 2.54$, $p=0.11$; Figure 1a; Table 1), after controlling for a significant positive effect of subordinate age (GLMM: $\chi^2_1 = 7.50$, $p = 0.006$; Table 1). While inspection of the data (Figure 1a) suggests that subordinate males and females might respond differently to dominant female replacement, there was no statistical support for an interaction between dominant female replacement and subordinate sex (GLMM: $\chi^2_3 = 5.56$, $p = 0.14$; Table 1). 8% of the variance was explained by the fixed factors. 9% of the variance was explained by the fixed and random factors.

ii) Does the probability of natal subordinates disappearing increase when there is a replacement of the dominant male compared to years with no replacement?

17 incidences of dominant male replacement were recorded in 14 groups. The mean (\pm SE) percentage of natal subordinates disappearing per group after a dominant male replacement in the year-long windows under study was 48 (\pm 3) % (range 0 – 100%). There was a significant effect of the loss of the dominant male on the probability of subordinates disappearing from their natal group, and its effect differed significantly for subordinate males and females (dominant male replacement x subordinate sex interaction: $\chi^2_1 = 5.18$, $p = 0.02$; Figure 1b, Table 2), after controlling for a significant positive effect of subordinate age (GLMM: $\chi^2_1 = 7.07$, $p = 0.008$; Table 2). Female subordinates were *less* likely to disappear from their natal group in the year following the loss of the dominant male (likely their genetic father: Harrison *et al.* 2013a, b) than in control years, while there was no clear effect of dominant male replacement on the probability that subordinate males disappeared. 4% of the variance was explained by the fixed factors. 4% of the variance was explained by the fixed and random factors.

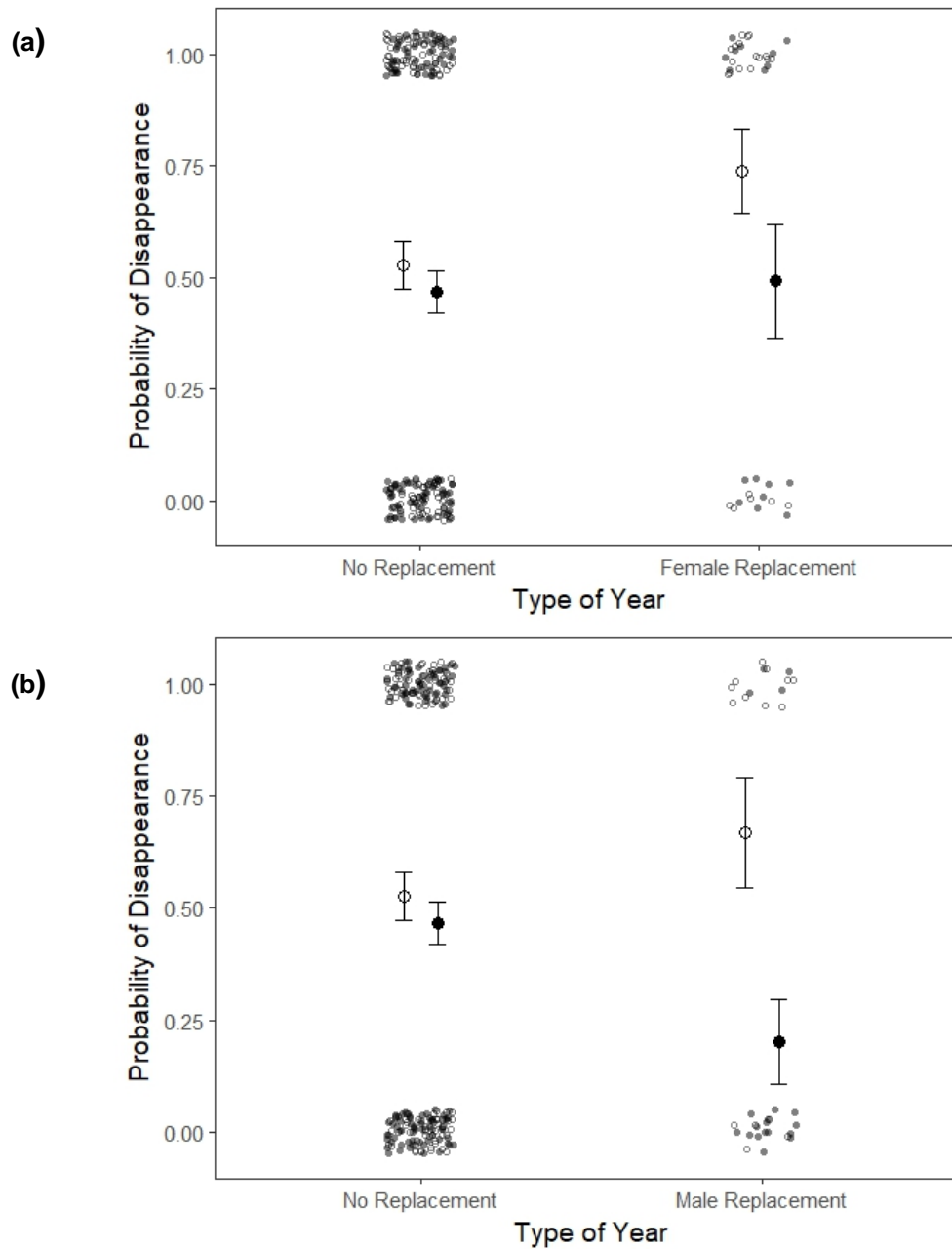


Figure 1 – The effect of (a) female and (b) male breeder replacement on the probability of natal subordinates disappearing from their natal group compared to years where no breeder replacement occurred. The open points represent male subordinates and the closed points represent female subordinates. Means and standard errors are predictions from the minimal GLMMs described above.

Table 1 - Generalized linear mixed model investigating the effect of dominant female (DF) replacement on the probability of subordinates disappearing from their natal group (N = 253 subordinates monitored over 23 dominant female replacement years and 79 non-replacement years for 31 groups across 8 breeding seasons). Terms in bold were retained in the minimal model (p values show the significance of the change in variation explained on dropping this term from the minimal model), while terms in normal type-face were not retained in the minimal model (p values show the significance of the change in variation explained on adding this term to the minimal model).

	Intercept	Average Effect	Standard Error	χ^2	df	P
Age	-0.41	0.41	0.16	7.50	1	0.0062
Age ²	-0.76	-0.20	0.11	3.28	2	0.070
DF Replacement (No Replacement)	0.09	-0.58	0.37	2.54	1	0.11
Sex (Male) * DF Replacement (No Replacement)	-0.53	-0.83	0.76	5.56	3	0.14
Sex (Male)	-0.62	0.39	0.26	2.20	1	0.14
Time Elapsed ²	-0.67	-0.02	0.02	3.30	2	0.19
Time Elapsed	0.02	-0.06	0.05	1.56	1	0.21
Start Group Size	-0.76	0.05	0.06	0.64	1	0.42
Rainfall	-0.70	0.69	1.23	0.32	1	0.57

Table 2 - Generalized linear mixed model investigating the effect of dominant male (DM) breeder replacement on the probability of subordinates disappearing from their natal group (N = 253 subordinates monitored over 17 dominant male replacement years and 79 non-replacement years for 31 groups across 8 breeding seasons). Terms in bold were retained in the minimal model (p values show the significance of the change in variation explained on dropping this term from the minimal model), while terms in normal type-face were not retained in the minimal model (p values show the significant of the change in variation explained on adding this term to the minimal model).

	Intercept	Average Effect	Standard Error	χ^2	df	P
Age	-1.88	0.44	0.17	7.07	1	0.0079
Sex (Male)	-1.88	2.07	0.80	8.26	1	0.016
Sex (Male) * DM Replacement (No Replacement)	-1.88	-1.84	0.85	5.18	3	0.023
DM Replacement (No Replacement)	-1.88	1.24	0.61	6.03	1	0.049
Time Elapsed	-1.54	-0.09	0.05	2.62	1	0.12
Time Elapsed ²	-1.84	-0.01	0.02	2.98	2	0.23
Start Group Size	-2.15	0.04	0.06	0.37	1	0.54
Age ²	-2.00	-0.07	0.15	0.23	2	0.63
Rainfall	-2.13	0.58	1.28	0.21	1	0.65

iii) Do groups end the year smaller in the year following a breeder replacement relative to control years?

There were 23 dominant female replacement years, 17 dominant male replacement years and 79 non-replacement years. The mean (\pm SE) end group size in the year-long windows under study was 5.22 (\pm 0.20) individuals (range 2 - 13 individuals). There was no effect of whether a breeder replacement occurred (fitted as a 3-level factor: DM Replacement, DF Replacement, No Replacement) on the group size at the end of the ensuing year (GLMM: $\chi^2_2 = 1.10$, $p=0.58$; Table 3), after controlling for a significant positive effect of the group size at the start of the year (GLMM: $\chi^2_1 = 26.2$, $p < 0.001$; Table 3) and maternal age (GLMM: $\chi^2_4 = 13.6$, $p = 0.009$; Table 3). 25% of the variance was explained by fixed factors. 25% of the variance was explained by both fixed and random factors.

Table 3 - Generalized linear mixed model investigating the effect of breeder replacement on group size (N = 119 group-years, comprising 23 dominant female (DF) replacement years, 17 dominant male (DM) replacement years and 79 non-replacement years (No Replacement), all from 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model. p values were obtained from anovas comparing the minimal model with and without the variable of interest.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Start Group Size	1.29	0.09148	0.02	26.21	1	<0.001
Maternal Age (years)	1.29			13.58	4	0.009
2-3 (compared to <2)		0.11	0.14			
3-4 (compared to <2)		-0.21	0.15			
4-5 (compared to <2)		-0.30	0.15			
5+ (compared to <2)		-0.16	0.15			
Type of Year	1.29			1.10	2	0.58
DM Replacement (compared to DF Replacement)		-0.07	0.15			
No Replacement (compared to DF Replacement)		0.06	0.11			
Start Group Size*Type of Year	1.45			2.68	4	0.61
Start Group Size, DM Replacement (Start Group Size, DF Replacement)		0.08	0.08			
Start Group Size, No Replacement (Start Group Size, DF Replacement)		0.04	0.04			
Time Elapsed ²	1.45	0.005	0.01	0.71	2	0.70
Rainfall	1.26	0.12	0.44	0.07	1	0.79
Time Elapsed	1.30	-0.001	0.02	0.006	1	0.94

1.4.2. Reproduction

i) Does breeder replacement increase the lag from the start of the replacement year to the laying of the first clutch compared to control years?

23 female replacements were recorded for 18 groups and 17 male replacements were recorded for 14 groups. 10 groups did not have any male or female replacements. The mean (\pm SE) minimum age of the dominant female (maternal age) at the start of the time window was 3.56 (\pm 0.15) years (range 1.08 to 7.57 years). The mean (\pm SE) lag from the start of the time window of interest (either “replacement” or “stable” years) to the laying of the first clutch was 162.80 (\pm 9.33) days (range 1 - 350 days). The mean (\pm SE) number of clutches laid was 2.34 (\pm 0.13) clutches (range 0 - 7 clutches). There was no effect of breeder replacement on the lag from the start of the time window of interest to the laying of the first clutch of eggs (LMM: $\chi^2_2 = 2.15$, $p = 0.34$; Table 4), after controlling for a significant positive effect of the time since the start of the breeding season (GLMM: $\chi^2_1 = 12.22$, $p < 0.001$; Table 4) and its quadratic which has a significant negative effect (GLMM: $\chi^2_2 = 20.01$, $p < 0.001$; Table 4). 19% of the variance was explained by the fixed factors. 33% of the variance was explained by the fixed and random factors.

ii) Does the dominant female lay fewer eggs in the year following breeder replacement events?

The mean (\pm SE) total number of eggs laid per group in the year-long time windows under study was 4.61 (\pm 0.26) eggs (range 0 - 16 eggs). There was a significant effect of breeder replacement on the total number of eggs laid in the ensuing year (GLMM: $\chi^2_2 = 7.50$, $p = 0.02$; Figure 2; Table 5). Figure 2 shows that the number of eggs laid was higher in the year following no breeder replacement than the years following both dominant female replacement and dominant male replacement. There was also a significant effect of maternal age on the number of eggs laid (GLMM: $\chi^2_1 = 12.71$, $p = 0.01$; Table 5). 12% of the variance was explained by the fixed factors. 12% of the variance was explained by the fixed and random factors.

Table 4 - Generalized linear mixed model investigating the effect of breeder replacement on the lag to laying the first clutch (N = 119 group-years, comprising 23 dominant female (DF) replacement years, 17 dominant male (DM) replacement years and 79 non-replacement years (No Replacement), all from 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model (p values show the significance of the change in variation explained on dropping this term from the minimal model), while terms in normal type-face were not retained in the minimal model (p values show the significant of the change in variation explained on adding this term to the minimal model).

	Intercept	Average Effect	Standard Error	χ^2	df	<i>P</i>
Time Elapsed	-58.75	66.35	15.70	12.22	1	<0.001
Time Elapsed ²	-58.75	-4.40	1.22	20.01	2	<0.001
Maternal Age (years)	-70.29			5.89	4	0.21
2-3 (compared to <2)		41.62	27.25			
3-4 (compared to <2)		1.77	26.42			
4-5 (compared to <2)		35.48	27.65			
5+ (compared to <2)		48.47	28.35			
Type of Year	-31.18			2.15	2	0.34
DM Replacement (compared to DF Replacement)		-19.87	29.94			
No Replacement (compared to DF Replacement)		-32.95	22.53			
Rainfall	-36.98	-62.98	75.515	0.692	1	0.41
Start Group Size	-48.86	-2.49	3.39	0.54	1	0.46

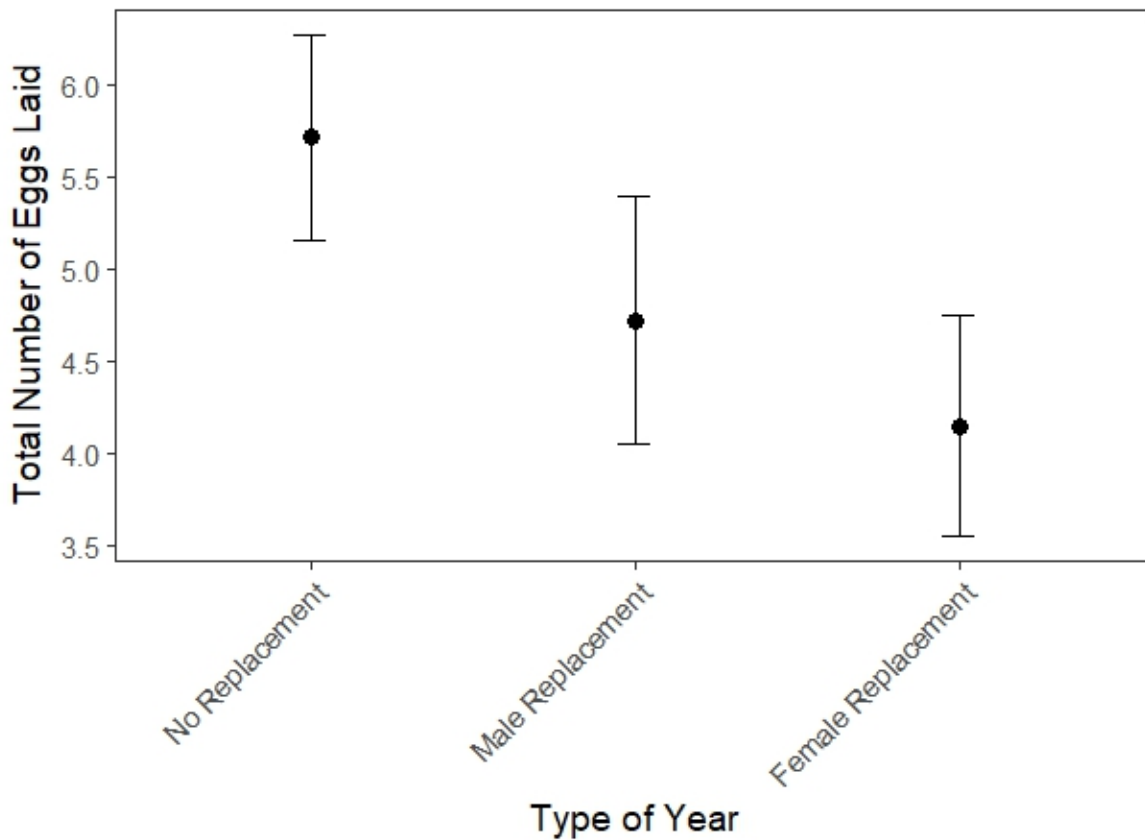


Figure 2 - The effect of breeder replacement on the total number of eggs laid compared to control years with no breeder replacement. Means and standard errors are predictions from the GLMMs described above. There was no interaction between maternal age and breeder replacement therefore results are shown for only one maternal age category (3-4 years) to aid visualisation.

Table 5 - Generalized linear mixed model investigating the effect of breeder replacement on the total number of eggs laid in the ensuing year (N = 119 group-years, comprising 23 dominant female (DF) replacement years, 17 dominant male (DM) replacement years and 79 non-replacement years (No Replacement), all from 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model (p values show the significance of the change in variation explained on dropping this term from the minimal model), while terms in normal type-face were not retained in the minimal model (p values show the significant of the change in variation explained on adding this term to the minimal model).

	Intercept	Average Effect	Standard Error	χ^2	df	P
Maternal Age (years)	1.38			12.71	4	0.013
2-3 (compared to <2)		-0.14	0.15			
3-4 (compared to <2)		0.043	0.14			
4-5 (compared to <2)		-0.44	0.16			
5+ (compared to <2)		-0.13	0.15			
Type of Year	1.38			7.50	2	0.024
DM Replacement (compared to DF Replacement)		0.13	0.17			
No Replacement (compared to DF Replacement)		0.32	0.13			
Time Elapsed	1.18	0.036	0.021	2.80	1	0.094
Time Elapsed ²	1.20	0.00066	0.0066	2.81	2	0.25
Rainfall	1.23	0.45	0.49	0.85	1	0.36
Start Group Size	1.39	-0.0029	0.021	0.019	1	0.89

iii) Is the hatching probability of eggs lower in the year following breeder replacement events?

The mean (\pm SE) total number of eggs that survived to the point of hatching successfully per group in the year-long windows under study was 2.88 (\pm 0.18) eggs (range 0 - 9 eggs). There was no effect of breeder replacement on the hatching probability of eggs in the ensuing year (GLMM: $\chi^2_2 = 1.92$, $p = 0.38$; Table 6), after controlling for the significant positive effect of group size (GLMM: $\chi^2_1 = 4.89$, $p=0.03$; Table 6) and the significant negative effect of the number of eggs laid (GLMM: $\chi^2_1 = 4.82$, $p=0.03$; Table 6). 3% of the variance was explained by the fixed factors. 3% of the variance was explained by the fixed and random factors.

iv) Is the probability that nestlings fledge lower in the year following breeder replacement events?

The mean (\pm SE) percentage of chicks that survived to hatching per group in the year-long windows under study was 56 (\pm 4) % (range 0 – 100%). There was a significant effect of breeder replacement on the probability of chicks fledging in the ensuing year (GLMM: $\chi^2_2 = 8.28$, $p = 0.02$; Figure 3; Table 7). Figure 3 shows that the probability was higher in the year following dominant male replacement than the years following either control years with no breeder replacement or dominant female replacement. There were no other significant effects (Table 7). 6% of the variance was explained by the fixed effects. 6% of the variance was explained the fixed and random factors.

Table 6 - Generalized linear mixed model investigating the effect of breeder replacement on the probability of eggs hatching (N = 119 counts of replacement, 23 female replacements, 17 male replacements, 79 non-replacements for 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model. p values were obtained from anovas comparing the minimal model with and without the variable of interest.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Start Group Size	0.63	0.11	0.048	4.89	1	0.027
Number of Eggs	0.63	-0.090	0.040	4.82	1	0.028
Time Elapsed	0.67	-1.68	1.07	2.39	1	0.12
Time Elapsed ²	0.02	-0.021	0.015	1.96	2	0.38
Type of Year	0.52			1.92	2	0.38
DM Replacement (compared to DF Replacement)		-0.047	0.42			
No Replacement (compared to DF Replacement)		0.33	0.33			
Maternal Age (years)	0.94			2.60	4	0.63
2-3 (compared to <2)		-0.56	0.39			
3-4 (compared to <2)		-0.55	0.38			
4-5 (compared to <2)		-0.49	0.43			
5+ (compared to <2)		-0.48	0.39			
Number of Clutches	0.65	-0.092	0.21	0.19	1	0.66
Rainfall	1.19	-0.0066	0.048	0.019	1	0.89

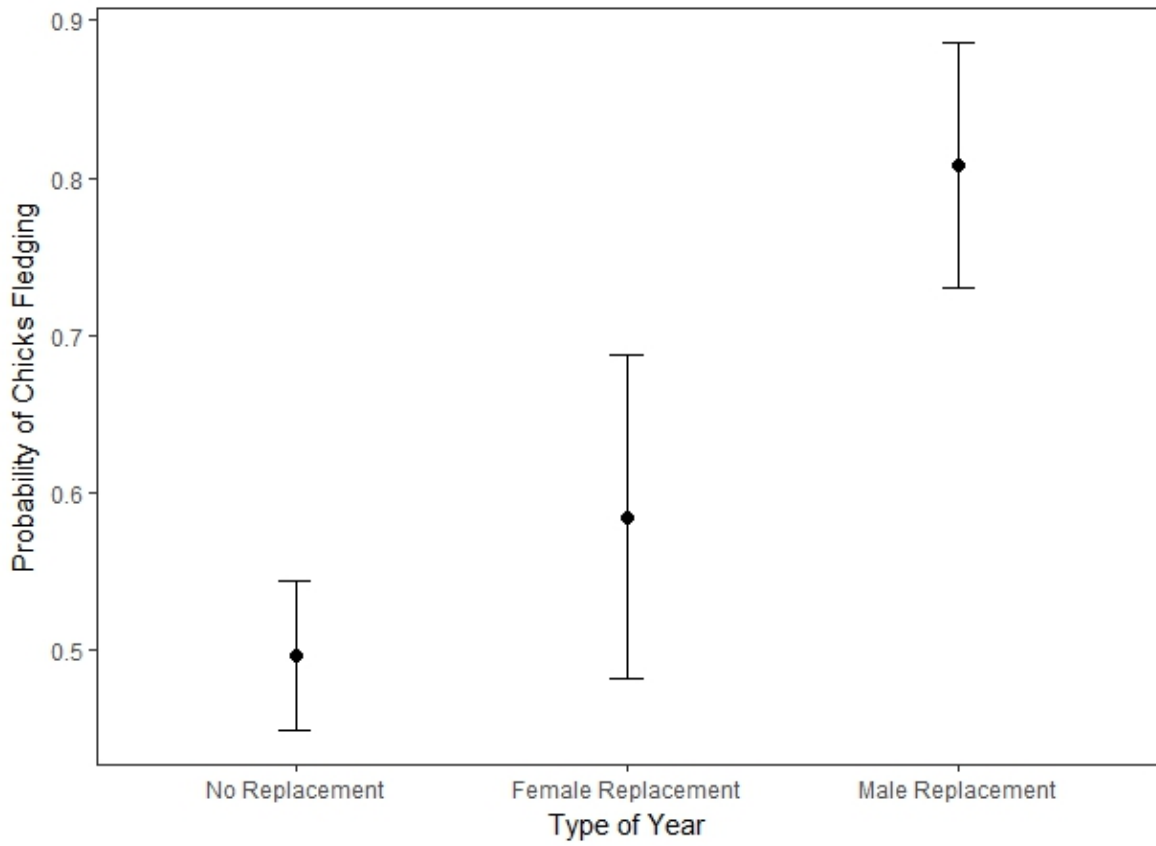


Figure 3 – The effect of breeder replacement on the probability of chicks fledging compared to control years with no breeder replacement. Means and standard errors are predictions from the GLMMs described above.

Table 7 - Generalized linear mixed model investigating the effect of breeder replacement on the probability of nestlings fledging (N = 119 group-years, comprising 23 dominant female (DF) replacement years, 17 dominant male (DM) replacement years and 79 non-replacement years (No Replacement), all from 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model. p values were obtained from anovas comparing the minimal model with and without the variable of interest.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Type of Year	0.34			8.28	2	0.016
DM Replacement (compared to DF Replacement)		1.10	0.65			
No Replacement (compared to DF Replacement)		-0.36	0.47			
Rainfall	1.45	-2.61	1.60	2.85	1	0.091
Number of Eggs that Hatched	0.63	-0.076	0.092	0.69	1	0.41
Number of Eggs	0.54	-0.040	0.061	0.44	1	0.51
Time Elapsed	0.54	-0.032	0.071	0.21	1	0.65
Number of Clutches	0.44	-0.035	0.13	0.076	1	0.78
Maternal Age (years)	0.26			1.38	4	0.85
2-3 (compared to <2)		0.22	0.53			
3-4 (compared to <2)		-0.14	0.50			
4-5 (compared to <2)		0.39	0.57			
5+ (compared to <2)		0.22	0.55			
Time Elapsed ²	0.37	-0.0049	0.022	0.26	2	0.88
Start Group Size	0.36	-0.0036	0.066	0.0029	1	0.96

v) Do the dominant pair fledge fewer young in the year following breeder replacement events?

The mean (\pm SE) number of chicks that fledged per group in the year-long windows under study was 1.54 (\pm 0.13) chicks (range 0 - 6 chicks). There was no effect of breeder replacement on the number of offspring reared to fledging in the ensuing year (GLMM: $\chi^2_2 = 1.74$, $p = 0.42$; Table 8). No other variables in the model significantly affected the number of offspring reared (Table 8). 2% of the variance was explained by the fixed effects. 2% of the variance was explained by the fixed and random factors

Table 8 - Generalized linear mixed model investigating the effect of breeder replacement on the number of offspring fledged in the ensuing year (N = 119 group-years, comprising 23 dominant female (DF) replacement years, 17 dominant male (DM) replacement years and 79 non-replacement years (No Replacement), all from 37 groups across 8 breeding seasons). Terms in bold were retained in the minimal model (p values show the significance of the change in variation explained on dropping this term from the minimal model), while terms in normal type-face were not retained in the minimal model (p values show the significant of the change in variation explained on adding this term to the minimal model).

	Intercept	Average Effect	Standard Error	χ^2	df	<i>P</i>
Start Group Size	0.22	0.040	0.030	1.73	1	0.19
Time Elapsed ²	-0.11	-0.016	0.010	2.52	2	0.28
Type of Year	0.20			1.74	2	0.42
DM Replacement (compared to DF Replacement)		0.40	0.26			
No Replacement (compared to DF Replacement)		0.25	0.21			
Rainfall	0.62	-0.43	0.67	0.41	1	0.52
Maternal Age (years)	0.55			2.06	4	0.73
2-3 (compared to <2)		-0.20	0.24			
3-4 (compared to <2)		0.013	0.22			
4-5 (compared to <2)		-0.24	0.25			
5+ (compared to <2)		-0.16	0.24			
Time Elapsed	0.37	0.0085	0.029	0.086	1	0.77

1.5. DISCUSSION

Together our findings reveal that, contrary to expectation, the replacement of dominant breeders does not precipitate the breakdown of socially monogamous nuclear family groups in this cooperatively breeding bird. Indeed, we found no evidence that subordinates were more likely to leave their natal groups following the disappearance of the dominant female (their mother) or male (likely their father, Harrison *et al.* 2013a, b). Accordingly, replacement of the dominant female or male did not significantly impact either (i) the size of the social group at the end of the ensuing year relative to control years, or (ii) the reproductive success of the group (total number of offspring fledged) over the ensuing year relative to control years. Subordinate females were actually significantly *less* likely to disappear from their natal groups in the year following the replacement of the dominant male (likely their father) and the probability of chicks fledging was increased following male breeder replacement. These latter findings are consistent with the expectation that replacement of the opposite-sex dominant breeder may impact natal subordinate dispersal and helping decisions by offering them the prospect of future outbreeding opportunities within their natal territory. Indeed, our finding that the number of eggs laid is reduced in the year following breeder replacement raises the possibility that breeder replacement also intensifies social conflict (over rank or reproduction), especially between natal subordinate females and their mother (the resident dominant female). I discuss these findings regarding the impact of dominance replacement on the cohesion of cooperative groups and the incidence of conflict within them in more detail below.

1.5.1. Breeder replacement and the cohesion of cooperative groups

Reductions in relatedness between natal subordinates and their resident dominants, which occurs after breeder replacement, may give rise to negative consequences on helper retention and reproduction through the departure of subordinates. Nepotism may decrease (Ekman and Griesser 2002; Eikenaar *et al.* 2007), potentially leading to natal subordinates being driven out of their groups or leaving voluntarily due to reduced toleration of foraging competition (Dickinson *et al.* 2009; Chiarati *et al.* 2011) and assistance in future reproduction (Brown 1987; Woolfenden and Fitzpatrick

1990). However, this study shows that subordinate sparrow weavers of both sexes are *not* more likely to leave following breeder replacement of either sex. Our findings suggest that breeder replacement may not reduce the benefits of philopatry for subordinates sufficiently to make their voluntary dispersal favourable. This could be the case simply because (i) the costs of dispersal and/or (ii) the benefits of philopatry arising *independent* of relatedness to breeders are sufficiently high in this species that any reduction in kinship to breeders associated with breeder replacement does not render dispersal favourable. For example, there could be potential survival benefits of group living rather than floating, or there may be direct benefits arising from cooperation (Ridley *et al.* 2008; Kigama *et al.* 2014). Breeders are also known to forcibly evict subordinates in a number of other cooperative vertebrates (e.g. meerkats (*Suricata suricatta*, Young *et al.* 2006), banded mongooses (*Mungos mungo*, Cant *et al.* 2001, 2010), Arabian babblers (*Turdoides squamiceps*, Zahavi 1990) and Southern pied babblers (*Turdoides bicolor*, Ridley *et al.* 2008). As such, our findings suggest that, to the extent that dominants in this species are capable of evicting, any rank-related conflict arising from breeder turnover may not be sufficiently strong as to render evictions adaptive. This may be because dominants (i) can effectively defend their reproductive monopoly without driving subordinates out, and/or (ii) may stand to benefit sufficiently from helping by resident subordinates to outweigh the costs of allowing them to stay. Previous work on white-browed sparrow-weavers suggests that dominants of both sexes are able to completely monopolise reproduction within their groups even when subordinates have access to unrelated breeding partners (Harrison *et al.* 2013b).

Female white-browed sparrow-weaver subordinates may be more likely to continue to delay dispersal after male breeder replacement because of future reproductive opportunities, such as territory inheritance or budding (Woolfenden & Fitzpatrick 1978; Dickinson & Hatchwell 2004). Despite the fact that territory inheritance is of importance in the evolution of group living (Wiley and Rabenold 1984; Lindstrom 1986; Dickinson and Hatchwell 2004), it is not common in cooperatively breeding birds (e.g. Koenig *et al.* 1999; Komdeur and Edelaar 2001) and this is reflected in the white-browed sparrow-weaver system where inheritance of natal territories is rare for both males and females (14.8%, Harrison *et al.* 2014). However, territory

inheritance by subordinate females might be much more common in circumstances where their father has been replaced by an unrelated immigrant male because a female subordinate may gain reproductive success by filling the breeding vacancy left by her mother (Balcombe 1989). Another explanation as to why female subordinates are more likely to stay after male breeder replacement is that females might gain reproductive opportunities through 'budding off' (Woolfenden and Fitzpatrick 1978) part of the territory with a new mate. Budding has been demonstrated in a number of species (e.g. *Neolamprologus pulcher*, Heg *et al.* 2005; Florida scrub jays, Woolfenden and Fitzpatrick 1978; Seychelles warblers, *Acrocephalus sechellensis*, Komdeur and Edelaar 2001; western bluebirds, Dickinson *et al.* 2014), including white-browed sparrow-weaver females who frequently bud off part of their natal territory to establish a new territory (Harrison *et al.* 2014). A female subordinate may pair up with an unrelated male, who remains in the group as a non-breeding helper (Lewis 1982), after a coalition of males immigrates into the group to fill a breeding vacancy after the departure of the original breeder. Coalition dispersal has been shown in mammals (Pusey and Packer 1987; Doolan and Macdonald 1996) and birds (Hannon *et al.* 1985; Koenig and Stacey 1990; Ligon and Ligon 1990; Williams and Rabenold 2005; Ridley 2012). Furthermore, similar to behaviours observed in brown jays (*Psilorhinus morio*, Williams and Rabenold 2005), males may also disperse into a group where a related male is already established as the breeder (Young, personal communication). These future reproductive benefits may give female subordinates an incentive to remain within their natal group after male breeder replacement, even though group relatedness is reduced.

Given the lack of a reduction in group size following breeder replacements, it is perhaps not surprising that reproductive success did not drop. However, it might be expected that subordinates that remained would reduce their cooperative contributions given the expected two-fold reduction in their relatedness to offspring produced after the replacement of one of their parents (and thus reduced indirect benefits of helping). Additionally, one might expect greater reproductive conflict to emerge. Reproductive success may hold up despite the reduction in relatedness because parents may compensate for reduced contributions of helpers. Helper

removal experiments have shown that parents compensate, to some extent, for the loss of helpers through increased provisioning rates (e.g. long-tailed tits, Hatchwell & Russell 1996), visits to the breeding shelter (e.g. *Julidochromis ornatus*, Brintjes *et al.* 2013) and brood care effort (e.g. *N. pulcher*, Zöttl *et al.* 2013). Although there was no increase in subordinate dispersal following breeder replacement, subordinates may have reduced their contributions to cooperation. However, our findings in this study show that chicks are more likely to fledge after the dominant male has been replaced suggesting that helpers, especially female subordinates (the more helpful sex in white-browed sparrow-weavers), may not reduce their contributions to cooperation. Male breeder replacement also makes female subordinates more likely to stay, therefore, perhaps the additional retention of female helpers could explain why dominant male replacement boosts fledging success. Subordinates may continue to contribute to offspring care to gain direct benefits from living in a group, for example, improved survival (Stacey and Ligon 1987; Clutton-Brock *et al.* 1999; Dierkes *et al.* 2005; Ridley *et al.* 2013) and subordinates might help to increase group size via group augmentation (Kingma *et al.* 2014). The impact of breeder replacement on helping and cooperative behaviours were not investigated in this study but could prove interesting subject material for future work in white-browed sparrow-weavers. In the next section, I will discuss reproductive conflict in more detail.

1.5.2. Reproductive Conflict

Male breeder replacement could increase reproductive conflict between subordinate natal females and their mothers by providing subordinate females with outbreeding opportunities within their social group. There is evidence of reduced numbers of eggs being laid following breeder replacement (this study), consistent with the possibility of escalated reproductive conflict. If females break each other's eggs immediately after laying, then we wouldn't have detected these 'eggs laid', therefore, it is possible that the reduction in eggs laid actually reflects competitive egg breaking among dominant and subordinate females. Previous work in this system has never detected subordinate maternity of nestlings (Harrison *et al.* 2013a, b). However, subordinates may be occasionally responsible for laying eggs that don't survive to

hatching due to egg destruction by the dominant. Additionally, there may be increased competition for social dominance between the dominant female and female subordinates which may increase dominant female investment in maintaining dominance (Koenig 1982) and thereby disrupt egg laying. However, contrary to other cooperative breeders (e.g. acorn woodpeckers, Koenig 1982; Southern pied babblers, Nelson-Flowers *et al.* 2013), our findings show no effect of breeder replacement on egg hatchability, which suggests that the dominant is able to invest just as much in incubation after breeder replacement as in control years and that dominance is secure by this stage of reproduction.

Reproductive conflict between remaining breeder and subordinates can have profound effects on the time it takes to re-establish dominance, form a new breeding pair and for reproduction to resume. However, there was no effect of breeder replacement on the lag from the start of the time window of interest (either “replacement” or “stable” years) to the laying of the first clutch in this study, which is perhaps surprising, given evidence of such lags in other species (e.g. acorn woodpeckers, Hannon *et al.* 1985; common marmosets Lazaro-Perea *et al.* 2000). Our findings might suggest that breeding vacancies are rapidly filled. Female breeder replacement was rapid after the removal of the breeding female in superb fairy-wrens (*Malurus cyaneus*, Ligon *et al.* 1991) and previous studies of white-browed sparrow-weavers have shown that breeding males that disappeared were replaced very quickly by another male; always within a month and usually within a week (Lewis 1982). Moreover, the short time to breeding may be an artefact of not monitoring over winter because more breeder replacements may occur over the winter season, possibly as a result of increased mortality, and this period can be used to establish new pairs and dominance hierarchies post-replacement.

1.5.3. Conclusions

To conclude, our findings reveal that white-browed sparrow-weaver families are robust to the breakdown of monogamy. While breeder replacement affected helper retention, the effect was not markedly negative, with female subordinates being more likely to stay after male breeder replacement and a non-significant trend for male

subordinates to be more likely to disappear after female breeder replacement. There was no difference in the probability of natal subordinate disappearance if the parent of the same-sex was replaced. Reproduction was also impacted by breeder replacement, though again, not in a markedly negative manner: while the number of eggs laid after breeder replacement was significantly lower than when no breeder replacement occurred and a significant increase in the probability of chicks fledging after male breeder replacement, there was no effect on when eggs were laid, the hatchability of eggs and the number of fledglings produced. This shows that perhaps that the ability to help rear offspring that are equally related to your own would not appear to be essential for the maintenance of delayed dispersal in this species.

Contrary to the growing view that long-term monogamy is important to the formation and stability of cooperative groups, breeder replacement in this nuclear family cooperative breeder gives rise to neither group dissolution nor reductions in annual reproductive success (total number of offspring fledged in the year). The anticipated negative effects of breeder replacement on helper retention and reproductive success might have been expected to select for diverse tactics within nuclear families to keep existing breeders in place (e.g. the breeding pair assisting with the defence of each other's breeding positions and offspring defending their parent's positions; Sharp & Clutton-Brock 2011). However, our findings of minimal effects of breeder turnover on helper retention and reproductive success highlight that selection on such tactics may actually be weaker than might otherwise be anticipated, at least in this nuclear family cooperative breeder. Our findings highlight too that the implications of divorce (where both birds are still alive but are no longer paired with each other; Jeschke *et al.* 2007; Jeschke & Kokko 2008) for the reproductive success of breeders and the success of former offspring may also be lower than might otherwise have been expected.

Chapter Two: Larger social groups dominate competition for space in a cooperatively territorial bird

2.1 ABSTRACT

Cooperative territorial defence is among the most widespread forms of cooperation, but the mechanisms by which it yields benefits to the co-operators remain unclear. While larger groups are frequently more likely to win contests, whether doing so allows larger groups to accrue territory over the long-term has rarely been shown. Here we investigate whether larger social groups are better able to monopolise space, using longitudinal data from 34 groups of the cooperatively territorial white-browed sparrow-weaver (*Plocepasser mahali*). Using a within-group centring statistical approach to isolate the spatial consequences of within-group changes in group size and relative group size over time, we report three key findings. First, larger groups live on significantly larger territories, and, accordingly, within-group changes in group size among years positively predict within-group changes in territory size. Second, relative group size between neighbouring groups predicts the location of the territory boundary between them, and, accordingly, within-neighbour-pair variation in relative group size among years predicts within-neighbour-pair variation in their boundary location among years. Finally, while larger groups occupy larger territories the relationship is not proportional; the *per capita* area utilised significantly decreases with increasing group size. Together, our findings provide rare support for the hypothesis that larger groups are better able to monopolise space, but highlight a need for caution when assuming that individuals will accrue *per capita* resource benefits from cooperating to increase group size because the latter yields benefits in inter-group competition for space.

2.2 INTRODUCTION

Cooperative territorial defence is among the most widespread forms of cooperation, but the mechanisms by which it yields benefits to the co-operators remain unclear. Group-living species often defend resources within territories from intrusions by rivals and neighbouring groups (Boydston *et al.* 2001; Mares *et al.* 2012), resulting in the formation and defence of distinct territorial boundaries (Adams 1990). The number of individuals in a group is likely to influence the group's capabilities in defending a territory and each group may be trying to expand its territory at the expense of the neighbouring groups (Adams 1990). Territorial conflicts involving antagonistic intergroup interactions over boundary disputes have been observed in many species, including lions *Panthera leo* (McComb *et al.* 1994; Grinnell *et al.* 1995), chimpanzees *Pan troglodytes* (Wilson *et al.* 2001), meerkats (Young 2003; Mares *et al.* 2012), red-cockaded woodpeckers *Leuconotopicus borealis* (Walters 1990), Galápagos mockingbirds *Mimus parvulus* (Curry and Grant 1990) and *Azteca trigona* ants (Adams 1990). A large number of studies now suggest that larger groups are more likely to win territorial contests (e.g. Woolfenden and Fitzpatrick 1990; Radford 2003; Thompson *et al.* 2017) and that intruding groups are numerically assessed based on group size relative to the territory owners (e.g. McComb *et al.* 1994; Wilson *et al.* 2001; Benson-Amram *et al.* 2011; see Table 1). If larger groups are able to win such inter-group interactions with smaller groups, larger groups might be able to expand their territories to the detriment of smaller neighbours. However, the ability of larger groups to gain territory over the long-term has rarely been shown.

Positive relationships between group size and territory size have now been described in numerous bird (e.g. Parry 1973; Rabenold 1990; Jansen 1999; Duca and Marini 2014; see Table 2) and mammal species (Bowen 1982; Marino *et al.* 2012; see Table 2), and a small number of studies have also shown that experimentally weakened groups lose territory to their larger neighbours (e.g. Carlson 1986; Adams 1990). Together these findings suggest that larger groups may indeed enjoy space use benefits arising from their differential success in inter-group conflict. However, very few studies have specifically isolated the relationship

between within-group variation in group size over time and within-group variation in territory size over time, from among-group variation in both traits (e.g. Woolfenden and Fitzpatrick 1978; Brooker and Rowley 1990; Ligon and Ligon 1990; Radford and Du Plessis 2004a; see Table 2). This is important, as groups may vary markedly in their territory quality, leaving groups on higher quality territories potentially both better placed to compete for space (given higher local resource availability) and larger (given higher reproductive success born of higher territory quality), yielding potentially non-causal positive associations between among group variation in group size and territory size. Furthermore, the effect of the relative group size of competing neighbouring groups on the location of their shared territorial boundary location has rarely been studied (Table 1), and few studies, have established whether changes in relative group size among neighbouring pairs over time predict the movement of their shared territorial boundary over time (Adams 1990). Findings of this kind would help to implicate inter-group competition *per se* as a driving force in generating positive relationships between group size and territory size, given that such a relationship could also arise in the absence of inter-group competition if larger groups simply needed to range more widely (e.g. to meet their nutrition needs; Bowen 1982; Kruuk and Parish 1982). Longitudinal spatial studies are therefore needed to specifically investigate the effects of within-group variation in group size over time on within-group variation in space use over time, in species whose territory locations (and hence likely relative qualities) change little over time.

Studies investigating the spatial consequences of group size under inter-group competition are essential for understanding the direct and indirect fitness payoffs from some of the most pervasive forms of cooperation in animal societies. For example, by contributing to cooperative activities with the potential for positive effects on group size (such as offspring care and anti-predator vigilance), individuals may stand to gain downstream direct fitness benefits arising from the opportunity to live in a larger group as a result (the group augmentation hypothesis for the evolution of cooperation; Kingma *et al.* 2014). One mechanism through which such group augmentation benefits are often thought to accrue is positive effects of group size on territory size (e.g. arising via enhanced success in inter-group conflict, Clutton-Brock *et al.* 1999; Heg and Hamilton 2008; Mosser and Packer 2009). Such effects

could, for example, afford individuals in larger groups with improved access to resources (e.g. if larger groups enjoy improved *per capita* space in which to access resources, Marino *et al.* 2012) and/or the opportunity to inherit part or whole of a larger territory in which to breed downstream (Woolfenden and Fitzpatrick 1978). Arguments of this kind thereby require that within-group increases in group size over time are indeed associated with within-group increases in territory size (which has rarely been shown; Table 2). Such arguments also highlight a need to better understand whether the differential success of larger groups in spatial competition translates in to *per capita* increases in available space (and hence resources) with increasing group size; a point that has attracted limited attention to date (e.g. Marino *et al.* 2012).

Here we investigate whether larger groups are better able to monopolise space in a species that shows cooperative territorial behaviour, the white-browed sparrow-weaver (*Plocepasser mahali*). White-browed sparrow-weavers are group territorial cooperatively breeding birds that defend year-round territories in the semi-arid areas of southern Africa (Collias and Collias 1978; Lewis 1982b). Social groups actively compete for territory and all group members are involved in territorial intergroup interactions (Collias and Collias 1978; Lewis 1982b; Wingfield and Lewis 1993). However, the immediate consequences of intergroup interactions are often unclear as the majority of border disputes end by each group flying back to toward the centre of its territory (Collias and Collias 1978), and hence it is not clear in this species whether larger groups necessarily 'win' individual interactions. Groups contain 2-12 individuals, including a dominant male and female and subordinates of both sexes that have typically delayed dispersal from their natal group (Collias and Collias 1978; Lewis 1982b; Ferguson 1988; Harrison *et al.* 2013b, 2014). The dominant pair completely monopolise reproduction within the group, but dominant males lose approximately 15% of paternity to extra-group males, principally dominant males in other groups (Harrison *et al.* 2013a, b; Cram *et al.* 2015). Subordinate helpers engage in a number of different cooperative behaviours including offspring provisioning, sentinelling, weaving and territorial defence (Collias and Collias 1978; Lewis 1982a, b; Walker *et al.* 2016).

The aims of this study are to use longitudinal spatial data from wild sparrow-weaver groups to investigate (i) whether larger groups occupy larger territories, (ii) whether relative group size among neighbours influences the location of their mutual territorial boundary, and (iii) whether members of larger groups enjoy increases in the *per capita* space available. In each case I utilise a within-group centring statistical approach (Van de Pol and Wright 2009) to investigate the relationship between within-group variation over time in group size (and relative group size) and within-group variation over time in the territorial traits in question (territory size, boundary location and *per capita* territorial space). This technique can be used in mixed models to separate between-subject effects (i.e. evolutionarily fixed behavioural responses based on the individual or its class) from within-subject effects (i.e. facultative behavioural responses or phenotypically plastic) (Van de Pol and Wright 2009). This separation is important because it allows differentiation between alternative biological hypotheses and prevents us from inaccurately generalizing within-subject relationships to between-subject relationships, or vice versa (Van de Pol and Wright 2009).

Type	Species	Contest outcome for larger groups	Change in territory size or boundaries tested?	Reference
Willingness to approach	<i>Monias benschi</i>	+	N	Seddon and Tobias 2003
	<i>Callithrix jacchus</i>	+	N	Lazero-Perea 2001
	<i>Pan troglodytes</i>	+	N	Wilson <i>et al.</i> 2001; Wilson and Wrangham 2003
	<i>Crocuta crocuta</i>	+	N	Benson-Amram <i>et al.</i> 2011
	<i>Cebus capucinus</i>	+/0	N ^b	Crofoot <i>et al.</i> 2008
	<i>Mungos mungo</i>	+	N	Furrer <i>et al.</i> 2011
Non-physical Contest	<i>Campylorhynchus nuchalis</i>	+	N ^c	Rabenold 1990
	<i>Psilorhinus morio</i>	+	N	Hale <i>et al.</i> 2003
	<i>Aphelocoma coerulescens</i>	+	N	Woolfenden and Fitzpatrick 1990
	<i>Monias benschi</i>	+	N	Seddon and Tobias 2003
	<i>Phoeniculus purpureus</i>	+	N	Radford 2003
	<i>Castor fiber</i>	+	N	Campbell <i>et al.</i> 2005
	<i>Canis lupis</i>	+	N	Harrington and Mech 1979
	<i>Panthera leo</i>	+	N	McComb <i>et al.</i> 1994; Grinnell <i>et al.</i> 1995; Heinsohn 1997
	<i>Suricata suricatta</i>	+	N	Young 2003
	<i>Canis simensis</i>	+	N	Sillero-Zubiri and Macdonald 1998
Physical Contest	<i>Azteca trigona</i>	+	Y ^a	Adams 1990
	<i>Panthera leo</i>	+	Y	Mosser and Packer 2009
	<i>Mungos mungo</i>	+	N	Thompson <i>et al.</i> 2017
	<i>Suricata suricatta</i>	+	N	Young 2003

Table 1. Studies that examined the relationship between relative group size and performance in inter-group conflict (specifically willingness to approach the opposing group, and success in non-physical and physical contexts). ^aExperimental removal of group members. ^bOutcome depended upon location in territory (see Crofoot *et al.* 2008) ^cInvestigated changes in boundary location or territory size but did not test statistically.

Species	Relationship between group size and territory size	Within-group variation tested?	References
<i>Dacelo gigas</i>	+	N	Parry 1973
<i>Melanerpes formicivorus</i>	+	N	MacRoberts and MacRoberts 1976
<i>Aphelocoma coerulescens</i>	+	Y	Woolfenden and Fitzpatrick 1978
<i>Neothraupis fasciata</i>	+	N	Duca and Marini 2014
<i>Parus niger</i>	+	N	Tarboton 1981
<i>Campylorhynchus nuchalis</i>	+	N	Rabenold 1990
<i>Nesomimus parvulus</i>	+	N ^a	Curry and Grant 1990
<i>Orthonyx spaldingii</i>	+	N	Jansen 1999
<i>Malurus splendens</i>	+	Y	Brooker and Rowley 1995
<i>Phoeniculus purpureus</i>	+	Y	Ligon and Ligon 1990 (Kenya)
	0	Y	Radford and Du Plessis 2004a (South Africa)
<i>Cisticola chiniana</i>	0	Y ^b	Carlson 1986
<i>Leuconotopicus borealis</i>	0	N	Hooper <i>et al.</i> 1982
<i>Porphyrio porphyrio melanotu</i>	0	N	Craig 1979
<i>Opisthocomus hoazin</i>	0	N	Strahl and Schmitz 1990
<i>Buteo galapagoensis</i>	0	N	Faaborg and Bednarz 1990
<i>Crotophaga sulcirostri</i>	-	N	Vehrencamp 1978
<i>Hydrochoerus hydrochaeris</i>	+	N	Herrera and Macdonald 1989
<i>Canis latrans</i>	+	N ^a	Bowen 1982
<i>Panthera leo</i>	+	N	Mosser and Packer 2009
<i>Canis simensis</i>	+	N	Marino <i>et al.</i> 2012
<i>Castor fiber</i>	0	N	Campbell <i>et al.</i> 2005

Table 2. Studies that examined the relationship between group size and territory size. All studies examined among-territory variation. Those studies that also investigated the effects of within-group variation in group size over time on territory

size are indicated with a 'Y'. ^aEffects of within-group variation mentioned but not evidently tested statistically. ^bExperimental removal of group members.

2.3 METHODS

2.3.1 Study Population

Data were collected on a population of 40 white-browed sparrow-weaver groups, which have been monitored since 2007 and inhabit an area of about 1.5 km² in the semi-arid Kalahari desert at Tswalu Kalahari Reserve, South Africa (27°16'S, 22°25'E). Group size was determined by establishing the number of birds consistently seen foraging together and roosting in the central trees of a territory (Cram *et al.* 2015) and group compositions were recorded on a weekly basis (Harrison *et al.* 2013b). Individual birds were fitted with a metal ring and 3 colour rings for identification purposes (SAFRING licence 1444) (Cram *et al.* 2015), and males and females could be distinguished by beak colour (Leitner *et al.* 2009; Cram *et al.* 2015).

2.3.2 Ranging Data

Ranging data was collected over the course of three consecutive breeding seasons spanning the Southern summers of 2012-13, 2013-14, and 2014-15. The locations of key features in the landscape, such as trees and burrow systems (hereafter termed 'reference marks') were collected using a Garmin GPS (accuracy $\pm < 5$ m) to create a printed map with these features on, on which the location of the group could be plotted by hand by the observer in the field. Field trials confirmed that this approach was a more spatially accurate means of recording group locations than observers using a GPS to record their own position and then estimating the distance and bearing to the group's location for use in subsequently adjust the GPS-derived location to provide that of the focal group. Prior to the start of ranging data collection each season, a set of distinctive reference marks were recorded within and in the immediate surroundings of each focal group's territory. This was performed by the same observer that ultimately collected the ranging data for those focal groups, to ensure that the reference marks were clear to the end-user. All observers were given a plant identification guide (information taken from van Rooyen, 2001) to facilitate the use of key species as reference marks, including shepherd's tree

(*Boscia albitrunca*), camel thorn (*Acacia erioloba*), grey camel thorn (*Acacia haematoxylon*), black thorn (*Acacia mellifera*; subspecies *detinens*), raisin bush (*Grewia flava*), three thorn (*Rhigozum trichotomum*), candle thorn (*Acacia hebeclada*) and Kalahari current (*Rhus tenuinervis*). Reference marks also included dead trees, trees with roosts and nests, areas of open ground, and large holes and burrow systems.

Ranging data collection was conducted for one continuous 30-minute period per week for each focal group, during which time the location of the focal group was recorded at successive 5-minute intervals. The ranging observation periods started between 06:45 and 09:00 in the morning and were all conducted between October and April (the principal breeding season of the birds). Once the social group had been located, a period of 5 minutes was left before the collection of the first location point (hereafter termed 'fixes'), to allow the group to settle following the observer's arrival (though every effort is made throughout our fieldwork to avoid influencing the movements of the birds). Throughout each ranging observation period the observer followed and recorded the location of the group's dominant pair (or the dominant male if the dominant female was incubating), as subordinates are known to occasionally conduct exploratory movements outside their group's territory.

2.3.3 Inter-Group Interaction Data

During weekly group visits, all inter-group interactions (hereafter termed 'IGIs') observed were recorded. These are defined as incidents in which multiple members of more than one group interact, typically in aggressive territorial disputes. They typically occur when both groups are at the borders of their territories (Wingfield *et al.* 1993), and will most likely involve vocal and visual displays, which may escalate to aggression between specific individuals. For each IGI, the location midway between the locations of the two groups engaged in the dispute was recorded using a handheld Garmin GPS (accuracy $\pm < 5$ m).

2.3.4 Territory Mapping and Territory Size Calculation

The fixes collected as described above were then used to map and estimate the areas (in hectares; Ha) of each focal group's territory in each of the three breeding seasons. Territories were mapped by creating minimum convex polygons (hereafter termed 'MCPs') (Seaman *et al.* 1999) around the fixes collected, using the Home Range Tools extension (Rodgers *et al.* 2007) in ArcGIS version 10 (ESRI, Redlands, California, USA), with one MCP being calculated for each group for each breeding season. MCPs were created by joining the peripheral points of a group of fixes with straight lines, so that external angles were always greater than 180° (Mohr 1947; Rodgers *et al.* 2007). As 100% MCPs, in which all the fixes are included within the polygon, are likely to over-estimate territory size through the inclusion of spatial outliers born of the visitation of rarely used areas (Harris *et al.* 1990; Radford and du Plessis 2004a), we followed other authors in calculating 95% MCPs (e.g. Jansen 1999, Seddon *et al.* 2003, Radford and du Plessis 2004a). Duplicate points (e.g. if the dominant pair remained in the same location for >5 minutes) were removed from the data set to avoid division by zero errors during the calculation of 95% MCPs (Rodgers *et al.* 2007). 95% MCPs were chosen for the assessment of territory size (and subsequently boundary locations; see below) as (i) there were no physical boundaries to restrict the birds' movements within our study site (e.g. mountains or water bodies), and (ii) the location data were auto-correlated within observation sessions (as successive locations within a session were recorded just 5 mins apart), rendering MCPs more suitable than kernel methods (Seaman *et al.* 1999). The 95% MCPs were regarded in subsequent analyses as reflecting the groups' territories for a given breeding season (Figure 1).

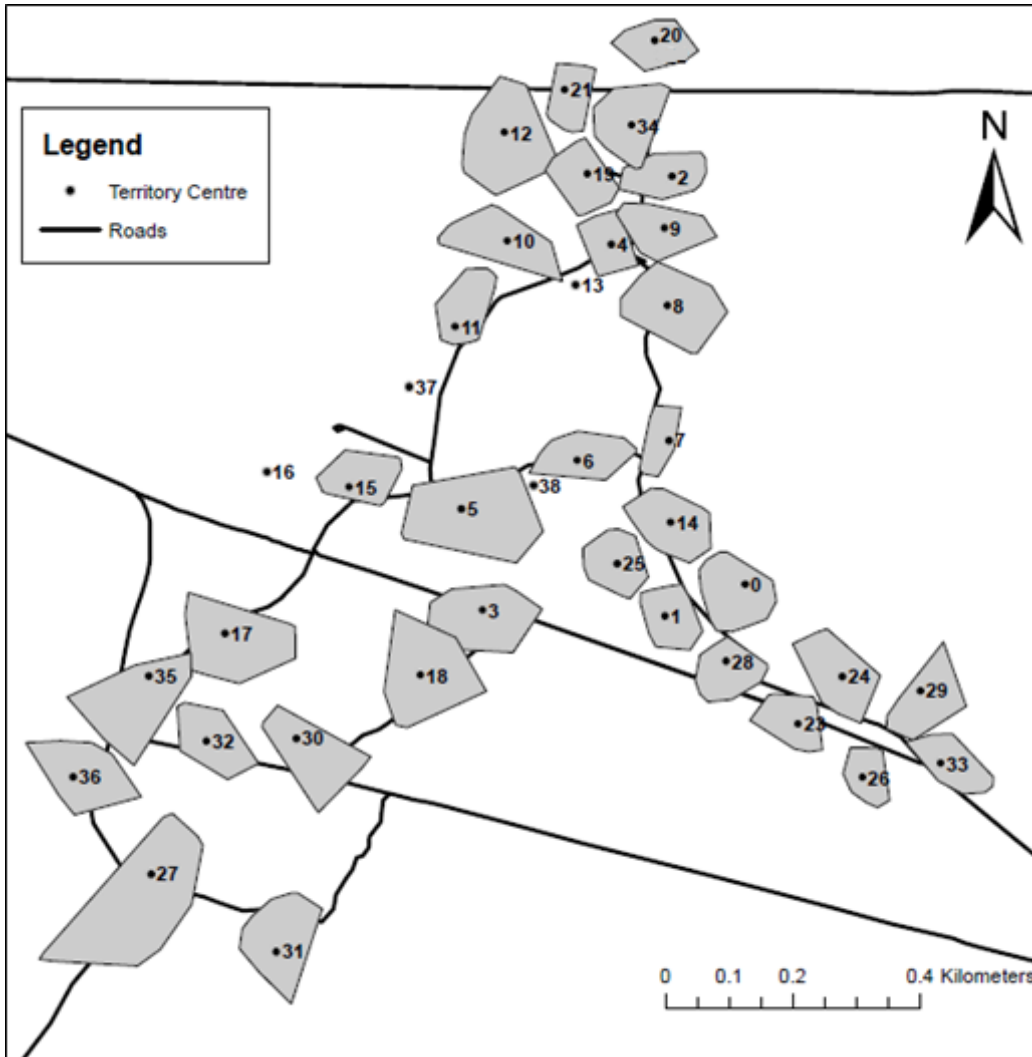


Figure 1 - Map of territories on the study site at Tswalu Kalahari Game Reserve from the 2014-15 breeding season. Each numbered point represents the centroid of the group's ranging points during this season. Grey minimum convex polygons represent a group's mapped territory. Territories were not mapped for the groups that lack grey polygons.

2.3.5 Boundary Location Mapping

The centre of each focal group's territory was calculated separately for each season by calculating the arithmetic mean of all x (longitude) and y (latitude) co-ordinates from the 95% MCPs and these locations were then averaged across seasons for each group to determine an overall 'territory centroid' for each group for the entire study. Groups were included in the 'boundary location' calculations (and subsequent analyses) in any seasons in which they were considered to be a neighbour to another group. Neighbours were defined as groups whose 95% MCP borders lay at some point within 50 m of another group's 95% MCP border, with no third group's territory lying in between. To avoid pseudoreplication in the boundary location analyses, one group in each pair of neighbours was termed the 'Focal group' and the other the 'Neighbour group', and the location of their shared boundary in a given season was then calculated only from the perspective of the Focal group. As such, each unique pair of neighbouring groups contributed just one 'boundary location' data point per season to the analysis. The Focal group was arbitrarily assigned as the group in each neighbouring pair whose group-name's first letter came earliest in the alphabet (e.g. the group 'Aye-Aye' would be the Focal group in the neighbouring pair of groups 'Aye-Aye' and 'Bongo'; social groups were arbitrarily assigned group-names for ease of recall in the field). As each group could have multiple neighbours, a given group in a given season could have been considered the 'Focal group' in one or more neighbouring pairs, while also being considered the 'Neighbour group' in one or more other neighbouring pairs (e.g. while 'Bongo' would be the 'Neighbour group' in its interactions with 'Aye-Aye' it would be the 'Focal group' in its interactions with 'Chimp').

The 'boundary location' for each neighbouring pair in each season was calculated from the perspective of the Focal group as follows. Using ArcGIS version 10 (ESRI, Redlands, California, USA), a straight line was drawn connecting the territory centroids of the two neighbouring groups. The territorial boundary between the two groups was then defined as being located mid-way between (i) the point at which this line intersected the Focal group's 95% MCP border, and (ii) the point at which this line intersected the Neighbour group's 95% MCP border. For the purposes of

analysis, the 'boundary location' was then calculated as the distance from the Focal group's territory centroid to this mid-way point, divided by the total distance between the Focal and Neighbour groups' territory centroids. Boundary locations are therefore proportions, ranging from 0-1, with boundary locations of <0.5 being closer to the Focal group's territory centroid than the Neighbour group's territory centroid, locations of 0.5 being halfway between the Focal and Neighbour groups' territory centroids, and locations of >0.5 being closer to the Neighbour group's territory centroid.

2.3.8 Statistical Analysis

All statistical analyses were conducted in R (version 3.3.0, R Core Team, Vienna, Austria). Linear mixed effect models (LMMs) were used for the majority of analyses (lme4, Bates *et al.* 2014; exceptions are described below). All predictor terms of interest were initially entered to create a full model and then they were dropped sequentially, the least significant term first, until only the terms whose removal would have significantly weakened the explanatory power of the model remained, yielding the final model. The significance of a term was derived by dropping it from the final model (if it was part of the final model), or adding it to the final model and then dropping it (if it was not part of the final model). Random terms were defined to take into account repeated measures (e.g. of groups and seasons) and were not subjected to model selection. All full models were subjected to a visual inspection of their residual plots, which did not reveal clear deviations from homoscedasticity or normality (following the application of normalising transformations to the response term in some cases; see below). Conditional (total variance explained by the best-supported model, i.e. both fixed and random factors) and marginal (variance explained by fixed effects alone) R^2 formulations were calculated for all models to provide meaningful information with regard to the fixed and random factors (Nakagawa & Schielzeth 2013). In all model tables, the 'average effect' refers to the model coefficient for a given independent variable.

Locations of inter-group interactions

For each IGI involving a given group, two distances were calculated: (i) the distance between the IGI location and the group's territory centroid for that season; and (ii) the distance between the IGI location and the nearest point on the group's 95% MCP territory boundary for that season. For each group that was involved in more than 1 IGI during the entire study, an average was taken of the distance to the centroid values and the distance to the boundary values for all of the IGIs in which that group was involved, yielding one value for each metric for each group. A paired t-test was then used to test whether IGIs occur closer to territorial boundaries than centres.

Do larger groups have larger territories?

A LMM was used to investigate the relationship between group size and territory size (N = 85 territory size measures for 34 groups across 3 breeding seasons). Each group's group size was calculated as the number of adults (>1 year old), with an average value calculated for each group in each breeding season (i.e. the period running 1 September to 30 April). Territory size was calculated from the areas of the 95% MCPs (see above). The distribution of territory sizes was normalised for analysis using a square-root transformation. In addition to group size, the following predictor terms were included as fixed effects: rainfall (the total amount for the season in question), minimum number of neighbouring groups (i.e. the number of other groups with mapped territories whose 95% MCP territory boundaries came within 50m of that of the focal group; see also below), group sex ratio (the number of group members known to be male divided by group size), presence of known immigrants (the number of group members known to be immigrants divided by group size) and the total number of location fixes collected for that group in that season (to control for variation in sampling effort among groups and years). Variation in group sex ratio and the presence of immigrants were controlled for in the model to allow for the possibility that different classes of individual contribute differing amounts to cooperative territorial defence. Group ID and Season (2012-13, 2013-14 or 2014-15) were fitted as random effects. Ranging data was not collected for all groups in all years due to logistical constraints in the field, and so the minimum number of

neighbouring groups (see above for definition) is a minimum because in some cases there were candidate neighbouring groups whose territories were not mapped in certain years (and hence these groups could not be formally classified as neighbours by this definition). Variation in the number of neighbouring group was controlled to allow for the possibility that groups with fewer neighbouring groups are less constrained in their territory size, independent of their group size (as they may be surrounded by more uncontested space). Table 3 shows the full model, with the terms in bold being in the final model.

Do within-group changes in group size over time predict variation in territory size?

We then complemented the above analysis with an explicit test of whether *within-group* variation in group size over time predicts variation in territory size, using the same data set (N = 85 territory size measures for 34 groups across 3 breeding seasons). As for the previous model, an LMM was used containing all the same terms with the exception of group sex ratio and the presence of immigrants which were excluded, and group size, which was partitioned into *mean group size* (the mean group size value for that group over all of the seasons in which it appeared in the analysis) and *delta group size* (the group size of that group in the focal season minus the group's *mean group size*). This within-group centring approach, following Van de Pol and Wright (2009), leaves the *delta group size* term reflecting the effect of within-group variation in group size. Table 4 shows the full model, with the terms in bold being in the final model.

Does the relative group size of neighbouring groups predict variation in the location of their shared boundary?

A LMM was used to investigate the relationship between relative group size and boundary location (N = 100 boundary location measures for 27 focal group-neighbour pairs across 3 breeding seasons). Relative group size was calculated as the Focal group's group size divided by the Neighbour group's group size (see above for the classification of pairs in to Focal and Neighbour groups). Boundary location was calculated as the distance from the Focal group's territory centroid to the shared

boundary, divided by the distance from the Focal group's territory centroid to the Neighbour group's territory centroid (see above for details). In addition to the relative group size of the Focal group, the following predictor terms were included as fixed effects: rainfall, total number of fixes for the Focal group, total number of fixes for the Neighbour group. Focal group ID, Neighbour group ID and Season were also fitted as random effects. Table 5 shows the full model, with the terms in bold being in the final model.

Do within-group changes in relative group size to neighbours over time predict variation in the location of their shared boundary?

We then complemented the above analysis with an explicit test of whether *within-group* variation in relative group size to neighbours over time predicts variation in boundary location, using the same data set (N = 100 boundary location measures for 27 focal group-neighbour pairs across 3 breeding seasons). As for the previous model, an LMM was used containing all the same terms with the exception of the Focal group's relative group size which was partitioned into *mean relative group size* (the mean relative group size value for each Focal group over all of the data points for that Focal group) and *delta relative group size* (the relative group size of the Focal group for a given data point minus the Focal group's *mean relative group size*), following Van de Pol and Wright (2009). Table 6 shows the full model, with the terms in bold being in the final model.

Do larger groups have more territorial space per individual?

A LMM was used to investigate the relationship between group size and territory size per individual (N = 85 territory size per group member measures for 34 groups across 3 breeding seasons). The territory size per individual was calculated as the area of the mapped 95% MCP divided by group size, with one value calculated for each group mapped in each season. The distribution of territory size per individual was normalised for analysis using a square-root transformation. In addition to group size, the following fixed effects were included: rainfall, minimum number of neighbouring groups, group sex ratio, presence of known immigrants and the total number of

location fixes collected for that group in that season. Group ID and Season were fitted as random effects. Table 7 shows the full model, with the terms in bold being in the final model.

Do within-group changes in group size over time predict variation in territorial space per individual?

We then complemented the above analysis with an explicit test of whether *within-group* variation in group size over time predicts variation in territory size per individual, using the same data set (N = 85 territory size per group member measures for 34 groups across 3 breeding seasons). As for the previous model, an LMM was used containing all the same terms with the exception of group sex ratio and the presence of immigrants, which were excluded, and group size which was partitioned into *mean group size* and *delta group size* (see above for details). Table 8 shows the full model, with the terms in bold being in the final model.

2.4 RESULTS

Over the three breeding seasons of ranging data collection, territory sizes were estimated using 95% MCPs for an average of 28.3 (range 22 - 32) social groups per season. Mapping of the social group territories (e.g. see Figure 1) confirmed that groups' territories are frequently bounded by those of neighbouring groups and that there is virtually no spatial overlap between neighbouring territories, suggesting that exclusive access to space is contested between groups. Indeed, across all three seasons a total of 77 inter-group interactions (IGIs) were recorded involving a total of 24 different social groups. These IGIs were led by the dominant male and female in each group, typically involved several birds in each group engaging in long, intense and coordinated "chorus" vocalisations, flights to high perches in trees, and grass-carrying behaviours (see Wingfield *et al.* 1993 for further details), and in some cases escalated into chases and physical fights (personal observation). Across all three seasons, all recorded IGIs occurred close to the territorial boundaries of the groups involved (within 25m of their territorial borders, as mapped by 95% MCP), with not a single IGI being recorded in the core area of a group's territory (>25 m inside their territorial border). Accordingly, IGIs were found to occur significantly closer to groups' territory boundaries (mean \pm S.E. distance = 11.5 ± 2.4 m) than their territory centroids (mean \pm S.E. distance = 70.7 ± 3.2 m; Paired *t*-test; *n* = 24 groups, $t_{23} = 25.13$, d.f. = 23, $p < 0.001$).

A mean of 60.2 ± 2.15 fixes (range 18-104) were collected for each group per season (totalling 5117 fixes for 34 groups over the course of the three seasons). All analyses conducted below controlled for potential effects of variation among groups in the number of fixes collected, by including the number of fixes as covariate predictors in the models. The findings presented are those arrived at subjecting the 'number of fixes' terms to model selection (like all other fixed effects fitted). However, we also verified that the statistical significance of the group size and relative group size terms across all models presented were qualitatively unchanged if we took the conservative measure of forcing the retention of the 'number of fixes' terms in the final model regardless of their significance. This was true in all but one case, and that case is detailed in the following paragraph. The 95% MCP territories calculated

from these fixes ranged in size from 0.2 to 3.12 ha, and averaged (mean \pm S.E.) 1.18 \pm 0.07 ha over the 3 breeding seasons. Territory sizes were at their smallest in 2013-14 (mean \pm S.E. = 0.89 \pm 0.06 ha; n = 31 social groups) when group sizes were also at their smallest (mean \pm S.E. = 2.55 \pm 0.12 individuals; N = 31 social groups), and were at their largest in 2012-13 (mean \pm S.E. = 1.64 \pm 0.14 ha; n = 22 social groups) when group sizes were also at their largest (mean \pm S.E. = 3.79 \pm 0.28 individuals; n = 22 social groups).

Do larger groups have larger territories?

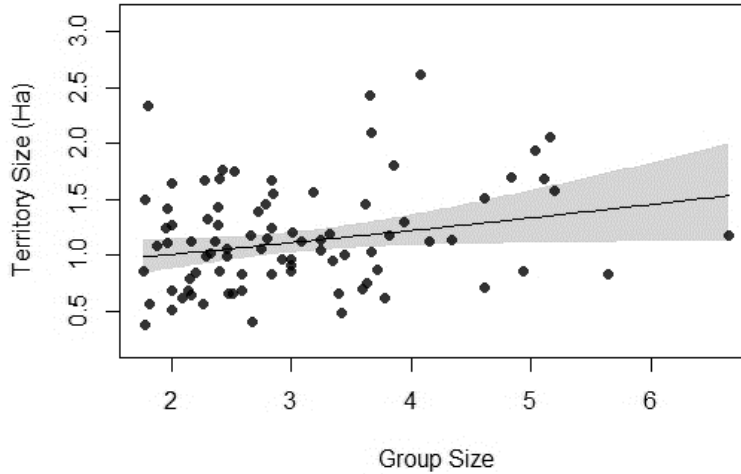
Statistical modelling of territory sizes revealed that there was a significant positive relationship between group size and territory size (LMM: $\chi^2_1 = 4.21$, $p = 0.040$; Figure 2a; Table 3), after controlling for significant negative effects of both rainfall (LMM: $\chi^2_1 = 7.1$, $p = 0.008$; Table 3) and minimum number of neighbouring groups (LMM: $\chi^2_1 = 10.36$, $p = 0.001$; Table 3). Variation among groups in the number of location fixes collected did not explain significant variation in their resulting territory size (LMM: $\chi^2_1 = 2.14$, $p = 0.14$; Table 3). If we took the conservative step of forcibly retaining this 'number of fixes' term in the final statistical model, the effect of group size on territory size changed from being marginally significant ($p=0.040$) to marginally non-significant ($p=0.083$). However, in our partitioned version of this analysis (presented immediately below) the specific effect of interest (within-group variation in group size over time; delta group size) did remain a significant predictor of territory size even when the number of fixes was forcibly retained in that final model. 37% of the variance was explained by the fixed factors. 37% of the variance was explained by the fixed and random factors.

Do within-group changes in group size over time predict variation in territory size?

Partitioning variation in group size into within- and among-group variation revealed that within-group variation in group size (i.e. changes in a given group's size between seasons; 'delta group size') significantly positively predicted variation in territory size (LMM: $\chi^2_1 = 5.49$, $p=0.02$; Figure 2b; Table 4), after controlling for the significant negative effects of rainfall (LMM: $\chi^2_1 = 6.30$, $p = 0.01$; Table 4) and minimum number

of neighbours (LMM: $\chi^2_1 = 10.60$, $p = 0.001$; Table 4). The significant positive effect of within-group variation in group size was not accompanied by a significant positive effect of among-group variation in group size (LMM: $\chi^2_1 = 0.48$, $p = 0.49$; Table 4). This suggests that groups that are generally large don't generally have larger territories. 38% of the variance was explained by the fixed factors. 38% of the variance was explained by the fixed and random factors.

(a)



(b)

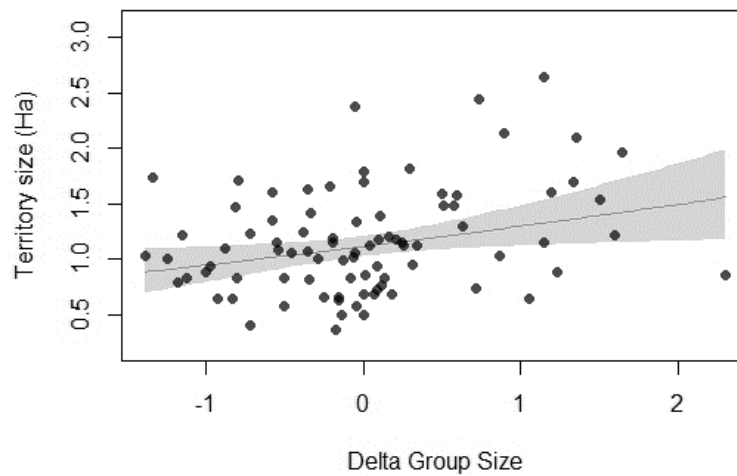


Figure 2 - (a) The model predicted relationship between group size and territory size (see Table 3). **(b)** The model predicted relationship between the within-group change in group size (delta group size) and territory size (see Table 4). In both plots the points show model residuals (i.e. data after being corrected for all terms present in the final model), lines are model predictions for the focal relationship, and shaded areas represent 95% confidence intervals around the model predicted relationship having accounted for the effects of any other significant terms in the models (see Tables 4 and 5).

Table 3. General Linear Mixed Model investigating the effect of group size on territory size (N = 85 territory size measures for 34 groups across 3 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Min Number Neighbouring Groups	1.48	-0.087	0.021	10.36	1	0.0013
Rainfall	1.48	-0.0011	0.00032	7.10	1	0.0077
Group Size	1.48	0.051	0.024	4.21	1	0.040
Total Number of Fixes	1.36	0.0018	0.0012	2.14	1	0.14
Group Sex Ratio	1.45	0.10	0.19	0.29	1	0.59
Presence of Known Immigrants	1.45	0.027	0.085	0.10	1	0.75

Table 4. General Linear Mixed Model investigating the effect of within-group change in group size on territory size (N = 85 territory size measures for 34 groups across 3 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Min Number Neighbouring Groups	1.58					
Groups		-0.085	0.021	10.60	1	0.0011
Rainfall	1.58	-0.00093	0.00033	6.30	1	0.012
Delta Group Size	1.58	0.083	0.035	5.49	1	0.019
Total Number of Fixes	1.46	0.0016	0.0012	1.77	1	0.18
Mean Group Size	1.51	0.022	0.032	0.48	1	0.49

Does the relative group size of neighbouring groups predict variation in the location of their shared boundary?

Territorial boundaries between neighbouring groups ranged from 31.09 to 182.60 m away from the territory centroid of the 'Focal group' of the pair (mean \pm S.E. = 71.6 \pm 1.7 m; n = 27 neighbouring pairs of groups over 3 seasons). The territory centroids of neighbouring group pairs ranged from 81.4 to 218.7 m away from each other (mean \pm S.E. = 139.2 \pm 2.8 m; n = 27 neighbouring pairs of groups over 3 seasons). The relative group size of the 'Focal group' in a neighbouring pair compared to the 'Neighbour group' significantly predicted the location of the boundary between the two groups; the larger the relative group size of the Focal group the closer the boundary was (proportionally; see methods) to the centroid of the Neighbour group (LMM: $\chi^2_1 = 12.38$, $p = <0.001$; Figure 3a, Table 5). There were no other significant predictors of boundary location (Table 5). 11% of the variance was explained by the fixed factors. 33% of the variance was explained by the fixed and random factors.

Do within-group changes in relative group size to neighbours over time predict variation in the location of their shared boundary?

Partitioning variation in relative group size to neighbours into *within-* and *among-group* variation revealed that *within-group* variation in the relative group size of the Focal group (i.e. changes between seasons in a given Focal group's size relative to that of its Neighbour; termed 'delta relative group size') significantly positively predicted variation in boundary location (LMM: $\chi^2_1 = 7.56$, $p=0.006$; Figure 3b; Table 6), after controlling for the significant positive effects of among-group variation in relative group size (LMM: $\chi^2_1 = 5.60$, $p = 0.02$; Table 6). 11% of the variance was explained by the fixed factors. 33% of the variance was explained by the fixed and random factors.

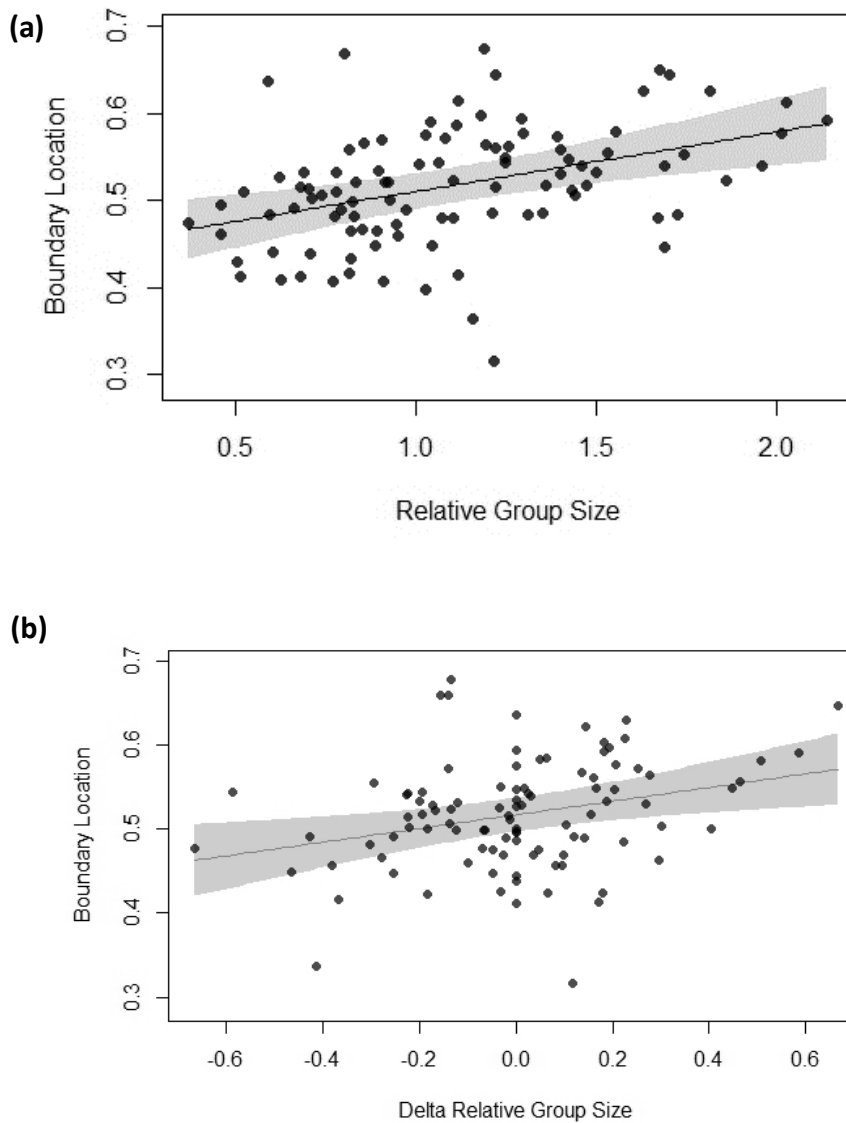


Figure 3 – Model predicted relationships between **(a)** relative group size and boundary location (see Table 5), and **(b)** within-group change in relative group size (delta relative group size) and the boundary location (see Table 6). In both plots the points show model residuals, the lines show model predictions for the focal relationship, and the shaded areas represent 95% confidence intervals around the model predicted relationship, having accounted for the effects of any other significant terms in the models (see Tables 5 and 6).

Table 5. General Linear Mixed Model investigating the effect of relative group size on boundary location (N = 100 boundary location measures for 27 focal group-neighbour pairs across 3 breeding seasons). Terms in bold were retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Relative Group Size	0.44	0.0684	0.0189	12.38	1	<0.001
Number of Other Neighbours	0.45	-0.0078	0.0082	0.90	1	0.34
Number of Focal Group Fixes	0.43	0.0002	0.0004	0.34	1	0.56
Rainfall	4.48E-01	-1.88E-05	8.88E-05	0.04	1	0.83
Number of Neighbour Group Fixes	0.44	1.28E-05	0.0004	0.001	1	0.97

Table 6. General Linear Mixed Model investigating the effect of within-group change in relative group size on boundary location (N = 100 boundary location measures for 27 focal group-neighbour pairs across 3 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	P
Delta Relative Group Size	0.45	0.0815	0.0289	7.43	1	0.006
Mean Relative Group Size	0.45	0.0587	0.0248	5.60	1	0.02
Number of Other Neighbours	0.47	-0.0083	0.0082	1.04	1	0.31
Number of Focal Group Fixes	0.44	0.0002	0.0004	0.32	1	0.57
Rainfall	4.55E-01	-8.60E-06	9.04E-05	0.01	1	0.92
Number of Neighbour Group Fixes	4.51E-01	2.29E-05	0.0004	0.004	1	0.95

Do larger groups have more territorial space per group member?

The mean territory size per group member averaged 0.41 ± 0.03 ha and ranged from 0.11-1.68 ha ($n = 34$ social groups across three breeding seasons). Statistical modelling of territory space per group member revealed that there was a significant negative relationship between group size and territory size per group member (LMM: $\chi^2_1 = 14.28$, $p < 0.001$; Figure 4a; Table 7), after controlling for significant negative effects of both rainfall (LMM: $\chi^2_1 = 9.45$, $p = 0.002$; Table 7) and minimum number of neighbouring groups (LMM: $\chi^2_1 = 6.21$, $p = 0.01$; Table 7). 35% of the variance was explained by the fixed factors. 37% of the variance was explained by the fixed and random factors.

Do within-group changes in group size over time predict variation in territorial space per individual?

Partitioning variation in group size into within- and among-group variation revealed that within-group variation in group size (i.e. changes in a given group's size between seasons; termed 'delta group size') significantly negatively predicted variation in territorial space per individual (LMM: $\chi^2_1 = 4.60$, $p = 0.03$; Figure 4b; Table 8), after controlling for the significant negative effects of rainfall (LMM: $\chi^2_1 = 5.66$, $p = 0.02$; Table 8), among-group variation in group size (LMM: $\chi^2_1 = 11.58$, $p < 0.001$; Table 8) and minimum number of neighbours (LMM: $\chi^2_1 = 9.94$, $p = 0.002$; Table 8). 37% of the variance was explained by the fixed factors. 38% of the variance was explained by the fixed and random factors.

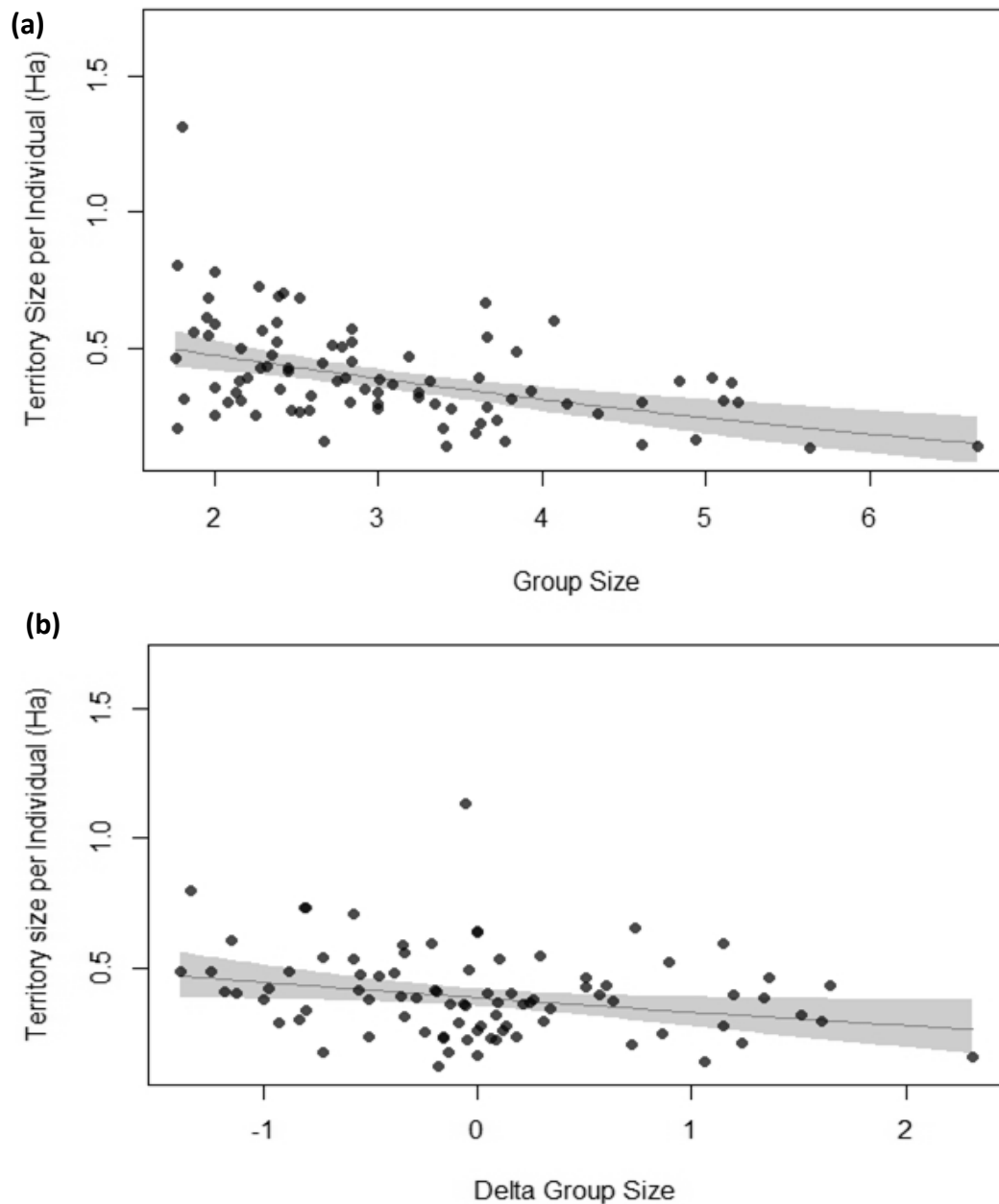


Figure 4 Model predicted relationships between **(a)** group size and territory size per individual (see Table 7) and **(b)** the within-group change in group size (delta group size) and territory size per individual (Table 8). In both plots the points show model residuals, the lines show model predictions for the focal relationship, and the shaded areas represent 95% confidence intervals around the model predicted relationship, having accounted for the effects of any other significant terms in the models (see Tables 7 and 8).

Table 7. General Linear Mixed Model investigating the effect of group size on territory size per group member (N = 85 territory size per group member measures for 34 groups across 3 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	<i>P</i>
Group Size	1.17	-0.065	0.015	14.28	1	<0.001
Min Number Neighbouring Groups	1.17					
		-0.055	0.013	9.45	1	0.0021
Rainfall	1.17	-0.00063	0.00019	6.21	1	0.012
Total Number of Fixes	1.08	0.0014	0.00073	3.50	1	0.06
Presence of Known Immigrants	1.14					
		0.035	0.053	0.44	1	0.51
Group Sex Ratio	1.15	0.073	0.12	0.36	1	0.55

Table 8. General Linear Mixed Model investigating the effect of within-group change in group size on territory size per group member (N = 85 territory size per group member measures for 34 groups across 3 breeding seasons). Terms in bold were retained in the minimal model, while terms in normal type-face were not retained in the minimal model.

	Intercept	Average Effect	Standard Error	χ^2	df	<i>P</i>
Mean Group Size	1.19	-0.082	0.020	11.58	1	<0.001
Min Number Neighbouring Groups	1.19	-0.055	0.013	9.94	1	0.0016
Rainfall	1.19	-0.00055	0.00020	5.66	1	0.017
Delta Group Size	1.19	-0.046	0.021	4.60	1	0.032
Total Number of Fixes	1.11	0.0013	0.0007	2.96	1	0.086

2.5 DISCUSSION

Our ranging data highlighted that groups' territories are frequently bounded by those of neighbouring groups and that there is virtually no overlap between neighbouring territories, suggesting that exclusive access to space is likely to be contested between groups. Indeed, large numbers of aggressive inter-group interactions (IGIs) were observed and these were concentrated in the boundary areas between groups. Our statistical analysis of the causes of variation in territory size revealed a significant positive relationship between group size and territory size. By partitioning group size into mean group size and delta group size, our results suggest that the 'within-group' change in group size positively predicts territory size. Moreover, we found a significant positive relationship between relative group size and boundary location, which suggests that groups that are relatively larger than their neighbours had their territory boundaries closer to the territory centroid of their neighbouring groups. By partitioning relative group size into mean and delta relative group size, our analyses show that relative group size positively predicts boundary location, indicating that groups compete with their neighbouring groups for space. By having a numerical advantage, larger groups can expand the size of the territory by pushing boundaries shared with neighbours towards their neighbours' territory centroid. Furthermore, our results showed that there is a significant negative relationship between group size and territory size per individual, and that this relationship holds for within-group variation in group size too (allowing us to rule out the possibility that among-group variation in some factor correlated with group size, such as territory quality, could be driving this relationship). Together these findings show that inter-group competition *per se* is a driving force in generating positive relationships between group size, territory size and boundary location. While there were changes in territory size and boundary locations of the groups over time, the locations of the groups' territories remained broadly similar over the three years of this study, and indeed have done so over the 10 years of monitoring of this population to date.

2.5.1 Intergroup Interactions

From the results of this study, it seems likely that IGIs reflect competition for control of land area to secure defensible resources, such as food and the materials required to build nests and roosts. White-browed sparrow-weavers forage and gather the materials required for weaving almost exclusively on their territories and vigorously defend their territory (Collias and Collias 1978). This suggests that the outcome of IGIs may impact the formation of distinct territorial boundaries and where they are located. These territories are vigorously defended by groups and yet intrusions are common by rivals (Collias and Collias 1978). Intruders could use IGIs to assess resource holding power of other neighbouring groups with a view to expand into neighbouring groups' territories (Carlson 1986; Adams 1990). In green woodhoopoes (*Phoeniculus purpureus*), while there is no evidence that permanent changes in territory size arising from IGIs (Radford and du Plessis 2004a), successful intruding groups often forage and examine roosts/nests in the neighbouring territory (Ligon and Ligon 1990). However, in white-browed sparrow-weavers, the immediate consequences of IGIs are often unclear as the majority of border disputes end by each group flying back to toward the centre of its territory (Collias and Collias 1978).

Alternate functions of IGIs could include the assessment of the presence or absence of breeding vacancies, potential breeding partners and dispersal opportunities in neighbouring groups, as has previously been suggested for white-browed sparrow-weaver IGIs (Lewis 1981; Lewis 1982b). In common marmosets (*Callithrix jacchus*), the involvement of helpers in both territorial defence and non-aggressive IGIs suggests that IGIs may function in part in this species in the assessment of extra-group breeding opportunities (Lazaro-Perea 2001). Additionally, in green woodhoopoes, the experimental removal of breeding individuals from a group increased the vocal territorial rallying contributions of the remaining group members, leading to the suggestion that vocalisation during IGIs could advertise breeding vacancies (Radford 2003). In order to better understand the function and consequences of IGIs in white-browed sparrow weaver societies, future studies should investigate the determinants of both individual variation in contributions to IGIs and IGI outcomes (in particular whether larger groups are more likely to 'win').

2.5.2 Impacts of Group Size on Territorial Defence

Previous investigations of the relationship between group size and territory size have produced a variety of results (Table 2). Groups may vary markedly in their territory quality which leaves groups on higher quality territories potentially better placed to compete for space (given higher local resource availability) and larger (given higher reproductive success born of higher territory quality). Studies have shown that territory quality is an important correlate of group size in birds (e.g. Gaston 1976; Carlson 1986; Walters 1990) and mammals (e.g. Mosser and Packer 2009; Marino *et al.* 2012). Large territories could be the most productive enabling the groups holding these territories to produce more offspring and harbour larger group sizes, which potentially explains a positive relationship between group size and territory size (Woolfenden and Fitzpatrick 1978). However, few studies have investigated the effect of 'within-group' changes in group size on territory size (Table 2). It is important to remove such factors which may influence variation in group size and territory size relationships due to the non-causal positive associations formed. By conducting this within-group centring approach, this study has shown that group size predicts territory size and we are able to rule out the possibility that among-group variation in some factor correlated with group size, such as territory quality, could be driving the relationship between group size and territory size. Intriguingly, while groups occupied larger territories in years when they were larger (as indicated by the positive effect of delta group size in Table 4), groups that were larger on average did not live on territories that were larger on average (as indicated by the lack of an effect of mean group size in Table 4). This might be the case if, for example, groups that were larger on average tended to live on better quality territories (indeed this could explain why they tended to be large) that were consequently able to support a higher density of resident birds.

While numerous studies have shown that larger groups are more likely to win competitive territorial interactions, very few have investigated whether large relative group size conveys long-term spatial benefits as a consequence (see Table 1). In *A. trigona* ants, after contests at the boundary, losing colonies retreated when outnumbered and boundary locations shifted so that larger colonies claimed a greater share of the territory (Adams 1990). While we did not look at the immediate

effects of IGIs, there may be long-term effects of IGIs resulting in neighbours competing for space. If groups that are larger than their neighbours they may need to range more to meet the nutritional demands (e.g. Bowen 1982; Kruuk and Parish 1982) which may result in moving boundary locations, expanding into neighbouring territories. However, we might expect to see few, if any, territorial disputes and territorial defence from neighbouring groups. Alternatively, relatively larger groups may live on better quality territories they may be in a better condition and can invest more in territorial defence and possible expansion through aggressive intergroup interactions. Our partitioned result shows that the movement of boundary locations is a product of inter-group competition for space, favouring larger groups expanding at the expense of smaller neighbouring groups.

The amount of resources a group is able to defend depends on its competitive ability. By winning contests at the boundary, larger groups may be able to maintain their relatively larger group size compared to their neighbours through the recruitment of members of neighbouring groups. A certain amount of space within a territory is required to satisfy resource needs to survive, for example, foraging (Hixon 1980) and roosting (Williams *et al.* 1991; du Plessis and Williams 1994) for each individual group member. By expanding into a smaller neighbour's territory after aggressive IGIs and moving the boundary closer to a neighbour's territory centroid, there is increased intra-group competition in the losing group (Fitzpatrick and Bowman 2016) and more space available in the winning territory. Therefore, the recruitment of willing individuals from the losing groups ensures that winning groups increase their group size relative to their neighbour (Müller and Bell 2009). However, it has been suggested, in white-browed sparrow-weavers, individuals are more likely to successfully recruit into smaller groups rather than large groups, possibly as a result of better territory defence in larger groups (Lewis 1982b). Additionally, the majority of white-browed sparrow-weavers subordinates delay dispersal and monitor for neighbouring breeding vacancies in the safety of the natal territory (Lewis 1982b; Harrison *et al.* 2014), potentially resulting in greater recruitment into smaller groups. A few studies have shown that subordinate males often defect to neighbouring groups after territorial conflicts apparently in pursuit of better breeding opportunities (e.g. pale-winged trumpeter, *Psophia leucoptera*, Sherman 1995; subdesert

mesites, *Monias benschi*, Seddon and Tobias 2003). A group with a surplus of males may always approach intruding groups; allowing the non-breeding males to assess potential breeding opportunities, and the dominant pair approaching with a purpose to expel the intruding group to which valuable group members (i.e. helpers) may defect (Seddon and Tobias 2003).

Having lots of neighbours may increase the risk of losing territory, especially as the number of neighbours had a significant negative effect on both territory size and territory size per individual. For example, lion prides are at greater risk of losing territory when they have many neighbours (Mosser and Packer 2009). Therefore, in white-browed sparrow-weavers, having a larger group may prove to be particularly beneficial when groups have many neighbours because they are able to protect maintain their territory boundaries against intruding groups (Collias and Collias 1978; Lewis 1982b). Like lions (McComb *et al.* 1994) and chimpanzees (Wilson *et al.* 2001), white-browed sparrow-weavers may be able to assess their numerical advantage/disadvantage in relative group size in comparison to neighbouring groups using IGIs using acoustic signals during chorusing. It is important to avoid unwinnable contests to avoid costs such as injury, death, reduced survival prospects or lost reproductive opportunities (McComb *et al.* 1994; Wilson *et al.* 2001). An accurate assessment of intruders may allow individuals and groups to predict contest costs without actually incurring them (Adams 1990; Wilson *et al.* 2001) If a group knew they were larger than the intruding group, they might be more willing to approach (McComb *et al.* 1994; Wilson *et al.* 2001; Seddon and Tobias 2003) and may be more likely to expand into neighbouring territories (Adams 1990). However, this needs to be experimentally tested, possibly using playback experiments, as demonstrated in green woodhoopoes (Radford 2003) and subdesert mesites (Seddon and Tobias 2003).

2.5.3 Implications for the Benefits of Cooperation

Numerical advantages over neighbouring groups in territorial intergroup competition may give rise to long-term advantages of sociality and cooperation (Mosser and

Packer 2009). One mechanism which may yield direct fitness benefits of cooperation to co-operators is group augmentation, where helpers work to increase group size (e.g. by helping to rear offspring that are not their own and/or engaging in cooperative anti-predator vigilance) in order to enjoy the benefits of living in a large group downstream, such as improved survival and future reproductive success (Kingma *et al.* 2014). Through the positive effects of group size on territory size, which could conceivably yield increases in resource availability for all group members, group members may gain direct benefits by improving their survival. Consistent with this logic, our study has provided rare evidence that within-group increases in group size are indeed associated with within-group increases in territory size, and that within-group increases in relative group size are associated with the expansion of territorial boundaries with neighbours. However, our findings have also highlighted that the *per capita* space available to group members appears to decrease with increasing group size, suggesting a need for caution when invoking *per capita* resource acquisition benefits to individuals from cooperative investments in group augmentation. Therefore, it is possible, that group augmentation in this species actually involves reductions in total *per capita* resource availability within the territory. However, under this scenario, group augmentation could still yield net direct fitness benefits overall if any reduction in predation risk arising from increased group size (i) increased individuals' ability to access these resources (e.g. by increasing *per capita* foraging success by affording opportunities for reduced vigilance; Bertram 1980; Elgar 1989) or simply (ii) yielded survival benefits which more than offset any fitness costs arising from any reduction in *per capita* space.

Alternatively, even if *per capita* resource availability does indeed fall with increasing group size, asymmetries among individuals in their ability to compete for those resources may still leave more dominant individuals standing to benefit from cooperative group augmentation. For example, helpers in cooperatively breeding vertebrates are invariably older than the offspring that they are helping to rear, and in many species older age and/or larger size convey advantages in social competition (e.g. Galapagos mockingbirds, Curry 1988; Arabian babblers; Zahavi 1990; Mexican jays, *Aphelocoma wollweberi*, Brown and Brown 1990; Florida scrub jays, Woolfenden and Fitzpatrick 1990). As such, helpers might actually suffer little

reduction in resource availability (or possibly enjoy net resource benefits) from rearing additional group members, given that they may ultimately be able to dominate them in resource competition. As is frequently the case in cooperative breeders, the resources that larger territories might offer white-browed sparrow weavers constitute not only food but breeding sites. Indeed, it has been suggested that one major potential downstream direct benefit to non-breeding subordinates of increases in territory size is an associated increase in the likelihood of being able to carve out part of the natal territory to form a breeding territory of their own, in a process known as budding (Woolfenden and Fitzpatrick 1978). Territorial budding from the natal territory is frequently observed in white-browed sparrow weavers, particularly among females (Harrison *et al.* 2014); the more philopatric sex in this species (Harrison *et al.* 2014). The opportunity for subordinate female sparrowweavers to gain differential downstream direct benefits from cooperation in this way would provide one potential explanation for the fact that subordinate females in this species contribute significantly more to cooperative offspring care than subordinate males (Young, unpublished data). While rearing more group members could also entail a risk of increasing competition for such budding opportunities, preliminary analyses suggest that only the oldest subordinates in a group engage in budding, and so helpers may actually face little risk of competition from the additional group members that they rear (Young, unpublished data).

2.5.4. Conclusions

To conclude, white-browed sparrow-weaver groups actively defend their territories against neighbouring rival groups (Collias and Collias 1978; Lewis 1982b) and our study shows that group size determines the size of territories and that relative group size determines the location of boundaries, suggesting that larger groups can hold on to, defend and expand their territories to create larger territories, thus gaining control of limited space. Our findings have also highlighted that the *per capita* space available to group members appears to decrease with increasing group size, suggesting a need for caution when invoking *per capita* resource acquisition benefits to individuals from cooperative investments in group augmentation.

Numerical advantages over neighbouring groups in territorial intergroup competition may give rise to long-term advantages of sociality and cooperation by providing fitness benefits of living in a large group (Mosser and Packer 2009). Helpers in many cooperative societies and group-living species may therefore work to augment group size (Mosser and Packer 2009; Kingma *et al.* 2014).

Thesis Discussion

In this thesis, I have examined the impacts of conspecific out-group threats on group behaviour in a cooperative species, the white-browed sparrow-weaver. Firstly, I investigated the effects of out-group breeder replacement on helper retention and reproductive success and I found that neither is negatively impacted by out-group breeder replacement, even though breeder replacement was expected to destabilise cooperative groups due to reductions in relatedness. I then investigated the role of group size in between-group conflict over space and I found that larger social groups dominate competition for space. Below, I discuss the major findings of this thesis, the implications for our understanding of out-group threats, including individuals and groups, on within- and between-group behaviours. Additionally, I discuss how cooperation may reduce the potential costs of out-group rivals and, where appropriate, suggest future research objectives.

Out-group individuals may challenge the breeding position of group members (Koenig *et al.* 1983; Raihani *et al.* 2010; Mares *et al.* 2011; Lowney *et al.* 2017), which may give rise to costs to the remaining group members. Such costs may include increased within-group conflict over resources and reproduction, and reductions in nepotistic behaviours and relatedness (Hannon *et al.* 1985; Ekman *et al.* 1994; Cockburn 1996; Emlen 1997; Russell 2004; Eikenaar *et al.* 2007). These increased costs are generally expected to erode the net benefits of delayed dispersal, resulting in a reduction in the retention of helpers, with potentially negative impacts on within-group reproductive success (Emlen 1997; Cornwallis 2010). However, in Chapter 1, I found that helper retention was not negatively affected by out-group breeder replacement. In fact, females were *more* likely to remain in the group after the replacement of their father than in control periods. Chapter 1 also showed that breeder replacement did not have overall negative effects on within-group reproductive success. Breeding was not delayed and there were few negative impacts upon reproductive success (the total number of fledglings produced). However, after a breeder replacement, there was a decreased number of eggs laid but there was no change in egg hatchability. Together, these results may suggest that there is increased reproductive conflict after breeder replacement between

mothers and daughters (Koenig & Stacey 1990; Emlen 1997) for access to unrelated breeding partners in family groups, including the new dominant male. However, further work investigating sexually-related aggression and within-group reproductive conflict, is required because we don't know to what extent this occurs, in this species. After a male breeder replacement, the probability of chicks fledging actually increased, which may suggest that subordinates continue to contribute to the care of offspring even after a decrease in relatedness to any subsequent offspring from the new dominant pair. The change in probability in the disappearance of subordinates suggests that subordinate helpers are not leaving their natal group after breeder replacement, even with potential increased within-group conflict. Therefore, subordinates may still be able to gain direct fitness benefits from group-living, for example, improved survival (Stacey and Ligon 1987; Clutton-Brock *et al.* 1999; Dierkes *et al.* 2005; Ridley *et al.* 2013) or future reproductive opportunities where a subordinate female may "bud off" (Woolfenden & Fitzpatrick 1978) part of the territory with an immigrant male.

Many studies of cooperative breeders have reported low rates of divorce (e.g. Stacey & Koenig 1990; Walters 1990). When dominant individuals are monogamous, their successive generations of offspring are as related to each other as any of them would be to their own young (Bourke 2014). Therefore, subordinates may employ strategies to help prolong the tenure of the dominants (who are usually their parents), and to help them raise future offspring (who are usually their full siblings) because, if they lose their tenures to outsiders, the subordinates will suffer a loss in inclusive fitness (Woolfenden and Fitzpatrick 1984; Sherman and Jarvis 2002; Williams 2004). In meerkats, it has been suggested that female dominants might receive assistance from other female group members in deterring any potential challengers, due to a reduction in inclusive fitness should the dominant be displaced by an immigrant female, whose offspring they would be less related to (Broom *et al.* 2009; Sharp & Clutton-Brock 2011). By helping the dominants to maintain their position, subordinates can maximize their indirect fitness benefits if they are unable to take the breeding position for themselves or there is a lack of access to unrelated breeding partners within their groups (Young 2009; Sharp & Clutton-Brock 2011). However, the lack of marked negative impacts of breeder replacement on helper

retention and reproductive success, in the study species in this thesis, may mean breeders do not need to align their interests with their mate or subordinate philopatric offspring if their reproductive tenure and success can be maintained independently.

A large number of studies suggest that larger groups are more likely to win territorial contests (e.g. Woolfenden and Fitzpatrick 1990; Radford 2003; Thompson *et al.* 2017) and that there are positive relationships between group size and territory size in numerous species (e.g. Parry 1973; Rabenold 1990; Jansen 1999; Marino *et al.* 2012; Duca and Marini 2014). However, prior to this study, it was not well known whether large groups winning intergroup interactions translates into success in spatial competition. Groups often defend against neighbouring or unfamiliar groups that might attempt to acquire the group's resources or encroach into their territory (Radford 2003; Wilson & Wrangham 2003; Mosser & Packer 2009). In Chapter 2, the results revealed three key findings. First, larger groups lived on significantly larger territories, and, accordingly, within-group changes in group size among years positively predicted within-group changes in territory size. Second, relative group size between neighbouring groups positively predicted the location of the territory boundary between them, and, accordingly, within-neighbour-pair variation in relative group size among years predicted within-neighbour-pair variation in their boundary location among years. Finally, while larger groups occupy larger territories the relationship is not proportional; the per capita area utilised significantly decreases with increasing group size. This suggests that larger groups dominate smaller groups in competition for space.

Cooperative territorial defence is among the most widespread forms of cooperation. The amount of resources a group can secure is dependent in part on its competitive ability against other neighbouring groups in the population (Carlson 1986) and larger groups are frequently more likely to win contests across species (e.g. Radford 2003; Seddon & Tobias 2003; Young 2003; Mosser & Packer 2009; Thompson *et al.* 2017). In this species, further work is required to improve our understanding of between-group conflict, such as investigating the causes of variation in the characteristics of intergroup interactions (i.e. duration, intensity, outcome), studying individual contributions to these interactions, and establishing whether white-browed sparrow-

weavers can assess numerical advantage or disadvantage in contests using playback experiments. Groups may employ strategies to maintain a large group size, relative to that of neighbouring groups. To maintain a large group size, subordinate helpers may work to increase group size by improving the reproductive success of the dominant (known as group augmentation) in order to enjoy the benefits of living in a large group, such as improved survival and future reproductive success (Woolfenden and Fitzpatrick 1978; Clutton-Brock *et al.* 1999; Kingma *et al.* 2014). Therefore, by using group augmentation to increase group size to maintain a relatively larger group compared to neighbours, there may be strong selection for cooperative territorial defence, especially if success in conflict relies on cohesion between group members, to overcome the threat of between-group territorial competition (Reeve & Hölldobler 2007; Radford 2008).

To conclude, this thesis aimed to investigate the impacts of conspecific out-group threats on within- and between-group behaviours. We have shown that out-group breeder replacement does not have negative impacts on family cohesion and reproduction and that larger groups dominate smaller groups in between-group competition for space in the cooperatively breeding white-browed sparrow-weaver. Future work needs to address questions comparing the impacts of out-group threats within- and between-group conflict across species, will allow a greater understanding about the evolution of cooperative behaviour and how it is maintained (Radford 2016; Thompson 2017).

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