Cooperative Breeding in the Southern Anteater-Chat

Sexual Disparity, Survival and Dispersal

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Abstract

Group-living sets the scene for complex social behaviours such as cooperative breeding, and exploring the factors that shape group-living is crucial in understanding these behaviours. This thesis explores the ecology of a population of the facultative cooperative breeding southern anteater-chat (Myrmecocichla formicivora), a group-living bird species endemic to southern Africa. It reveals a breeding system based around a breeding pair and up to three auxiliary males. Despite equal numbers of males and females produced as fledglings there was a surplus of adult males, which remained philopatric. Dispersal was strongly female biased. Females dispersed within their first year, they dispersed further than males, and they lost the benefits of the natal site. The sex skew in the population suggested that these factors drive differential mortality, with juvenile females having much lower annual survival than juvenile males. Adult survival was higher, with female survival only slightly lower than male survival. Dispersal distances suggested that males selected the breeding location, nearer to their natal site. There was no evidence of surplus non-breeding females. On the loss of a breeding female there was no replacement until new females entered the population, yet if a breeding male disappeared the female promptly re-paired with a male from another group. There was no indication of birds floating in the population, and if males were orphaned or widowed they joined other groups as unrelated helpers in preference to floating. There was no sign of inter-group or individual aggression among chats, and unrelated helpers were peacefully accepted into groups, suggesting mutual benefits. In fact all birds in a group helped raise offspring of the breeding pair, and groups with more helpers fledged more offspring, which implies that both direct and indirect fitness benefits can be gained through joining a group and helping. There was surprisingly little inheritance of breeding position by auxiliaries, and strikingly low levels of extra-pair paternity. This study suggests that the Southern anteater-chat group structure arises through male philopatry due to a shortage of breeding females, the benefits of remaining on the natal site and helping, and the potentially high costs of living alone.

Keywords: Southern anteater-chat, Myrmecocichla formicivora, cooperative breeding, social evolution, behavioural ecology, delayed dispersal, family living, Africa


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List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.


Publications not included in this thesis


Introduction

Cooperative breeding, delayed dispersal and helping

Cooperative behaviour occurs in a large number of vertebrate species, and living in cooperative groups has both costs and benefits (Krause & Ruxton 2002). Cooperative breeding groups are most often family groups in which cooperation is between relatives. In such groups individuals can benefit from helping relatives, thereby enhancing their own fitness through kin selection mechanisms (Hamilton 1964). However interactions between close relatives are just one type of group social behaviour and cooperative groups often contain unrelated individuals. There is growing evidence that related and unrelated individuals can gain direct fitness benefits from living in groups and also even from helping to rear unrelated offspring (Clutton-Brock 2002). Direct and indirect fitness benefits can both arise through a multitude of processes, and it appears that complex evolutionary mechanisms give rise to and maintain cooperative breeding in vertebrates.

The wide range of cooperative breeding systems found among birds is a consequence of complex interactions between evolutionary history, life-history traits, and ecological relationships. The strategy of a particular bird species is expected to be determined by the costs and benefits of each of these components in each specific situation (Covas & Griesser 2007). Historically it has been suggested that 3% of birds breed cooperatively (Arnold & Owens 1998), but recent estimates have put the number much higher, at 9% of all avian species, with 6.5% known to be cooperative, and a further 2.5% inferred as breeding cooperatively (Cockburn 2006). This is a conservative figure with respect to delayed dispersal and family living since both can occur without cooperative breeding, and both delayed dispersal and family living have probably been frequently overlooked (Griesser & Barnaby 2010). One pattern which emerges is that the proportion of cooperatively breeding birds is high in the Southern Hemisphere (Russell 2000; Russell 2004), particularly Australia (Rowley 1976), but also in Sub-Saharan Africa (Edwards & Boles 2002; Ekman 2006). Yet detailed studies of species residing in these southern regions are relatively scarce.

Cooperative breeding is closely linked both with family living and delayed dispersal, and it is worthwhile briefly outlining these three phenomena. Cooperative breeding is commonly described as when two or more breeding birds are together with one or more non-breeding individuals who help to
raise offspring which are not their own (Brown 1987). Most frequently these auxiliaries are offspring of the breeding individuals, but they can be siblings or other relatives, or unrelated individuals (Ekman et al. 2004). The term cooperation is taken here to involve interaction behaviour which is mutually beneficial (West & Griffin 2007). Where group members are related to the breeding pair, I use the term family living. The situation is further complicated because family living does not necessarily entail cooperative breeding, and offspring can stay in a family yet not engage in helping (Ekman et al. 2001), although the exact nature of cooperation among group members can be difficult to identify (Hatchwell 2009). These situations can still involve cooperation, even if it is not distinctly cooperative breeding. This separation leads to the definition of a third term, delayed dispersal, which is said to occur when offspring remain with their parents, usually on the natal territory, beyond the time at which they would have good survival prospects independent of their parents (Griesser & Barnaby 2010).

Indirect fitness benefits gained by auxiliaries helping to raise the offspring of relatives have been a major focus of many early studies of cooperative breeding species (Dickinson & Hatchwell 2004). There is little evidence that indirect benefits are sufficient to give rise to cooperative breeding in the first place (Ekman et al. 2004), although these benefits may be sufficient to sustain it (Cockburn 1998; Ekman 2006). However the majority of helpers gain a lower fitness, in the short term, by helping than they do by breeding independently (Dickinson & Hatchwell, 2004; Emlen et al., 1991). This leads to the crucial question of why do they stay?

One of the key theories on cooperative breeding proposes that delayed dispersal is the result of constraints on dispersal opportunities (Emlen 1982), the idea being that individuals stay because there are no viable options for breeding independently. These constraints include a lack of suitable habitat, a shortage of breeding partners, high dispersal costs and a low probability of successful independent reproduction (Koenig et al. 1992; Emlen 1995; Hatchwell & Komdeur 2000). Constraints appear to explain dispersal choices in many species (Emlen 1982; Emlen 1994), but in parallel many species which face constraints do not delay dispersal (Ekman et al. 1994), and it appears that constraint-based theories are too broad to have much predictive power (Kokko & Ekman 2002). Whereas constraints are seen as the ‘best of a bad job’ situation where dispersal is delayed because dispersal costs are high, there is increasing evidence that delaying dispersal can have intrinsic benefits (Emlen 1994; Ekman et al. 2000; Dickinson 2004), and can be seen as an adaptive decision (Covas & Griesser 2007). Such benefits include the benefits of staying on the natal site, such as familiarity with food sources and safe roosting sites (Stacey & Ligon 1991; Perrin & Lehmann 2001). However family formation does not come about solely on the decisions of the offspring; in order to stay offspring have to be allowed to stay by their parents, which in effect requires parental facilitation (Brown & Brown
Cooperative breeding in the southern anteater-chat

In addition to permissive facilitation parents can also provide nepotistic benefits to their offspring (Brown & Brown 1984; Ekman et al. 1994). This can include nepotistic predator protection, aided access to food and possible thermal roosting benefits (Du Plessis & Williams 1994; Ekman et al. 2000; Griesser & Ekman 2004). Benefits can also be obtained independent of kin structure, through group augmentation, including the formation of social alliances, and deterrence and dilution effects (Stacey & Ligon 1991; Kokko et al. 2001). In addition to these benefits group members may also benefit from learning opportunities, in terms of rearing young, foraging and predator avoidance, and the potential indirect genetic benefits of helping to rear related individuals (Dickinson & Hatchwell, 2004). If breeding opportunities are restricted or early breeding is costly, an alternative to remaining in a breeding group as a non-breeder is to float. A floater is defined as an unpaired bird with a more variable range and itinerant behaviour (Koenig et al. 1992; Kokko & Sutherland 1998; Pen & Weissing 2000). More recent ideas incorporate life history, phylogeny and ecology in a cost benefit appraisal, with delayed dispersal being considered an adaptive decision based on a multitude of factors, considering the whole lifespan of an individual (Covas & Griesser 2007). This complexity hints at why it has been so difficult to find general correlates to the occurrence of cooperative breeding (Bennett & Owens 2002; Koenig & Dickinson 2004).

The path to cooperative breeding requires a number of life-history choices, including to forgo independent reproduction, to delay dispersal, or to disperse into, or return to an already established breeding group, instead of floating, and to engage in helping behaviour (Griesser & Barnaby 2010). In an adaptive framework, these decisions are based not only upon a balance between the cost and benefits with respect to being an auxiliary in a group, but also on the cost and benefits to the breeders in a group, and potentially the other group members (Covas & Griesser 2007). It would appear that phylogenetic history predisposes a species to family living (Russell 1989), but that both life-history and ecological factors create a complex web of interactions which determine the specific family dynamics (Hatchwell & Komdeur 2000; Covas & Griesser 2007). Detailed investigations into a relatively small number of cooperative species have given rise to different and wide-ranging ideas as to the mechanisms which lead to family formation, often with strong support for particular proximate factors influencing the species in question, but there has so far been little success in predicting the occurrence of cooperative breeding based on overarching ecological or life-history characteristics (Ekman et al. 2004). However there are some general features which characterise a significant proportion of cooperative breeding bird species including low fecundity, long developmental periods, extended parental care and high survival (Du Plessis et al. 1995; Arnold & Owens 1998; Hatchwell & Komdeur 2000; Hatchwell 2009). These features also
predominate among birds in the southern hemisphere regions (Martin 1996; Russell 2000; Peach et al. 2001; Covas 2002). Different workers have made conflicting predictions based on the idiosyncrasies of their own particular species, nevertheless each study is valuable as it adds to the sum of knowledge and increases the power of comparative studies to identify overarching factors (Bennett & Owens 2002). Key questions in studies of cooperative breeders are: What are the origins of the extra group members? Why when physiologically capable do certain individuals not disperse or breed? For almost all species it has been shown not to be a case of physiological immaturity (Stacey & Koenig 1990). The answers lie in long-term investigations of demography and genetic structure of specific populations along with studies of behaviour within these populations.

The objectives

This thesis focuses on gaining a deeper understanding of the ecology of a wild population of Southern anteater-chat *Myrmecocichla formicivora*, a passerine endemic to southern Africa. I examine the bird’s social structure using a combination of demographic data, behavioural observations and genetic information, and investigate their dispersal and helping decisions.

The Southern anteater-chat is an opportunistic cooperative breeder which inhabits semi-arid, predominantly grassland habitats. Pedigree data, home range, group composition, mortality and nesting information, along with behavioural observations were gathered, on my study site near Kimberley in South Africa, over a period of four years (2008-2011), and a suit of microsatellite markers was developed to complement and extend the pedigree data, allowing investigation of survival, parentage patterns and dispersal strategies within the population. The basic breeding biology and diet of the Southern anteater-chat has been studied on a small scale elsewhere (Herholdt 1987; Earle & Herholdt 1988; Earle & Louw 1988). Here I compare and contrast some of these results, but look more specifically and in more detail at aspects specifically relating to their cooperative breeding system.

The main objectives were to identify key mechanisms behind cooperative breeding in this species. The overarching questions are which individuals delay dispersal and why? Of those individuals who disperse, when do they disperse and where do they go? Of the non-breeding individuals which individuals help, what do they gain from helping? What alternative choices do they have?

I examine data on family group structure and the nature of cooperation within this species. In particular I was interested to see the variation in group structure, and who the helpers were, including their sex, age and within-group relationships. I wanted to examine the breeding system in terms of whether it was predominantly monogamous, or if there was evidence of po-
lygamous breeding patterns, extra-pair paternity or incestuous relationships, all of which influence the patterns of helping (Davies 1985; Hartley & Davies 1994). I also wanted to investigate dispersal choices, including the options open to birds other than to disperse to breeding opportunities, or to stay and help. To understand the evolution of cooperative breeding it is crucial to gain insights into why capable individuals forgo independent breeding (Komdeur et al. 2008a).

I was also interested in the option for chats to float either alone or with groups of none breeders, to remain as a non-helper, or to join another group as an unrelated helper. Floating is a costly activity (Ridley et al. 2008) and as such is often involuntary and a result of being actively driven out from a group (Ekman et al. 2002; Ridley et al. 2008), and it can be informative about the costs and benefits of living in groups. Joining another group as an unrelated helper can indicate competition within the family group (Ekman et al. 2002), or potential access to reproduction through becoming a non-family group member (Whittingham et al. 1997; Cockburn 2004). Another question of interest was that of sex skew within the population. There is a predominant skewed sex ratio among birds in favour of males (Mayr 1939; Donald 2007). Cooperation and helping behaviour is a life-history trait, and has been shown to be positively correlated with longevity (Arnold & Owens 1998).

This study investigates survival in the chats, and examines the differential survival between males and females and different age groups. It also explores how this may relate to the sex ratio in fledglings and adult birds in the study population. Many avian cooperative breeders also have sex biased dispersal, with the bias being more frequently towards female dispersal (Greenwood & Harvey 1982). Sex skew in numbers and dispersal can affect both the availability of breeding partners and the propensity to delay dispersal (Cockburn 1998). Within this context I explore potential costs and benefits to individuals with contrasting dispersal opportunities and breeding prospects. The key to understanding how different factors interact in any particular situation is through detailed studies of specific species and populations.

Paper I looks at overarching features of the population structure, the sex composition, group arrangement, breeding biology and predation, of the Southern anteater-chat. Paper II investigates differential survival with respect to sex, age and environmental parameters. Papers III and IV investigate female and male choice respectively with particular regard to dispersal, helping, female replacement and breeding. Paper V describes the development and implementation of a suite of microsatellites allowing pedigrees and pairwise relationships to be assigned.
Study site and species

The Southern anteater-chat *Myrmecocichla formicivora* is one of eight species of bird in the little studied genus *Myrmecocichla*, members of the Muscicapidae family (Dickinson 2003; Aliabadian et al. 2012), all of which appear to breed cooperatively (Hoyo del et al. 2005; Cockburn 2006). It occurs over large areas of southern Africa from Botswana southwards (Hockey et al. 2005; Hoyo del et al. 2005). Southern anteater-chats are medium sized birds (45 – 50g), with uniform dark-brown plumage (Fig. 1). Both sexes have white bases to the primaries, and the males have a white carpal patch (lesser coverts) from mid-nestling stage onwards, although this patch is not always visible since males can display or hide the patch at will. However it can readily be seen when the bird is flying or in the hand, and allows accurate sexing of both adults and nestlings.
b. Female southern anteater-chat, showing pale edges to contour feathers typical of adults.

c. Juvenile southern anteater-chat, with typical uniform dark-brown plumage, and remnants of gape.

Figure 1. Southern anteater-chat Myrmecocichla formicivora. a. Male southern anteater-chat; b. Female southern anteater-chat (banded); c. Juvenile southern anteater-chat.
Southern anteater-chats are known to be facultative cooperative breeders (Earle & Herholdt 1988), and in my focal population breed either in pairs or in groups of up to five birds (plus fledglings of the current breeding season). Southern anteater-chats breed between September and February, with the majority of breeding taking place between October and December (Herholdt 1987; Earle & Herholdt 1988). The exact timing is to some extent dependent upon the early spring rains, the rains being associated with an increase in invertebrates, but heavy rains can also inflict high nest mortality resulting in re-nesting (J. Barnaby, unpublished data). The chats breed in tunnels excavated horizontally into the walls of holes dug by aardvarks *Orycteropus afer*. They are also reported to use natural banks and gully edges (Earle & Herholdt 1988; Rubenstein & Hobson 2004; Hockey et al. 2005). They feed mainly on a wide variety of invertebrates, predominantly termites (*Isoptera*), ants (*Formicidae*), grasshoppers (*Caelifera*) and solifuges (*Solifugae*), but also occasionally eat berries (Earle & Louw 1988). Southern anteater-chats are active diurnal birds, hunting invertebrates both by foraging directly on the ground, or by hovering and swooping from the air, or hawking from elevated perches in their environment, commonly termite mounds. They frequently sing while perched and in flight, particularly at dusk, and males have also been observed singing together in groups of up to around a dozen birds.

The study was carried out over four years, 2008 to 2011, from October to December each year, on Benfontein Nature Reserve (28°53’S, 24°89’E), located eight kilometres south east of Kimberly in the Northern Cape of South Africa (Fig. 2). The site is situated in a transitional Karoo-Kalahari Sandveld vegetation zone, an area peripheral to the Kalahari Desert. The seven square kilometre study area is a mixture of open grassland (including *Eragrostis, Aristida* and *Stipgrostis* species) and low karoo-type scrub - Eastern mixed nama karoo (Mucina & Rutherford 2006), with patches of eroded bare ground along runoff channels, and a small number of trees (largely along the drainage lines) forming a gradually sloping transitional zone between Camelthorn (*Acacia erioloba*) savannah woodland and vast areas of open pan veld (endorheic pan). This area of the reserve has relatively high concentrations of termites and termiteria and is heavily frequented by aardvark with which the Southern anteater-chat is ecologically connected for both nesting and feeding (Taylor & Skinner 2001). The area has a semi-arid climate, with a mean annual rainfall of 454 ± 117 mm (range 270 – 789mm, period 1994 – 2011, data supplied courtesy of the South Africa Weather Service). The rainfall is both highly seasonal, the majority falling in the southern hemisphere summer (November to February), and highly variable (e.g. October 0 – 84mm, November 6 – 142mm, December 10 – 161mm, period 1994 – 2011). Temperatures range from -8.5°C to 40.9 °C, with a mean daily temperature of 18.4 ± 6.2 °C, the coldest months being in June/July.
Field methods

This study relied on having the large majority of the birds on the study site uniquely identifiable. This was achieved through comprehensive capture and colour banding. Since the chats roost in tunnels at night, by locating these tunnels one can target these roosting birds. Each year a survey was taken of all aardvark diggings on the study site considered suitable for a chat tunnel (over 500mm deep, not significantly overgrown and not in the process of collapse). No chat tunnels were found outside these criteria, and no chat tunnel was found apart from in aardvark excavations. Each excavation was recorded and uniquely referenced using a portable global positioning system (GPS), with an accuracy of ± 2m. The adult chats were then caught at night by revisiting the tunnels several times over the three months field season. At the same time the nest chambers were inspected to check for any breeding activity (fresh nest, eggs or nestling). Night time catching was the most effective way of catching chats. If birds were present they were caught by covering the entrance to the tunnel with a transparent bag, and flushing the birds into the bag using a long flexible wire “snake” inserted towards the rear of the tunnel. Frequently several birds would be caught at night roosting together. Each bird was given a unique combination of three coloured rings, as well as a numbered metal band. Morphological measurements (mass, tarsus, wing and tail length, bill and head length) were taken of all birds, and they
were sexed by the presence of a white carpal patch in males. This was possible even for nestlings from around seven days old. 50μl of blood was taken from each bird by brachial venipuncture, and the blood was stored in 96% ethanol at room temperature. The nestling period was 15-18 days in agreement with earlier studies (Earle & Herholdt 1988). Nestlings were caught around fledging (15-17 days old). At this stage the fledglings were robust and the risks to the birds were minimised. The fledglings could fly, but not strongly, and remained in the nest when returned. The number of fledglings banded at this time was taken to be the number of nestlings fledged.

Data on home ranges, group composition and nest attendance was gathered directly by observers in the field. Each chat encountered was identified by its colour rings, its location was recorded using GPS, and group associations and significant behaviours were noted. Active nests were located by observing chats feeding during the day, and during night catches. All active nests were observed during 1-3 hour long nest watches during the morning when nest attendance was at its busiest. It was most effective to carry out the observations from a vehicle as the chats had become partly habituated to the presence of vehicles. When this was not possible camouflaged hides were used. Southern anteater-chats on the study site were found to be very wary of human presence especially in proximity to active nests. Active nests, containing either eggs or nestlings, were inspected daily. Group attendance, hatching dates, fledgling growth (visual scoring) and any nest predation / mortality were recorded.

Survival (Manuscript II)

Mark-capture-recapture analysis is carried out following the methods of Lebreton (Lebreton et al. 1992), whereby captured individuals are uniquely marked and released back into the population. Marked individuals may be then subsequently recaptured and released along with newly marked individuals. Such encounter histories of individuals are used to generate both survival probabilities (φ) and recapture probabilities (p) for each successive capture-recapture session. Mark-capture-recapture methods are more precise than return rates due to taking into account recapture/resight probabilities in calculating the survival probabilities, improving their accuracy. A standard Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965) in Program MARK (Version 6.1, build 7601) (White & Burnham 1999; Cooch & White 2010) was used to compare the fit of the different legitimate, survival hypotheses based candidate models and to calculate survival and recapture parameters using maximum likelihood estimates. This primarily tested for the effect of year of capture and age and sex of individuals. Additional continuous variables of rainfall and temperature were also incorporated as linear constraints in the models, to examine the effects of climate on survival
and recapture probability. Using only birds of known age i.e. banded as fledglings, allowed the investigation of a key hypothesis regarding age-related survival. The data set includes the capture-recapture history of 728 such individuals. The data was tested for goodness-of-fit using Parametric bootstrapping of simulated encounter histories, and software program U-CARE (Unified Capture-Recapture) (Choquet et al. 2009; Cooch & White 2010). Both tests suggested that the data fitted the Cormack-Jolly-Seber model well. Program MARK allows model comparison using Akaike Information Criterion (AIC) (Akaike 1973). AIC values allow the selection of the “best” model taking account of both descriptive accuracy and parsimony – that is the best fit with the fewest parameters (Anderson & Burnham 1999). Models with lower AIC values are considered better fitting the data without over-fitting, and are taken as being better at explaining patterns in the data (Akaike 1973; Lebreton et al. 1992). By balancing the precision and fit of good approximating models, AIC value usually selects a model that is closest to the “unknown reality” from which the data came (Bozdogan 1987; Manly et al. 2003; Cooch & White 2010). The relative importance of individual parameters was examined using Akaike weights, which indicate the degree of support for each model (Burnham & Anderson 2002; Wagenmakers & Farrell 2004).

Statistical analysis

In addition to the mark-capture recapture analysis above, statistical analysis was performed in R version 2.14.2 (R-Development-Core-Team 2012), ESRI Spatial Analyst (ArcMAP 9.3 build 1770, 1999-2008), and microsatellite based analysis software described in laboratory methods. The numbers of adults, juveniles, nestlings, groups, and nests varies between some analyses where the data was considered not adequate for certain measures. The relationship of fledgling output to group size, and first year survival of fledglings, were investigated using a generalised linear mixed model in R – package glmmADMB (Bolker et al. 2009; R-Development-Core-Team 2012) (Manuscript V). Using glmm allowed the choice of an appropriate error distribution, and the controlling for several random effects. The analysis of fledgling output is based on the sample of nests which successfully fledged young, i.e. groups where there was high confidence of group composition and fledgling number. They are therefore count data suggesting modelling with a Poisson error distribution. However since the data include only successful nests (at least one individual fledged), it was model using zero-truncated Poisson distribution (Long 1997; Bolker et al. 2009) using a log link function. The dependant variable fledgling number was modelled against group size with the addition of age of breeding female, age of breed-
ing male, rainfall (annual and breeding season), density of aardvark holes and temperature (mean minimum breeding season) as independent variables. I controlled for the effect of year, breeder identity and territory in all models by assigning them as random categorical variables. This controlled for pseudo-reciprocity, and by incorporating the effects of territory and breeder in the model as random variables it also controlled for the possible confounding effects of these variables, since both territory and breeder quality can result in an increase in fledgling output and the number of helpers, without the need for a helper contribution to fledgling productivity (Cockburn 1998; Cockburn et al. 2008). The variances of the random variables (kept in all models) were very low, with a much higher associated standard error, suggesting that the associated effects were not measurably different from zero, and they had little impact on model selection. Diagnostic plots were used to check for homogeneity of variance and tested for over dispersion, and no transformation or correction was necessary. First year survival was modelled in a similar way, but the response variable was a proportion and the model used a binomial error distribution and a logit link function. Models were compared using Akaike information criteria. Models with a ΔAIC of greater than two were considered to have little support with respect to the best model. AIC values were corrected for finite sample sizes, using AICc (Burnham & Anderson 2002), which adds a greater penalty for extra parameters. To investigate the influence of the different parameters the Akaike weights for the different parameters were summed over all models.

Genetic analysis (Manuscript V)

A suite of microsatellite markers was developed by testing the cross-amplification of existing microsatellite markers from other bird species for their suitability in genotyping the Southern anteater chat. Markers were chosen based on previous successful cross amplification and from relatively closely related species. The selection was also made on the basis of the degree of polymorphism, and the predicted size of the markers in order to allow the creation of a small number of multiplexes from the markers. Out of 37 markers tested, 14 microsatellite markers were identified as being polymorphic in the chat with only minor deviation from Hardy-Weinberg equilibrium and little evidence of null alleles as evaluated in MICROCHECKER (Van Oosterhout et al. 2004) and CERVUS (Kalinowski et al. 2007). The number of alleles ranged between 3 and 34 alleles per locus, and observed heterozygosity ranged from 0.45 to 0.93. Primers for these 14 markers were combined in 4 multiplexes (Manuscript V).

Of the 1036 chats caught over the period 2003 to 2011, 944 individual birds were successfully genotyped. Seventy-eight samples collected 2003 – 2007 were missing, and 10 other samples failed to amplify. Four samples
from the period 2008 – 2001 were missing or of insufficient amount to genotype. DNA was extracted from the blood samples using the high salt purification method (Aljanabi et al. 1997). These samples were then amplified using Polymerase Chain Reaction (PCR), with Qiagen Multiplex PCR Master Mix (Qiagen 2010). Genotyping was carried out using a megaBACE 1000 machine (GE healthcare) and the output analysed using MegaBACE Fragment Profiler Version 1.2, (Amersham Bioscience). The program CERVUS (Kalinowski et al. 2007) was used to calculate maximum likelihood parent offspring relationships for all sampled offspring, adult females (potential mothers) and adult males (potential fathers) (Slate et al. 2000). Where mothers could be assigned from observations (incubating eggs) this was in 100% agreement with the microsatellite results, giving good support for the accurate assignment of parentage in the study population. The program KINGROUP was also used to estimate relatedness between all individuals present in a given year (Queller & Goodnight 1989; Konovalov et al. 2004; Konovalov & Heg 2008).

The validity and accuracy of sexing the chats, as both adults and fledglings, using the presence or absence of the white carpal patch, was tested on a sample of 80 birds using a DNA based identification method (Griffiths et al. 1998). This confirmed that the morphologically assessed sex was equal to the genetic sex, and there is little doubt that this is a reliable indicator of sex from as early as the feathers appear, around nestling day seven.
Results and discussion

Population and group composition (Manuscript I).

This is the first large-scale study of the Southern anteater-chat. During the four year study, the adult population size varied between 122 and 168 birds and fledgling production between 36 and 93 birds (Table 1). There was a consistent significant sex skew within the adult population over the four years ($\chi^2 = 34.6$, $df = 7$, $p = 0.00001$), with a mean proportion of 0.59 ± 0.03 males and 0.41 ± 0.03 females. There is no evidence of the sex ratio ever reversing between years in this population, although this is seen in a number of other species (Stacey & Koenig 1990). The sex skew was not a result of differential fledging rates, since the sex ratio in fledging birds was equal with a mean proportion of males 0.51 ± 0.05 and females 0.49 ± 0.05 ($\chi^2 = 1.67$, $df = 7$, $p = 0.975$). These figures suggest post fledging sex biased mortality (Manuscript II). This adult sex skew has potential repercussions on the group structure, since if the breeding system is based around pair breeding it would suggest that approximately 30% of adult males in any one year are without a breeding partner.

Southern anteater-chats live in groups of 2 – 5 individuals - a breeding pair and up to three additional male none-breeders (Fig. 3), with a mean successful breeding group size of 3.22 ± 0.89 (SD). The majority of groups observed successfully breeding had at least one helper, which immediately hints that groups with helpers are more capable of fledging young, however pair breeding was also a feasible option. All birds observed in a group attended the nest, and non-helping group members were never observed except for dependant offspring from the same breeding season (Manuscript IV). Both sexes were commonly recorded breeding at age of one year, suggesting that delayed maturity was not a crucial factor in remaining as a helper (Manuscript III & IV). There was no sign of aggression either between groups or individuals in a group, and the chats did not appear territorial. However, individuals and groups were usually found within the same area (approx. 0.2km$^2$). The large majority of helpers were males (94.7%). The retained females (5.3%) were all less than one year old, and had dispersed by the end of the following breeding season (Manuscript III).
Table 1. Southern anteater-chat population by sex and age status on Benfontein, 2008-2011.

<table>
<thead>
<tr>
<th>Year</th>
<th>Adults</th>
<th>Adult females</th>
<th>Adult males</th>
<th>Juveniles</th>
<th>Juvenile females</th>
<th>Juvenile males</th>
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</tr>
</tbody>
</table>

Figure 3. Group size vs. frequency of occurrence, 2008 – 2011 (breeding groups feeding fledglings).

Breeding biology (Manuscript I)

Breeding pairs were typically unrelated (mean r = -0.06 ± 0.20 (SD)), with only 1 out of 43 pairs being between putative first degree relatives. Pedigree data suggest that this pair was not a parent and an offspring, or nest mates, but they could have been offspring from separate clutches. Some insight into mate choice in the chats comes from observations of gatherings of males (≈ 8 – 12 males) attended by single females. The males were observed displaying, and the gatherings would dissolve shortly after the female left with one male. These gatherings were observed once or twice each breeding season, but may be more common during the peak period of female dispersal (Manuscript III). In the study population 100% of nests were excavated into the walls of aardvark holes despite the availability of other options found elsewhere (Earle & Herholdt 1988), suggesting that aardvark holes are the preferred location. Although both aardvark holes and the chat tunnels in them were found to be clustered (Nearest neighbour analysis, $z = -32.40$, $p < 0.0001$; $z = -11.72$, $p < 0.0001$ respectively, null hypothesis - features are...
randomly distributed), active chat nests in any one season exhibited a dispersed, evenly spaced, spatial distribution (Nearest neighbour analysis $z = 2.32, p = 0.02$). The lack of territoriality and aggression between chat groups suggests the possibility of this distribution arising through predator dilution mechanisms (Lima 2007).

Females were the sole incubator of eggs, which may be one factor in the slightly reduced survival of adult females over adult males, and predation avoidance could be a reason why they roost separately from the nestlings 3 – 4 days after hatching (Manuscript II). The clutch size varied from 1 – 5 eggs, with a mean of $3.9 \pm 0.6$. Incubation was 14 – 15 days, and fledging took a further 14 – 17 days. Nest mortality was just over 50%, with similar proportions lost at the egg and nestling stages. The key nest predators were snakes, since the nest tunnels are inaccessible to most other predators. Brood parasitism by a Greater Honeyguide *Indicator indicator* was recorded once, although being on the edge of this species range such parasitism could be more common elsewhere. As well as using the tunnels for breeding the chats use them as roosts, often roosting in groups (mean group size $1.5 \pm 0.8$ (SD), $n = 301$). No significant link was found between roosting group size and minimum night time temperature ($F_{1,292} = 2.95, p = 0.087, r^2 = 0.007$). However the effect may be stronger in winter when temperatures can drop to -8.5°C and nest predating snakes are largely inactive (Eloff 1984). Delayed dispersal in the Southern anteater-chat appears to be a strategy of waiting for a breeding opening in response to a poor quality of current dispersal opportunities, which in this situation means the lack of breeding partners (Emlen 1994).

**Survival: sex, age and climate (Manuscript II)**

My study gives the first detailed information on the survival rates of the Southern anteater-chat. Clear differences were found in survival for both male and female, and adult and juvenile chats. There was strong support in the most parsimonious models for an effect of sex and of age, and an interaction between the two terms, on chat survival (Table 2). Models containing explicit age had much less support than models containing age as two classes, first year and adult (over one year old). Annual adult survival probability (mean ± SE) was $0.71 \pm 0.03$ for males and $0.60 \pm 0.04$ for females. Juvenile survival was lower for each sex, with juvenile female survival ($0.36 \pm 0.04$) being 35% lower than juvenile male survival ($0.55 \pm 0.04$) (Fig. 4). Using these estimates gave a mean life span (MLS) in years for male Southern anteater-chat to be $4.0 \pm 0.7$, considerably higher than that for females at $2.0 \pm 0.4$. When survival was modelled using the constraining variables of rainfall and temperature, annual rainfall and annual mean minimum daily temperature both had support in the most parsimonious model (Table 3).
Higher annual mean temperature was associated with higher survival, whereas higher annual rainfall was associated with lower survival for both sex and age classes (Fig. 5).

The results fit well with the hypothesis of higher juvenile mortality, and prompt female dispersal reducing survival, and the overall pattern of female-biased dispersal in birds (Greenwood 1980; Clarke et al. 1997), and reflects the significant sex skewed population structure I found. Given the lack of sex skew among fledglings, the sex skew in the population of 60% males would appear to be due to post-fledging survival differences. Predation is expected to be higher in juveniles as the figures support (Bonte et al. 2012), however this in itself does not explain the difference in survival between the sexes. Female survival, particularly female juvenile survival, may be reduced due to prompt dispersal and longer dispersal distances, and the additional costs of breeding early in life. The dispersal process itself, moving across and settling in unfamiliar territory can be costly (Delgado et al. 2010), and also early dispersal of less experienced birds has been suggested in a number of species to increase mortality (Belichon et al. 1996; Dieckmann et al. 1999; Yoder 2004). The cost balance may be particularly high for first year females where the costs of losing the benefits of the natal site and parental facilitation (Ekman & Griesser 2002) and dispersal per se add to those of inexperienced females attempting to breed (Pietiäinen 1988; Brommer et al. 2003; Ekman 2007). Reduced survival with colder temperatures could be connected with reduced food supplies (Newton 1998), however studies in similar environments suggest that reductions in food supply due to climatic variation are may not be critical to post fledgling and adult survival in similar African environments (Covas et al. 2004). Daytime temperatures rarely fail to rise above 15°C, and daytime thermal stress is low for both the birds and their prey species. The effect of reduction in survival of the chats with minimum temperatures is possibly due to thermoregulatory costs during night-time roosting (Beauchamp 1999; McGowan et al. 2006; Hawn et al. 2007). Southern anteater-chats are often found roosting in groups, and this behaviour may be in order to reduce thermal costs (Williams et al. 1991). Higher rainfall is often associated with increased food supply, and that may be the case here, however, as already discussed, food supply may not be the critical factor. The seasonal and sporadic nature of rain, with it often falling in intense storms, frequently leads to local surface saturation and flooding. During such periods the birds roosting tunnels can get flooded, forcing the birds to roost out in the open where they are more prone to predation and they may be more thermally stressed due to the wet conditions. Increased vegetation due to higher rainfall may also decrease survival by providing more cover for predators, and the number of predators, particularly birds of prey, appears to increase in years of high rainfall (Barnaby, unpublished data).
Knowledge of differential survival rates between males and females and juveniles and adults give insights into the costs and benefits of different behavioural and life-history strategies. Given the potential multiple mechanisms of increased female mortality it would be interesting to investigate these components in more detail by examining survival on a monthly basis, particularly during their first year. The difference in adult survival between males and females is surprisingly small. It was expected that the reproductive burden, particularly the costs associated with incubation (Owens & Bennett 1994), and greater distances from the natal site, would reduce female survival by a larger extent in comparison to adult male survival. It may be that for females the extra burden of egg laying and incubation are small, and that breeding females are usually able to avoid being taken when their eggs or nestlings are predated. This could be due to the sentinel behaviour of other group members, as they are frequently seen giving warning calls and mobbing predators, which is common among cooperative breeders (Wright et al. 2001; Ridley et al. 2010). Survival is a key factor behind life-history variation, and is a major influence on sociality in species which delay dispersal and live in family groups (Hatchwell & Komdeur 2000; Covas & Griesser 2007). A long lifespan allows individuals to forgo independent reproduction since it increases future opportunities, and allows parents to invest more time in rearing offspring (Arnold & Owens 1998). The survival figures for adult male Southern anteater-chats are relatively high, particularly compared to northern passerines (Peach et al. 2001), and differential survival, between sexes, can promote philopatry (Greenwood 1980) which in turn could well encourage the cooperative breeding observed in the Southern anteater-chat.

Table 2. Models (Cormack-Jolly-Seber) fitting survival and recapture parameters for Southern anteater-chats banded as Juveniles (n = 728). Sex = male or female; age = 1 – 8 (years); age class = first year or adult, year = 2004 – 2011. φ = survival, p = recapture probability.

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>QAICc Weights</th>
<th>No. of estimable parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>φ(sex,2ageclasses)p(year)</td>
<td>1350.34</td>
<td>0.000</td>
<td>0.508</td>
<td>11</td>
</tr>
<tr>
<td>φ(sex*2ageclasses)p(year)</td>
<td>1350.43</td>
<td>0.086</td>
<td>0.487</td>
<td>12</td>
</tr>
</tbody>
</table>

Differential sex biased dispersal is widespread among cooperatively breeders (Eikenaar et al., 2007; Koenig & Dickinson, 2004), potentially driving differential survival rates. If this differential dispersal is, as is common, driven by some constraint on breeding to the philopatric sex (Hatchwell & Komdeur 2000), it indicates that there are benefits in remaining philopatric, over the choice of dispersing to a non-breeding position as an unrelated helper, or floating while waiting for a breeding opportunity. These benefits
may include indirect benefits of helping rear related offspring as has been shown in many species (e.g. Dickinson 2004; Covas et al. 2006), however particularly for juvenile birds they may also include direct fitness benefits related to increased survival (Walters et al. 1992; Ekman et al. 2000; Richardson et al. 2002), as suggested by this study. The dispersal distances of southern anteater-chat are comparatively short (Manuscript III), and only a few marked birds were found breeding adjacent to the study site, and none at greater distances despite open easily surveyed habitat. Therefore the large majority of birds which disappeared are expected to be dead, and the survival estimates are likely to be highly accurate.

![Figure 4. Survival probability (Φ) by sex and age (model averaged parameters), with standard error (SE), averaged over models φ(sex,2ageclasses)p(year) and φ(sex*2ageclasses)p(year).](image)

Table 3. Models (Cormack-Jolly-Seber) fitting survival and recapture parameters for Southern anteater-chats banded as Juveniles (n = 728). Showing models within ΔQAICc = 2 of the best model. Sex = male or female; age = 1 – 8 (years); 2ageclass = first year or adult, year = 2004 – 2011; rainfall = annual rainfall; mintemp = annual mean minimum daily temperature. φ = survival probability, p = recapture probability.

<table>
<thead>
<tr>
<th>Model of Survival</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>QAICc Weights</th>
<th>Num. Par</th>
</tr>
</thead>
<tbody>
<tr>
<td>φ(sex+2ageclasses+min TEMP+rainfall)p(year)</td>
<td>1349.78</td>
<td>0.0</td>
<td>0.320</td>
<td>14</td>
</tr>
<tr>
<td>φ(sex+2ageclasses)p(year)</td>
<td>1350.43</td>
<td>0.6</td>
<td>0.231</td>
<td>12</td>
</tr>
<tr>
<td>φ(sex+2ageclasses+min TEMP)p(year)</td>
<td>1350.80</td>
<td>1.0</td>
<td>0.192</td>
<td>13</td>
</tr>
<tr>
<td>φ(sex+2ageclasses+rainfall)p(year)</td>
<td>1351.80</td>
<td>2.0</td>
<td>0.115</td>
<td>13</td>
</tr>
</tbody>
</table>
Figure 5. Effect of climatic variables on survival of a. mean minimum daily temperature (Slope = -0.071 ± 0.056, \( r^2 = 0.05 \)), b. annual rainfall (Slope = -0.0007 ± 0.0003, \( r^2 = 0.22 \)). Data includes adult male and female survival, 2004 – 2011.

Female dispersal and breeder replacement: the rarer sex (Manuscript III)

The sex skew in the southern anteater-chat population suggests that the lack of females is a major constraint on males dispersing to breeding openings, thus being the immediate cause of philopatry and the associated cooperative breeding. That all adult females identified were in apparent breeding groups with one or more males further suggests that there are no surplus females waiting for breeding opportunities. The absence of a non-breeding female surplus to these observations is reinforced by the lack of replacement of females during the breeding season. Dispersal in the Southern anteater-chat was strongly female biased, with females dispersing within their first year whereas many males remained philopatric.

Despite thorough surveys of the study site no evidence was found of floating females nor replacement of disappeared breeding females. Surveying an extensive area beyond the study site showed no evidence of long-range dispersal. If a female disappeared in the breeding season they were not replaced until new females matured and dispersed after the breeding season (Table 4). This suggests that there are no females waiting during the breeding season for a breeding opportunity, since the loss of a breeding female should open up both a suitable breeding site, and an available breeding male. The only replacement of females to become breeders occurred between breeding seasons (Table 5). In contrast, if a male breeder disappeared during the breeding season he was replaced by another male within the same breeding season (Table 6). This supports the hypothesis that these males were “waiting” for an available female, and there is no evidence that auxiliaries...
exist because of their incapability to become breeders. The lack of floating females is also supported by the fact that there was also a complete absence of floating males, suggesting the costs of floating are high in comparison to joining a group either as a breeder or as a helper, with even unrelated males joining groups rather than choosing to float. Annual recruitment matched annual losses, with some yearly variation. Annual replacement of females does occur and population numbers of both sexes have been relatively stable over the four years of the study, but it appears that all of the female breeder replacement happens outside of the breeding season. The data indicate that all females disperse and attempt to breed in the season following fledging and that there are no available females until fledglings become independent, whereas males regularly remain philopatric for at least one season. The modal age of breeding females was one year old whilst the modal age of breeding males was three years, supporting the hypothesis of prompt female dispersal (Doerr & Doerr 2005).

Dispersal distances were significantly higher for females than for males, particularly natal dispersal distances (Fig. 6). Natal dispersal, the mean dispersal distance (+ SD) of first year birds into a breeding opening, was for females 757 ± 462m, over six times that for males at 114 ± 132m (Mann-Whitney U Test, U = 40, p = 0.006). Breeding dispersal, the mean distance (+ SD) between consecutive nest locations when a bird changed breeding partner, was for females higher at 1012 ± 429m, over four times that of males at 227 ± 189m (Mann-Whitney U Test, U = 18, p = 0.024), and the mean distance (+ SD) of a breeding female from her natal site was 625 ± 363m, just over twice that for males of 302m ± 220m (Mann-Whitney U Test, U = 554.5, p = 0.002). The mean distance from the natal site is small in comparison to the separation of groups (mean distance (+ SD) between active nests = 407 ± 117m).

Inbreeding avoidance has been suggested to affect dispersal choices in a number of cooperatively breeding birds and mammals (Clutton-Brock & Lukas, 2012; Daniels & Walters, 2000; Nelson-Flower, Hockey et al., 2012). The near absence of closely-related breeding pairs (Manuscript I), the absence of extra-pair paternity between close kin (Manuscript IV), and the relocation of females on loss of partners suggests that chats avoid breeding with family members. It is unclear to what extent this is a dilution effect due to dispersal, or if it is also due to the avoidance of kin, via kin recognition mechanisms (Komdeur et al. 2008b; Clutton-Brock & Lukas 2012). Although a dilution effect occurs rapidly with increasing distance and the propensity to disperse (Szulkin & Sheldon 2008), patterns of dispersal separating close relatives have not inevitably evolved as an inbreeding avoidance mechanism (Pusey & Wolf 1996), and inbreeding alone is thought unlikely to account for dispersal (Perrin & Mazalov 1999; Daniels & Walters 2000). Short distance sex-skewed dispersal can be effective in avoiding high costs
of inbreeding, and at the same time balancing inbreeding against the costs of dispersal (Pusey 1987; Heinsohn 2012).

Cooperative species like the Southern antechat are regularly in close proximity to kin, and in such species kin recognition is often highly developed (Komdeur & Hatchwell 1999; Nelson-Flower et al. 2012). It may be that female chats do not have to disperse far to find a suitable mate, and the proximity of breeding males to their natal site points towards these males determining the breeding site and taking advantage of the benefits of familiarity (Stacey & Ligon 1991). Further study is required to determine if the sex differences in dispersal distances in the chats are sufficiently distinct to prevent inbreeding on their own, and to investigate other factors such as mate choice in determining dispersal distances. It appears that the sex skew in this population allows all females access to breeding opportunities, that females disperse and breed as soon as they are sexually mature, and, crucially, that there are no surplus non-breeding adult females.

Figure 6. a. Distance (m) of breeding birds from natal site (males and females). b. Natal dispersal distance (m) (distance of one year old breeding birds from natal site) (males and females). c. Breeding dispersal distance (m) (distance moved by breeding birds on change of breeding partner) (males and females). Box = 1\textsuperscript{st} and 3\textsuperscript{rd} quartile, bold line = median.
Table 4. Fate of females (2008 – 2011), indicating replacement breeding partner.

<table>
<thead>
<tr>
<th>Category</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult females (2008-2011) - all in pair/group as sole adult female</td>
<td>122</td>
</tr>
<tr>
<td>Alive at the end of 2011 (final breeding season, seen December)</td>
<td>43</td>
</tr>
<tr>
<td>Disappeared between breeding seasons (January – September)</td>
<td>47</td>
</tr>
<tr>
<td>Disappeared during breeding season* (October – December, not seen</td>
<td>32</td>
</tr>
<tr>
<td>subsequent years)</td>
<td></td>
</tr>
<tr>
<td>- no new breeding female in group/territory same season</td>
<td></td>
</tr>
<tr>
<td>- no new female seen with group</td>
<td></td>
</tr>
<tr>
<td>- male disappeared at approximately the same time as female</td>
<td>4</td>
</tr>
</tbody>
</table>

*Birds are recorded as disappeared during the breeding season if they are not seen during December of the season in question, and not seen in the following years.

Table 5. Recruitment and loss of females over four breeding seasons and three inter-breeding periods, 2008 – 2011.

<table>
<thead>
<tr>
<th></th>
<th>number lost</th>
<th>number recruited</th>
</tr>
</thead>
<tbody>
<tr>
<td>During breeding season</td>
<td>32</td>
<td>0</td>
</tr>
<tr>
<td>Between breeding seasons</td>
<td>47</td>
<td>62</td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td>62*</td>
</tr>
</tbody>
</table>

*There were slightly fewer females in the population in 2011 as compared to 2008

Table 6. Fate of breeding males lost (2008 – 2011) during the breeding season, indicating replacement (acquisition of breeding partner by widow).

<table>
<thead>
<tr>
<th>Category</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disappeared during breeding season*(October – December, not seen</td>
<td>12</td>
</tr>
<tr>
<td>subsequent years)</td>
<td></td>
</tr>
<tr>
<td>- female disappeared at approximately the same time as male</td>
<td>4</td>
</tr>
<tr>
<td>- female with a new potential breeding male during current season</td>
<td>8</td>
</tr>
</tbody>
</table>

*Birds are recorded as disappeared during the breeding season if they are not seen during December of the season in question, and not seen in the following years.

Male choices: delayed dispersal and helping (Manuscript IV)

The effect of auxiliaries on fledgling productivity and survival

All mature auxiliaries in the Southern anteater-chat groups are male, and the sex ratio in the overall population indicates around 50% more males than females. These males join breeding pairs as auxiliaries, with groups ranging from a pair to a pair with three helpers. All auxiliaries in groups with nestlings fed at the nest, and the number of offspring fledged is positively corre-
lated with group size (Table 7; Fig. 5a). The number of auxiliaries appeared to explain 15% of the variation in fledgling output. All auxiliaries were observed feeding at the nest, and many took part in predator mobbing. However, parents can also use the help provided to reduce their workload and increase their own survival or allow more rapid re-nesting, thereby masking the positive effects of helping (Heinsohn 2004). In successful breeding groups 75% of groups have one or more auxiliary, suggesting that groups with auxiliaries are more likely to fledge young, and it may indicate that pair breeders are less likely to attempt to breed in the first place. The analysis also gave support for an effect of breeding season rainfall on fledgling output (Table 7), with higher rainfall increasing fledgling production (Fig. 7). It is likely that breeding season rainfall is linked to increasing food abundance (Dean & Milton 2001; Covas et al. 2008), and the preceding months are characterised by extremely low rainfall (modal rainfall in July, August and September 2008-2011 is zero). Rainfall has also been shown to be positively correlated with clutch size in a number of South African birds (Lloyd 1999). This response can be very rapid, with some species laying larger clutches within one week of a rainfall (Lloyd 1999). The interaction between rainfall and group size indicated that as auxiliary number increases the effect of rainfall on fledgling production decreases (Fig. 7). The positive effect of rainfall appeared to depend upon the number of helpers. Groups with zero and one helper showed a positive correlation between rainfall and fledgling production. However, for groups with two helpers rainfall had no effect on fledgling output. This suggests that auxiliaries have a stronger effect when breeding conditions are poorer, and auxiliaries may buffer some aspects of the adverse effects of climate on fledgling production, as found for Sociable weavers *Philetairus socius* species in adjacent habitats (Covas et al. 2008). There was also a positive correlation between group size and the proportion of fledglings surviving over the first year (Fig. 8). Again there is the potential for masking the positive effects of helping due to reductions in the costs to the breeding pair. During the fledgling period an increased number of auxiliaries could shorten the time to re-nesting by reducing the effort of the parents in feeding the fledglings, or accelerate the development of the fledglings so that they become independent sooner (Heinsohn 2004).
Table 7. Generalised linear model of number of offspring fledged. Models within ΔAICc of 2 of the best model shown. Group size (number of adults in breeding group), bbrain (breeding season rainfall).

<table>
<thead>
<tr>
<th>Modelling of fledgling number</th>
<th>k</th>
<th>Loglik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>fledglings ~ group size</td>
<td>6</td>
<td>-136.68</td>
<td>286.40</td>
<td>0.00</td>
<td>0.151</td>
</tr>
<tr>
<td>fledglings ~ group size + bbrain</td>
<td>7</td>
<td>-135.59</td>
<td>286.58</td>
<td>0.18</td>
<td>0.138</td>
</tr>
<tr>
<td>fledglings ~ bbrain</td>
<td>6</td>
<td>-137.24</td>
<td>287.52</td>
<td>1.12</td>
<td>0.086</td>
</tr>
<tr>
<td>fledglings ~ group size + bbrain + group size: bbrain</td>
<td>8</td>
<td>-134.94</td>
<td>287.70</td>
<td>1.31</td>
<td>0.079</td>
</tr>
</tbody>
</table>

Figure 7. a. The relationship between group size and number of offspring fledged, (2008 – 2011). a. (estimate = 0.4 ± 0.1, r² = 0.15, n = 86, p = 0.0002); and the relationship between rainfall during the breeding season and the number of offspring fledged, (2008 – 2011). b. groups with no auxiliaries (estimate = 0.007 ± 0.003, r² = 0.17, n = 22, p = 0.03); c. groups with one auxiliary (estimate = 0.006 ± 0.003, r² = 0.09, n = 29, p = 0.06), d. groups with two auxiliaries (estimate = 0.0005 ± 0.002, r² = -0.03, n = 31, p = 0.8).
Dispersal choice, genetic relationship and age of auxiliaries

All males in the population were confirmed as breeders or auxiliaries in a breeding group. The majority of auxiliaries in the Southern anteater-chat were related to the breeding pair (54.2%), with 25.4% of auxiliaries related to only one of the breeders, and 20.4% unrelated to either breeder (Fig. 9). The modal age of auxiliaries was one year, but there were non-breeding individuals helping in groups which were seven years old, although these birds may have been breeders at some point in their history. Non-kin auxiliaries (3.2 ± 1.7(SD) years) were significantly older than kin auxiliaries (1.9 ± 1.3 (SD) years) (Kruskal-Wallis $\chi^2 = 6.05$, df = 1, p = 0.01; Fig. 10).

A constraint on independent reproduction does not necessarily entail that an individual delays dispersal. Individuals have the option to leave the natal group and float while waiting for a breeding opportunity, or disperse and join another group as an auxiliary (Ekman 2006). There was no evidence of this. It seems that until a chat disperses to a breeding opportunity it remains philopatric. However it appears that if a male loses its group due to mortality it will join another group as an unrelated non-breeding auxiliary rather than float. This suggests that floating is costly in comparison to remaining philopatric or joining a group as an unrelated auxiliary. It would appear that chats always can and do choose the option to be in a group. Floating has been shown to be costly in an increasing number of vertebrate species (Ridley et al. 2008). Of the chats related to only one of the breeders 87% are related only to the male breeder. The predominance of male only relatives could be due to extra pair paternity or inheritance of breeding positions, but both are very low. Males remain philopatric for up to several years and when dispersing to breed males remain much closer to the natal site or subsequent breed-
ing sites (Manuscript III), facilitating the continued association with or joining of male relatives.

![Figure 9. Auxiliary group members and their relationship (first degree relatives) to the breeding pair, 2008 – 2011.](image1)

![Figure 10. Age composition of kin auxiliaries and non-kin auxiliaries, 2009 – 2011.](image2)
Unrelated auxiliaries participate in both feeding and predator mobbing. This behaviour is interesting since in many species unrelated auxiliaries refrain from helping (Emlen & Wrege 1988; Emlen et al. 1991), although this inference may change as a broader spectrum of helping behaviour is identified (Bennett & Owens 2002). It is striking that no aggression was observed between individual Southern anteater-chats, either between or within groups, and chats appear to join groups as unrelated members without conflict. Tolerance between group members is commonly inferred to be a result of mutuality (Clutton-Brock 2002), suggesting that breeders benefit from the presence of the unrelated auxiliaries. If survival is higher in larger groups, then joining and helping to raise young increases group size and leads to increased survival of all group members (Clutton-Brock et al. 1999). Or it could be that by helping, unrelated individuals are effectively paying to stay in the group (Dickinson & Hatchwell 2004). There is growing evidence to suggest that direct benefits are as important in the maintenance of cooperation as kin selection (Ekman et al. 2002; Dickinson 2004). Inheritance of breeding positions does not appear to be an important reason why unrelated auxiliaries help since there was very little evidence of inheritance by auxiliaries. Out of 24 male helpers unrelated to the female only one inherited a breeding position on the loss of the breeding male. Extra pair paternity in Southern anteater-chats was also very low (2.4% of offspring), especially for a cooperatively breeding species, suggesting that it is not direct breeding opportunities promoting unrelated auxiliaries to join groups. However the data hint that gaining extra pair paternity is facilitated by being closely related to the primary breeding male. In fact although the actual numbers are small, all the extra-pair males resident in the groups where they gained paternity were first degree relatives of the primary breeding male. Mating preference could be more female mediated, and may explain why close relatives of the breeding male, with overlapping phenotypes, have a higher chance of mating with the female.
Summary and concluding remarks

Field studies are a crucial tool for investigating ecological systems, and this is the first in-depth study of the Southern anteater-chat. This thesis explores many aspects of the chats ecology, but focuses on group living. Group living sets the scene for complex social behaviours such as cooperative breeding, and exploring the factors that shape group living is crucial in understanding these behaviours. The study has been based on a comprehensively identified population of birds over an extensive area, both through individual recognition (colour banding) and via genetic analysis using microsatellite markers. Microsatellite markers developed for other bird species were tested for cross amplification, as an economic method of creating a suite of markers. This has enabled the examination of individual choice within a larger population context, with knowledge of family and group structure, and also the investigation of dispersal decisions by monitoring the movements of a large number of individuals.

Sexual dimorphism in the chat has facilitated the identification of a consistent sex skew in the population, one which appears to be a key feature in a complex web of effects influencing, and influenced by, the connected social system. The chat is a facultative cooperative breeder, capable of breeding in pairs, but the large majority of successful breeding groups had one or more helpers. The sex skew might suggest that the helpers would be predominantly male, and indeed mature adult helpers were found to be exclusively male. The majority were philopatric offspring, but some were apparently unrelated to the family they joined. It appeared that females disperse directly into a breeding opportunity within the first year, while males disperse into a breeding position if they can, but those which cannot choose to remain in the family group with their parents. The system appears to be driven by ecological constraints, with helpers making the “best of a bad job” (Emlen 1982). This is common to many cooperative breeders (Dickinson & Hatchwell 2004), but each specific case encompasses a wide range of influencing factors, with cost-benefits, particular to each species and population, influencing specific behaviour.

Survival is a major influential life history trait in species which delay dispersal and live in family groups (Covas & Griesser 2007), yet little is known about survival in most wild bird populations (Koenig et al. 2000). Modern statistical methods using mark-recapture data enable the estimation of sur-
vival parameters of various categories of chats in a much more accurate way than simple return rate calculations, allowing an integration of both survival and re-observation probabilities. The results suggested that survival was lower among first year birds than adults, but most strikingly that first year females had a substantially lower survival than first year males. This fitted well with observation of females dispersing more promptly and further than males. In fact overall dispersal distances were short, with most males remaining within their natal area, but females on average travelled twice as far. The nature of the open semi-arid landscape has allowed accurate monitoring on a large scale. The dispersal distances of Southern anteater-chat are comparatively short and only a few marked birds were found breeding adjacent to the study site. None were observed at greater distances despite open easily surveyed habitat, the large majority of birds which disappeared were expected to be dead, and the survival estimates are likely to be highly accurate. These results are one step in addressing the shortage of studies accurately assessing survival in cooperatively breeding birds (Kesler et al. 2010), and fits the pattern of male biased sex skew, and female biased dispersal and mortality found in many cooperatively breeding birds (Greenwood 1980).

I found no evidence of individuals floating in the Southern anteater chat. All females appeared to be lone breeding females in breeding groups, and all males were either breeders or auxiliaries in groups. This makes it difficult to assess the cost benefits between floating or joining a group. Floating individuals may be much harder to detect than social group members, however a complete absence of replacement of breeding females during the breeding season supports the hypothesis that there are no surplus females waiting for a breeding opportunity. All replacement of females appears to occur when fledglings mature and disperse. Prompt replacement after the disappearance of male breeders supports the observation that auxiliary males are capable of breeding, as it is from this pool of auxiliaries that replacement of breeding males took place. The sex skew in the population hints that females have no shortage of mates. I found no indication of other constraints on prompt female dispersal, and this may suggest that there are no territorial quality constraints, at least at the population sizes experienced. The Southern anteater-chat does not appear to be limited for breeding opportunities in terms of territories or a lack of suitable males, since the disappearance of a currently breeding female during the breeding season should open up both prospects.

I found that all the auxiliary males in a group helped rear the nestlings, and modelling gave good evidence that helpers made a positive contribution to both fledgling production, and the survival of these fledglings over their first year. For the related auxiliaries this provides indirect benefits, but the presence of unrelated auxiliaries suggests that there are direct benefits as well. The fact that unrelated auxiliaries helped is unusual in cooperative breeders (Cockburn 2004). However a very low level of both inheritance of breeding position by auxiliaries and extra-pair paternity suggests that these
two factors are not major incentives to join groups and help. It hints at the potentially high costs of floating and potential direct benefits due to group membership. Future work would be needed to determine if, in addition to increasing fledgling production, auxiliaries allow breeders to reduce their costs and increase future reproductive output. However this study implies multiple potential effects of both direct and indirect benefits influencing group membership and helping in this species. It is interesting that the interaction between rainfall and group size indicated that as auxiliary number increases the effect of rainfall on fledgling production reduces. This suggests that auxiliaries have a stronger effect when breeding conditions are poorer, and auxiliaries are in effect a buffer against the effects of climate on fledgling production. In addition there was notably no evidence of aggression either within or between groups of chats, and no sign of aggression preventing unrelated auxiliaries associating with family groups. This apparent lack of aggression, along with the fact that southern anteater-chats appear to be non-territorial, is unusual in non-colonial cooperatively breeding birds (Stacey & Koenig 1990), and may be closely linked to female mate choice and fidelity.

On a number of occasions gatherings of males were observed where the white carpal patches of the male birds were prominently displayed, with much singing, aerobatic display flights and chasing. These gatherings were attended by single females, suggesting the possible choice of a mate by the female, and the events appear to end with the female leaving with a single male and the gatherings dissolving. This behaviour could suggest that the sex skew observed on this study site is the norm and that the behavioural ecology of the chat has evolved around this constraint. Mate choice could be a key area for future study in the Southern anteater-chat. Detailed studies outside the breeding season could also give insights into systems which can only be guessed at from breeding season observations, since much of the dispersal and group social organisation may happen outside the breeding season (Griesser et al. 2009). Such studies of the Southern anteater-chat may shed light on exactly how females assess and choose males, and subsequently how the pairs and family groups determine nesting territories. Low levels of inbreeding suggest that either the short range sex skewed dispersal is effective, or that there is active kin recognition and avoidance, or a combination of the two (Pusey & Wolf 1996).

There have been suggestions that other populations of Southern anteater-chat may have neutral or the opposite sex skew, and that these populations do not exhibit delayed dispersal beyond the next breeding season (Earle & Herholdt 1986; Earle & Herholdt 1988). However, these observations may have been carried out on chats in a more marginal habitat with both lower productivity and survival. It has been shown in other species that social structure varies between populations, for example Carrion crows Corvus...
corone in Switzerland do not live in cohesive year round family groups, but those in northern Spain do (Baglione et al. 2005). Crucial information concerning the breeding dynamics of the chats and the mechanisms involved in their family structure could be gathered by studying a population with the opposite sex skew, or by manipulating the sex skew in a population.

Many studies have shown that particularly a scarcity of breeding openings promotes delayed dispersal (Koenig et al. 1992; Emlen 1994; Hatchwell & Komdeur 2000). This study provides strong evidence that delayed dispersal in the Southern Anteater chat is driven by an ecological constraint, namely differential mortality between the sexes and a shortage of breeding females. It appears that the sex skew in the population allows all females’ access to breeding opportunities, that females disperse and breed as soon as they are sexually mature, with no surplus non-breeding adult females. Adult males where possible remain on the natal site with philopatric benefits, gaining both direct and indirect fitness benefits, and avoiding the potential costs of floating, until they can obtain a breeding partner (Fig. 11).

![Figure 11](image_url)

Figure 11. Overview of dispersal options taken by male and female southern anteater-chats. Arrows indicate main dispersal routes and subsequent choices/events. Dotted box indicates no floating birds. Only males remain philopatric or join groups as a helper. Females only disperse to breeding position and if loose mate disperse to another breeding position.
Sammanfattning på svenska


Vid ett flertal tillfällen har vi observerat samlingar av hanar där den vita skulderfläcken är iögonfallande framhävd, något som sker med mycket sjungande, akrobatiska uppvisningsslagsmål och jagande. Dessa samlingar var besökt av ensamma honor, vilket pekar på möjligheten av ett honligt val i valet av partner, och händelserna förefaller sluta med att honan avlägsnar sig med en hane medan resten av gruppen upplöses. Detta beteende kan tyda på att den sneda könsfördelningen vi observerade är normen och att beteendekologin hos skvättan har evoluerat runt denna begränsning. Partnerval kan vara ett nyckelområde för en framtidens studie av den sydliga termitskvätten. Detaljerade studier som utförs utanför häckningsperioden kan även ge insikter i system vilka man endast kan gissa sig till utifrån observationer gjorda under häckningsperioden. Detta eftersom mycket av spridningen och gruppororganisationen kan ske utanför häckningen (Griesser et al. 2009). Sådana studier av den sydliga termitskvätten kan sprida ljus över exakt hur honor värderar och väljer hanar, och därefter hur paren och familjegrupperna bedömer boterritorier. Låga nivåer av inavel antyder antingen att det korta,
snitt könsfördelade spridningsavståndet är effektivt, eller att det finns ett aktivt släktspåndigenkännande och undvikande, eller att det är en kombination av de två (Pusey & Wolf 1996). Det har antyts att andra populationer av den sydliga termitskvättan kan ha neutral eller den motsatta skeva könsför-
delningen, och att dessa populationer inte uppvisar försenad spridning utan-
för nästa häckningsperiod (Earle & Herholdt 1986; Earle & Herholdt 1988).
Emellertid kan dessa observationer ha utförts på skvättor i ett mer marginali-
serat habitat med både lägre produktivitet och överlevnad. Det har visats
inom andra arter att social struktur varierar mellan populationer. Ett exempel
är svartkräka, *Corvus corone*, som i Schweiz inte lever i kohesiva familjer
året om, samtidigt som svartkräkorna i norra Spanien gör det (Baglione et al.
2005). Essentiell information angående häckningsdynamiken hos skvättorna
och mekanismen involverad i deras familjestruktur kan bli insamlad genom
att studera en population med den motsatta sneda könsfördelningen, eller
genom att manipulera könsfördelningen i en population. Många studier har
visat att framförallt brist på häckningsmöjligheter främjar försenad spridning
(Koenig et al. 1992; Emlen 1994; Hatchwell & Komdeur 2000). Denna stu-
die tillhandahåller starka bevis för att den försenade spridningen hos den
sydliga termitskvättan drivs av ekologiska begränsningar, nämligen olika
grad av dödlighet mellan könen samt en brist på häckande honor. Det före-
faller som om den sneda könsfördelningen i populationen låter alla honor ha
tillgång till häckningsmöjligheter, och att honor sprider sig och häckar så
fort de blir könsmogna, något som i sin tur leder till att det inte finns ett
överskott av icke-häckande adulta honor. Adulta hanar stannar emellertid
kvar på födelseplatsen när det är möjligt och erhåller filopatriska fördelar till
dess att de kan få en häckningspartner; hanarna vinner både direkta och indi-
rektta fitnessfördelar och de undviker den potentiella kostnaden av lösdriveri.
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