

**Effect of group size and composition on individual behavior, group dynamics and population regulation in the Arabian babbler (*Turdoides squamiceps*)**



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Department of Biology



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# Abstract

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Cooperative breeding is a social system in which individuals help care for young that are not their own. Considerable research has found that cooperation can result in a number of benefits for group members, including enhanced reproductive success and greater longevity. These benefits lead to the possibility that the social structure of the group an individual comes from may have important long-term fitness consequences. However, little is known about the relative importance of social and environmental factors on individual fitness traits and group dynamics in the long-term in cooperatively breeding species. Thus, long-term studies on how social and environmental factors influence the costs and benefits of cooperative behaviour are of extreme importance. In this thesis I explore how social and environmental factors influences the individual, the group and the population in cooperatively breeding Arabian babblers (*Turdoides squamiceps*). I did that by (a) experimentally investigating the factors influencing individual foraging strategies and innovative behaviour, (b) analysing a long-term database to study the effect of social and environmental factors on individual fitness traits and group dynamics, and (c) determining whether inverse density dependence (Allee effects) occurs at both the group and population level. I found that dominant and subordinate individuals differ in both foraging and cognitive strategies, and that novel foraging skills may be socially transmitted, outlining an important benefit of group-living. I also found that group size and reproductive competition significantly affected reproductive success and group dynamics, suggesting that social factors are important influences on both individual fitness and group demography. Finally, I found the existence of both group and demographic Allee effects in the study population, which represents an important consideration for the management and

protection of cooperatively breeding species. These findings provides novel approaches that may benefit further studies on individual fitness and group dynamics in cooperative breeders.

## Statement of candidate

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I certify that the work carried out in this thesis, entitled, ‘Effect of group size and composition on individual behaviour, group dynamics and population regulation in the Arabian Babbler (*Turdoides squamiceps*)’ has not been previously submitted for a degree, nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research and during the preparation of this thesis has been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis. The research presented in this thesis was approved by Macquarie University Ethics Review committee under reference number 2011/038 (appendix 5).

A handwritten signature in dark ink, consisting of a stylized 'A' shape with a horizontal line crossing it, and a long, sweeping horizontal stroke extending to the right.

Oded Keynan

Student Number: 42270650

November 2014

# Preface

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All empirical chapters have been submitted for publication to peer-reviewed Journals. Chapter 3 was accepted for the journal '*Behavioral ecology*', Chapter 4 was submitted to the journal '*Behavioral ecology*'. Chapter 5 was submitted to the journal '*Ecology*', chapter 6 was submitted to the journal '*Journal of animal ecology*', and chapter 7 was submitted to the journal '*PLoS Biology*'. They are formatted here to meet the requirements of the respective journals.

The chapters of this thesis were reviewed and revised with the assistance of my academic supervisors, Dr. Amanda Ridley (University of Western Australia, former in Macquarie University) and Prof. Arnon Lotem (Tel-Aviv University).

Although the behavioral observations, experiments and dataset analysis were collected and executed by me, I was working within an established research project, founded in 1971 by Prof. Amotz Zahavi. The population was already color- ringed, and habituated to human presence and this work was certainly aided by the contribution of those that have worked on the research project since 1971.

My personal estimated contribution to each chapter is indicated below:

Chapter 1 & 2- conception 90%, writing 90%

Chapter 2- conception 100%, writing 90%

Chapter 3- conception 90%, data collection 100%, writing 70%

Chapter 4- conception 90%, data collection 100%, writing 70%

Chapter 5- conception 80%, data preparation and analysis 80%, writing 80%



Chapter 6- conception 80%, data preparation and analysis 90%, writing 80%

Chapter 7- conception 90%, data preparation and analysis 95%, writing 90%.

Chapter 8- conception 90%, writing 85%

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I'll start from the top with the key figures in this thesis, my supervisors, Mandy Ridley and Arnon Lotem, without whom I couldn't have brought this thesis together.

Since I first met Mandy in 2001, when she conducted her own PhD in Hazeva, I admired her scientific work, her efficiency and her ambitiousness. Having Mandy as a supervisor was a great honour. I feel that Mandy has managed to turn me into a real scientist, and gave me the tools to become an independent researcher. She has been the main figure who worked with me on this thesis, and has been through numerous drafts, written in relatively poor English. These drafts were always returned with comments within a few days (and sometimes within the same day), and they always gave the right guidance for how to improve my writing skills and my scientific abilities. Mandy is by all means one of the best teachers I have ever had in my life. Mandy is not only an excellent supervisor but also a dear friend, always generous and sensitive to my needs as an “older” student with a family.

I really don't know how my family and I could have survived our first two months in Perth if it wasn't for Mandy letting us stay in her house while she was conducting her research in the Kalahari.

Four years ago I sat with Arnon at his home in Haifa and begged for him to become my supervisor. I am extremely grateful that my begging was answered with a positive reply. Arnon is one of the most inspiring scientists I have ever met, and each conversation with him is an educational journey. Arnon has introduced me to the fascinating world of animal cognition and always challenges me to further investigate the philosophy that underlines scientific research. Although Arnon wasn't committed to any financial support of my project initially, he eventually invested a substantial amount of money in supporting both this research and my own scholarship. I believe that although Arnon didn't expect that in the beginning, he became seriously involved and enthusiastic about this research and its results.

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# 1.Introduction

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## 1.1 Cooperative breeding

Cooperative breeding is a social system in which more than two individuals help care for the young raised from a single brood, sometimes at the expense of their own reproduction (reviewed in Koenig & Dickinson 2004; Cockburn 2013; Riehl 2013). Numerous variations in social structure have been identified in cooperatively breeding societies, including alloparental care by offspring that delay dispersal and remain with their parents, and various forms of cooperative polygamy, in which more than a single male or female compete over breeding status within the same social unit (e.g. Carlisle & Zahavi 1986; Koenig *et al.* 1992; Ridley 2007; Nelson-Flower *et al.* 2013; Margraf & Cockburn 2013). The extent to which reproduction is shared among individuals within a group, also known as “reproductive skew”, depends on the ability of subordinates to gain access to inter or intra-group breeding opportunities, and the ability of the dominant breeding individuals to prevent them from doing so (reviewed by Hager & Jones C. B 2009). In general, cooperatively breeding bird species have higher rates of reproductive skew than mammals (Raihani & Clutton-Brock 2010), and in many avian species a dominant pair may monopolize most, if not all of the intragroup breeding activity (Raihani & Clutton-Brock 2010). A necessary step in the development of a cooperative group is the retention of grown offspring in the parental unit, otherwise known as delayed dispersal (Koenig *et al.* 1992; Kokko & Ekman 2002). The conditions favouring delayed dispersal may be viewed as the costs and benefits of two opposing options: (1) dispersing and attempting to breed independently, and (2) postponing dispersal and remaining as a non-breeder in the natal group (Kokko & Ekman 2002). At least four factors should influence the decision to leave the natal group: the cost (risks) of dispersal; the probability of successful establishment on a suitable territory following dispersal; the probability of obtaining a mate; and the likelihood of successful reproduction after the dispersal event



(Emlen 1994; Kokko & Johnstone 1999; Cant & English 2006). Whether or not an individual will disperse often depends on how these costs compare to the prospect of gaining direct or indirect fitness by remaining in the natal territory (Stacey & Ligon 1991; Koenig *et al.* 2000; Legge & Cockburn 2000; Pen & Weissing 2000; Ekman *et al.* 2001; Raihani *et al.* 2010; Nelson-Flower *et al.* 2012a; Ridley 2012a).

Identifying the costs which lead to delayed dispersal, together with the direct and indirect fitness benefits that individuals gain through group living, is of great value for understanding the selective forces involved in the evolution of cooperatively breeding societies (Pen & Weissing 2000; Kokko & Ekman 2002). Many studies have highlighted the importance of environmental factors in influencing individual fitness traits in social species (e.g. Koenig *et al.* 1992, 2011; Canário, Matos & Soler 2004; Ridley 2007; Shen *et al.* 2012; Gonzalez, Sheldon & Tobias 2013), with an accumulation of evidence leading to the recent proposal that cooperative breeding evolved in order to enhance individual fitness under environmental uncertainty (Rubenstein & Lovette 2007; Rubenstein 2011; Jetz & Rubenstein 2011). However, there is an increasing awareness of the influence of social factors (i.e. group size and reproductive competition) on both individual fitness and group dynamics (e.g. Hodge *et al.* 2008; Spong *et al.* 2008; Kazahari & Agetsuma 2010; Lardy *et al.* 2012; Bateman *et al.* 2013). Surprisingly, little is yet known about the relative importance of environmental factors and social factors, and how they influence the variation in individual fitness and group dynamics in cooperative breeders.

## **1.2 Social foraging and social learning**

A useful first step towards understanding how social factors influence individual fitness would be to investigate the benefits that group-living has on an individual's daily activities, in particular foraging success and its relationship with learning ability (in terms of learning novel foraging techniques). Previous studies have found that group-living benefits

individuals through higher biomass intake, due to the benefits of shared sentinel activity and increased vigilance (Roberts 1996; Hollén, Bell & Radford 2008; Sorato *et al.* 2012). In a direct comparison of living socially versus living alone, individuals who left their group to live alone suffered a reduction in both body mass and foraging efficiency, as well as an increase in stress levels (Ridley, Raihani & Nelson- 2008; Young & Monfort 2009), suggesting that individuals benefit from being part of a group. Additional evidence for the benefits of living socially have been provided through the discovery of teaching behaviour between group members (Thornton & McAuliffe 2006) and cooperative hunting (Creel & Creel 1995). Surprisingly, the effect that group-living has on individual foraging strategies and learning ability has been relatively under-studied, particularly in wild, cooperatively breeding species. Patterns of learning behaviour during foraging are of particular interest in cooperative breeders because (a) there is an extended period of post-fledgling care where individuals have an opportunity to learn foraging skills from other group members (Heinsohn 1991; Rapaport 2005; Thornton & McAuliffe 2006; Raihani & Ridley 2008) and (b) the presence of multiple individuals foraging closely together throughout the day could facilitate the efficient transmission of foraging techniques (similar to those observed by Langen (1996) in the White-throated magpie jay, *Calocitta formosa*). The study of social foraging has been developed mostly within the framework of the producer-scrounger (PS) game (Barnard & Sibly 1981, reviewed by Giraldeau & Dubois 2008). In this game, individuals can forage either as searchers (producers) or joiners (scroungers) and these social foraging tendencies may be influenced by both group size (Vickery, Giraldeau & Templeton 1991; Giraldeau & Caraco 1993) and social dominance (Liker & Barta 2002). Scrounging behavior may facilitate or inhibit social learning; Caldwell & Whiten (2003) found that common marmosets (*Callithrix jacchus*) that had the chance to scrounge on an individual who was trained to gain access to a food reward learnt this behavior faster than those who didn't have the chance to scrounge. On the other hand, both Giraldeau &

Lefebvre (1987) and Lefebvre & Helder (1997) found that scrounging inhibited social learning and the acquisition of novel foraging behavior in pigeons (*Columba livia*) by causing the scrounger to be dependent on the producer without being able to learn the task by itself. Recent work showed that individual learning ability in young house sparrows (*Passer domesticus*) is correlated with a future tendency to forage as a producer (Katsnelson *et al.* 2011), and that in both house sparrows and nutmeg mannikins (*Lonchura punctulata*), the relative use of producing and scrounging is affected by the relative success experienced while applying each strategy (Katsnelson *et al.* 2008; Morand-Ferron & Giraldeau 2010; Belmaker *et al.* 2012; Ilan *et al.* 2013). These results suggest that both individual foraging strategies and learning ability are highly influenced by social characteristics. This social influence may be particularly strong in cooperatively breeding species, where social interactions among group members occur frequently.

In social species, there is evidence that some individuals are consistently more innovative than others (Laland & Reader 1999; Liker & Bókonyi 2009; Morand-Ferron *et al.* 2011; Cole & Quinn 2012; Griffin *et al.* 2013). It is not clear however, whether such differences persist throughout life, in personality types (Sih & Del Giudice 2012), or are determined by factors such as age, social rank, or local conditions. For example, Thornton & Samson (2012) found that in meerkats (*Suricata suricatta*) male adult subordinates were better at acquiring novel foraging skills than either juvenile subordinates or dominants individuals. Similarly, Brickner (2008) found that subordinate Arabian Babblers (*Turdoides squamiceps*) are more innovative and explorative than dominant ones, and Midford, Hailman & Woolfenden (2000) found that juvenile free-living Florida scrub jays (*Aphelocoma coerulescens*) that were exposed to adult novel foraging behavior, learnt this behavior much faster than naïve juveniles. Individual success in both innovation and learning skills may also be influenced by the size of the group, since it may lead to a skill-

pool or ‘pool of competence’ effect (Giraldeau 1984; Morand-Ferron & Quinn 2011). This describes an effect where larger groups may be more likely to contain individuals with the ability to solve a novel task, thus increasing problem-solving efficiency at the group level. Therefore, group size may have an important influence on individual learning ability and thus the likelihood of acquiring novel foraging techniques. This is a novel way in which group-living may benefit individuals, yet it has rarely been empirically measured in cooperatively breeding species.

### **1.3 Individual success, group dynamics and Allee effects**

As noted in 1.1 and 1.2, group-living can influence individuals in many ways. Therefore, understanding the factors that affect individual life history and group dynamics is essential to our understanding of the evolution and maintenance of cooperative breeding behaviour. This can only be answered through the use of long-term studies that are able to document individual success, and group and population dynamics over a prolonged time frame (Clutton-Brock & Sheldon 2010; Cockburn 2014). Analysis of long-term databases enables us to study detailed social and ecological influences on cooperative breeding behaviour from diverse perspectives, and may therefore provide a more detailed overview of the costs and benefits of group living in comparison to short-term studies.

In cooperatively breeding species with high reproductive skew, the primary way to reproduce is by becoming a dominant (reviewed in Hager & Jones C. B 2009). Factors like low adult mortality and high territory saturation leads to considerable variation in the number of individuals that both achieve and are able to maintain a dominant breeding position (Arnold & Owens 1998; Pen & Weissing 2000). While individual morphology and body condition is a strong factor influencing longevity and competitive ability among individuals in non-cooperatively breeding species (Carrascal *et al.* 1998; Buston 2003a; Blums *et al.* 2005; Verhulst *et al.* 2014), the influence of body condition on the ability to both attain and maintain a dominant position (and achieve higher lifetime reproductive

success (LRS) appears not as important for cooperative breeders (Hodge *et al.* 2008; Spong *et al.* 2008). Rather, it seems that social factors such as dispersal decisions, group size and reproductive competition are more influential (Cant & English 2006; Raihani *et al.* 2010; Lukas & Clutton-Brock 2014). While many studies have illustrated the benefits of group size on lowering the cost of parental care (Heinsohn 1992; Wright & Dingemanse 1999; Canário *et al.* 2004; Ridley & Raihani 2007), the effect of group size and environmental factors on variation in the annual reproductive success (ARS) and LRS of breeding individuals has only recently started to emerge. (e.g. Hodge *et al.* 2008; Spong *et al.* 2008; Lardy *et al.* 2012; Bateman *et al.* 2013).

Both the size of the group and the type of social interactions occurring within it may influence individual survival and reproductive success. Therefore, by looking at group dynamics (i.e. immigration and emigration patterns, reproductive success and group extinction events) we can better understand the factors that generate stable, long lasting groups. This is especially important for cooperatively breeding species, that primarily inhabit areas that are characterised by environmental uncertainty (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011). Indeed, studies have found that the size of the group and the social interactions within it (mainly reproductive competition) influence individual survival and reproductive success most strongly during severe environmental conditions (Shen *et al.* 2012; Angulo *et al.* 2013; Ebensperger *et al.* 2014). Therefore, we would predict that larger groups have a greater likelihood of successful reproduction and persistence when environmental constraints are high (Covas, Doutrelant & du Plessis 2004), (Heg *et al.* 2005), compared to small groups. At the moment, there is still limited information on the mechanisms by which group living influences individual survival and reproductive success during severe environmental conditions (Rubenstein 2011; Bateman *et al.* 2013; English *et al.* 2013) and further research is needed in order to better understand it.

Since cooperatively breeding species are characterised by populations that are clumped into groups of individuals, to gain an understanding of long-term demographics in such breeding systems it is important to understand the relationship between population dynamics, group dynamics and individual survival and reproductive success. An increase in individual reproductive success and survival with an increase in population density is known as *inverse density-dependence*, or the Allee effect (Allee 1931). According to this effect, more individuals in a population will result in higher fitness per individual, until negative density dependence effects (such as competition over reproduction or resources) will take place (Stephens, Sutherland & Freckleton 1999; Courchamp, Clutton-Brock & Grenfell 1999). An Allee effect could influence small populations by several mechanisms such as mate limitation, inbreeding depression, higher per capita risk of predation, and higher vulnerability to both environmental stochasticity and genetic drift (reviewed by Stephens *et al.* 1999; Courchamp *et al.* 1999; Courchamp, Berek & Gascoigne 2008; Stephens & Sutherland 1999). The relative strength of the Allee effects affecting individual fitness components will determine the overall influence of Allee effects on the population. Therefore Stephens *et al.* (1999) suggested that in order to better study Allee effects in animal populations, it would be useful to distinguish between component Allee effects, which are manifested by individual fitness traits (increased individual fitness with population size), and demographic Allee effects, which is the level of total fitness represented by population growth rate in relation to population size. Cooperatively breeding societies are likely to prove an excellent model for understanding Allee effects since the more the individuals of a species need to cooperate in order to survive and reproduce, the more intense Allee effects are expected to be in that species (reviewed in Courchamp *et al.* (2008).

However, while component Allee effects have been documented in a number of cooperative breeders (Somers *et al.* 2008; Gusset & Macdonald 2010; Bateman *et al.* 2012;

Angulo *et al.* 2013), there is an absence of empirical evidence for demographic Allee effects (Gregory *et al.* 2010; Angulo *et al.* 2013). As a result, Bateman, Coulson & Clutton-Brock (2011) suggested that in cooperative breeders, component Allee effects may not translate to the population level (demographic Allee effects) since group growth rates are asynchronous with population growth rates, resulting in different factors influencing group and population dynamics. Similarly, Angulo *et al.* (2013) suggested that since individual fitness is more dependent on group dynamics than overall population size, the concept of a ‘group Allee effect’ should be considered in order to better understand Allee effects in cooperative breeders.

Thus, by developing a framework that would enable us to examine the social and environmental factors that influence individual LRS and group dynamics, and by looking at the relationship between population dynamics, group dynamics and individual LRS, we can create a thorough overview that will enhance our understanding of the causes of variation in individual life history traits, group persistence and population decline in cooperatively breeding species.

#### **1.4 Thesis structure**

In this thesis I investigate the cost and benefits of group living at three levels of resolution.

I start by looking at the individual level, identifying how group living influences individuals during both foraging and social interactions. I then determine the causes of variation in fitness values among individuals according to prevailing social and environmental conditions. Following this, I investigate the causes of variation in group dynamics over the long-term, and determine how they are shaped by social and environmental conditions. Finally, I look at long-term population dynamics, trying to identify Allee effects, and looking at how they affect the individual, the group and the population. The overall findings from these empirical investigations will not only provide an extensive, multi-dimensional overview allowing us to better understand some of the

costs and benefits of group-living, but will also generate a better understanding of population dynamics, enabling better informed management decisions when attempting to conserve cooperatively breeding species. **1.5 Thesis outline**

In chapters three, four and five I focus on the individual as the level of analysis. In chapters three and four I focus on cognitive questions. I conduct three field experiments to investigate individual differences in social foraging strategies, learning and innovation abilities. In chapter three I experimentally investigate the relationship between foraging strategy and the acquisition of novel foraging skills. In chapter four I experimentally investigate whether the propensity to innovate varies among individuals, and between different cognitive tasks.

In chapter five I consider the factors causing variation in fitness among individuals. I use an extensive database covering 35 years of observation to investigate how social factors (such as dispersal, group size and reproductive competition), together with environmental factors (such as rainfall and drought) affect individual variation in the acquisition of a dominant breeding position, dominance tenure, and lifetime reproductive success.

In chapter six I focus on the group level. I use a long-term database to determine the relative influence of social and environmental factors on group dynamics (nesting success, survival of young, changes in adult group size and likelihood of group extinction).

Finally, in chapter seven, I investigate population dynamics by determining whether Allee effects exist in the study population, how they affect individual reproductive success and group dynamics, and the implications of these findings for understanding the importance of Allee effects on population fluctuations over time and thus the management of cooperatively breeding species.



## 2. General methods

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## 2.1 Study species:

The Arabian Babbler (*Turdoides squamiceps*) is a medium-sized passerine (65-85 g) from the family *Leiothrichidae* (Gelang *et al.* 2009). It is a territorial, obligate cooperatively breeding bird, that inhabits the Arabian desert and Sinai peninsula (Zahavi 1989, 1990; Anava *et al.* 2000). Groups range in size from 2-20 adult individuals of both sexes, with linear dominance hierarchies within each sex. The dominant pairs in each group form monogamous bonds. Young birds delay dispersal for an average of 1–3 years. All adult group members cooperate to provision young, detect and defend against predators, and share sentinel duties (Wright 1998). Arabian babblers are sexually dimorphic, males are relatively larger and heavier (Males 70-85g, females 64-77 g, Ridley 2007) and may be recognized in the field by their yellow iris and dark beak, while females have a dark eye and a more gently curved and yellow beak (Figure 2.1).

The Arabian babbler is not considered to be threatened, and is classified as ‘least concern’ on the IUCN red list of threatened species (IUCN, version 3.1)



**Figure 2.1:** Female (left) and male (right)  
Arabian babblers engaged in allopreening

### 2.1.1 *Breeding behaviour*

Breeding in Arabian babblers is almost entirely monopolized by the dominant pair, and breeding by subordinates is extremely rare (Lundy, Parker & Zahavi 1998). As predicted by models of reproductive skew (Vehrencamp 1983; Keller & Reeve 1994), as genetic relatedness between the dominant and same-sex subordinate increases, so does the degree of reproductive monopolization by the dominant (Lundy et al. 1998). Non-breeding helpers participate in a number of activities related to helping to raise young produced by the dominant pair, including incubation, feeding of nestlings and dependent fledglings, and defending the young from predators (Zahavi & Zahavi 1997; Ostreiher 1999; Wrigh, Maklakov & Khazin 2001). The breeding season typically spans the period between February and July, although breeding attempts are occasionally observed as early as October and as late as August (Zahavi 1989, 1990). Breeding activity is initiated by courting displays by the dominant pair: this includes the presentation of nesting material to one another, and an increase in the frequency of allopreening bouts, and continues to the mutual building of a nest. Nests are usually built from dried grass and other soft vegetation, and are usually built in dense or thorny bushes and trees, mainly *Acacia totrollis*, *Acacin radianna*, *Nitraria retusa*, and *Lycium Shawii*. (Ostreiher 2001) Copulation occurs privately, without the presence of subordinate group members (Ostreiher 1997). Pre-copulation, the male presents a nuptial gift to the female (usually a small branch or other inedible object) and then copulation will take place, this ritual usually repeats itself several times over the course of the morning (Zahavi 1989, 1990). The dominant female will typically lay a single clutches of four eggs, although clutches of three or five eggs are not uncommon (Ridley 2007). Joint clutches of two or more females are rare and may contain up to 13 eggs in one nest (Zahavi 1989, 1990). Incubation usually starts after the

last egg is laid (Figure 2.2), and although all group members participate in incubating the eggs, the dominant female is the only one that incubates during the night (Ostreiher 1997).

Three stages of offspring development are identified in Arabian babblers: (1.) Nestling stage. Nestlings remain in the nest for 12-14 days after post hatching, (2.) Fledgling stage. Once fledged, the young are unable to fly for up to x days post-fledging, and are dependent on adult group members for food, (3.) Independent stage. Fledglings start to become independent foragers approximately eight weeks post-fledging. They are defined as independent when more than 95% of their food is obtained through self-foraging (Ridley 2007). Independent juveniles are considered adults when they reach 12 months of age (Ridley 2007).



**Figure 2.2:** Young Arabian babbler nestlings  
(5 days old)

### 2.1.2 Territoriality

Arabian babblers are highly territorial, and a group may occupy the same territory during its entire lifespan. Territory size is highly variable, (some larger territories may reach approx. 1km<sup>2</sup>. (Zahavi 1990) and are primarily located along dry riverbeds or in areas where ground water is closer to the surface, resulting in greater vegetation cover. Groups monitor their territory borders daily, and interactions between neighboring groups are frequent (Ridley 2012b). Most interactions are peaceful and characterized by ritualized chorusing and occasional short chases (Zahavi 1990). In rare events the interaction may escalate and lead to fights, which may, in rare cases, result in injury or even death. (Zahavi 1990; Zahavi & Zahavi 1997)

### 2.1.3 Foraging and diet

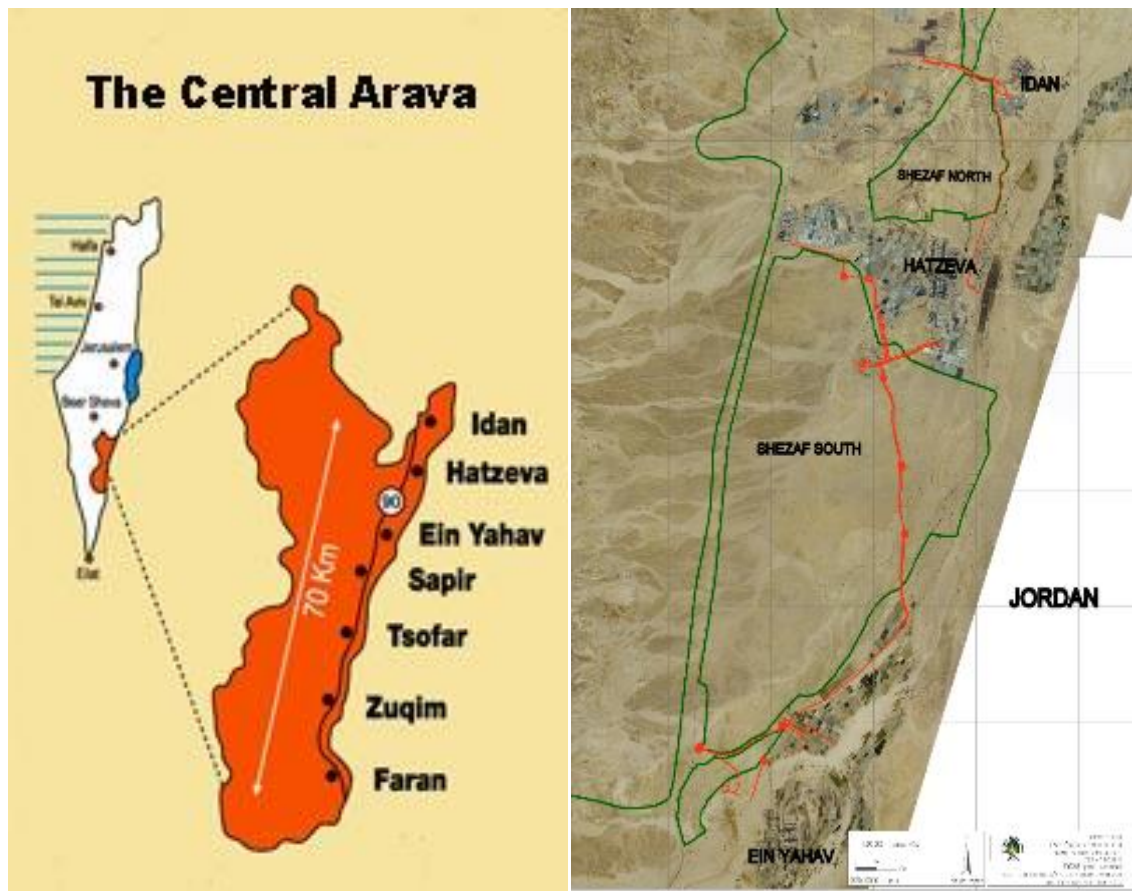
Babblers are omnivorous and forage on different types of flowers, fruits, insects and vertebrates. They have been observed feeding on nectar from *Loranthus acaiae* and *Lycium shawii*, the flowers of *Acacia radianna*, *Acaia tortilis*, and the fruits of *Nitaria retusa*. Nevertheless, invertebrates make up for most of their diet (Keynan, Ridley & Lotem 2014), and they may feed on small vertebrates such as lizards, geckoes, small snakes and the nestlings of small bird species. Cooperative hunting is extremely rare and has been observed only when relatively large vertebrates are caught, such as diadem snakes (*Spalerosophis diadema*) and on one occasion a wounded White spectacled Bulbul (*Pycnonotus xanthopygus*, O. Keynan, *personal observations*). Babblers are primarily terrestrial foragers, using their bill to dig in the substrate or to glean through vegetation in order to locate food items (Zahavi 1990, O. Keynan *personal observations*). Other, less common foraging techniques include probing inside tree stems to locate tree-dwelling caterpillars and hawking for flying insects. Arabian babblers do not need to drink water and can derive all their water requirements from their food

### 2.1.5 Conflict over reproduction and routes to breeding

The dominant pair in each social group are monogamous, and reproduction by subordinates is extremely rare (Lundy *et al.* 1998). Therefore, the only way for a subordinate to achieve reproductive success is by finding a dominant position, either in its natal group or by dispersing to a neighboring group (Kokko & Johnstone 1999; Raihani *et al.* 2010; Nelson-Flower *et al.* 2012b). Since Arabian babblers avoid inbreeding (Zahavi 1990; Lundy *et al.* 1998), and most groups are highly kin-structured, vacancies within the group are typically filled by an unrelated individual dispersing from a neighboring group (Zahavi 1989, 1990). Dispersal in Arabian babblers is female-biased, with female dispersal accounting for about 70% of all dispersal events (Ridley 2012b). The most successful dispersal events occur when a coalition of individuals invade a smaller group and overthrow the existing breeding pair (Ridley 2012b), similar to what occurs in lions (*Panthera leo*; Bygott, Bertram & Hanby 1979). Subsequently, after the coalition has successfully invaded the group, there is a battle for dominance, with one individual eventually becoming the sole breeder. The remaining coalition members (who are now reproductive competitors) are usually evicted or accepted as non-reproductive helpers (Zahavi 1989, 1990). While competing over reproduction, females negatively impact group reproductive success. Competing females were witnessed breaking each other's eggs or chasing an incubating female from the nest (Koenig *et al.* 1995; Lundy *et al.* 1998; Nelson-Flower 2013).

## 2.2. Study site

The study was conducted at the Arava rift valley, Negev desert, Israel, ~30km south of the Dead Sea, between the settlements of Idan (30°48N, 35°17E) Hazeva (30°46N, 35°16E) and Ein Yahav (30°45N, 35°15E). The study site is approximately 60 km<sup>2</sup>, covering a 40 km<sup>2</sup> nature reserve (the Shezaf Nature Reserve) and surrounding, unprotected areas. (Figure 2.3)



**Figure 2.3:** A map of the central Arava region and its location in Israel (left) and a detailed satellite image of the study site (right). Maps are courtesy of the Arava regional council and Israel Nature & Parks Authority



### 2.2.1 Climate

The Arava Valley is defined as a hyper-arid habitat (UNESCO, 1977) with a mean annual winter rainfall of 35mm, with rainfall occurring on average 6-9 days per year, primarily between October and May (Ginat *et al.* 2011). There are large annual variations in both the total rainfall recorded as well as its temporal and spatial distribution in the Arava Valley (Figure 4, Anava *et al.* 2000)). The climate is immoderate and characterized by strong solar radiation, high air temperature (annual average > 23°C; summer daily average > 38°C), extremely low rainfall and high evaporation potential (~ 3000-3,500 mm/year; Goldreich & Karni 2001). Daily temperatures may rise to 49°C ( Goldreich & Karni 2001, Figure 2.4). In spite of these climatic extremes, the region is dotted with small agricultural communities that use groundwater to grow horticultural crops and support dairy herds (Ginat *et al.* 2011).

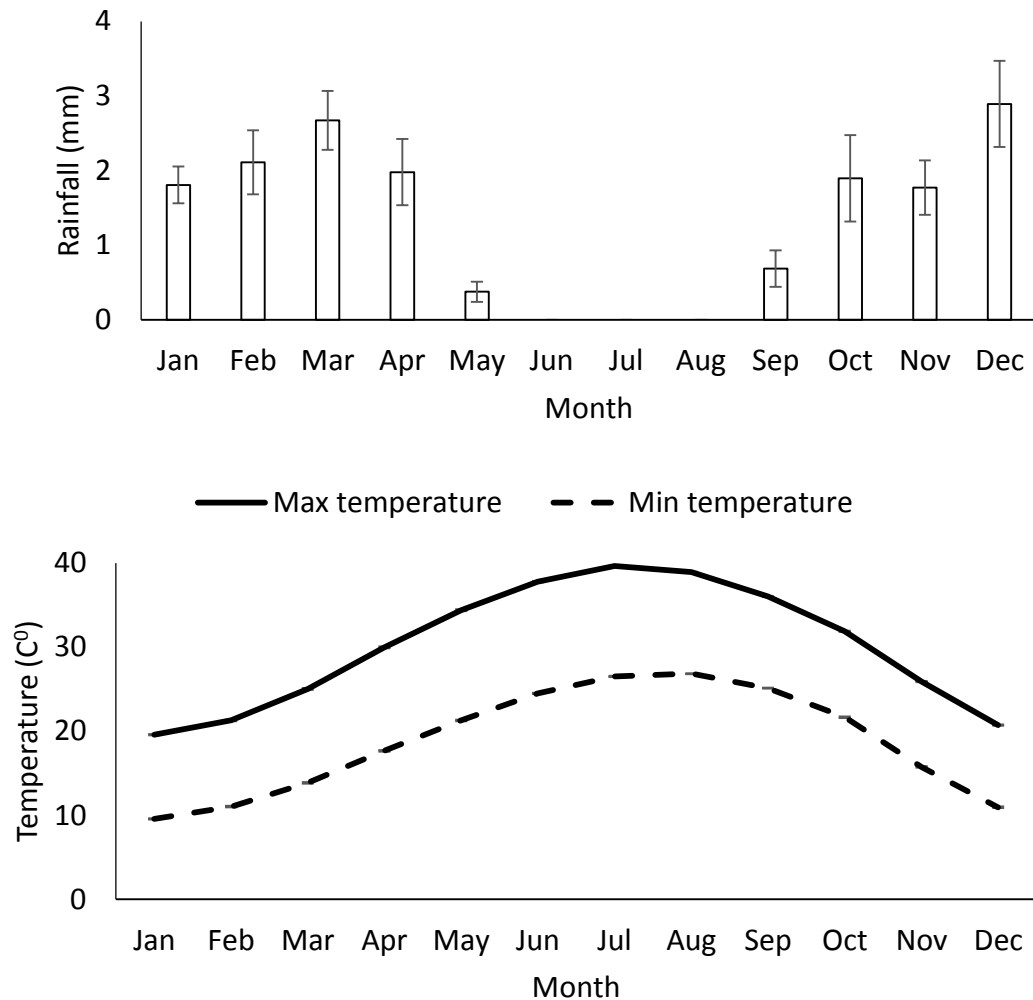
### 2.2.2 Habitat

The Arava valley is part of the Dead Sea rift, a topographical depression that separates the Negev desert in the west from the Edom Mountains at the east. The Arava valley is the northern part of the Great Rift Valley. The region encompasses a diverse range of microhabitats, including dry riverbeds, small springs, marl rocks and sand dunes. The natural flora of the region is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, and *Haloxylon persicum*), that occur primarily in the dry riverbeds (wadis). The local fauna of the Arava region is diverse and includes more than 30 species of reptiles, two hundred species of birds (migrating and local), and dozens of mammal species (Israel Nature & Park Authority).

In the past two decades the region has suffered from a considerable increase in human activity, resulting in the extensive development of a road network, horticultural farmland, and urban expansion. This had led to direct natural habitat loss, as well as indirect habitat



loss though the increased mortality of trees and other local vegetation in the remaining natural habitats due to edge effects and a lowering of the water table due to unsustainable pumping (Ward & Rohner 1997; Lahav-Ginott, Kadmon & Gersani 2001).



**Figure 2.4:** Average monthly rainfall (+SE) and average monthly maximum and minimum temperature at the study site. Figures are based IMS data, covering the years 1972-2013

### 2.3. The Arabian babbler research station

The Arabian babbler study population that this research is based on was established by Professors Amotz & Avishag zahavi in 1971, and the population has been monitored continuously since then. The population currently contains 128 individuals in 22 groups, but population size fluctuates between years from a minimum of 89 individuals in 19 groups in 2009, to approximately 230 individuals in 34 groups in 1996.

Each individual in the population is ringed with a uniquely numbered metal ring and three additional plastic rings for individual identification. Individuals are ringed either as chicks in the nest (at 9-12 days post hatching), or as adults caught using a walk-in trap. The walk-in traps are baited with bread crumbs and mealworms, and are triggered automatically by the babblers stepping on a lever inside the trap, or by hand by an observer. Walk-in traps are never left unattended. During ringing, blood samples (ca 50µl) are collected through brachial venipuncture for use microsatellite analysis. All birds have been captured and ringed under a ringing license from the Israeli Nature and Parks Authority. The current research of this thesis was approved by the Israeli Nature and Parks Authority (License numbers 2011/38268, 2012/38711), and by the Australian Research Authority (ARA, License number 2011/038).

The study population is habituated to the presence of human observers, allowing behavioural observations and data collection from close range (within 2-3m) without causing any perceivable behavioral change or stress. The process of habituation aims to ensure that the observer is not perceived as a threat, nor as a source of food, and consequently the birds act naturally in the presence of the observer (*sensu* Ridley & Raihani 2007). Therefore, small portions of food were given to the birds only when they were first encountered at the start of each observation session. Behavioral observations and data collection occurred in the mornings, while the afternoon sessions were devoted to

following group to their roosting trees in preparation for observation from dawn the next morning. Observing effort fluctuated between years but each group was observed at least once a month during the non-breeding season and once a week during the breeding season.

### *2.3.1 Determining sex, rank and breeding status*

Dominance within the groups of Arabian babblers can be determined through age (age linear hierarchies exist in the group, social interactions and breeding behavior (Ridley 2007). Dominant individuals assert their dominance over subordinates through aggressive behavior (such as pecking and physical attacks, (Carlisle & Zahavi 1986). Dominance can also be determined through breeding behaviors such as courting, nest building or overnight incubation (the latter which is performed solely by dominant females).

## **2.4 Data collection**

### *2.4.1 Long-term group and individual database*

Over the 35 years of data collection on the study population, a standardized structure life history of data collection was mandatory for all researchers. During each observation life history data was collected on: group size, individual identity of all birds present, sex, rank (dominant/subordinate). In addition, for every breeding event the following details were collected: breeding status (nest-building, incubating, number of eggs, nestling, and fledglings), offspring survival, adult survival, dispersal events, eviction events, encounters between neighboring groups, and the location of the nest and roost tree.

Each life history observation was entered into a database, which took three forms: a chronological catalogue of handwritten life history events for each group, an entry into the calendar event for each group, or by entering the data onto a Microsoft Access database that was developed at the station. The data presented in this thesis was extracted and cross-examined from those three sources. Only groups that had a complete record of the event in question in all three forms were used for the analysis of group dynamics and individual reproductive success (Table 1). All groups that existed in the population for more than

three breeding seasons and had continuous data on group size analyzed for population data (Table 2.1).

**Table 1:** description of the different parameters extracted from the Arabian babbler dataset

Data collected	Description
Social rank	Dominant or subordinate (determined by age, social interaction and breeding activity)
Sex	Male/ female (for all individuals who survived their first year of life)
Age	In days post-hatching, measured for each individual that hatched in the population
Dispersal	Whether the focal individual dispersed from its natal group
Dominant tenure	The total period (days) that an individual spent in the dominant rank for a group
Pair tenure	The total amount of time (days) that a dominant male and female were present as a breeding pair
Reproductive competition	The presence and identity of multiple potential breeders of the same sex in the same group (where potential breeders are adults that are not related to a within-group adult of the opposite sex, <i>sensu</i> Nelson-Flower et al 2013)
Group sex ratio	Number of adult females divided by the total number of

	adults in the group
Group size	Number of adults (all individuals > 1 year old) present in the group
Relative group size	Adult group size of the focal group divided by the average adult group size in the study population for each year.
Breeding attempt	A breeding attempt was considered to have occurred when at least one egg was laid in a nest. The identity of the dominant pair was collected for each breeding attempt.
Brood overlap	Presence of dependent young in the group when another breeding event is initiated
Breeding characteristics	Number of eggs laid, number of nestlings hatched, and number of fledglings fledged. Breeding characteristics were collected for each group and for each dominant individual.
Survival to adulthood	<p>Number of young that survived to the end of their first year post-hatching. Individuals that disappeared before completing their first year of life were considered dead due to extremely low chances for successful dispersal at this age (Zahavi 1989, 1990; Lundy <i>et al.</i> 1998; Ridley 2007)</p> <p>Survival of young to adulthood was collected for each group and for each dominant individual.</p>

Emigration	Number and identity of individuals dispersing from the focal group for a period of longer than 30 days, and re-sighted in another group in the population.
Immigration	Number and identity of individuals joining a group for a period of longer than 30 days.
Extinction	A group was defined as extinct when all individuals had dispersed or disappeared, and repeated investigations found no further evidence of the group.
Individual density	Number of individuals in the population per km <sup>2</sup>
Group density	Number of groups in the population per km <sup>2</sup>
Population per capita growth rate (PCG)	Number of individuals in the population in year t+1/ number of individuals in the population in year t.

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## 2.5 Statistical analysis

Statistical analyses were carried out primarily in IBM SPSS statistics version 22. See table 2.2 for a list of the statistical techniques employed in this thesis.

**Table 2.2:** A brief description of the statistical techniques employed in this thesis

<b>Statistical test</b>	
<b>Binomial test</b>	Chapter 4
<p>The binomial test is used to explore the significance of an observed distribution from a theoretically derived expected distribution. I used it in order to see whether individuals learned to prefer white lids over black lids.</p>	
<b>Spearman rank correlation coefficient</b>	Chapter 4
<p>The spearman rank correlation coefficient is a non-parametric measure for statistical dependence between two variables. I used this test to check for the consistency of an individual tendency to scrounge between experimental trials.</p>	
<b>Linear regression</b>	Chapter 7
<p>Linear regression is a statistical test to determine the strength of the relationship between one dependent variable and one or more independent variables. I used it in order to check for significant trend in the study population (i.e. rainfall, annual reproductive success, group size and group and individual density) I</p>	
<b>Linear Mixed Models (LMM) with AICc</b>	Chapters 3-7
<p>When conducting experiments with wild animals, a range of environmental and social factors can come into play, and are potentially important for explaining response terms. LMM's is used to simultaneously explore multiple explanatory terms and statistically</p>	

control for both random (repeated measures) and fixed effects on normally distributed data. I have used LMM's on normally distributed data (or data that was transformed to achieve normality). Models were compared using model selection with Akaike's information criterion adjusted for small sample size (AICc). All candidate models were compared to the AICc basic model (with no predictors). Any candidate models that did not have AICc values of less than five from the basic model were considered as having no significant influence on the distribution of data. The model with the lowest AICc value provided the best fit to the data. When models scored within 5 AICc values of the best model, multi-model averaging was employed to determine significant predictors. Model averaging is a technique to calculate a weighted average of each parameter estimate (Grueber et al 2011).

### **Generalized Estimating Equations (GEEs)**

Chapters 3-7

Similar to LMM's, GEEs are a technique to explore multiple explanatory terms and statistically control for both random (repeated measures) and fixed effects. However, GEEs focus on population averages rather than subject-specific responses. Therefore GEE as may be used for binomial or poisson data. Similarly to the LMM analysis described above, I compared candidate models using model selection, but with GEE analysis I used Correlated Quasi Likelihood under independence model criterion (QIC; Pan 2001) corrected for small sample size (QICc). When models scored within 5 QICc values of the best model, multi-model averaging was employed to determine significant predictors. Model averaging is a technique to calculate a weighted average of each parameter estimate (Grueber et al 2011).



Similar to LMM's and GEE's, GLM's is a technique used to explore multiple explanatory terms. I used GLM's on data that was transformed to achieve normal distribution when there were no repeated measures and only fixed factors were involved. I used Akaike's information criterion for small sample size (AICc) to compare models.

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### 3. Social foraging strategies and acquisition of novel foraging skills in cooperatively-breeding Arabian babblers.

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Co- authored by: Amanda R. Ridley and Arnon Lotem

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### 3.1 Abstract

Social foraging strategies and their association with learning and innovation abilities have been studied extensively in flocking birds, but their importance for cooperatively breeding birds has remained relatively unexplored. The high degree of sociality typical of cooperative societies may indicate an important role of social foraging for learning and innovation. We studied (a) social foraging strategies and (b) the acquisition of a novel foraging skill in 16 groups of wild, cooperatively-breeding Arabian babblers (*Turdoides squamiceps*). In Experiment 1 we provided a foraging grid of 96 feeding wells to each group, allowing them either to search for food individually (producer) or join other birds (scrounger). Subordinates scrounged significantly more than dominant individuals, spent longer on the foraging grid, and had a higher proportion of their foraging steps rewarded (due to the effect of successful scrounging). However, scrounging was not related to poor learning ability, because almost all the individuals that learned the novel foraging skill in Experiment 2 (removing a rubber lid to reach food) were scroungers. These findings suggest that group members differ in their foraging strategies and learning abilities according to their rank and that subordinate group members may be more opportunistic and flexible in their behavior than dominants, making use of both scrounging and novel foraging opportunities.

### 3.2 Introduction

Living in a group results in complex interactions between individuals, who need to both cooperate and compete with conspecifics for food resources (Hatchwell & Komdeur 2000). While sociality provides benefits such as anti-predator defense, mating opportunities, and increased foraging efficiency, it also entails costs, mainly through competition and depletion of resources (Hatchwell & Komdeur 2000; Krause & Ruxton 2002; Giraldeau & Dubois 2008). The costs of competition may nevertheless be reduced when group members have different repertoires of foraging behaviors, as suggested by the “niche variation

hypothesis” (Bolnick *et al.* 2003). Moreover, different individual niches may not only reduce competition but may also benefit group members by creating a “skill pool effect” (Giraldeau 1984) or a “pool of competence”(Morand-Ferron & Quinn 2011), which allow social foragers to exploit a greater variety of food resources by joining each other’s food findings (Giraldeau 1984; Giraldeau & Lefebvre 1986).

The potential benefits of social foraging, or the skill pool effect, can be effectively studied within the framework of the “producer-scrouter game”. This game was first envisioned by Barnard & Sibly (1981), and subsequently analyzed and studied extensively by others (reviewed by Giraldeau & Caraco 2000; Giraldeau & Dubois 2008). According to the producer-scrouter game, group-living animals can employ one of two social foraging strategies: as producers, which search for food by themselves (and thus “produce” food for the group); or as scroungers (joiners), which exploit the findings of the producers. The success of each strategy depends on the frequency of the other strategy, which makes it a game with evolutionarily, or behaviorally, stable outcomes (Giraldeau & Dubois 2008). Group foraging success may be reduced due to producer-scrouter dynamics when scrounging comes at the expense of producing (Giraldeau & Caraco 2000). However, the same dynamics may actually increase group foraging success when producing and scanning for scrounging opportunities are not mutually exclusive (Fernández-Juricic, Erichsen & Kacelnik 2004), when scrounging facilitates social learning (Arbilly *et al.* 2011), and when food patches are hard to find and provide more food than a single individual is likely to consume (Vickery *et al.* 1991). Thus, under such circumstances social foraging may be viewed as cooperative.

The success of social foraging depends not only on the number of producers in the group but also on their experience and foraging skills. It has been suggested that producers may be more efficient foragers than scroungers (Coolen 2002; Beauchamp 2006), and that the

tendency to produce may be associated with better learning abilities (Arbilly *et al.* 2010; Katsnelson *et al.* 2011) or with bold or explorative behaviors (Kurvers *et al.* 2010; Kurvers, Hamblin & Giraldeau 2012). Furthermore, scrounging is typical of young and inexperienced individuals that follow their parents or other group members (e.g. Midford, Hailman & Woolfenden 2000; Moscovice & Snowdon 2006; Katsnelson *et al.* 2008; Thompson & Ridley 2012 but see Liker & Barta 2002; Belmaker *et al.* 2012, for the effect of dominance that may reverse this trend). Thus, producers are often viewed not only as those that find food, but also as those that produce the knowledge that can be transmitted to the rest of the group through social learning (Giraldeau 1997; Laland 2004; Lehmann & Feldman 2009). However, this view of “producer to scrounger” information transfer is complicated by two lines of evidence: first, scrounging individuals may often fail to learn the food-related cues used by the producer, which means that successful scrounging does not guarantee social learning (Giraldeau & Lefebvre 1987; Beauchamp & Kacelnik 1991; Ilan *et al.* 2013). Second, when it comes to innovation and the acquisition of new skills, young and inexperienced individuals may perform better than adults (Thornton & McAuliffe 2006; Biondi, Bó & Vassallo 2010; Morand-Ferron *et al.* 2011), but see Reader & Laland 2001) for opposite results in primates). Thus, the relationship between producing/scrounging tendencies and the ability to acquire new skills is not clear. In fact, despite extensive work on each of these behaviors separately (reviewed by Giraldeau & Caraco 2000; Reader & Laland 2003), to our knowledge there are only a handful of studies in which the same individuals were tested for both producing/scrounging tendencies and for their ability to acquire new foraging skills (Giraldeau & Lefebvre 1987; Giraldeau & Templeton 1991; Katsnelson *et al.* 2011)

Here we studied social foraging strategies and the acquisition of novel foraging skills in groups of wild, cooperatively breeding Arabian babblers (*Turdoides squamiceps*). The study of social foraging strategies and learning abilities in cooperatively breeding birds is

still in its infancy (Langen 1996; Midford *et al.* 2000; Ratikainen *et al.* 2012). Cooperative breeders commonly live in stable groups that forage socially in a year-round, all-purpose territory (reviewed by Cockburn 2013), which allows close monitoring of social foraging and learning strategies in relation to a range of social and life-history parameters (such as group size, dominance, and reproductive success, reviewed in Pen & Weissing 2000). In order to determine the factors affecting producer-scrounger strategies of individuals in groups, we tested groups of Arabian babblers on a foraging grid, allowing them to search for food (produce) or join other individuals (scrounge). To determine the effect of social or individual characteristics on the ability to learn a novel task, we conducted a second experiment in which the birds needed to acquire a new foraging skill (removing a rubber lid) in order to reach food. We discuss our results in light of the social and individual characteristics that influence social foraging behavior and novel skill acquisition in a wild, cooperatively-breeding species.

### 3.3. Materials & methods

#### *Study site and foraging ecology*

The study was conducted at the Shezaf Nature Reserve, a 40 km<sup>2</sup> area in the Arava region, Negev desert, south-east Israel (30°48'N, 35°13'E). A long-term research project on the social behavior of the cooperatively-breeding Arabian Babbler (*Turdoides squamiceps*) has been conducted in the area since 1971 by Amotz & Avishag Zahavi (Zahavi 1989, 1990; Zahavi & Zahavi 1997). The area is an extremely arid desert savanna with mean annual rainfall of 35mm (Anava *et al.* 2000; Keynan & Yosef 2010). The flora of the site is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, and *Haloxylon persicum*), found only in the dry riverbeds (wadis).

The habitat used by the babblers is highly diverse, including different soil types and topographic conditions (Peled, Ben-Shlomo & Shanas 2014), ranging from round

sandstone hills and intercalations of clay, to shallow valleys, dry river beds (wadies), and small springs. The ground surface may be covered by alluvium silt cover, sand dunes, semi-stable sands or salt flats (Kam *et al.* 2003; Peled *et al.* 2014). Each of these habitats is characterized with a specific type of flora and fauna, and all are subjected to marked seasonal changes in composition (Anava *et al.* 2000). This diversity and variability of the babblers' habitat is highly relevant for their foraging ecology because the babblers are omnivores. They feed on almost any type of arthropods found on the ground or within the vegetation, as well as on a range of fruits, seeds and soft parts of plants (Zahavi 1990; Kam *et al.* 2003). They spend much of their time digging for food in the ground or under the bark of trees and their diet may also include small vertebrates such as lizards, geckoes, small snakes and even small birds (Zahavi 1990; Kam *et al.* 2003). During the spring and summer they also feed on berries (e.g. *Ochradenus*, *Lycium*, and *Nitraria*) and on flowers of *Acacia* and nectar of *Loranthus*. Groups of babblers may also feed on garbage dumps in the villages that surround the reserve (Zahavi 1990; Anava *et al.* 2000). The variable environment and diverse diet of the babblers, as well as their social life (see below) suggest that individual and social learning may be important for the acquisition of foraging skills, making them an ideal species for the study of social foraging and social learning in the wild.

Arabian babblers are a group-territorial, cooperatively-breeding bird species, with age-related linear dominance hierarchies within each sex class (Zahavi & Zahavi 1997). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to the dominant individuals may gain reproductive success on rare occasions (Lundy, Parker & Zahavi 1998).

The study population comprised 21 groups, with group size ranging between 2- 13 adult individuals. All individuals were ringed with a unique combination of one metal and three



colored rings, and were habituated to human presence (for a description of habituation, see (Ridley 2007; Ridley & Raihani 2007), allowing close-range observations.

### *Experiment 1: Producer-Scrounger Game*

Between Oct-Nov 2011 we presented 16 groups of wild Arabian babblers (85 individuals) with a 100x120cm foraging grid (Figure 3.1) containing 96 wells (3cm diameter, 2cm deep, and 12cm center-to-center). Such a foraging grid allows individuals to forage on the ground and thus mimics natural foraging behaviour. Food (one piece of “Nestle Cheerios” cereal, divided into 4 portions) was provided only in 10 of the 96 wells (~10%). During experimental sessions individuals could either search for food (producers) or join other birds that had already successfully found food (scroungers). Each individual in each group was exposed to the grid for two sessions (representing two experimental trials per focal bird). The first session comprised the first exposure of the group members to the grid. We used the latency to first approach to the grid as a measurement of object neophobia (*sensu* Greenberg 2003). Sessions were conducted in the first two hours of the morning, the most active foraging period for babblers (Ridley 2007). A high-definition video camera (Sony HDR-CX115) in front of the grid provided a view of its entire surface and allowed recognition of color rings. To avoid recognition errors, an observer with binoculars seated next to the video camera and approx. 3 m from the grid, recorded the color bands and location of each bird using the video camera’s internal microphone. This allowed verbal identification to be matched with the bird’s image (during video analysis), which could then be followed throughout its movement on the grid.

To score each individual’s tendency to produce or to scrounge, we analyzed the videos on a computer screen using “Python”- based software (*Perspective Birdy 1.0*, <http://ibis.tau.ac.il/twiki/bin/view/Zoology/Lotem/TechnicalToolsandCode>), developed at our lab by Y. Perry and E. Shellef). Following earlier studies in the field (e.g. Barnard &

Sibly 1981; Beauchamp 2001; Coolen, Giraldeau & Lavoie 2001; Liker & Barta 2002; Ilan *et al.* 2013), each visit to a well (a foraging event or a foraging step) was classified as either a producing or a scrounging event. Producing was classified as visits to an unoccupied well, while scrounging reflected visits to a well already occupied by another individual at the moment of arrival or up to five seconds before arrival of the second individual (we thus assume that delaying the act of scrounging for more than 5 sec after the first bird has left is rare, and that such cases are more likely to represent independent foraging). Data collection for each individual continued until food was depleted or until the group left the grid and did not return for over ten minutes. The social foraging strategy of each individual was measured as the proportion of joining events (number of joining events divided by the sum of searching and joining events) throughout the first two sessions. Individual food intake was measured as the number of foraging steps rewarded

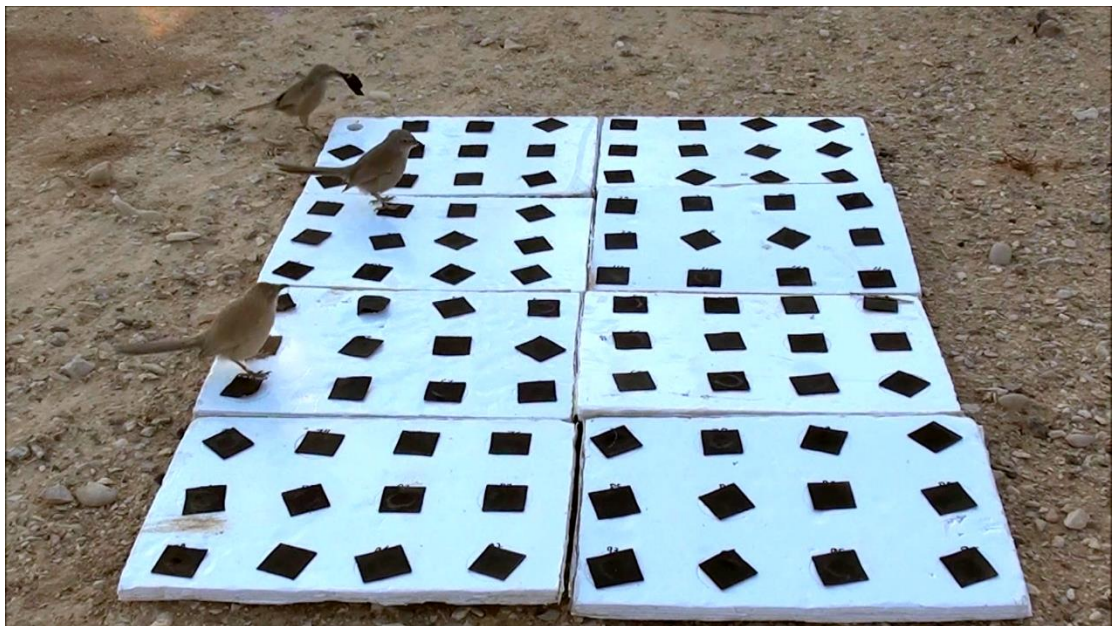


**Figure 3.1:** Arabian babblers foraging on the grid during the producer-scrounger game. Food items were provided only in ten out of 96 wells. The experiment was recorded using a video camera and analysed later in the lab.

with food items per second.

### *Experiment 2: Acquisition of a novel foraging skill*

To determine the characteristics influencing acquisition of a novel foraging skill, we presented 14 of the 16 groups used for Experiment 1 (the remaining two could not be used as they disappeared from the study area) with the same foraging grid, but this time all wells contained food (same food as in Experiment 1), and were covered with black rubber lids (Figure 3.2). While removing rubber lids is certainly a novel task for the babblers, it requires motor actions that are typical to their natural foraging behavior that includes the removal of leaves, branches and stones. Individuals needed to learn to remove the rubber lids in order to obtain food. Each group was presented with the grid for four different sessions on four separate mornings, with each session lasting for up to 30 min or until all lids had been removed or the group had left. Data were collected in the same method as in Experiment 1. Data were analyzed only for the first 15 steps on the grid of each individual, thus excluding steps performed after most of the lids had already been removed.



**Figure 3.2:** Arabian babbler removing lids during the acquisition of a novel foraging skill experiment. Food was provided in all foraging wells and covered with black lids.

### *Statistical analyses*

Statistical analyses were conducted using IBM SPSS statistics version 22. All data were checked for normality and transformed if needed using square root-arcsine transformation for proportional data and  $\text{Log}_{10}$  or square root transformation for integers.

We used Linear Mixed Models (LMM) for multivariate analyses to test the effect of the following parameters on individual foraging steps taken: rank (dominant or subordinate-defined by agonistic interactions and breeding behaviors (*sensu* Nelson-Flower *et al.* 2011), sex, linear age (days post-hatching), group size (total number of independent foragers present during the experiment), time to reach the foraging grid (sec), time spent on the foraging grid (sec) and trial number.

Since the number of other individuals on the grid may determine the potential number of birds that could be joined, and it could therefore be a confounding variable of strategy choice, we calculated for each focal individual the average number of other individuals pecking on the grid in the 5 seconds before it made a foraging step. This factor, labeled “number of other individuals on the grid” was incorporated in our statistical analyses.

We determined a set of candidate models and compared them using Akaike’s Information Criterion corrected for small sample size (AICc) (Burnham & Anderson 2002). We included group and individual identity as random factors to account for the potential influence of repeated measures within the same group and individuals on the distribution of data. The model with the lowest AICc value provided the best fit to the data; models with an AICc value of 5 or more than this best model were considered as insufficient fit for further interpretation. All candidate models were compared to the AIC basic model (with

no predictors). If candidate models did not have AICc values  $> 5$  lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data.

When models scored within 5 AICc values of the best model, multi-model averaging was employed to determine significant predictors (*sensu* Grueber *et al.* 2011). All terms in the top model set were checked for significance using 95% confidence intervals (CI). A term was considered a good predictor of data patterns (i.e. significant) if its CI's did not intersect zero (Burnham & Anderson 2002).

To determine the best candidate models for Experiment 2, we used Generalized Estimating Equations (GEE) to test the effect of the same parameters as in experiment 1 on individual success in removal of lids. We compared candidate models using QICc (Corrected Quasi Likelihood under independence model criterion, Pan 2001) for binomial analysis. We included group and individual identity as random terms to account for the potential influence of repeated measures within the same group and individuals on the distribution of data. The model with the lowest QICc value provided the best fit to the data; models with a QICc value of 5 or more than this best model were considered an insufficient fit for further interpretation. All candidate models were compared to the QICc basic model (with no predictors). If candidate models did not have QICc values  $> 5$  lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data. As for the AICc analysis, when models scored within 5 QICc of the best model, multi-model averaging was employed to determine significant predictors.

### 3.4. Results

#### *Experiment 1: producer-scrounger game.*

In total, we analyzed 152 focal trials of 85 individuals from 16 groups (some individuals did not participate in both sessions so they contributed only one trial rather than two). Mean trial time ( $\pm$ SE) was  $419.9 \pm 18.26$  sec. Mean group size was 5.98, ranging from 3 to 11 individuals (all groups included a dominant pair plus subordinate helpers). Individuals were consistent in their propensity to scrounge as indicated by the significant correlation between proportion of time spent scrounging in the first and second trials (Spearman correlation coefficient = 0.356,  $N = 70$  individuals who participated in both trials,  $p = 0.002$ ).

Dominant individuals spent less time on the grid than subordinates (Table 3.1, means  $\pm$  SE:  $95.4 \pm 7.5$  and  $143.1 \pm 11.1$  s for dominants and subordinates respectively), and had fewer foraging steps (i.e. visits to wells) rewarded per second than subordinates (Table 3.2, means  $\pm$  SE:  $0.013 \pm 0.015$  and  $0.019 \pm 0.012$  steps rewarded/sec for dominants and subordinates, respectively). Dominants also scrounged significantly less than subordinates (Table 3.3, means  $\pm$  SE:  $0.077 \pm 0.015$  and  $0.177 \pm 0.018$  scrounging proportion for dominants and subordinates, respectively) and did not show any apparent aggression toward subordinates during the experiment. Both subordinates and dominants scrounged only on individuals in wells containing food, suggesting that scrounging occurs only upon seeing food discoveries by others. Scrounging proportion was also related to the number of other individuals foraging on the grid, but this effect did not confound the effect of dominance that remained significant also when both factors were included in the model (see Table 3.3).

**Table 3.1:** Top model set of model selection (AICc) of the terms influencing the amount of time spent on the grid per individual during the producer-scrouter game. Only models with  $\Delta\text{AICc} < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	AICC	$\Delta\text{AICc}$	Weight
Basic	4	635.24	8.03	
Dominance	5	554.495	0	1

**Table 3.2:** Top model set of model selection (AICc) of the terms influencing the number of rewarded foraging steps/second for each individual in the producer-scrouter game. Only models with  $\Delta\text{AICc} < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	AICC	$\Delta\text{AICc}$	Weight
Basic	4	-467.21	4.71	
Dominance	5	-471.92	0	1
Parameter	Estimate	SE	Low 95% CI	High 95% CI
<b>Dominance</b>				
Subordinate	0	0		
Dominant	-0.03	0.008	-0.05	-0.02

Parameter	Estimate	SE	Low CI 95%	High CI 95%
<b>Dominance</b>				
Subordinates	0	0		
Dominant	-0.18	0.05	-0.29	-0.08



**Table 3.3:** Top model set of model selection (AICc) for the terms influencing the proportion of individuals joining (scrounging) during the producer-scrounger game. Only models with  $\Delta\text{AICc} < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	AICC	$\Delta\text{AICc}$	Weight
Basic	4	27.58	9.37	
Dominance	5	20.045	1.835	0.285
Dominance + No. of other individuals on grid	6	18.21	0	0.715

Parameter	Estimate	SE	Low 95% CI	High 95% CI
<b>Dominance</b>				
Subordinate	0	0		
Dominant	-0.16	0.05	-0.25	-0.06
<b>No. of individuals on grid</b>	0.07	0.03	0.01	0.13

#### *Experiment 2: acquisition of a novel foraging skill*

In total, we conducted 227 trials on 66 individuals from 14 groups. Mean group size was 5.48, ranging from 3-10 individuals. Mean trial time ( $\pm\text{SE}$ ) was  $341.12 \pm 20.15$  sec.

As in the producer-scrounger game, dominance was the main factor affecting behavioral differences: only 3 out of 28 (10.7%) dominant individuals learned the task, whereas 22 out of 38 (57.9%) subordinates learned it (Table 3.4). The total amount of time that individuals spent on the grid had no effect on the ability to learn (Table 3.4). Another indication that lack of time was not a limiting factor for learning: individuals that failed to learn spent significantly longer periods on the grid than the average time it took those who did learn to remove the first lid (means $\pm\text{SE}$  for non-learners and learners were  $103.3 \pm 6$  sec to leave the grid and  $48.38 \pm 12$  sec to remove their first lid, respectively, Table 3.5). All individuals showed a reduction in the time they spent on the grid as trial number increased (Table 3.5)

Although individuals that learned to remove lid had a higher food intake than non-learners ( $0.11 \pm 0.02$  pieces/second for learners and  $0.05 \pm 0.01$  for non-learners), the non-learners achieved food intake by scrounging on others or visiting lids that had been removed but not depleted (non-learners mean food intake of  $0.05 \pm 0.01$  pieces/trial was entirely due to lid removal by learners).

**Table 3.4:** Top model set of model selection (QICc) of the terms influencing whether an individual learnt the novel foraging task (0 = didn't learn, 1 = learned). Only models with  $\Delta\text{QICc} < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICc	$\Delta\text{QICc}$	Weight
Basic	4	274.16	13.73	
Dominance	5	260.43	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% CI
<b>Dominance</b>				
Subordinate	0	0		
Dominant	1.86	0.68	0.51	3.2

**Table 3.5:** Top model set of model selection (AICc) of the terms influencing the time that it took each individual to remove its first lid (for learners) or its total time on the grid (for non-learners). Only models with  $\Delta\text{AICc} < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	AICc	$\Delta\text{AICc}$	Weight
Basic	4	1253.35	71.03	
Trial number + Learning	6	1182.32	0	1
Parameter	Estimate	SE	Low 95% CI	High 95% CI
<b>Trial number</b>	-0.99	0.22	-1.4	-0.5
<b>Learning to remove a lid</b>				
Learnt	0	0		
Didn't learn	4.68	0.56	3.56	5.79

### 3.5 Discussion

Our experimental results show that although subordinates scrounged more than dominant individuals, they were also better at learning a novel foraging skill. In the first experiment, subordinates had a higher success rate (more foraging steps rewarded per sec), which can be explained by their tendency to scrounge more (recall that scrounging occurred only from individuals that had already found food, while searching was less likely to yield success as only ~10% of the feeding wells in the first experiment contained food). The more frequent successes experienced by subordinates in Experiment 1 may also explain why they remained longer on the foraging grid than dominants.

The proportion of scrounging in our study was affected by both dominance (i.e. subordinates scrounged more) and by the mean number of other birds that foraged on the grid (Table 3.3). The second effect is consistent with previous theoretical and empirical work on the producer-scrounger game (Caraco & Giraldea 1991; Vickery *et al.* 1991; Giraldeau & Dubois 2008), reflecting an increase in scrounging with an increase in scrounging opportunities. The first effect, on the other hand, is inconsistent with the findings of previous studies, in which subordinates scrounged less than dominants (Stahl *et al.* 2001; Liker & Barta 2002; Beauchamp 2006; Brown, Jablonski & McCormack 2007), or avoided direct scrounging (Belmaker *et al.* 2012). There are three possible, and not mutually exclusive, reasons for this difference. First, in cooperative breeding species, scrounging by subordinates may be tolerated more than in non-cooperative breeding species because of their tendency to have high genetic relatedness to dominant individuals (Lundy *et al.* 1998; Nelson-Flower *et al.* 2011, 2012). This notion is consistent with the absence of aggression towards scroungers in our study, and with recent evidence relating tolerance towards scroungers with genetic relatedness (Mathot & Giraldeau 2010; Chiarati *et al.* 2012). Second, scrounging may be adaptive for subordinates if it can facilitate social

learning of food-related cues or food-related behaviors (Giraldeau 1997; Laland 2004; Arbilly *et al.* 2011). Although social learning from poor foragers may be maladaptive (Lehmann & Feldman 2009), the risk of following poor foragers is reduced in cooperative breeders, where the individuals are familiar with each other and forage together in a cohesive group throughout the day (Ridley & Raihani 2007; Thompson & Ridley 2012). A third possible explanation may be related to the fact that scrounging had a lower variance in payoff, and thus to possible differences in variance-sensitive preferences between subordinates and dominants (e.g. Lendvai *et al.* 2004; but see Kacelnik & El Mouden 2013 for a critical review of such predictions).

In contrast to Experiment 1, the results of Experiment 2 show that despite the subordinates' tendency to scrounge more and to search less, when faced with a novel foraging task they were much more likely to succeed at solving the task than dominants. Consequently, they became the 'producers' of the group, and by removing the rubber lids allowed the individuals that didn't learn to access food on the experimental array. Our finding that subordinates were more successful than dominants at learning a new foraging skill is not consistent with other studies conducted on European starlings (*Sturnus vulgaris*) and domestic chickens (*Gallus gallus*) (Spencer *et al.* 2004; Boogert, Reader & Laland 2006; Croney, Prince-Kelly & Meller 2007); but is consistent with studies performed on primates, such as chimpanzees (*Pan troglodytes*, reviewed in (Reader & Laland 2001)). One possible explanation for this is that the subordinate individuals in our study were more motivated to search for food than dominants, and therefore showed a greater propensity to explore new objects (Biondi *et al.* 2010), as suggested by the "necessity drives innovation" hypothesis (Reader & Laland 2003). A higher motivation to search for food may be expected if individuals have limited access to high-quality resources, a possibility that is also consistent with the fact that subordinates were significantly lighter than dominants (O. Keynan, unpublished data). It should be noted, however, that the non-learning individuals

in our study (mostly dominants) explored the foraging grid for longer than it took the learners (mostly subordinates) to learn (see Results). Thus, insufficient time to explore the grid cannot explain why the dominants failed to learn, suggesting that differences in motivation may not explain our findings.

An alternative explanation for the subordinates' better learning of the new skill may be related to their cognitive strategies. It has been suggested that group-living affects and constrains subordinates most, so that low-ranking individuals might have been forced to 'make the most of the genetic predisposition for intelligence and learning' (Kummer & Goodall 1985). In the case of Arabian babblers, subordinates may not necessarily be more "intelligent" than dominants, or better than dominants in all types of learning, but may simply be more flexible and explorative in their foraging behavior. This may be adaptive as it increases the chances of finding new resources not monopolized by dominants. Interestingly, behaviors that are more explorative and neophilic are frequently associated with young age (e.g. Heinrich 1995; Thornton & Raihani 2008). Although chronological age *per se* was not found to be a significant factor in our analyses, from a mechanistic point of view, it is possible that subordinates adopt a cognitive strategy that is juvenile-like, which is interestingly consistent with some studies' suggestions of delayed development and maturation in non-breeders among cooperatively-breeding birds (Lawton & Lawton 1986; Koenig *et al.* 1992).

Surprisingly, group size in our study had no effect on scrounging rate or innovation rate (i.e. lid removal). This is in contrast to both theoretical and empirical work suggesting that scrounging should increase with flock size (reviewed by Giraldeau & Caraco 2000; Giraldeau & Dubois 2008; Beauchamp 2014) and studies that found that larger groups are better at problem-solving (Liker & Bókonyi 2009; Morand-Ferron & Quinn 2011). It is possible that a group size effect existed, but that our sample size was too small to detect it

(as hinted by the fact that scrounging was influenced by the number of other birds on the grid but not by group size). It could also mean that social foraging behavior in Arabian babblers depends mostly on the interactions between dominants and subordinates and less on group size.

Our findings suggest that subordinate group members may be more opportunistic and flexible in their behavior than dominants, making use of both scrounging and novel foraging opportunities as they arise. From the perspective of the group, this can lead to an interesting dynamic that is consistent with the “skill pool effect” suggested by Giraldeau (1984) and later demonstrated by further studies (Giraldeau & Lefebvre 1986; Morand-Ferron & Quinn 2011). When foraging in their familiar habitat, dominants may be faster at finding food than subordinates, but subordinates may then scrounge from dominants. When food patches are hard to find and provide more food than a single individual is likely to consume, this dynamic may increase group foraging success. Similarly, when foraging in a rarely used or novel habitat, subordinates may be faster at discovering novel resources, which can also increase group foraging success through scrounging and food sharing. Although the foraging behavior of each group member may be determined by individual trade-offs in relation to social rank and experience, the suggested “skill pool effect” may benefit the group as a whole, which is especially likely in the case of omnivorous birds, like Arabian babblers, that utilizes a diverse and changing environment. Further work is needed to determine whether scrounging in this system facilitates social learning of foraging skills or, rather, whether dominants and subordinates maintain differential specialization.

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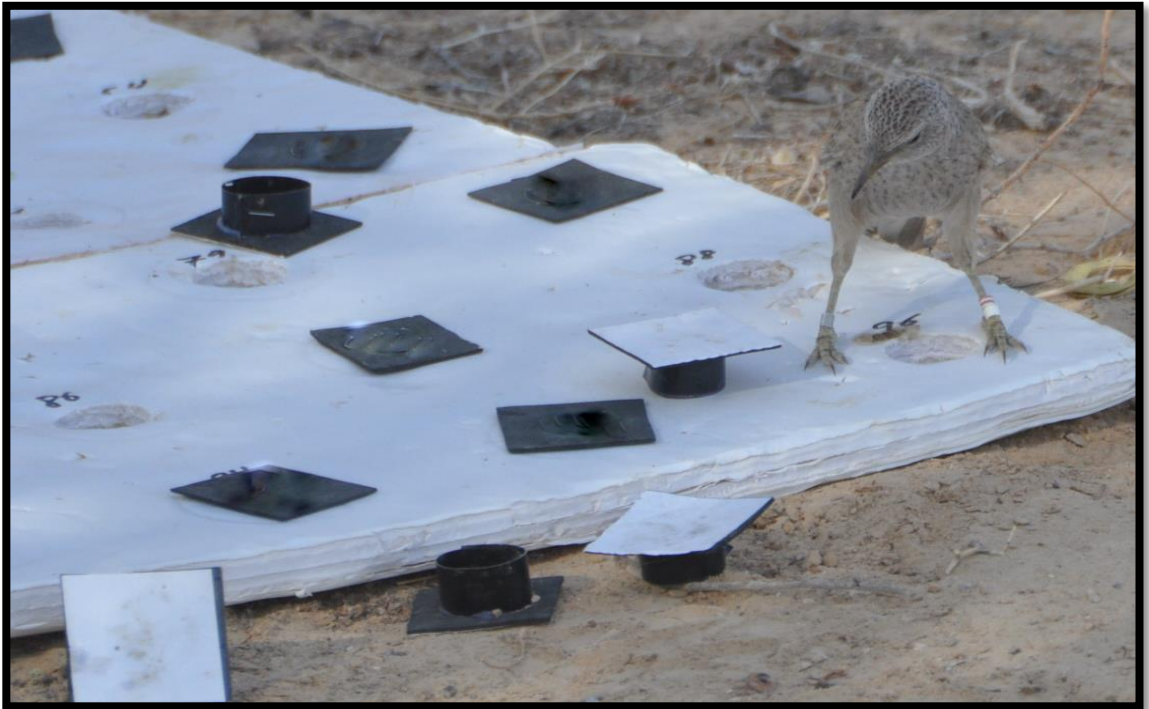
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## 4.Task-dependent differences in innovation abilities by subordinate and dominant wild Arabian babblers

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#### 4.1 Abstract

Learning and innovation abilities have been studied extensively in flocking birds, but their importance and relevance in cooperatively breeding birds has been relatively unexplored. We studied the acquisition of novel foraging skills in 14 groups of wild, cooperatively breeding Arabian babblers (*Turdoides squamiceps*). While in a previous study we found that subordinate individuals were usually the first to learn to remove black rubber lids from a foraging grid, here we show that dominant were the first to succeed in shifting from these black rubber lids to newly introduced white rubber lids. We also found that in all groups where one forager learned to shift to the white lids, the rest of the foragers also learned to do so, suggesting that this type of innovation is quickly transmitted among group members. Although dominant individuals were almost always the first to remove white lids, once starting to remove white lids, dominants and subordinates learned equally well to prefer white over black lids based on differential reinforcement (food was provided only under white lids). Together with our previous study, our results suggest that differences in innovation abilities between dominants and subordinates are task-specific, which may represent different cognitive strategies: subordinates may explore a more diverse range of foraging opportunities, while dominants may be better at generalizing from familiar tasks to similar ones.

#### 4.2 Introduction

Recent years have seen increasing interest in research on animal cognition and social learning in the wild (Thornton & McAuliffe 2006; Rutz *et al.* 2007; Morand-Ferron *et al.* 2011; Allen *et al.* 2013; Pennisi 2014) for a recent perspective). While it has long been recognized that basic aspects of animal cognition, such as the ability to learn to find food or to avoid predators are important for survival and reproduction (reviewed by Shettleworth 2012), the way that individual cognitive abilities evolve under different social contexts is potentially complex and not fully understood (e.g. Danchin *et al.* 2004; Laland

2004; Giraldeau & Dubois 2008; Arbilly *et al.* 2010; David *et al.* 2014). One important aspect of animal cognition is related to the animals' ability to solve new problems, or to adapt to novel situations. This ability is especially important for animals that move across different habitats where discovering new resources or learning new skills can contribute to their fitness (Dunlap & Stephens 2009). Adapting successfully to novel situations may be facilitated by a wide range of cognitive mechanisms, including simple ones such as reinforcement learning or taste aversion (Shettleworth 2012). However, because novel situations often call for new behavioural responses, some of which may appear cognitively demanding (such as milk-bottle opening in great tits, or tool use in primates and crows), much effort has been made to characterize and study animals' ability to generate new behaviours- an ability that is commonly referred to as 'innovation' (Kummer & Goodall 1985; Lefebvre *et al.* 1997; Reader & Laland 2003).

Refining an earlier definition by Reader & Laland (2003), Ramsey, Bastian & van Schaik (2007) suggested that animal innovation should be defined as the process that generates a novel learned behaviour in an individual that is not simply a consequence of social learning or environmental influence. The last two conditions confirm the independence and uniqueness of the innovation (i.e. it is not copied from others, and is not immediately induced by environmental cues in all individuals alike). The term animal innovation may thus provide an umbrella for a wide variety of novel behaviours that may be cognitively simple or complex, but meet the criteria of this operational definition. Note that this approach bypasses the need to specify or to fully understand the cognitive mechanisms involved, and implies that innovative abilities can be compared across species, populations, or individuals (Lefebvre *et al.* 1997; Reader & Laland 2002, 2003; Overington *et al.* 2011). Indeed, there is evidence suggesting that innovative ability has a direct effect on individual fitness (Goodall 1990; Mateos-Gonzalez, Quesada & Senar 2011; Keagy, Savard & Borgia 2011; Cauchard *et al.* 2013), as well as on the fitness of other individuals that learn socially

from innovators (Fisher & Hinde 1949; Goodall 1964; Aplin *et al.* 2012; Allen *et al.* 2013). Yet, little is known about how innovations emerge or why individuals differ in their propensity to innovate.

In social species, there is evidence that some individuals are consistently more innovative than others (Laland & Reader 1999; Liker & Bókonyi 2009; Cole, Cram & Quinn 2011; Morand-Ferron *et al.* 2011; Griffin *et al.* 2013b). It is not clear however, whether such differences persist through life or personality types (Sih & Del Giudice 2012), or rather determined by factors such as age, social rank, or local conditions. According to the *necessity drives innovation* hypothesis (Reader & Laland 2003; Bokonyi *et al.* 2013), good competitors may be less innovative since they already enjoy better access to limiting resources. On the other hand, the *social inhibition* hypothesis (Overington *et al.* 2009; Griffin *et al.* 2013b) predicts a decrease in innovation by poor competitors that may be preoccupied with fear and risk avoidance in the presence of others, thus inhibiting innovation.

While innovative ability is often viewed as a single trait, given the wide variety of novel behaviours that can fall under the definition of animal innovation (see above) it is possible that the same individual may be innovative in one type of task but not in others. Indeed, recent studies suggest that at least in some cases innovation ability may be context- or task-specific. For example, in great tits (*Parus major*), fast innovators in captivity were not fast innovators in the wild (Morand-Ferron *et al.* 2011), and in Indian mynas (*Sturnus tristis*), innovativeness was not related to behavioural flexibility (Griffin *et al.* 2013a). If innovative abilities are task-specific, different individuals may express different types of innovations, creating a skill pool effect (Giraldeau 1984), or a pool of competence in social groups (Morand-Ferron & Quinn 2011). These possibilities may explain why previous



research has found that innovations were more likely to occur in larger groups (Liker & Bókonyi 2009; Morand-Ferron & Quinn 2011).

In light of the above, variable innovative abilities within a group may benefit group members in two ways. First, it may allow social foragers to exploit a greater variety of food resources by simply joining each other's food findings (Giraldeau 1984; Giraldeau & Lefebvre 1986). Second, innovations themselves can be learned socially (Reader 2004; Ramsey *et al.* 2007; Boogert *et al.* 2008; Aplin, Sheldon & Morand-Ferron 2013), allowing social learners to use the new skill and to access the new food type in future foraging attempts. Although these potential benefits of having variable innovative abilities in a group seem intuitive, direct evidence for task-dependent differences in innovation ability within groups are scarce (Morand-Ferron *et al.* 2011; Griffin *et al.* 2013a).

A potentially useful model system to study the interplay between innovation abilities and group dynamics is offered by cooperatively breeding birds, which commonly live in stable groups that forage socially in a year-round, all-purpose territory (Stacey & Ligon 1991; Ridley & van den Heuvel 2012). This type of group-living allows close monitoring of social foraging and learning strategies in relation to a range of social and life-history parameters (such as group size, dominance and reproductive success, reviewed in Pen & Weissing 2000). To the best of our knowledge, however, no study on innovative behaviour in wild cooperative breeding birds has been carried out thus far (and the first field study on innovation abilities in a cooperative breeding mammal is also very recent; see Thornton & Samson 2012).

Here we study the acquisition of novel foraging skills in groups of wild, cooperatively breeding Arabian babblers (*Turdoides squamiceps*). While in a previous study (Keynan, Ridley & Lotem 2014) we found that subordinate individuals tended to scrounge more, and were usually the first to learn to remove black rubber lids from a foraging grid, here we test

how quickly subordinates and dominant that already know to remove black rubber lids, learn a slightly different task: removing newly introduced white rubber lids they have never seen before. We also assess how the removal of white lids by the first individual in the group affects the behaviour of other group members (i.e. whether the innovation is socially transmitted), and by providing a food reward only under white lids, we compare how fast subordinates and dominants learn to prefer white over black lids based on simple reinforcement learning.

### 4.3. Materials & methods

#### *Study site and population:*

The study was conducted at the Shezaf Nature Reserve, a 40 Km<sup>2</sup> area in the Arava region, Negev desert, in the south-east of Israel (30°48'N, 35°13'E). A long-term research project on the biology, ecology, and social behavior of the cooperatively-breeding Arabian Babbler (*Turdoides squamiceps*) has been conducted in the area since 1971 by Amotz & Avishag Zahavi (Zahavi 1989, 1990; Zahavi & Zahavi 1997). The area is an extremely arid acacia desert savannah with a mean annual rainfall of 35mm (Anava *et al.* 2000; Keynan & Yosef 2010). The flora of the Shezaf Nature Reserve is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, and *Haloxylon persicum*) that occur only in the dry riverbeds (wadis). The habitat used by the babblers is highly diverse, including different soil types and topographic conditions and different combinations of flora and fauna, all of which are subjected to marked seasonal changes in composition. This diversity and variability of the babblers' habitat is relevant for their foraging ecology because the babblers are omnivores, feeding on almost any type of arthropods found on the ground or within the vegetation, as well as on small vertebrates such as lizards, geckoes, small snakes and even small birds, and on a range of fruits, seeds and soft parts of plants (see Keynan *et al.* 2014 for more details). The variable environment

and diverse diet of the babblers, as well as their social life, suggests that individual and social learning may be important for the acquisition of foraging skills.

Arabian babblers are a group territorial, cooperatively breeding bird species (Zahavi 1989, 1990). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to dominant individuals may gain reproduction on rare occasions (Lundy, Parker & Zahavi 1998). Dominance is defined by age (since age-structured dominance hierarchy exists in Arabian babblers) and by observations of aggressive interactions (Zahavi 1989). The current study population comprises 14 groups, with group size ranging between 2 – 7 adult individuals. All individuals are ringed with a unique combination of one metal and three colored rings, and are habituated to human presence (for a description of habituation, see (Zahavi & Zahavi 1997; Ridley 2007; Ridley & Raihani 2007), allowing close-range observations.

#### *Experimental procedure:*

During Apr-Jun 2013 we presented 14 groups of Arabian babblers (57 individuals in total), with a foraging grid containing 96 feeding wells ( $8 \times 12$ ), covered with an equal number (i.e. 48) of black and white rubber lids (the white lids had black edges in order to separate them from the white grid itself), distributed randomly (Figure 4.1). The grid was presented only when all group members were around and potentially available to interact with it. All birds were familiar with the grid from previous experiments (Keynan *et al.* 2014), and showed no signs of fear from the test apparatus. All birds were familiar with the black rubber lids from the previous study (Experiment 2 in Keynan *et al.* 2014, conducted 2-5 months earlier but not with the white rubber lids that were entirely new for them. Food (a quarter of a dead mealworm) was provided only under the white lids, thus, the birds needed to learn two things: first, to remove white lids (not only black lids), and second, to prefer white lids over black lids based on the different reward (one food item versus zero).

Note that while the second task can only be learned after the first task, only the first task tests for innovation.

It is also important to note that despite previous experience with removing black lids, learning to remove white lids can still be qualified as an innovation (*sensu* Ramsey *et al.* 2007) because: a) it is a novel learned behaviour that is not simply a consequence of social learning (the first to remove white lids in a group cannot learn it from other birds), and b) as confirmed by our results (see below), it cannot be the consequence of environmental influence because some of the birds never learned to remove white lids despite being exposed to them as long as those who did learn.

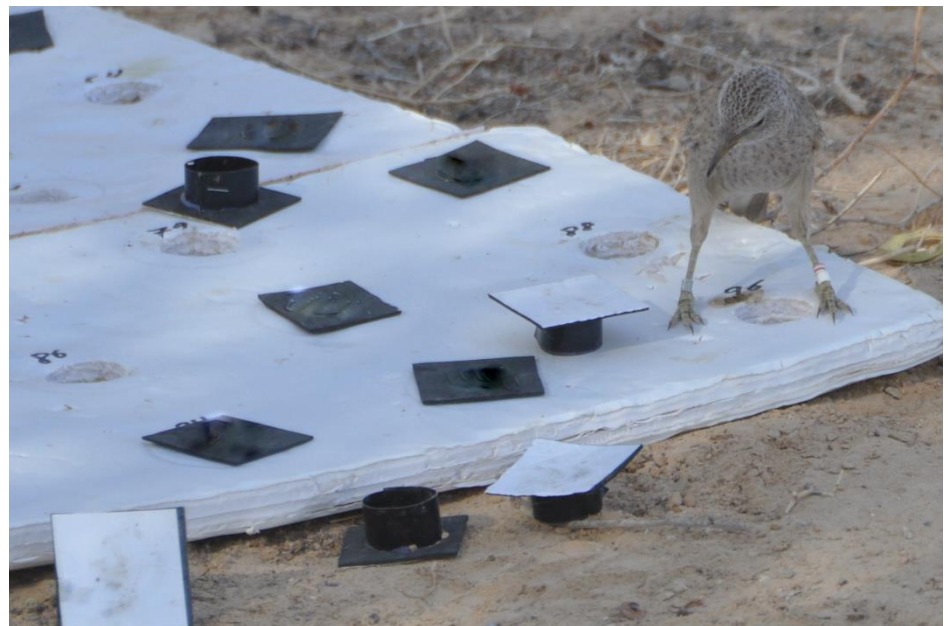
Each group was presented with the foraging grid four times on four consecutive mornings. The presentations (hereafter trials) took place during the first two hours of the morning, (the most active foraging period for babblers; (du Plessis *et al.* 2012)), and each trial lasted for up to 30 min or until the group left the experimental array. A High Definition video camera (Sony HDR-CX115) was located in front of the grid, allowing observers to recognize lid removals and the identity of the individuals engaging in the task from the videos. To further minimize the risk of recognition errors in video analysis, an observer with binoculars sitting next to the video camera, approx. 3 m from the grid, recorded the colour bands and location of each bird into the video camera's internal microphone. This method allowed the verbal identification to be matched with the bird's image during video analysis.

#### *Behavioural analysis:*

The behaviour of each bird was analysed from the videos using its first 20 steps on the grid (which usually occurred when there are still lids to remove), or until the individual left the grid, whichever came first. A step was defined as a removal of a lid (either black or white). To record each individual's arrival to the grid, and removal of lids of different colour,

video analysis was done using the *Birdy 1.0* software, coded by Y. Perry and E. Shellef, Tel Aviv University (see Keynan *et al.* 2014 for further details)

An individual was considered as the innovator of its group if it was the first in the group that removed white lids (which usually occurred in the first trial). For each group we also recorded the identity of the bird that was first to remove white lids in each of the four trials (i.e. in each morning). While these additional first removals may no longer represent the truly first innovation (most of which occur in the first trial), it may nevertheless indicate a tendency to adopt the novel alternative. Each individual was also classified as a learner or a non-learner of the white lid removal task, and among those, each was also tested for whether it learned to prefer white lids over black lids.



**Figure 4.1:** An Arabian babbler on the foraging grid, after removal of several black and white lids

### *Statistical analyses:*

Statistical analyses were conducted using IBM SPSS statistics version 21. To test the effects of social and individual characteristics on a) the probability of being the first to remove white lids, b) the probability of removing white lids in general, and c) the probability of learning to prefer white over black lids, we determined a set of candidate models, based on a set of biologically feasible hypotheses, and compared between their goodness of fit using Generalized Estimating Equations (GEE). We compared candidate models using Corrected Quasi Likelihood under independence model criterion (QICc, Pan 2001). We included group and individual identity as random terms to take into account the potential influence of repeated measures within the same group and individual on the distribution of data. The model with the lowest QICc value provided the best fit to the data; models with a QICc value of 5 or more than this best model were considered to provide an insufficient fit for further interpretation. All candidate models were compared to the QICc basic model (with no predictors). If candidate models did not have QICc values more than 5 lower than the basic, then we concluded that none of the terms tested had a significant influence on the distribution of the data. When models scored within 5 QICc values of the best model, multi-model averaging was employed to determine significant variables (*sensu* Symonds & Moussalli 2010).

Models testing the effects of various terms on the probability of being the first to remove white lids, or to remove white lids in general, included only individuals that already learned to remove black lids during the previous study (thus ensuring that all individuals in the analysis were equal in respect to the level of novelty presented by the new task). Models testing the effect of social rank on the probability of being the first to remove white lids, or to remove white lids in general, included only groups containing both dominant and subordinate individuals. Similarly, models testing the probability of learning to prefer

white over black lids included only individuals that learned to remove both black and white lids.

#### 4.4 Results

In total, we analyzed 153 focal trials of 57 individuals from 14 groups (some individuals did not participate in all four trials). Mean group size during the experiments was 4.07, ranging between 2-7 individuals (adults and sub-adults, all independent foragers). Out of the 57 individuals that were presented with the grid, 32 individuals (15 dominant and 17 subordinates), 56.14% were individuals that learned previously to remove black lids (in the previous study: Keynan *et al.* 2014). Out of those, 25 individuals learned to remove white lids (which is 43.8% of all individuals and 78.1% of those who learned to remove black lids, respectively). Finally, among the 25 individuals that learned to remove white lids, 16 individuals (64%) also learned to significantly ( $p < 0.05$  in a binomial test) prefer white over black lids

##### *Who are the innovators?*

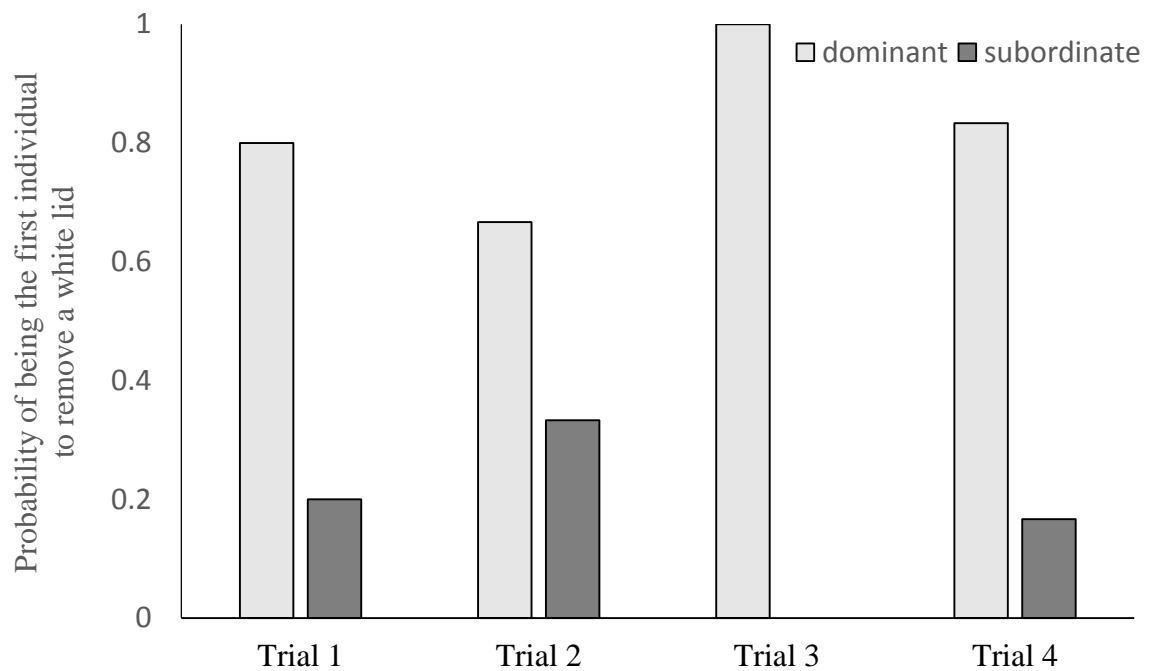
Out of the eight groups that contained both subordinates and dominants that had learned previously to remove black lids, the removal of white lids (i.e. the innovation) occurred in six groups. In five of these six groups the first removal of white lids occurred in the first trial (first morning) and in one group it occurred in the second trial (second morning). Interestingly, five of the six innovators were dominant, and the only group where the innovator was a subordinate was a group in which the dominant delayed interacting with the grid. Thus, in all five groups where both dominant and subordinates forage together on the grid, the dominant were always the innovators ( $p = 0.037$ , for drawing dominant in all five groups containing dominant and subordinates with a distribution of 2,2,1,1,1 and 1,1,1,2,1, dominant and subordinates respectively).

A more comprehensive analysis of several candidate models shows that dominance is the most likely predictor of being the first group member to remove white lids in any trial (Table 4.1, Figure 4.2). A comparison of the dominance model with other candidate models (ESM Table S1) show that being the first group member to remove white lids in a trial is not affected by age, sex, group size, time to approach the grid, number of steps on the grid until the first removal of white lids in the group, or by foraging speed (i.e. steps per second). It is worth noting that in some groups, the first to remove white lids in each of the four trials was not necessarily the same individual (see detailed information in Table S2 of the electronic supplementary materials (ESM)). In contrast to the effect of dominance on being the first to remove white lids, the probability of being the first to remove the familiar black rubber lids was not related to dominance or to any of the other factors that were tested (ESM Table S3). This result is consistent with our observation that both dominant and subordinates removed black lids as soon as they landed on the grid.

**Table 4.1:** Top model set of model selection (QICc) terms influencing the probability to be the first to remove a white lid (innovator). Individual and group identity were included as random terms. Data were based on 37 trials from 16 individuals from 6 groups that contained both dominants and subordinate who knew how to remove black lids. For details of the full model set tested, see ESM

Model	K	QICc	$\Delta$ QICc	Weight
Basic	1	51.9	6.85	
Dominance	1	45.05	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% CI
<b>Dominance</b>				
Subordinate	0			
Dominant	-2.25	0.59	-3.4	-1.1





**Figure 4.2:** The probability of being the first individual in the group to remove a white lid according to rank for each trial. Probability was calculated from raw data. N=37 trials on 7 dominants and 9 subordinate from six mixed groups (all of them knew how to remove black lids prior to the experiment).

**Table 4.2:** Top model set of model selection (QICc) of the terms influencing the probability to learn to remove white lid. Individual and group identity were included as random terms. Data were based on 111 trials on 32 individuals from 14 groups. For details of the full model set tested, see ESM

Model	K	QICc	ΔQICc	Weight
Basic	1	115.27	21.37	
Others learned in the group	1	93.9	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% CI
<b>Dominance</b>				
Others learned	0			
No others learned	2.4	0.9	0.63	4.3

*The distribution of learners and non-learners among groups:*

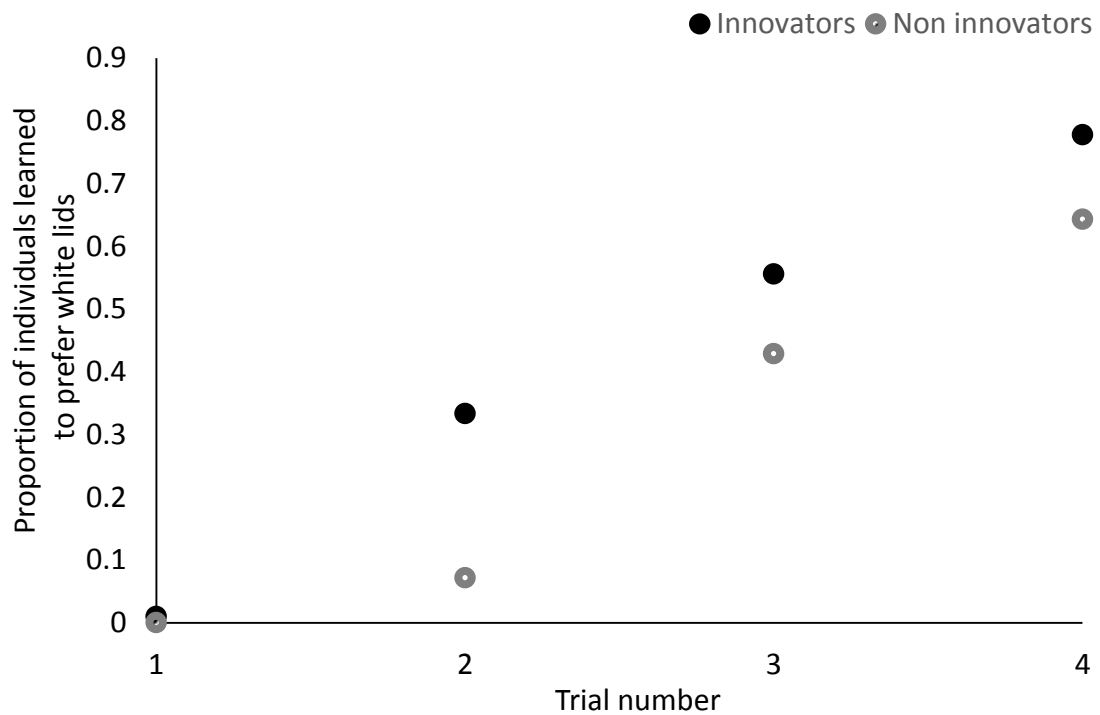
We found an “all or nothing phenomenon” in the distribution of learners and non-learners across babblers groups: either all group members that knew to remove black lids eventually learned the novel task of removing white lids (N=11 groups) or no individual in the group learned to do so (N=3 groups). Our analysis reveals that the best and only predictor to describe what affects the probability of becoming a learner was whether other individuals in the group had learned to remove white lids (Table 4.2; ESM table S4). Furthermore, time or steps on the grid weren't a limiting factor, since those who didn't learn spent more time on the grid, and removed more black lids, than the average time or steps that took for those who learned to remove their first white lid (average $\pm$ se of  $30.19 \pm 6.02$  sec for learners versus  $86.32 \pm 13.57$  sec for non-learners. and  $6.17 \pm 0.94$  steps for learners versus  $14.28 \pm 1.72$  steps for non-learners, respectively).

*Learning to prefer white lids over black lids:*

After learning to remove white lids, a learner's probability of developing a significant preference to white over black lids was positively related to trial number (Table 4.3; Figure 4.3), but not to dominance, whether the learner was the first in the group to remove white lids, or any other terms (see ESM table S5 for a full list of models tested). By the second trial, a greater proportion of innovators developed a significant preference to white lids, which was to be expected because they were the first to acquire experience with white lids (Figure 4.3). From the second trial to the fourth trial the increase in the proportion of individuals that learned to prefer white lids is similar for both innovators and non-innovators (Figure 4.3).

**Table 4.3:** Top model set of model selection (QICc) of the terms influencing the probability to prefer white lids. Individual and group identity were included as random terms. Data were based on 85 trials on 22 individuals from 9 groups who learned to remove white lids. For details of the full model set tested, see ESM

Model	K	QICC	$\Delta$ QICC	Weight
Basic	1	103.18	27.98	
Trial number	1	75.2	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% CI
Trial Number	-1.6	0.34	-2.2	-0.89



**Figure 4.3:** proportions of individuals in the population who learned to prefer white lids during each trial, for those who were first to remove white lids in the group (innovators) and for those who weren't (non-innovators) Proportion was calculated from raw data. N=85 trials on 22 individuals from 9 groups.).

#### 4.5. Discussion

Our study reveals three main findings, as well as an interesting contrast with a previous study carried out recently on the same groups of babblers. First, we found that among birds that already knew to remove black rubber lids, dominant individuals were the first to remove newly introduced white lids, both at the very first trial (as the innovators of their groups), and during subsequent trials. Second, among those birds that knew to remove black rubber lids, we found an “all or nothing” distribution of learners and non-learners across groups: either all in the group learned to remove white lids or no-one learned. Third, once starting to remove white lids, dominant and subordinates learned equally well to prefer white lids over black lids. The contrast of the present result with our previous study is that in the previous study subordinates were clearly the first to learn the novel task of removing a black rubber lid from the foraging grid (Keynan *et al.* 2014), while here, the dominant individuals were those more likely to perform the novel task of removing white lids. Before trying to explain these conflicting results, we should first discuss our recent findings.

According to our analysis, the fact that dominant individuals were the innovators in the present study cannot be explained by factors such as having more time to learn or to interact with the task, or by a lower level of fear. This is because an individual's probability of being the first to remove white lids was not related to the time it took it to approach the grid, to its foraging speed, or to the number of steps it managed to make on the grid before the first removal of white lids occurred in the group. Thus, it seems that innovators and non-innovators had equal opportunities to innovate. This claim is further supported by the fact that innovators and non-innovators (as well as dominants and subordinates) did not differ in how fast they developed a preference for white over black lids based on reinforcement learning (see further discussion below). In other words, there is no evidence that the difference between dominant and subordinates can be explained by

factors that impair learning or cognitive functioning in general. It is therefore difficult to explain our results by the *social inhibition hypothesis* (Overington *et al.* 2009; Griffin *et al.* 2013a)

It is also difficult to explain our results by the *necessity drives innovation* hypothesis (Reader & Laland 2003; Bokony *et al.* 2013). This is because there is no evidence for motivational differences between dominant and subordinate individuals in our study, and if anything, the *necessity drives innovation* hypothesis usually predicts subordinates to be the better innovators (see also Kummer & Goodall 1985). Our analysis also showed that in the current experiment, subordinates and dominants did not differ in the probability of being the first to remove black lids, again demonstrating similar motivation and opportunities to forage on the grid among individuals of different rank. This leaves us with the conclusion that at least in respect to shifting from the familiar task of removing black lids, to the novel task of removing white lids, dominant individuals were genuinely more successful.

Before considering why dominants may be faster in shifting to white lids, it is important to consider why despite being more likely to investigate white lids, they were not faster in learning to prefer white lids over black lids. The answer we suggest is that there is no reason to expect that reinforcement learning should be related to innovation ability. As one can learn from inspecting various models of reinforcement learning (see for example McNamara & Houston 1987; March 1996; Beauchamp 2000; Niv *et al.* 2002; Arbilly *et al.* 2011; Trimmer *et al.* 2012), such models are based on an updating rule that adjusts the value of a given option based on past experience, and a decision rule that chooses among options. Importantly, the options are always given to the model and there is nothing in the updating and decision rules that specify how to select new options. The mechanisms responsible for the acquisition of new input that is deemed relevant, and that can then be associated with a reward value by the reinforcement learning machinery, are usually not

part of the reinforcement learning mechanism itself and thus may be subjected to different selection pressures (see discussions by Lotem & Halpern 2012; Kolodny, Lotem & Edelman 2014). Thus, in terms of our present study, the probability of becoming an innovator is primarily a function of the propensity of approaching white lids and treating them as relevant to foraging. This must be done first without an external reinforcement. Only after it is done can the white lids be associated with a reward value, and the birds may then learn to prefer them. Our results suggest that this second process is done similarly by dominant and subordinates, while the first stage of viewing the lids as relevant to foraging was more likely to occur among dominants.

#### *Task-dependent differences in innovation abilities*

The question we have to address is not only why dominant individuals were more likely to approach the white lids in the present study, but also why they were worse than subordinates in learning to remove black lids for the first time, during our previous study (Keynan *et al.* 2014). In both studies we are unable to explain the effect of rank by immediate social or motivational factors, which leads us to suggest that subordinates and dominants may develop different cognitive strategies that result in task-dependent differences in innovation ability. This requires that despite their apparent similarity, the two novel tasks are sufficiently different in their cognitive demands, making the first easier for subordinates and the second easier for dominants. Given the wide variety of novel behaviours that can fall under the definition of animal innovation, it is quite possible that the same individual may be innovative in one type of task but not in others. While recent evidence for innovation being task-specific is starting to accumulate (Morand-Ferron *et al.* 2011; Griffin *et al.* 2013a), the different cognitive demands that cause innovative abilities to be task-specific are usually not clear. Interestingly, in a recent study on innovative problem-solving in wild meerkats, Thornton & Samson (2012) demonstrated that some

innovations may not be cognitively demanding, but instead may be explained by a combination of exploration, persistence and simple learning processes. In our case, the removal of rubber lids did not even require persistence. It was an easy task for babblers that are used to flip objects or to pill barks of trees in their daily foraging activity. The only innovation required was to attempt the task of flipping a novel item. Yet, there was still a difference between the two tasks: The first task of removing the black rubber lids required trying something entirely new, while the second task of shifting from black to white lids may be achieved through generalization (i.e. by treating white lids not as something new but as a new version of something familiar). Note that innovative problem solving may not always be based on trying to do something that is completely new. Frequently, it is achieved by adjusting familiar behaviour to a new context or by generalizing across different contexts (Shettleworth 2010; Brosnan & Hopper 2014). The conflicting results of our two studies may thus be explained by suggesting that dominant individuals are better in making generalizations from one task to another, while subordinates are simply more explorative and neophilic (as we already suggested in our previous study (Keynan *et al.* 2014). The adaptive reasons for such different cognitive strategies by dominant and subordinates may be related to the possibility that the first strategy requires more experience, which dominant individuals usually have, while the second strategy increases the chances of finding new resources not monopolized by dominant, which may benefit subordinates.

*Social transmission and other consequences of task-dependent innovation abilities for group-living*

The “all or nothing” distribution of learners and non-learners that we found across groups is highly consistent with the idea that innovation can be transmitted between group members (Aplin *et al.* 2013). Although the evidence is circumstantial rather than

experimental, the best predictor of becoming a learner was the presence of other learners in the group, and the non-learner groups could not be singled out by any other factor. Therefore, social transmission seems to be the most parsimonious explanation for our results.

The mechanism that may facilitate social transmission of the innovation in our study is not clear. It may be based on some form of social facilitation, stimulus enhancement, or observational learning (see Hoppitt & Laland 2008; Slagsvold & Wiebe 2011; Aplin *et al.* 2013). In the simplest case of social facilitation, observing a conspecific who finds a high quality food source on the grid may encourage other individuals to increase their searching attempts, which eventually lead them to succeed. In the case of stimulus enhancement or observational learning, the attention of the learners may be drawn by the open lids or by the removal actions of the innovator. Social learning of this kind seems highly plausible for Arabian babblers, which like other cooperatively breeding birds (Koenig and Dickinson 2004), forage together as a cohesive group at all times (Zahavi 1989, 1990,) and are very attentive to each other. It is also known from Pied babblers (*Turdoides bicolor*) that adult birds attract younger birds to high quality foraging patches by producing distinct calls (Radford & Ridley 2006), and that Arabian babblers also tend to produce calls when they find high quality food (Zahavi & Zahavi 1997) Thus, an intriguing possibility for social transmission of innovation in babblers is that it may also be assisted by recruitment calling.

It is worth noting that the “all or nothing” distribution of learners and non-learners that was found in the present study was not observed in our previous study where the innovators were subordinates (Keynan *et al.* 2014). This may indicate a situation in which subordinates learn socially from dominants (this study), but dominants are less likely to learn from subordinates (the previous study). This type of transmission bias has been discussed and demonstrated by several previous studies (Laland 2004; Aplin *et al.* 2013;



Kendal *et al.* 2014), and may reflect an adaptive choice of successful demonstrators to transmit information to other group members (Laland 2004).

Transmission biases of innovations may limit the spread of innovations in populations (Brosnan & Hopper 2014) and may therefore also limit the potential benefit of having variable task-dependent innovation abilities in the group. Nevertheless, even if innovations are not transmitted socially, variable task-dependent innovation abilities in a group can generate a skill pool effect (Giraldeau 1984) that allow social foragers to exploit a greater variety of food resources by simply joining each other's food findings (Giraldeau & Lefebvre 1986; Ilan *et al.* 2013). Thus, by providing the first evidence for task-dependent differences in innovation abilities between dominant and subordinates in a cooperative bird, our study also suggests an interesting cascading effect: different social ranks that display different cognitive strategies can increase the variety of innovations that may be generated in the group, which may then contribute to the benefits of group-living.

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## 5. Causes of variation in dominance acquisition, tenure, and lifetime reproductive success in a cooperatively breeding bird

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## 5.1 Abstract

In cooperatively breeding vertebrates with high reproductive skew, access to reproductive activity is typically monopolized by a few individuals within the group. In such breeding systems, selection will favour individuals that are more likely to both gain a breeding position and maintain it, thus optimising their lifetime reproductive success (LRS). We used a 35-year continuous, comprehensive life history database for cooperatively breeding Arabian babblers (*Turdoides squamiceps*), to investigate the influence of multiple social and environmental factors on the likelihood of an individual attaining a breeding position, maintaining tenure of that position, and reproducing successfully. We found that individuals who dispersed from their natal group were more likely to attain a dominant (breeding) position, suggesting that dispersal decisions play an important role in individual breeding success. Once an individual attained a dominant position, its lifetime reproductive success (LRS) was affected by both the duration of its dominance tenure and its annual reproductive success (ARS). We found that individuals in relatively larger groups (the size of the focal group compared to average group size in the study population) had longer dominance tenure and higher ARS. However, we found that reproductive competition had a negative effect on both tenure length and ARS. Our findings give vital insight into how social and environmental factors generate wide variation in individual fitness in a cooperatively breeding species, suggesting that dispersal decisions and the ability to maintain tenure once dominant are key factors promoting high lifetime reproductive success.



## 5.2 Introduction

Identifying the relative influence of social and environmental factors on the ability of an individual to successfully reproduce is crucial to our understanding of the evolution of social behaviour. This is especially important for the study of cooperatively breeding species, since reproduction in such breeding systems is often monopolized by a few dominant individuals, with subordinate adults delaying their own reproduction and instead helping to raise the young of others (Koenig & Dickinson 2004; Cockburn 2013; McDonald 2014). In these high-skew species, selection should favour strategies that increase an individual's chances of both gaining and maintaining a dominant breeding position, thus optimising lifetime reproductive success. A general understanding of the ontogenetic, physiological and morphological traits that influence individual variation in survival and reproductive success (RS) in cooperative breeders has progressed significantly in recent years (Ridley 2007; Nussey *et al.* 2011; Bateman *et al.* 2013; English *et al.* 2013a; b; Ozgul *et al.* 2014). For example, in cooperatively breeding meerkats (*Suricata suricatta*), long-term research found individual mass to be an important factor influencing individual reproductive success (English *et al.* 2013a; Ozgul *et al.* 2014). Although such studies have made an important contribution to our understanding of the physical and morphological factors affecting dominance acquisition and reproductive success (RS), there is still relatively little data available on the importance of social and environmental factors on dominance tenure, annual fecundity and lifetime reproductive success (but see Hodge *et al.* 2008; Spong *et al.* 2008; Lardy *et al.* 2012).

In cooperatively breeding species, subordinate individuals may gain both direct and indirect fitness benefits by delaying dispersal and reproduction (Cockburn 1998; Ekman *et al.* 2001; Komdeur 2006). However, the primary way to reproduce successfully in high-skew societies is by becoming a dominant individual (Lundy, Parker & Zahavi 1998; Hager & Jones 2009; Nelson-Flower *et al.* 2011). A dominant breeding position is most

commonly gained through one of the following strategies: passive or aggressive inheritance of the dominant position in the natal group (Shreeves & Field 2002), dispersal in order to found a new group, or dispersal to an already established group (Koenig *et al.* 2000; Raihani *et al.* 2010; Ridley 2012; Griesser *et al.* 2013). The frequency of each strategy (whether to stay and inherit, or disperse) may differ across species due to differences in life history traits such as longevity and incest avoidance mechanisms (Woolfenden 1984; Nelson-Flower *et al.* 2012). However, attempts to gain a dominant breeding position are also highly dependent on group demographic traits such as the length of the social queue and the position (social rank) of the focal individual within the social queue (Kokko & Johnstone 1999; Cant & English 2006; Raihani *et al.* 2010; Nelson-Flower *et al.* 2013). In addition, environmental constraints such as territory availability and food abundance affect an individual's likelihood of attempting to gain breeding access (Koenig *et al.* 1992; Kokko & Ekman 2002; Heg, Rothenberger & Schurch 2010). Exploring the factors that influence individual variation in the likelihood of attaining a dominant position may lead us to a better understanding of the benefits of group-living , and may assist in answering whether delayed dispersal is 'the best of a bad job' (as suggested by Russell 2004) or may instead be an adaptive behaviour by using the group as a safe haven while waiting for future dispersal opportunities (as suggested by Ekman & Griesser 2002; Kokko & Ekman 2002, Raihani *et al.* 2010)

While attaining a dominant position is often a vital first step in accessing breeding opportunities in high-skew cooperative breeding societies, once a position is occupied, different selection pressures may act on an individual's ability to maximize its lifetime reproductive success (LRS). Empirical studies have found that the key factors influencing individual LRS in cooperative breeders are the annual survival of offspring (Woolfenden 1984; Maccoll & Hatchwell 2004), and dominance tenure (Hodge *et al.* 2008; Lardy *et al.* 2012). Understanding both the social and environmental factors that influence ARS and

tenure may therefore be crucial to our understanding of individual variation in LRS in cooperative breeding societies. For example, dominants in large groups may achieve more reproductive success due to a larger number of helpers present to feed young (Emlen, Reeve & Sherman 1991; Cockburn 1998; Clutton-Brock, Russell & Sharpe 2001; Ridley 2007; Covas, du Plessis & Doutrelant 2008) or due to more individuals present to defend a high quality territory against neighbouring groups, intruders and predators (Kokko, Johnstone & T. H. 2001; Duca & Marini 2014). Conversely, other studies have found that dominant individuals in large groups may be more likely to incur a cost of reproductive competition, with such competition leading to a potential reduction in annual reproductive success (Setchell, Wickings & Knapp 2006; Nelson-Flower *et al.* 2013), or even the loss of the dominant position in some cases (Spong *et al.* 2008; Lardy *et al.* 2012). Bell *et al.* (2014) found that in meerkats (*Suricata suricatta*), when reproductive competition was low or absent, dominant individuals were less aggressive, gained more weight, and evicted subordinates less often, leading to higher pup survival. Therefore, it is likely that individual variation in dominance tenure, fecundity and LRS may be influenced both by the number of helpers in the group and existence of within-group reproductive competitors.

In this study, we use 35 years of life-history data to examine the factors that influence lifetime reproductive success in the cooperatively breeding Arabian babbler (*Turdoides squamiceps*). We begin by identifying the factors that influence the probability of an individual attaining dominance at some point in its lifetime. We then identify the factors that influence variation in dominance tenure and ARS. Finally, we look at how dominance tenure and ARS, together with social factors such as group size and intra-group reproductive competition, influence individual variation in lifetime reproductive success.

### **5.3 Materials & methods**

#### *Study site and population:*

This study was conducted at the Shezaf Nature Reserve, a 40 km<sup>2</sup> area in the Arava region of the Negev desert, south-east Israel (30°48'N, 35°13'E). The habitat is classified as hyper arid desert savanna with a mean annual rainfall of about 30mm (Anava et al. 2000, Keynan & Yosef 2010). The flora of the reserve is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, and *Haloxylon persicum*), found only in the dry riverbeds (wadis). A long-term research project on the biology, ecology, and social behavior of the cooperatively-breeding Arabian Babbler (*Turdoides squamiceps*) has been continuously conducted in the area since 1971 by Professors Amotz & Avishag Zahavi (Zahavi 1989, 1990; Zahavi & Zahavi 1997)

Arabian babblers are a group-territorial, cooperatively-breeding bird species, with age-related linear dominance hierarchies within each sex class (Zahavi 1989, 1990, Keynan, Ridley & Lotem 2014). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to the opposite sex dominant individual may gain reproductive success on very rare occasions (subordinate males produced less than 5% and subordinate females produced 0.5% of young hatched per season (Lundy *et al.* 1998). The breeding season starts around February each year and continues until July (Zahavi 1989, 1990). Only one nest is incubated at a time, and all adult group members help feeding the young produced from a single nest, and defend the nest area from intruders and predators (Ridley 2003). Arabian babblers may produce up to three successful clutches per year (Zahavi 1989, Zahavi & Zahavi 1997, Ridley 2007). Juveniles are considered adults when they reach 12 months old. At about this age it is possible to identify the sexes through sexual dimorphism in beak shape and sexual dichromatism in eye colour (Ostreiher 1999, Ridley 2007).

#### *Individual database collection*

We used data that was collected on each individual in each group of Arabian babblers present at the study site since 1978. The data was extracted and cross-examined from three resources- a Microsoft Access database that has basic data on every group observed, and every individual that was ever ringed in the population, field notes that were collected by researchers throughout the years, and large datasheets that contained each breeding event, significant life history events (e.g. dispersal, death) and adult group size during each observation for each group. Only individuals that had a complete life history in all three resources were used for analysis.

#### *Environmental data*

Weather data was collected from the long-term databases of the Israeli Meteorological Services (IMS) using the weather stations based close to the study site (within 10 km) in the villages of Hazeva, Ein Yahav and Sappir. Rainfall in the Arava region occurs only between October-May, with extremely rare events during June and September. Annual rainfall was measured between the months of August of consecutive years. We followed the IMS definition of drought as any year where the rainfall was 25% or less of the average annual rainfall. The average annual rainfall at the study site is 30.6 mm (calculated from IMS rainfall data for the past 35 years).

#### *Individual life history data*

We collated all data regarding each individual's social rank (dominance), dominance tenure, and annual and lifetime reproductive success. All individuals that didn't survive their first year post-hatching and/or their sex was not known were excluded from our analyses. Social rank was separated into two categories: dominant or subordinate. Dominance was defined by social interactions (agonistic interactions, including wing displays, physical attacks, and submissive postures, Zahavi 1989, Keynan et al *In press*). Age was determined only for individuals who hatched in our population. The group that each

individual fledged from was defined as its natal group, and individuals who entered the study population as adults were considered dispersers. A breeding event was defined as when a nest had at least one egg laid in it. We recorded the number of fledglings and number of young that survived their first year throughout the dominance period of each individual. We also calculated the time that a breeding pair spent together in order to see whether duration of the pair bond affected LRS. Individuals who attained a dominant position but did not hold it over the breeding season (and thus did not have a chance to breed before losing dominance) were excluded from our analyses of annual and lifetime reproductive success. Individual dominance tenure (in days) was calculated for each individual who achieved a dominant position.

#### *Group life history data*

Group size was measured as the number of adults in the group at the beginning of the breeding season, or averaged for each year (when the analysis was conducted on continuous and not annual data such as dominance tenure and lifetime reproductive success). Relative group size was measured as the average number of adults in the focal group divided by the average number of adults in all groups in the population for each year. We chose to include relative group size in our analysis because the size of neighbouring groups, and thus their ability to appropriate territory from the focal group, may be an important factor influencing reproductive success (Bateman et al. 2012). In addition, due to typically large fluctuations in group size between years, a characteristic of many cooperatively breeding species (Bateman et al. 2012), what group size represents a 'large group' in absolute numbers in some years may be a small group size in other years (Bateman et al. 2012). Within-group male:female ratio was calculated for each group at the beginning of the breeding season. Reproductive competition was defined as the presence of multiple potential breeders of the same sex (where potential breeders are adults that are not

related to a within-group adult of the opposite sex, *sensu* Nelson-Flower et al 2011). Competition over reproductive opportunities was defined as male competition (0 = no competition, 1 = male-male competition present) and female competition (0 = no competition, 1 = female-female competition present).

### *Statistical analysis*

Statistical analyses were conducted using IBM SPSS statistics version 22, and the R statistical package, version. 2.15.3. (R core team 2013)

To determine the parameters influencing (a) whether an individual attains a breeding position (dominant rank), (b) individual variation in annual reproductive success (fecundity) and (c) individual variation in lifetime reproductive success, we used Generalized Estimating Equations (GEE). We compared candidate models using Corrected Quasi-Likelihood-under-independence model criterion (QICc, Pan 2001) with a binomial distribution and a logit link function to determine factors affecting individual breeding status (where 0 = subordinate, 1 = dominant) per year of life. For variations in annual and lifetime reproductive success (where reproductive success was defined as the total number of fledglings produced per year for ARS, and the total number of young that survived their first year over the entire dominance tenure of an individual for LRS), we used a Poisson distribution with a log link function. We considered that the model with the lowest QICc value provided the best fit to the data; and that all models with a QICc value that was 5 or more units higher than the ‘best model’ were considered an insufficient fit for further interpretation. All candidate models were compared to the QICc basic model (with no predictors). If candidate models did not have QICc values  $> 5$  lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data.

To determine the parameters influencing dominance tenure we used Linear Mixed Models (LMM). Data were square-root transformed to achieve normality. We determined a set of candidate models and compared them using Akaike's Information Criterion corrected for small sample size (AICc, Burnham & Anderson 2002). We considered that the model with the lowest AICc value provided the best fit to the data; models with an AICc value of 5 or more than this best model were considered an insufficient fit for further interpretation. All candidate models were compared to the AIC basic model (with no predictors). If candidate models did not have AICc values  $> 5$  lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data. When models scored within 5 AICc units of the best model, multi-model averaging was employed to determine significant variables (*sensu* Grueber *et al.* 2011)). The best terms were checked for significance using 95% confidence intervals (CI). A term was not considered a good predictor of data patterns if its CIs did intersect zero (Burnham & Anderson 2002)

#### *Parameters influencing the attainment of dominant rank*

To determine what parameters influenced the likelihood of an individual attaining a dominant rank (and thus breeding position), we used GEEs with a binomial distribution (where 0 = each year that the individual did not become dominant, 1 = each year the individual spent as dominant). All individuals whose date of hatching, natal group size and identity, or fate (became dominant, dispersed to another group, or died) wasn't known were excluded from the analysis. We did not have body mass data for all individuals in our population; therefore, we took a subset of our data to determine the potential influence of early body mass on attainment of dominance rank as an adult. This gave us a sample size of 118 individuals whose body mass at time of ringing (11 days post-hatching) was recorded. For these individuals, we ranked their within-brood body mass measures (heaviest in brood = 1, second heaviest = 2, etc.). We used within-brood rank because the



variation in ecological conditions and group size between years meant that a comparison of body mass between broods and years on the eventual attainment (or not) of dominant rank was invalid. Our analysis of nestling body mass on the likelihood of becoming dominant in our sample of 118 individuals revealed that body mass was not a good predictor of our data patterns (see Table S1 in the supplementary data). Thus, we conducted the analysis with a larger sample size of individuals for which we did not have body mass data, but for which all other parameters described above were collected. We included the year, individual and group identity as random terms to account for the potential influence of repeated measures on the distribution of the data. We excluded group size and relative group size from this analysis since the mathematical probability of attaining dominant rank in a small group is higher than in a large group. We therefore considered the following parameters in our analyses: within-group female:male ratio, sex, natal group status, drought conditions per year (0 = yes, 1 = no) and yearly rainfall (mm).

#### *Parameters influencing dominance tenure*

Dominance tenure (in days) was transformed using a square-root transformation to achieve normality. We used Linear Mixed Models (LMMs) to determine the parameters influencing the total time (in days) an individual spent as a dominant. Since the study site is monitored on a daily basis, and since the chances of an individual losing dominance without an observed cause (e.g. eviction, dispersal, death, or group extinction) are extremely small, once an individual disappeared and no other record was found of it, we considered that dominance tenure had ended. We included group and individual identity as random terms to account for the potential influence of repeated measures on the distribution of data. Parameters tested during model selection were average group size and relative group size during dominance tenure, sex, natal group status and average ARS (average number of fledglings produced per year) during tenure.

### *Parameters influencing annual reproductive success (ARS)*

To determine what parameters influence variation in annual reproductive success (number of fledglings per breeding individual per year) between individuals that had attained a dominant breeding position, we used GEEs with a Poisson distribution and a log link function. We included in our analysis only individuals who invested in at least one breeding event (i.e. at least one egg was laid during their time in a dominant breeding position). We included individual identity, group identity and breeding year as random terms to account for the potential influence of repeated measures on the distribution of data. Parameters tested during model selection included absolute and relative group size during each breeding season, sex, natal group status, the presence of reproductive competition in the group at the start of each breeding season (yes/no), rainfall and drought (yes/no). In order to determine whether the age at which an individual attained dominant rank had an effect on annual reproductive success, a smaller analysis was conducted (containing only individuals of known age (days post-hatching)). Our analysis of age on ARS revealed that age was not a good predictor of our data patterns (see Table S4 in the supplementary data). Thus, we conducted the analysis on a larger sample size of individuals, in which age was not known for all individuals, but for which all other parameters described above were available.

### *Parameters influencing lifetime reproductive success (LRS)*

To determine what parameters influence LRS we used GEEs with a Poisson distribution. If the individual became dominant in a new group, we treated the new event separately from the previous, since the dynamics of the new group were different. We included group and individual identity as random terms to account for the potential influence of repeated measures on the distribution of data. Parameters tested in the model selection process were average absolute and relative adult group size throughout the years of dominance tenure,

sex, natal group status, average ARS, duration and the longest monogamous pair bond during tenure. As for our ARS analysis, a smaller analysis containing only individuals whose age at the beginning of their dominance period was known was conducted to determine the potential influence of age on LRS. However, age was not a good predictor of variation in LRS (see Table S6 in the supplementary data) and hence was not used in our subsequent analyses of the larger dataset.

## 5.4. Results

### *General:*

Overall, we had life history data available from 1237 adult individuals from 43 groups spanning the years 1978-2013. 753 individuals (60.87%) hatched in our study population and 484 (39.13%) arrived as adults. We analysed data on 544 females and 514 males (after excluding 179 subordinate individuals whose sex was unknown)

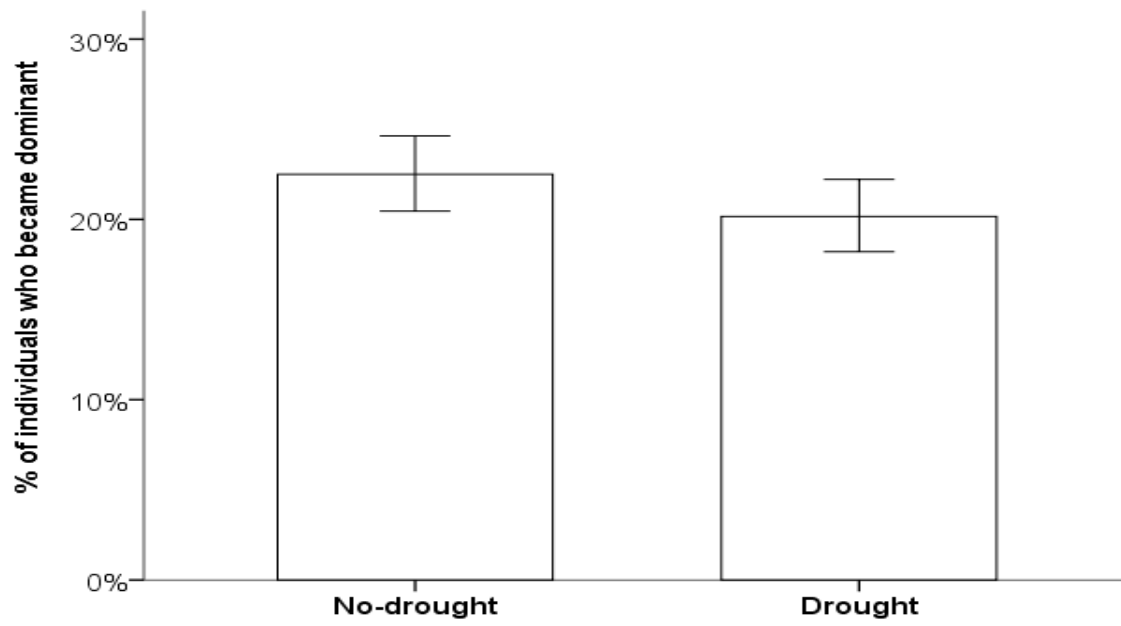
### *Probability of attaining a breeding position*

We analyzed data on a total of 1538 individual-years from 192 dominant and 238 subordinate individuals who were ringed in our population as nestlings and whose fate was known (died, moved, dispersed, evicted or became dominant). The average ( $\pm$ SE) age for an individual to become dominant was  $1541.76 \pm 44.22$  days ( $1351 \pm 60.12$  days for females and  $1670 \pm 66.5$  days for males). The minimum age to attain dominant rank in our population was 338 days, and the maximum age was 4482 days (~12 years old). The probability of becoming dominant was higher for individuals that dispersed from their natal group (Table 5.1). Only 8% of individuals who stayed at their natal territory became dominant, while almost 30% of those who dispersed became dominant. In addition, the probability of becoming dominant was higher during years with more rainfall (Figure 5.1).

There was no evidence that individuals that attained a higher body mass as nestlings were more likely to become dominant, nor were there sex differences in the probability of attaining dominance (Table S2, supplementary data)

**Table 5.1:** Top model set (QICc) of the terms influencing the probability of attaining a dominant breeding position per year of life. Group and individual identity were included as random terms. Data is based on 192 dominant and 238 subordinate individuals from 43 groups over the time period spanning 1978-2013. A complete set of candidate models are presented in Table S2 in the supplementary data.

Model	K	QICC	$\Delta$ QICC	Weight
Basic	3	2100.79	651.22	
Dispersal+ Drought	5	1440.57	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
<b>Natal status:</b>				
- Non-dispersers	0.0			
- Dispersers	3.2	0.15	2.9	3.5
<b>Droughts:</b>				
- Drought	0.0			
- No drought	0.4	0.13	0.13	0.66



**Figure 5.1:** The percentage of individuals ( $\pm$  SE) who became dominant during drought years and non-drought years. Data is based on 192 dominant and 238 subordinates from 43 groups over the time period spanning 1978-2013.

### *Dominance tenure*

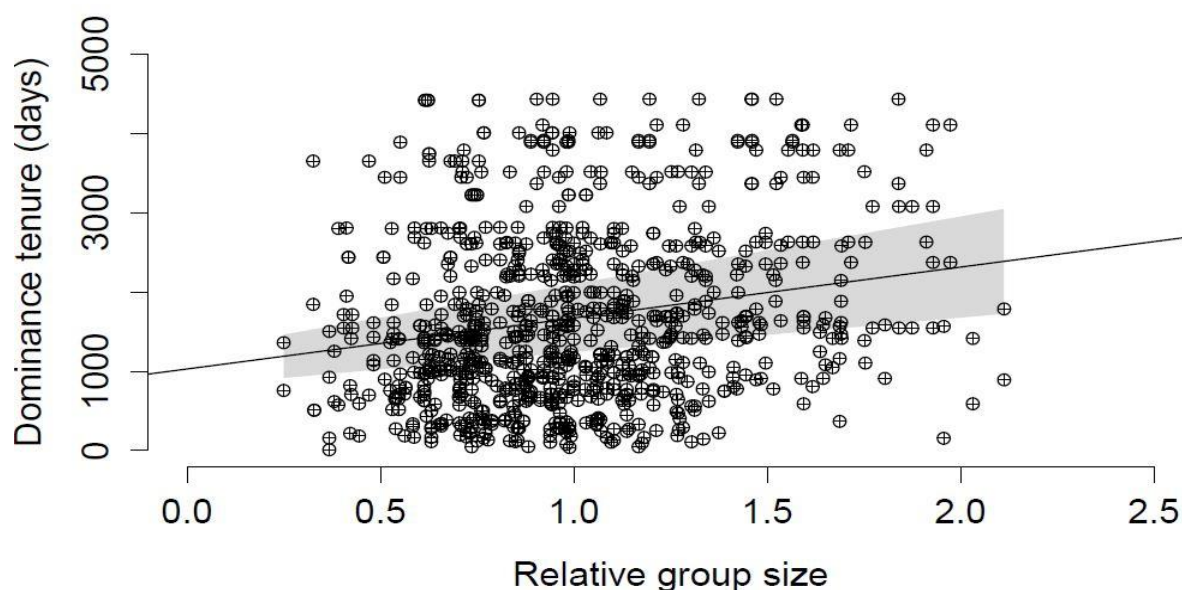
We analysed dominance tenure for 343 individuals: 171 females and 173 males. Average dominance tenure ( $\pm$ SE) was  $1131.15 \pm 49.7$  days. Minimum tenure was ten days, and maximum tenure was 4420 consecutive days (12.1 years). Individuals that attained dominance in relatively larger groups had longer dominance tenure. (Table 5.2, Figure 5.2)

**Table 5.2:** Top model set (AICc) of the terms influencing dominance tenure. Group and individual identity were included as random terms. Data is based on 343 individuals from 43 groups over the time period spanning 1978-2013. A complete set of candidate models are presented in Table S3 in the supplementary data

Model	K	AICC	$\Delta$ AICC	Weight
Basic	3	2739.7	19.04	
Average relative group size	4	2720.66	0	0.66
Average absolute adult group size	4	2722	1.34	0.34
Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
Relative group size	9.78	2.58	4.7	14.8

### *Annual reproductive success (ARS)*

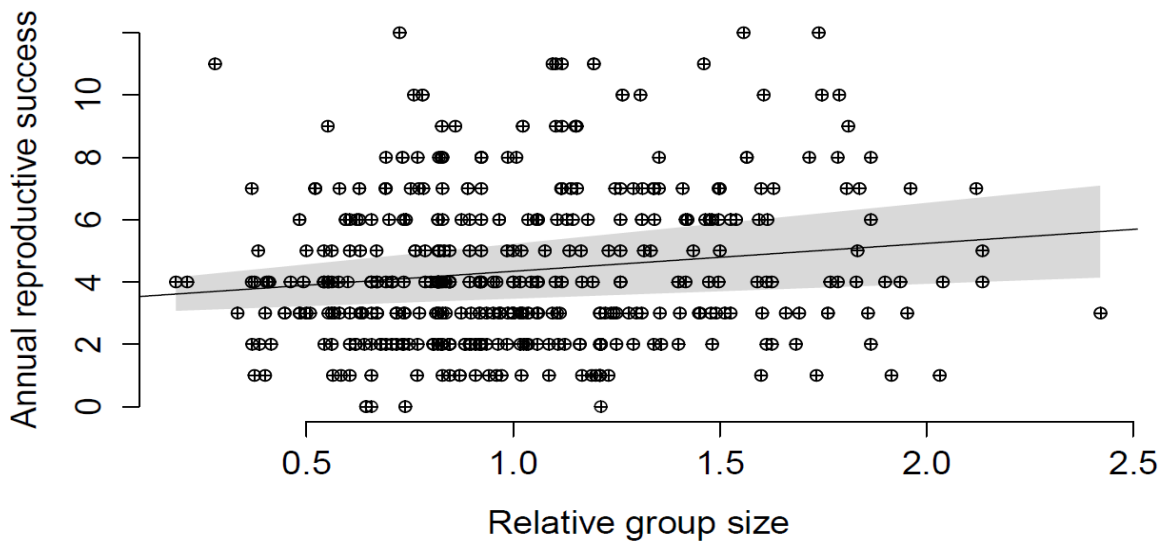
In total we analysed data from 863 individual breeding years for 158 males and 151 females. Annual reproductive success was between 0-12 fledglings, with an average ( $\pm$ SE) of  $4.36 \pm 0.08$  fledglings produced per dominant adult per year. Individuals in relatively larger groups had higher ARS, with more fledglings per year produced by dominant individuals in these groups (Table 5.3, Figure 5.3a). Droughts and reproductive competition also had a negative effect on ARS with individuals having lower ARS during drought years or when female reproductive competition was present in the group. (Table 5.3, Figure 5.3b,c).



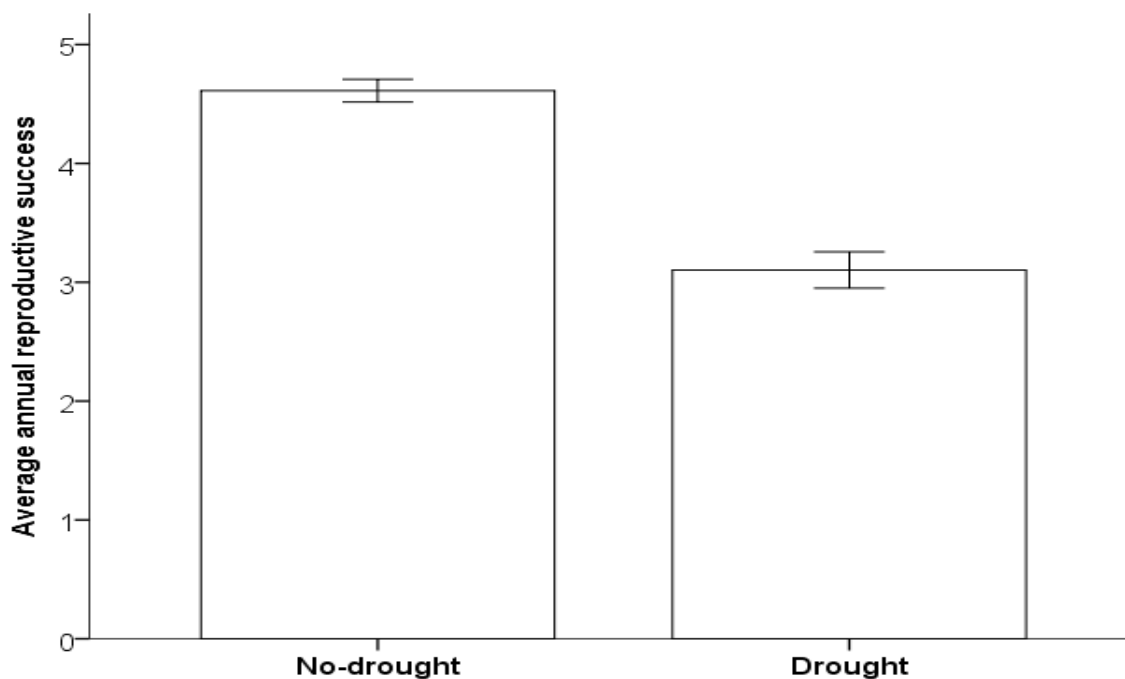
**Figure 5.2:** Effect of relative group size on individual dominance tenure (in days). Data is based on 343 individuals from 43 groups spanning 1978-2013. Grey background represents 95% confidence intervals

**Table 5.3:** Top model set (QICc) of the terms influencing annual reproductive success (ARS). Group identity, individual identity and breeding year were included as random terms. Data is based on 309 individuals who were dominant for at least 365 days. A complete set of candidate models are presented in Table S5 in the supplementary data

Model	K	QICC	$\Delta$ QICC	
Basic	3	1106.48	112.24	
Competition+ Drought+	6	994.24	0	1
Relative group size				
Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
Relative group size	0.2	0.05	0.1	0.29
- Female competition present	0.0			
- Female competition absent	0.15	0.04	0.08	0.24
- Drought	0.0			
- No Drought	0.42	0.05	0.32	0.53

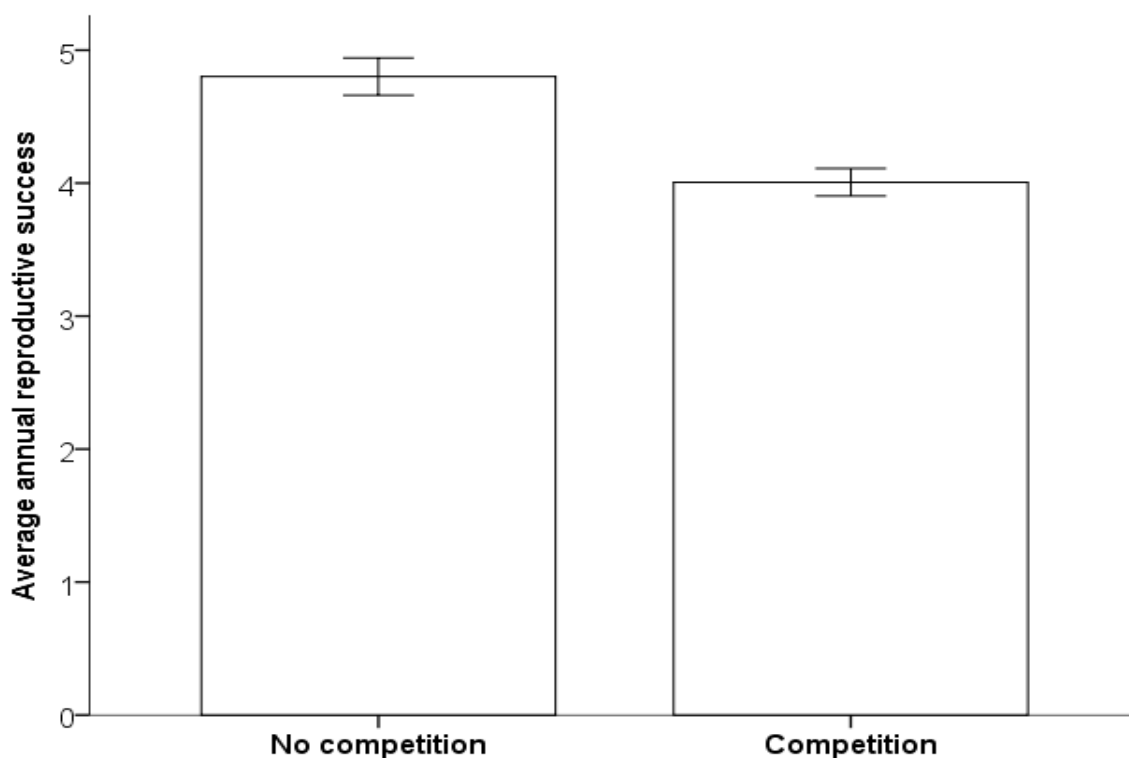


**Figure 5.3a:** Effect of relative group size on annual reproductive success (number of fledglings per year), Data is based on 309 individuals from 43 groups spanning the period 1978-2013. Grey background represents 95% confidence intervals.



**Figure 5.3b:** Effect of droughts on average annual reproductive success in dominant individuals (number of fledglings per year). Data is based on 309 individuals from 43 groups who were dominant for at least 365 days over the time period spanning 1978-2013.





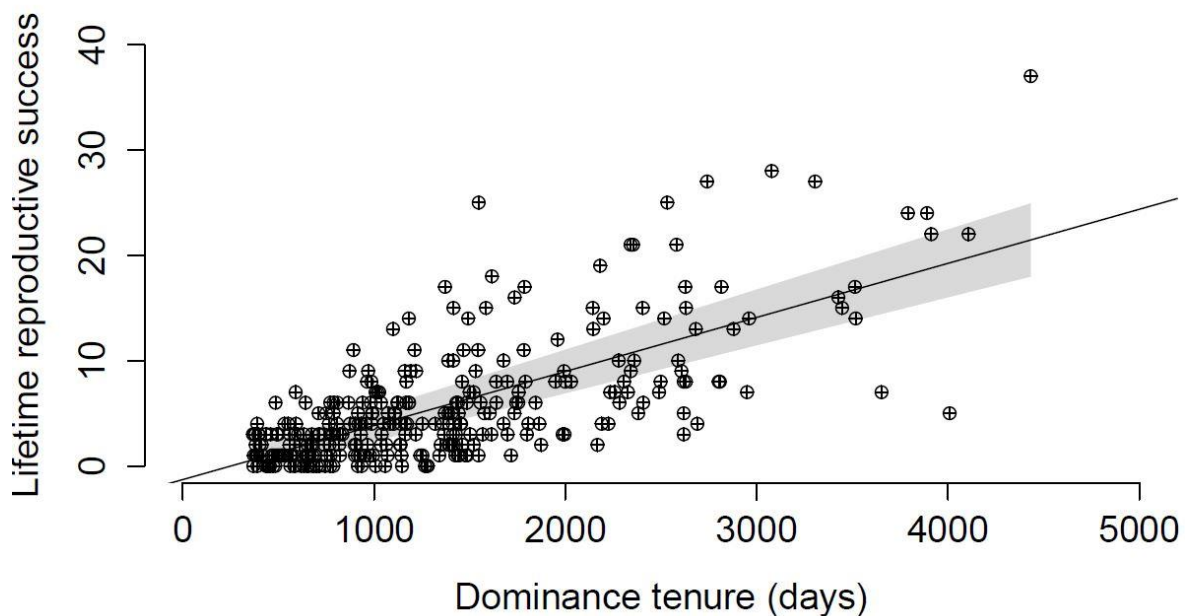
**Figure 5.3c:** Effect of within-group reproductive competition on average annual reproductive success in dominant individuals (number of fledglings per year). Data is based on 309 individuals from 43 groups who were dominant for at least 365 days over the time period spanning 1978-2013.

#### *Lifetime reproductive success (LRS)*

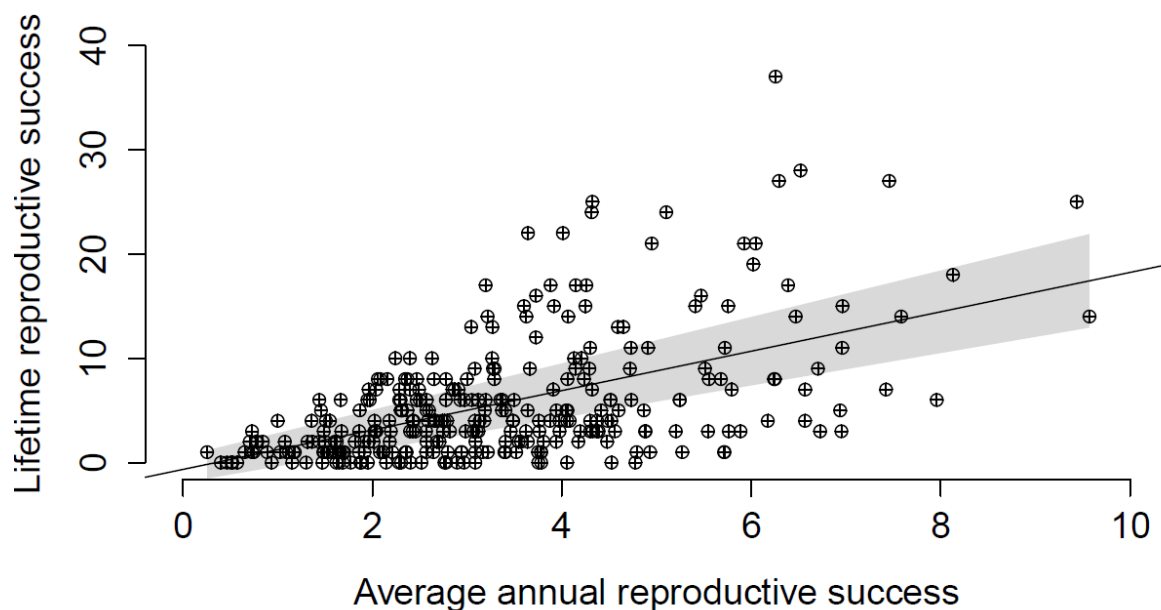
The average number of young fledged per dominant individual over their entire dominance tenure ( $\pm$ SE) was  $10.53 \pm 0.53$  fledglings (range = 1-76 fledglings). The number of young that survived to independence averaged ( $\pm$ SE)  $4.68 \pm 0.28$  (range = 0-37) per dominant individual. Dominance tenure and ARS were the most important factors affecting LRS (Table 5.4), where those individuals that experienced a longer dominance tenure and higher ARS had the highest LRS (Figures 5.4a,b). Relative group size also influenced individual LRS (Table 5.4), with individuals in groups that were larger than the population average producing more offspring over their lifetime (Figure 5.4c).

**Table 5.4:** Top model selection (QICc) of the main terms influencing individual variation in lifetime reproductive success. Group and individual identity were included as random terms Data is based on 309 individuals who were dominant for at least 365 days. A complete set of candidate models are presented in Table S7 in the supplementary data

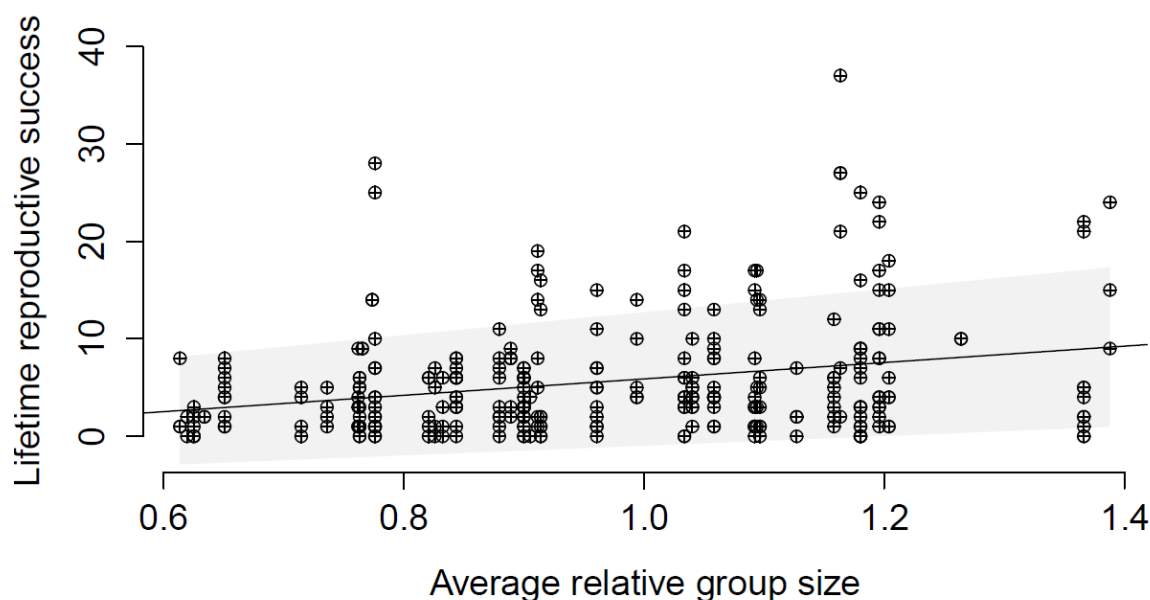
Model	K	QICC	$\Delta$ AICC	Weight
Basic	3	1604.06	196.07	1153.56
Dominance tenure+ ARS+ average relative group size	6	450.5	0	1
Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
Dominance tenure	0.001	3.5E-5	0.001	0.001
ARS	0.26	0.01	0.23	0.29
Relative group size	0.38	0.38	0.09	0.66



**Figure 5.4a:** Effect of dominance tenure on lifetime reproductive success (total number of fledglings that survived to adulthood). Data is based on 309 individuals from 43 groups who were dominant for at least 365 days over the time period spanning 1978-2013. Grey background represents 95% confidence intervals



**Figure 5.4b:** Effect of ARS on lifetime reproductive success (total number of fledglings survived to adulthood over the entire reproductive lifespan of each breeding adult) Data is based on 309 individuals from 43 groups who were dominant for at least 365 days over the time period spanning 1978-2013. Grey background represents 95% confidence intervals.



**Figure 5.4c:** Effect of relative group size on lifetime reproductive success (total number of fledglings survived to adulthood over the entire reproductive lifespan of each breeding adult) Data is based on 309 individuals from 43 groups who were dominant for at least 365 days over the time period spanning 1978-2013. Grey background represents 95% confidence intervals.

## 5.5 Discussion

Our extensive analyses have revealed that (a) the probability of attaining a dominant position are higher for those who disperse from their natal group, and (b) once an individual attains a dominant position, social factors like group size and reproductive competition play an important role in dominance tenure and reproductive success. These results accord with previous work on cooperatively breeding mammals, revealing that both group size and the presence of reproductive competition can play an important role in the ability of a dominant individual to maintain its dominance tenure (Hodge et al. 2008, Spong et al. 2008, Lardy et al. 2012). We found that some individuals were dominant for up to twelve years (and produced more than 30 young that reached adulthood), while others held dominance for a short period with extremely low or no breeding success. This demonstrates the huge variability among individuals in lifetime reproductive success, and suggests that social factors such as dispersal decisions and group size can have long-term influences on individual life history traits.

Our first aim in this study was to assess the causes of variation in individual ability to attain a dominant position, since this is the primary way to attain access to breeding opportunities in high-skew societies (Lundy et al. 1998, Maccoll & Hatchwell 2004, Spong et al. 2008, Nelson-Flower et al. 2013). Surprisingly, the condition of an individual in early life (measured as body mass in this study) did not influence the likelihood of attaining a dominant breeding position in later life. Previous studies have found a strong affect of body condition on dominance acquisition and reproductive success in non-cooperative species (Carrascal, Senar & Mozetich 1998; Buston 2003; Blums *et al.* 2005; Verhulst *et al.* 2014). However, our body mass result is similar to previous studies conducted on other cooperatively breeding species that found individual mass to be less important than social

context in determining dominance acquisition (Hodge *et al.* 2008; Spong *et al.* 2008; Ozgul *et al.* 2014; Lukas & Clutton-Brock 2014 but see Ozgul *et al.* 2014 for opposite results). Nevertheless, body mass is considered an important influence on an individual's ability to retain the dominant position and suppressing competitors in cooperatively breeding species and should thus be considered in any study concerning individual life history traits (Bradbury & Blakey 1998; Ridley & Raihani 2007; Ozgul *et al.* 2007, 2014)

Social interactions, in particular dispersal decisions, are the primary factors influencing the acquisition of dominance in Arabian babblers. As with many other long-lived, cooperatively breeding species, Arabian babblers may spend a substantial period of their life as non-reproductive helpers in their natal group (reviewed in Koenig *et al.* 1992; Koenig & Dickinson 2004), but the chances to reproduce with the opposite sex dominant, or replace the same sex dominant in their natal group are low (due to strong incest avoidance (Woxvold, Adcock & Mulder 2006; Nelson-Flower *et al.* 2012)). This means that for most individuals, the natal group acts as a 'safe haven' from which they are able to wait for and/or monitor breeding opportunities in other groups. (Koenig *et al.* 2000; Legge & Cockburn 2000; Ekman *et al.* 2001; Raihani *et al.* 2010). Nevertheless, although the chances to become dominant are significantly higher for those who disperse, only about one third of those who dispersed achieved dominance, while the rest either became subordinates in their new groups, returned to their natal group, or did not survive the dispersal event. This illustrates the costs of dispersal from the natal group and the importance of individual decisions on where, when and with whom to disperse (reviewed by Bonte *et al.* 2012). Having the natal group as a safe haven while waiting for an opportunity to disperse, or returning to it after an unsuccessful dispersal attempt may be considered an indirect fitness benefit of group-living, and may provide an adaptive explanation for the evolution of delayed dispersal in cooperative breeders (Ekman & Griesser 2002; Kokko & Ekman 2002)

Even for the small proportion of individuals who attain a dominant breeding position, there is large variation in lifetime reproductive success. Previously empirical studies have suggested that one of the best predictors of LRS in high-skew societies is the amount of time an individual is able to hold a dominant breeding position (i.e. dominance tenure, Hodge *et al.* 2008; Lardy *et al.* 2012), and this was supported by our results. Our analysis revealed that the primary factor affecting dominance tenure was relative group size, where dominants in relatively larger groups were able to maintain a longer dominance tenure. This effect may be explained by enhanced adult survival in larger groups (Clutton-Brock *et al.* 1999; Ozgul *et al.* 2006) where increased longevity equals longer tenure, and the ability of larger groups to protect against intruders from neighboring groups who may try to displace the dominant (Ridley 2012). Our finding that relative group size had a stronger influence on dominance tenure than absolute group size gives strong support to the latter and underlines the importance of between-group interactions on the ability of the dominant to maintain its tenure and achieve higher LRS. A second important factor affecting individual LRS was annual reproductive success (ARS). In Arabian babblers, dominant individuals who produce more offspring per year tend to have higher LRS. Similar to tenure, dominant individuals in relatively larger groups tended to produce more offspring per year. Again, this result emphasizes the importance of having helpers, not just for the benefits caused by increases in vigilance and defense against predators, or the amount of care offspring receive, but also by protection against intruders from neighbouring groups (Kokko *et al.* 2001; Kokko, Johnstone & Wright 2002; Kingma *et al.* 2014)

Our findings that individual ARS was lower during drought years reveals similar trends to previous studies, with fluctuations in rainfall recognised as an influence on individual reproductive success in both cooperative and non-cooperative species, particularly those inhabiting arid environments (Rotenberry & Wiens 1991; Morrison & Bolger 2002). In addition to rainfall we found that a social factor, reproductive competition, influenced

ARS. The presence of within-group reproductive competition is increasingly recognised as a social factor that may cause a decline in reproductive success (Cant *et al.* 2010; Nelson-Flower 2013; Bell *et al.* 2014). Within-group competition can also result in shorter dominance tenure due to aggressive interactions among competing individuals (Lardy *et al.* 2012; Lukas & Clutton-Brock 2014). Our results confirmed the negative influence of reproductive competition, but only between females, resulting in reduced ARS for both sexes. The potential reason for this effect is the increased rate of egg-breaking by competing females, as has been observed previously in other cooperatively breeding bird species (Koenig *et al.* 1995; Nelson-Flower 2013).

By analyzing the extensive long-term database available for Arabian babblers we were able to identify the social factors that increase an individual's chances to attain a dominant position, retain it and successfully reproduce. We have shown that successful dispersal positively influences the probability of an individual to become dominant, supporting the assumption that subordinates use their natal group as a “safe haven” until reproductive opportunities occur. Secondly, we have shown the importance of relative group size on dominant tenure, ARS and LRS, suggesting that inter-group interactions (i.e. the ability of a group to defend its territory against invasions by conspecifics from other groups) play an important role in reproductive success. Finally, our findings that female reproductive competition negatively affects ARS further highlight the increasing evidence for the importance of competition as a factor that should be addressed when considering variations in LRS among individuals. These findings give vital insight into how social and environmental factors generate wide variation in fitness levels among individuals in a cooperatively breeding species.

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## 6. Long-term analysis of social and environmental influences on group dynamics in a cooperative breeder

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## 6.1 Abstract

1. The relative importance of environmental versus social influences on group dynamics in cooperative breeders is not well understood, perhaps owing to a paucity of long-term databases that cover a wide variation of environmental extremes.
2. We used a 35-year continuous, comprehensive life history database for cooperatively breeding Arabian babblers (*Turdoides squamiceps*) to investigate how social and environmental factors affect group-level demographics such as reproductive success, recruitment rates, and likelihood of group extinction.
3. We found that both social and environmental factors influence group dynamics. Social factors (reproductive competition and number of helpers relative to the population average) influenced reproductive success, recruitment of young to the adult population, adult migration events, and the likelihood of group extinction. Environmental factors affected reproductive success and recruitment rate but not adult migration or group extinction.
4. Our results support recent studies suggesting that group-living buffers against environmental uncertainty. However our results suggest that the mechanisms underlying this process is not only through increased benefits to offspring, but also in the form of enhanced benefits to adult group members.
5. We conclude that while environmental factors do have an important influence on group-level demographics, social factors also play an important, and perhaps hitherto under-acknowledged role.

## 6.2 Introduction

Evolutionary theory predicts that individuals that employ strategies to successfully maximise their own survival and reproductive success will be favoured by natural selection (Darwin 1859). Such strategies depend strongly on the individual's ability to forage, avoid predators, find mates, defend a territory and invest in offspring (reviewed in Davies, Krebs & West 2013). It has long been suggested that group-living evolved as a strategy to protect against climatic extremes, reduce predation risk and enhance foraging efficiency (reviewed in Krause & Ruxton 2002). One of the most studied forms of group-living is cooperative breeding, a social system in which more than two individuals help care for the young raised from a single brood (reviewed in Koenig & Dickinson 2004; Cockburn 2013; Riehl 2013). By living in cooperatively breeding groups, individuals may gain both direct and indirect fitness benefits such as lower costs of parental care through the presence of helpers (Heinsohn 1991; Wright & Dingemanse 1999; Canário, Matos & Soler 2004; Ridley & Raihani 2007), access to parentage opportunities for helpers (Emlen, Reeve & Sherman 1991; Cockburn 1998), increased predator vigilance (Beauchamp 2008; Bell *et al.* 2009; Sorato *et al.* 2012; Ridley, Nelson-Flower & Thompson 2013), better access to food resources (Kokko, Johnstone & Clutton-Brock 2001) and greater access to dispersal opportunities (Ridley 2012).

Recent studies have suggested that cooperative breeding may have evolved in order to enhance on individual condition and fitness during prolonged periods of harsh or highly variable environmental conditions (Rubenstein & Lovette 2007; Rubenstein 2011; Jetz & Rubenstein 2011; Cockburn & Russell 2011; Angulo *et al.* 2013; Ebensperger *et al.* 2014 but see Gonzalez, Sheldon & Tobias 2013 for opposite results). As well as environmental conditions, empirical studies have revealed strong social influences on individual condition and fitness (Hodge *et al.* 2008; Spong *et al.* 2008; Lardy *et al.* 2012; DuVal 2012; Angulo *et al.* 2013; English *et al.* 2013; Ozgul *et al.* 2014) in cooperatively breeding species. It is

thus likely that a combination of both social and environmental factors may play an important role in within group dynamics. (Bateman *et al.* 2013). The ability of studies to successfully identify the primary factors influencing group dynamics in cooperative breeders is primarily due to the fact that they are based on long-term datasets. The importance of detailed long-term datasets in revealing important demographic patterns was emphasized in a recent review by Clutton-Brock & Sheldon (2010) and further supported by (Cockburn 2014). Our extensive long-term, continuous database on Arabian babblers, covering more than 35 years of data, represents a valuable resource towards understanding the importance of environmental and social factors on group dynamics over time.

Ecological factors influence the costs and benefits of group-living behaviour (reviewed by (Hatchwell & Komdeur 2000). For example, the ecological constraints (Koenig 1981; Emlen 1982) suggests that cooperative breeding evolved due to ecological constraints such as a shortage in high-quality breeding territories, low chances of successful breeding for lone individuals once group territories have been established, high mortality associated with dispersal, and low probability of finding a mate. Recently, Jetz & Rubenstein (2011) showed that cooperative breeding systems are more likely to evolve in species that inhabit areas of high environmental uncertainty; cooperative breeding may have therefore evolved as a ‘bet-hedging strategy’ to mediate against such uncertainty (Rubenstein 2011). If indeed cooperative breeding helps to mediate against environmental uncertainty during reproductive attempts, we would expect that the benefits of cooperative breeding would be especially prevalent during severe climatic events (such as heatwaves or droughts). This may be reflected for example in a greater delay in breeding attempts during dry breeding seasons by small groups, a greater likelihood of successful reproduction and persistence in large groups when environmental constraints are high (Covas, Doutrelant & du Plessis 2004), or a greater likelihood of allowing immigrants into the group when group size falls



under a certain threshold during years of high environmental variability (Korb & Roux 2012).

Group size is probably the most studied social factor influencing group dynamics in cooperative breeding studies to date. Previous research has provided empirical evidence that reproductive success is higher in larger groups through mechanisms such as load lightening. (e.g. Crick 1992; Cockburn 1998; Russell 2003; Ridley 2007; Brouwer, van de Pol & Cockburn 2014), greater detection of predators (Beauchamp 2008; Hollén, Bell & Radford 2008; Bell *et al.* 2009; Ridley, Raihani & Bell 2010), and higher quality (or larger) territories, thus buffering against food limitation during resource-poor years (Ridley 2007; Gusset & Macdonald 2010; Ebensperger *et al.* 2014) . However, when group size exceeds a certain threshold, the benefits of group-living may be outweighed by the costs, such as resource competition, length of the social queue and intra-group reproductive conflict (Courchamp, Grenfell & Clutton-Brock 1999; Kokko & Johnstone 1999; Nelson-Flower *et al.* 2013; Bell *et al.* 2014). Intra-group reproductive competition between potential breeders is increasingly recognised as an important factor affecting group dynamics (Shen *et al.* 2012, Nelson-Flower *et al.* 2013, Bell *et al.* 2014). Most cooperatively breeding animals live in simple family groups, but in a number of cases, especially in birds, groups may be composed of unrelated individuals (Raihani & Clutton-Brock 2010; Riehl 2013). In these cases, social groups may be formed through a combination of delayed dispersal, coalition dispersal and immigration, leading to complex aggregations of individuals that vary in both age and relatedness (Koenig 1981; Zahavi 1989, 1990; Ridley 2012; Riehl 2013). Competition between potential breeders may lead to reduced reproductive success due to a delay in breeding attempts, nest abandonment, infanticide, and suboptimal brood size (Zahavi 1989, 1990; Koenig *et al.* 1995; Cockburn 1998; Nelson-Flower *et al.* 2013; Bell *et al.* 2014). Therefore, analyses of the potential influence

of such potentially costly social factors on long-term group dynamics would be highly beneficial.

Here, we investigate the relative importance of ecological and social factors on group dynamics in cooperatively breeding Arabian babblers (*Turdoides squamiceps*) using an extensive and detailed 35-year continuous database of significant life-history events and group composition changes. Specifically, we investigate the factors affecting the initiation of breeding activity, reproductive success, migration events, and group extinction. Using this data, we aim to determine how long-term group dynamics in Arabian babblers are affected by environmental and social factors, which may contribute to a better understanding of the evolution and maintenance of cooperative breeding behaviour in general.

### 6.3 Materials & methods

#### *Study site and population:*

Our study was conducted at the Shezaf Nature Reserve, a 40 km<sup>2</sup> protected wildlife area in the Arava region, Negev Desert, south-east Israel (30°48'N, 35°13'E). The habitat is defined as a hyper-arid desert (rainfall<50mm per annum- UNESCO 1977). The flora of the reserve is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, and *Haloxylon persicum*), found only in the dry riverbeds (wadis). A long-term research project on the ecology of the cooperatively-breeding Arabian Babbler has been continuously conducted in the area since 1971 by Amotz & Avishag Zahavi (Zahavi 1989, 1990; Zahavi & Zahavi 1997).

Arabian babblers are a group-territorial, cooperatively breeding bird species with age-related linear dominance hierarchies within each sex class (Zahavi 1989, 1990). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to the dominant pair may gain reproductive success on rare occasions

(Lundy, Parker & Zahavi 1998). The breeding season usually starts around the end of February and continues until July (Zahavi 1989, 1990). Only one nest is incubated at a time, and usually all adult group members help in raising young (Ridley 2007). Arabian babblers may raise up to four successful clutches per year (Zahavi 1989, 1990; Zahavi & Zahavi 1997). Incubation continues for up to 14 days after the last egg was laid (synchronous hatching) and nestlings remain in the nest for up to 15 days before fledging (Ostreiher 1997). Newly fledged young are unable to fly and are entirely dependent on adults for food (Ostreiher 1999). Fledglings become independent foragers after approximately eight weeks post-fledging (Ridley 2007). Juveniles are considered adults when they reach 12 months old. At about this time it is also possible to discriminate between sexes through the colour of the eyes and beak shape (Ostreiher 1999; Ridley 2007)

#### *Group database collection*

We used data that was continuously collected on cooperative groups of Arabian babblers since 1978. The data was extracted and cross-examined from three sources- a Microsoft Access database that has basic data on every group and individual that was ringed in the population, field notes that were collected by researchers throughout the years, and large cardboard datasheets that contained each breeding event and group size during each observation. Only groups that had a complete group history in all three resources were used for analysis.

#### *Environmental data*

Weather data was collected from the long-term databases of the Israeli Meteorological Service (IMS) using the weather stations based close to the study site (within 10 km) in the villages of Hazeva, Ein Yahav and Sappir.

Rainfall in the Arava region occurs primarily between October-May, with extremely rare events during June and September. We measured annual rainfall between the months of August of consecutive years (no rainfall events occur between June and September, therefore the rainfall events that influence the next breeding season start in late September). We followed the IMS definition of drought as any year where the rainfall was 25% or less than the average annual rainfall. The average annual rainfall for the study site is 30.6 mm (calculated from local weather station data for the past 35 years). We also calculated the number of heatwaves during each breeding event (where a breeding event is defined from the point that the first egg was laid). Heatwaves were defined as three or more consecutive days of maximum temperature exceeding 38°C, *sensu* du Plessis *et al.* (2012).

#### *Group data- size and social structure*

Social rank was defined as either dominant or subordinate. Dominance was defined by age (since age-structured dominance hierarchies exist in Arabian babblers) and by observations of aggressive social interactions (Zahavi 1989). Reproductive competition was defined as the presence of multiple potential breeders of the same sex in the same group (where potential breeders are adults that are not related to a within-group adult of the opposite sex, *sensu* (Nelson-Flower *et al.* 2013). Group sex ratio was defined as the number of females divided by the total number of adults in the group.

Group size was measured as the number of adults (all individuals > 1 year old) in the group, averaged for each year. Relative group size was measured as adult group size of the focal group divided by the average adult group size in the study population for each year. We chose to use relative group size in our analysis because the size of neighbouring groups, and thus their ability to appropriate territory from the focal group, may be an important factor influencing reproductive success (Ridley & Huyvaert 2007; Bateman *et*

*al.* 2013). In addition, due to typically large fluctuations in group size between years, a characteristic of many cooperatively breeding species (Bateman *et al.* 2013), what size represents a ‘large group’ in absolute numbers in poor years may be a small group size in other years (Ridley & Huyvaert 2007; Bateman *et al.* 2013).

#### *Life history parameters*

A breeding attempt was considered to have occurred when at least one egg was observed to be laid in a nest, thus excluding events where some attempts to build a nest were made, but no further breeding activity occurred. In each breeding attempt we collected all available life history traits: number of eggs laid, number of nestlings hatched, number of fledglings fledged, number of young who survived their first year, emigration events (including the number of individuals emigrated in each event), and immigration events (including the number of individuals that immigrated in each event). We also noted brood overlap (defined as the presence of dependent young in the group when another breeding event is initiated, *sensu* (Ridley & Raihani 2008)).

#### *Statistical analysis*

Statistical analyses were conducted using IBM SPSS statistics version 21 and R version 2.15.3 (R core team 2013). To determine the terms influencing the initiation of breeding events, hatching success, survival to independence and group extinction, we conducted model selection using Generalized Estimating Equations (GEE). To determine the predictor terms influencing immigration and emigration, we used GEEs with a poisson distribution and a log link function. We compared candidate models using Corrected Quasi Likelihood under independence model criterion (QICc, Pan 2001)) using a binomial distribution and a logit link function. We considered that the model with the lowest QICc value provided the best fit to the data; and that all models with a QICc value that was 5 or more units higher than the ‘best model’ were considered an insufficient fit for further

interpretation. All candidate models were compared to the QICc of the basic model (a model that contains no predictor terms). If the basic model fell within the set of candidate models with QICc values  $< 5$  of the best model, we concluded that none of the terms tested had a significant influence on the distribution of data. When models scored within 5 QICc values of the best model, multi-model averaging was employed to determine significant variables (*sensu* Grueber *et al.* 2011). The best terms were checked for significance using 95% confidence intervals (CIs). A term was not considered a good predictor of data patterns unless its CI did not intersect zero (Burnham & Anderson 2002).

#### *Initiation of a breeding attempt*

To determine the parameters influencing the initiation of a breeding attempt (0= no breeding attempt, 1= breeding attempt initiated) we employed model selection as described above. We included group identity and the year in which the breeding attempt took place as random terms to account for the potential influence of repeated measures on the distribution of data. We used drought (yes or no) and rainfall (mm) as environmental predictors, and male: female ratio, reproductive competition (male or female competition, yes or no), group size, relative group size and group size squared (to check a quadratic effect) as social predictors of data patterns.

#### *Hatching success:*

To determine what terms affect hatching success (defined as the number of eggs successfully hatched per breeding event), we conducted model selection on binomial GEEs, with the number of nestlings that hatched from each brood as the dependent variable, and the total number of eggs in the clutch as the binomial denominator. All groups where either the number of eggs laid or the number of nestlings hatched was unknown during a specific breeding season were excluded from the analysis. We included group identity and the year in which the breeding attempt took place as random terms. We

used drought, heatwaves and rainfall (mm) as environmental predictors, male: female ratio, reproductive competition, group size, relative group size and group size squared (to check for a quadratic effect) as social predictors, and clutch number (representing number of previous breeding attempts by the group that season) and brood overlap (whether young from one or more previous breeding events in the same breeding season were present, yes or no) to check for reproductive factors influencing hatching success.

#### *Parameters influencing survival to adulthood*

To determine what terms affect survival to adulthood (defined as the survival from hatching to the end of the first year of life), we employed model selection using GEEs with a binomial distribution (where 0 = did not survive to end of first year, 1 = survived to end of first year) and a logit link function, with the number of individuals that survived from each brood as the dependent variable, and the number of nestlings that hatched as the binomial denominator. Although we didn't have an exact record for each individual death, we treated all individuals that disappeared from our study site before the end of their first year of life as though they didn't survive. Previous research on Arabian babblers found that individuals reach maturity only after their first year of life and that both dispersal events and reproductive success are extremely rare in sub-adults (Zahavi 1989, 1990; Zahavi & Zahavi 1997). to verify this we further analysed our data and found that the earliest age for an individual to attain a dominant position over 35 years of research was 338 days, and that the few dispersal events we found during the first year of life were always to a neighbouring group, and involved the young joining an adult individual from their natal group. Thus, we do not think it likely that we misclassified some individuals as dead when in fact they dispersed outside our study site. All groups where the number of nestlings that hatched was unknown were excluded from the analysis. We included the breeding year and group identity as random terms.

We used drought and rainfall (mm) as the environmental predictors, male:female ratio, reproductive competition (male and female, yes, no), group size, relative group size and group size squared (to check for a quadratic effect) as social predictors, and clutch number (representing number of previous breeding attempts by the group that season), and brood overlap (whether young from one or more previous breeding events in the same season were present, yes or no) to check for reproductive factors influencing survival to adulthood.

*Parameters influencing changes in annual adult group size*

To determine factors aside from juvenile survival to adulthood that may affect changes in group size between years, we analysed the factors affecting annual adult group size via emigration and immigration events. We conducted separate analyses for immigration and emigration events. For every year, we calculated the number of adult individuals who immigrated into the group or emigrated from it. All other changes in group size were excluded, as were all emigration or immigration events that were for a period of less than 30 days (i.e. the individual left the group it joined or returned to the group it left). A group that had no immigration or emigration event during the focal year was scored as zero. We used GEE with a poisson distribution and a log link function to test the effect of different parameters on immigration and emigration. Breeding year and group identity were included as random terms. We used drought and rainfall (mm) as the environmental predictors, and group size, relative group size and group size squared as social predictors.

*Parameters influencing group extinction*

We used model selection of GEEs with a binomial distribution and logit link function to determine the factors that affect the likelihood of groups going extinct on a per year basis. Each group was given a 0 or 1 for each year that the group was observed, where 0 = not extinct, 1 = extinct. A group that went extinct could not reappear in the database as extant



the following year. We defined a group as extinct when all individuals had dispersed or disappeared and repeated investigations found no further evidence of the group. All of the groups in our study population were observed at least once every two weeks, and all territories are located in places that are still monitored to this day. Thus, we do not think it likely that we misclassified some groups as extinct that were in fact still extant but had changed territory slightly. Arabian babblers are both poor fliers and highly territorial (Zahavi & Zahavi 1997). When a group goes missing, we search extensively for them well beyond their territory borders on repeated occasions. We included group identity and year as random terms.

We used drought and rainfall (mm) as the environmental predictors, male: female ratio, reproductive competition, group size, relative group size and group size squared, as social predictors, and both clutch number and the number of young that survived to adulthood to check for reproductive factors influencing extinction.

*Mayfield's survival probability:*

We calculated the Mayfield's survival probability (Mayfield 1961) for young at three different developmental stages: incubation, nestling and overall (from incubation until fledging). We considered the period over which survival probability could be considered started from the day the last egg was laid (Arabian babblers incubate synchronously, (Zahavi 1990). We used 14 days as the incubation period and 15 days as the nestling period (from hatching to fledging, *sensu* Ostreiher 1999). All breeding attempts that were observed only once or for which subsequent observation dates weren't known from database records were excluded from analysis.

## 6.4 Results

Overall, we had data available from 684 breeding attempts (where at least one egg was laid) from 43 groups spanning the years 1978-2013. Adult group size ranged from 2-14, with an average group size of  $4.95 \pm 0.35$  (SE).

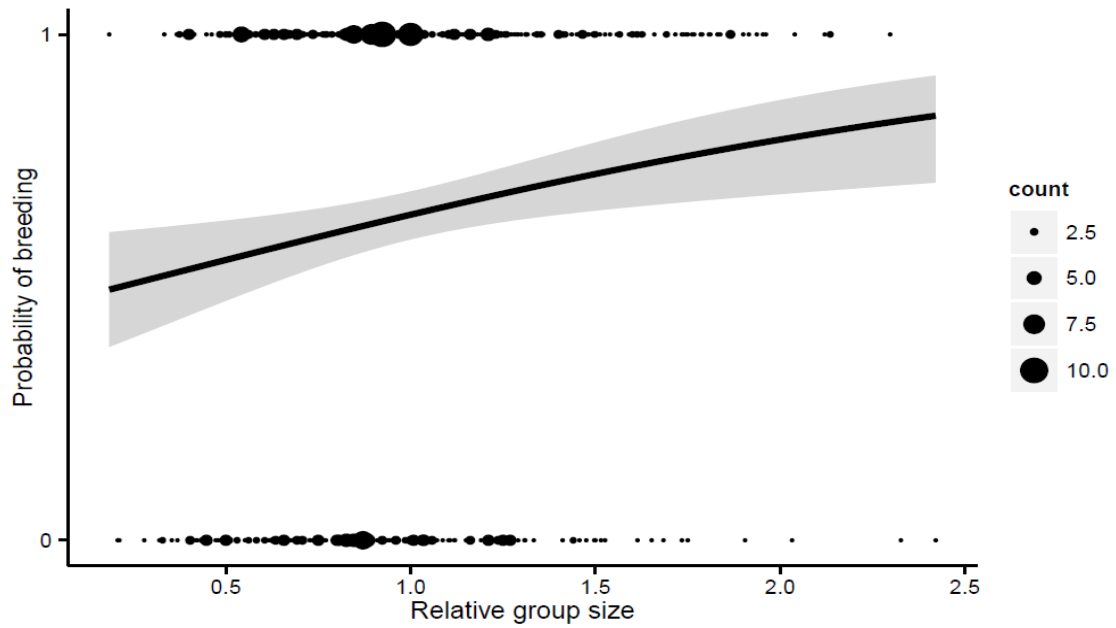
### *Initiation of breeding attempt*

In total, we analysed breeding attempts over 660 group-years, between the years of 1978-2013. On average, there were  $1.93 \pm 0.38$  (SE) breeding attempts/breeding season/group, ranging from no breeding attempts to four attempts per group per year.

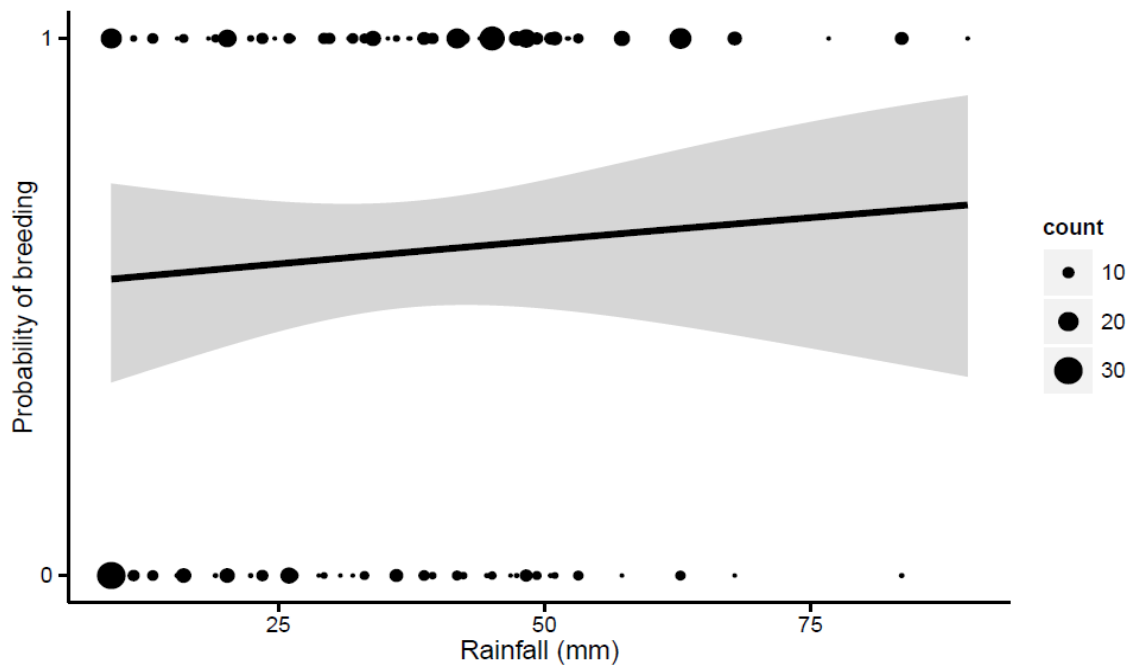
Rainfall and relative group size were the main factors affecting the initiation of a breeding attempt (Table 6.1). Initiation of breeding was more common when rainfall was high (Figure 6.1a). In addition, those groups that were on average larger than other groups in the population were more likely to initiate breeding attempts (Figure 6.1b). Relative group size was a better predictor of the initiation of breeding than absolute group size (Table 6.1)

**Table 6.1:** Top model set (QICC) of the terms influencing initiation of breeding. Group identity and breeding year were included as random terms. Data is based on 660 breeding years of 43 groups over the time period spanning 1978-2013. Only models with  $\Delta QICC < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICC	$\Delta QICC$	Weight
Basic	3	663.03	99.9	
Rainfall+	5	565.6	2.5	0.227
Absolute adult group size				
Rainfall +	5	563.1	0	0.773
Relative group size				
Parameter	Estimate	SE	Low 95% CI	High 95% CI
Rainfall	-0.06	0.007	-0.08	-0.05
Relative Group size	-0.8	0.28	-1.3	-0.2
Absolute adult group size	0.3	0.16	-0.1	0.4



**Figure 6.1a: Figure 1a:** The relationship between relative group size on the initiation of at least one breeding event during each year. N=660 group years of 43 groups. Grey area represents confidence intervals (Ci), thickness of dots represents the number of observations. The line of best fit is generated from the predictions of the top model presented in Table 1



**Figure 6.1b:** The relationship between annual rainfall and the initiation of at least one breeding event during each year. N=660 group years of 43 groups. Grey area represents confidence intervals (Ci), thickness of dots represents the number of observations. The line of best fit is generated from the predictions of the top model presented in Table 6.1

*Hatching success:*

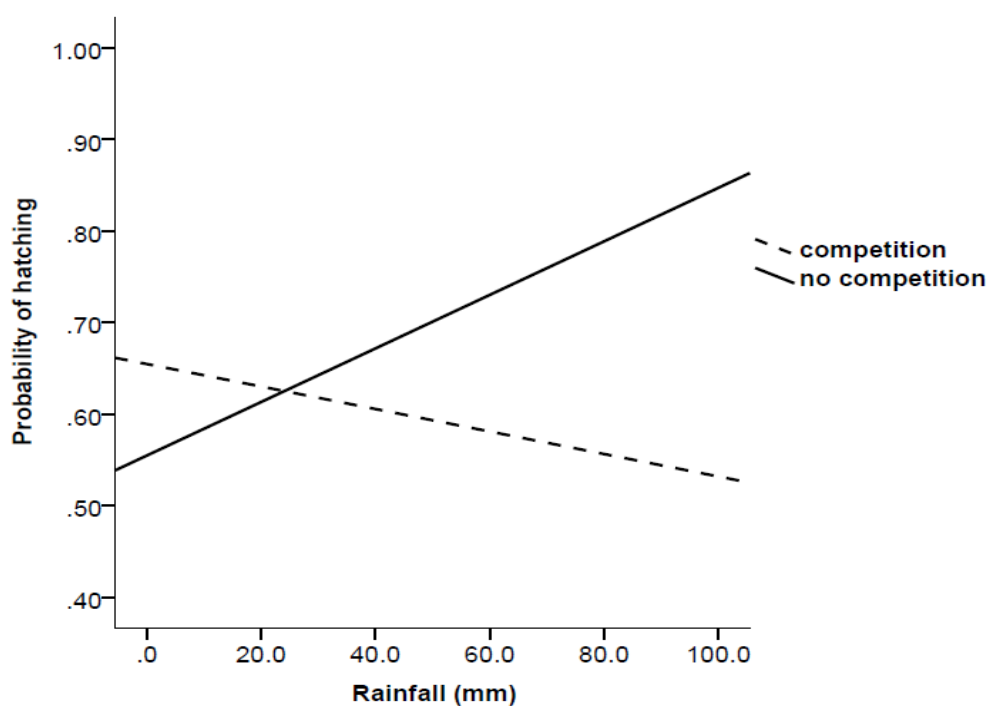
In total, we analysed the hatching success of 684 breeding attempts in 43 groups. Average clutch size per breeding attempt was  $3.58 \pm 0.04$  (SE) eggs, ranging from 1-12 eggs per attempt. The average number of nestlings that hatched per attempt was  $2.44 \pm 0.05$  (SE), ranging between 0-7 nestlings. The Mayfield probability for daily survival during incubation was 0.683 (Table 6.7).

Rainfall was a significant predictor of hatching success, but this varied according to the presence of within-group female reproductive competition (Table 6.2). When there was no intragroup female competition, hatching success was greater when rainfall was higher (Figure 6.2). However, this effect of rainfall was nullified when competing females were present (Figure 6.2).

When comparing Mayfield nest survival probability until hatching in rainy years vs drought years, survival probability was slightly higher in rainy years (0.693 vs 0.6040 than during drought years, Table 6.7).

**Table 6.2:** Top model set (QICc) of the main terms influencing hatching success. Group identity and breeding year were included as random terms. Data is based on 684 breeding attempts from 43 groups over the time period spanning 1978-2013. Only models with  $\Delta QICc < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICc	$\Delta QICc$	Weight
Basic	3	8664.98	362.58	
Rainfall* Female competition	5	8302.4	0	1
Parameter	Estimate	SE	Low 95% CI	High 95% CI
<b>Rainfall</b>				
-Female competition present	-0.002	0.004	-0.009	0.006
-Female competition absent	0.01	0.003	0.18	0.73



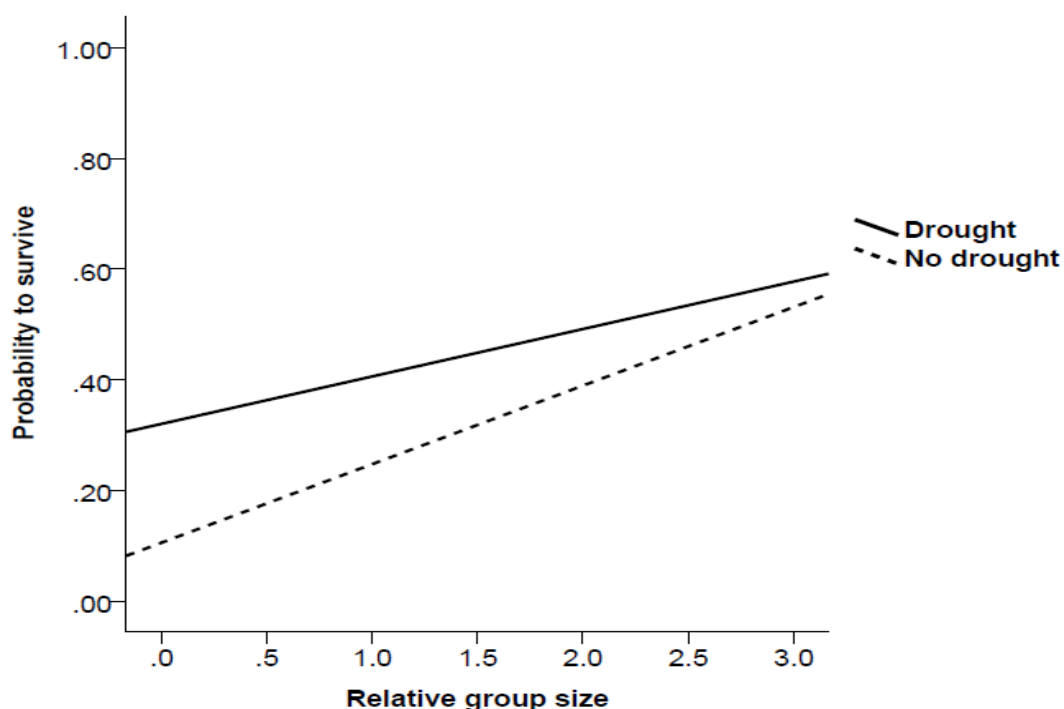
**Figure 6.2:** The relationship between annual rainfall (mm) and the hatching probability (number of nestlings hatched/number of eggs laid) according to the presence of intragroup female competition. N= 684 breeding events from 43 groups. The line of best fit is generated from the predictions of the top model presented in Table 6.2

### *Survival to adulthood:*

In total, we were able to analyse the survival of fledglings until adulthood in 504 breeding attempts that successfully hatched at least one nestling in 42 groups. The average number of nestlings per attempt was  $3.15 \pm 0.04$  (SE), ranging between 1-7 nestlings per attempt. Fledgling survival ranged between 0-5 individuals per attempt with an average of  $1.25 \pm 0.052$  (SE) fledglings survived per brood. Relative group size significantly affected survival (Table 6.3), with young more likely to survive to adulthood in groups that were larger than the population average. However, this effect was only during non-drought years, with no influence of relative group size on offspring survival during drought years (Figure 6.3). There was no influence of absolute group size on survival to adulthood. When considering only the period between hatching and fledging, Mayfield survival probabilities for fledging success (chances for hatched young to survive to fledging) for drought versus rainy years was 0.694 and 0.867 consecutively (Table 6.7).

**Table 6.3:** Top model set (QICc) of the terms influencing survival of young to first year. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold. Data is based on 504 breeding attempts from 42 groups over the time period spanning 1978-2013. Only models with  $\Delta QICc < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICc	$\Delta QICc$	Weight
Basic	3	3210.08	74.32	
<b>Relative group size* Drought</b>	5	3135.76	0	1
Parameter	Estimate	SE	Low 95% CI	High 95% CI
<b>Relative group size</b>				
-Drought	-0.05	0.14	-0.34	0.23
<b>-No drought</b>	<b>0.45</b>	<b>0.14</b>	<b>0.17</b>	<b>0.72</b>



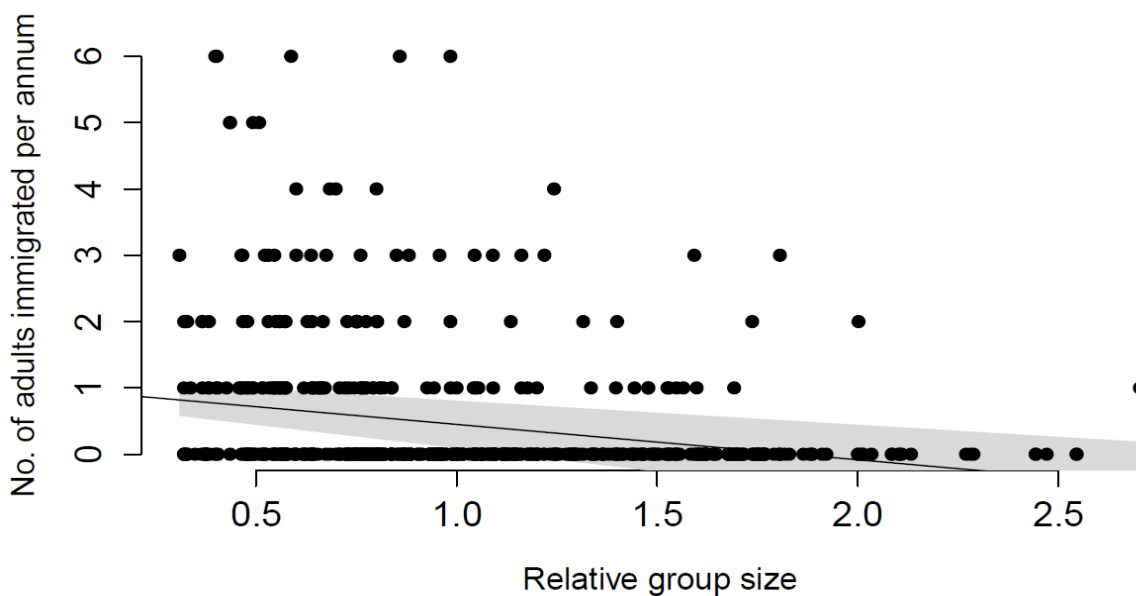
**Figure 6.3:** The relationship between relative group size and the survival rate of fledglings to adulthood during drought and non-drought years. N=504 successful breeding attempts (attempts that hatched successfully) from 42 groups. The line of best fit is generated from the predictions of the top model presented in Table 6.3

#### *Changes in adult group size*

We analysed a total of 618 group years. Immigration ranged from 0-6 adult individuals joining the focal group each year, and 0-7 individuals emigrating from the focal group in an event. Relative group size was the best predictor for immigration events where immigration events happened primarily in groups that were smaller than the population average (Table 6.4, Figure 6.4). Total adult group size was the only factor affecting emigration from the group, where emigration was primarily observed in large groups (Table 6.5, Figure 6.5)

**Table 6.4:** Top model selection (QICc) of the main terms influencing immigration to the group. Group identity and breeding year were included as random terms. Data is based on 618 group years from 43 groups over the time period spanning 1978-2013. Only the models with  $\Delta QICc < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICC	$\Delta QICC$	Weight
Basic	3	893.4	95.34	
Absolute adult group size	4	800.28	2.22	0.25
Relative group size	4	798.06	0	0.75
Parameter	Estimate	SE	Low 95%Ci	High 95%Ci
Relative group size	-1.6	0.28	-2.1	-1.06



**Figure 6.4:** The relationship between relative group size and the number of adults immigrating into established groups per annum. N=618 group years from 43 groups. Grey area represents confidence intervals (Ci). The line of best fit is generated from the predictions of the top model presented in Table 4

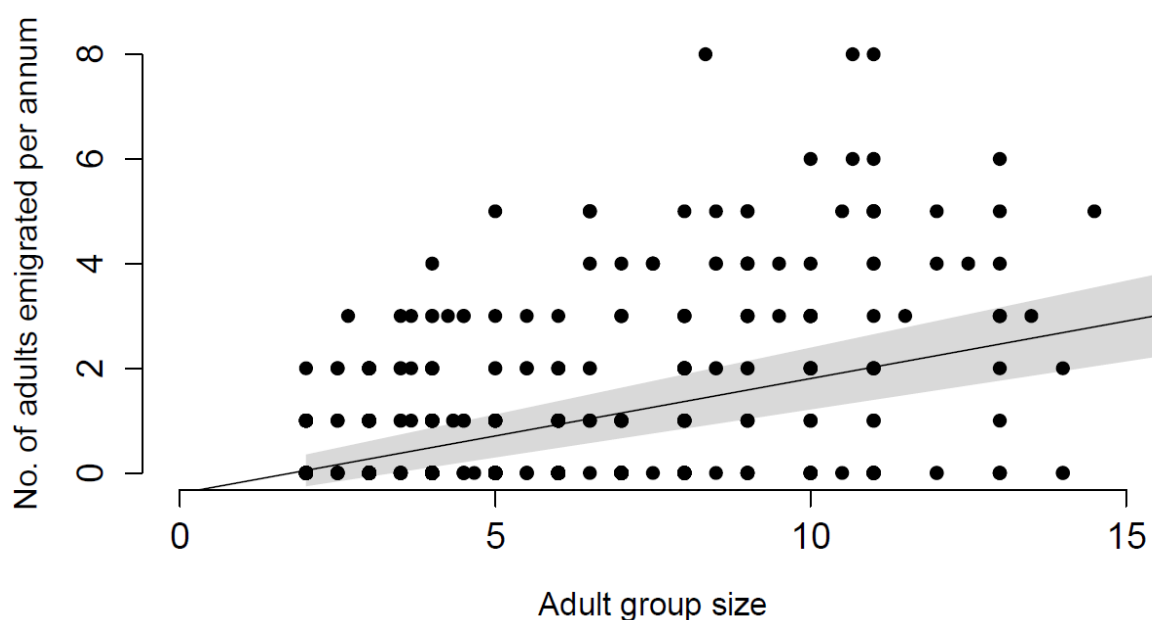


**Table 6.5:** Top model selection (QICc) of the main terms influencing emigration from the group. Group identity and breeding year were included as random terms. Data is based on 618 group years from 43 groups over the time period spanning 1978-2013. Only the models with  $\Delta QICc < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICc	$\Delta QICc$	Weight
Basic	3	1208.67	228.53	
Absolute adult group size	4	980.14	0	1

Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
Absolute adult group size	0.2	0.01	0.17	0.23



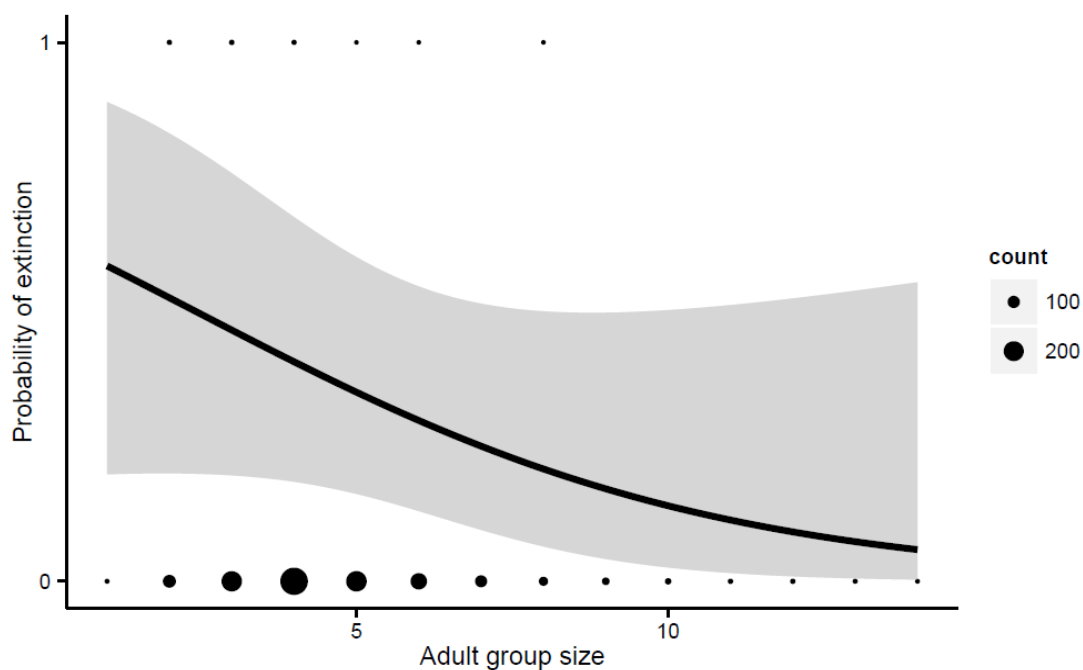
**Figure 6.5:** The relationship between absolute adult group size and the number of adults emigrating from the group per annum. N=618 group years from 43 groups. Grey area represents confidence intervals (Ci). The line of best fit is generated from the predictions of the top model presented in Table 5

*Parameters influencing likelihood of group extinction:*

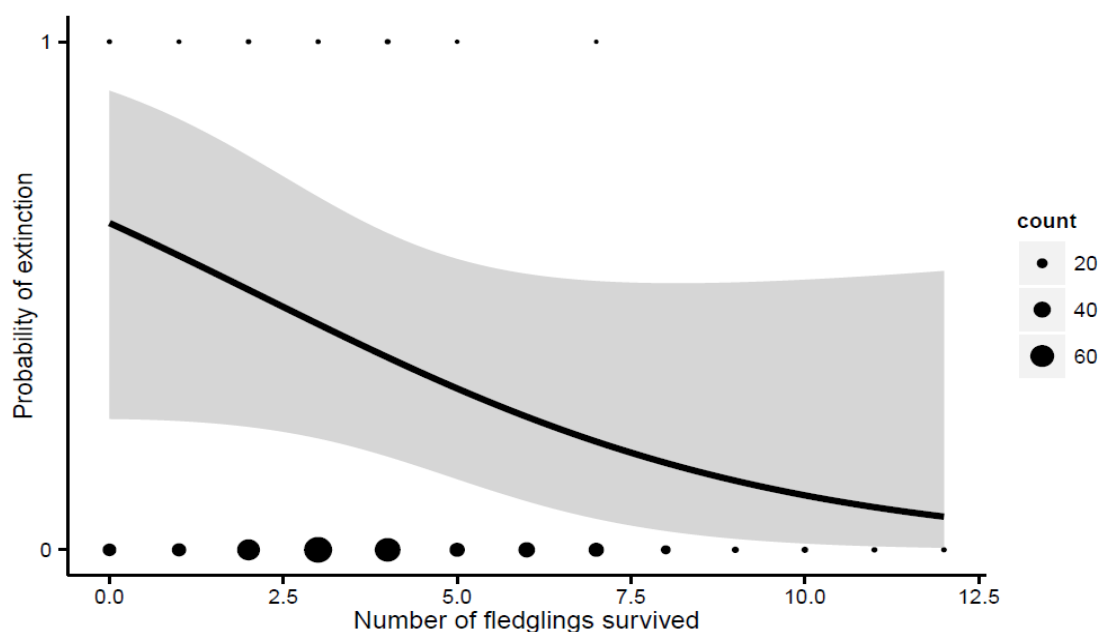
Over 660 group-years, we observed 36 group extinction events. Group size was an important predictor of the likelihood of a group going extinct, with smaller groups facing a higher probability of going extinct (Table 6.6, Fig 6.6a) The total number of young fledged per annum was also an important parameter influencing extinction (Table 6.6), with groups that fledged fewer young more likely to become extinct (Figure 6.6b). There was no effect of climatic factors on the likelihood of a group going extinct (Table 6.6).

**Table 6.6:** Top model selection (QICC) of the main terms influencing the likelihood of group extinction on an annual basis. Group identity and breeding year were included as random terms. Data is based on 660 group years from 43 groups and 36 extinction events over the time period spanning 1978-2013. Only models with  $\Delta QICC < 5$  are shown; a complete set of candidate models, as well as the basic model, are presented in the appendix.

Model	K	QICC	$\Delta QICC$	Weight
Basic	3	101.93	11.07	
Absolute adult group size+	5	90.86	0	1
Number of fledglings				
Parameter	Estimate	SE	Low 95% Ci	High 95% Ci
Absolute adult group size	0.56	0.27	0.04	1.08
Number of fledglings	0.34	0.14	0.07	0.6



**Figure 6.6a:** The relationship between absolute adult group size on extinctions event (0=no, 1=yes). N= 36 extinction events from 660 group-years for 43 groups. Grey area represents confidence intervals (Ci), thickness of dots represents the number of observations. The line of best fit is generated from the predictions of the top model presented in Table 6



**Figure 6.6b:** The relationship between the number of fledgling survived from the last breeding season on extinctions event (0=no, 1=yes). N= 36 extinction events from 660 group-years for 43 groups. Grey area represents confidence intervals (Ci), thickness of dots represents the number of observations. The line of best fit is generated from the predictions of the top model presented in Table 6

**Table 6.7:** Mayfield probabilities of nest survival for Arabian babblers during drought years and rainy years on the Shezaf nature reserve. Probabilities (P) of nest survival for  $P_i$  = incubation,  $P_n$  = nestling, and overall nest survival from incubation to fledging ( $P_{total}$ ).

period	Number of years	Nests	$P_i$	$P_n$	$P_{total}$
Droughts	11	113	0.604	0.694	0.419
Non-drought	24	573	0.693	0.867	0.606
Total	35	686	0.683	0.85	0.58

## 6.5 Discussion

Our results have revealed an important influence of both environmental and social factors on group dynamics. The effect of rainfall, although consistent and positive with respect to reproductive success traits, did not explain the observed changes in adult group size (immigration, emigration), nor did it affect the likelihood of a group's extinction. In comparison, social factors had a more consistent influence on the group-level demographic traits we measured. Group size and relative group size had an effect on the initiation of breeding, survival of young to adulthood, changes in adult group size, and group extinction, but no effect on the hatching success of young. Within-group female competition had a negative effect on hatching success when conditions were favourable (i.e. rainfall was high), but no effect on any other group-level demographics. This finding that all changes in adult group size that we measured are directly influenced by social but not environmental factors suggests that social factors play an important role in group dynamics in the Arabian babbler. These results support the findings of Ostreiher, Pruett-Jones & Heifetz (2012) who found that differences in breeding success between nests depend on social interactions within the group rather than food availability.

The ecological constraints hypothesis (Emlen 1982), and the benefits of philopatry hypothesis (Stacey & Ligon 1991) explain the evolution of cooperative breeding through the costs that an individual may face by trying to survive and reproduce outside of the

social group, and the benefits it gains from delayed dispersal and/or group-living behaviour (Hatchwell & Komdeur 2000). The interplay between these costs and benefits is predicted to determine the level of cooperation and conflict within the group. Our results suggest that individuals will benefit the most from group-living when their group size is large relative to the size of other groups in the population. Group size may improve reproductive success either through an increase in the number of helpers who supply more food to young (Emlen *et al.* 1991; Cockburn 1998; Clutton-Brock, Russell & Sharpe 2001; Ridley 2007; Covas, du Plessis & Doutrelant 2008) or by a larger number of individuals that can maintain a high quality territory and protect against neighbouring groups, intruders and (Kokko *et al.* 2001; Duca & Marini 2014). The fact that relative group size was a better predictor than absolute group size for the initiation of breeding, offspring recruitment rates and adult immigration rates, suggests that the number of individuals available to defend the territory against other groups and predators is more important than feeding at the nest alone. Ridley & Huyvaert (2007) found that Arabian babblers are sensitive to relative group size and preferentially invest in feeding male offspring (the philopatric sex) when their group size is relatively smaller than neighbouring groups. This study therefore confirms the importance of relative group size when considering social influences on within-group dynamics. The benefits of group-living may therefore be reduced when the size of the group an individual inhabits is relatively smaller than surrounding groups.

Our finding that immigration occurs more often in relatively small groups may suggest that when group size decreases to a level at which the benefits of group-living are reduced, small groups are more sensitive to invasion by individuals from neighbouring groups, or may accept extra-group individuals and the consequent reproductive competition that may occur as a result. Models of reproductive skew predict that under certain conditions, dominant individuals are more willing to share reproduction with subordinates in order to retain them in the group (Keller & Reeve 1994). Therefore, it is possible that when group

size decreases below a certain threshold, dominant individuals will accept extra-group individuals in order to maintain group size and prevent group extinction as a consequence. This was shown recently by Korb & Roux (2012) who discovered that small colonies of the termite *Cryptotermes secundus* fused with other small colonies in order to increase their survival. Our finding that more individuals emigrate from larger groups may be explained by the social queue and the consequent costs versus benefits of remaining in the group. Kokko & Johnstone (1999) suggested that the benefits of group-living are reduced when the social queue is longer. In these cases, subordinate individuals who are at the end of the queue are more likely to emigrate in order to improve their chances for future reproduction. This idea was further supported by Shreeves & Field (2002) who both modelled and showed empirically that a subordinate's tendency to help will be reduced if their chance to inherit the breeding position is low due to a long social queue. Group-living benefits may be reduced in larger groups not only due to an extended social queue, but also by scramble competition over reproduction or food resources (Cant & English 2006; Orbach, Packard & Würsig 2014; Balasubramaniam *et al.* 2014). The fact that immigration was influenced by relative group size while emigration was influenced by total adult group size emphasizes the need to consider both of these values, since it reveals how relatively smaller groups are more sensitive to invasion by individuals from neighbouring groups, while large groups are more sensitive to within-group competition.

Intragroup reproductive competition has been increasingly recognised as an important factor affecting group dynamics (Hodge *et al.* 2008, reviewed by Nonacs & Hager 2011). For example, Nelson-Flower *et al.* (2013) revealed that egg-breaking between within-group female competitors was an important cause of reduced reproductive success in the pied babbler. Egg-breaking behaviour has also previously been observed in the cooperatively breeding Acorn woodpecker (Koenig *et al.* 1995) and in our own research population of Arabian babblers (Zahavi 1990). Our long-term analysis of hatching success

has revealed that hatching success increases during years with high rainfall, but within-group female competition depresses this effect. During high rainfall years, groups with female competition did not experience significant increases in hatching success, in contrast to groups where female reproductive competition was absent. This confirms that competing females negatively impact group reproductive success in Arabian babblers, and is consistent with the findings for other cooperative breeding species mentioned above, providing further support for the idea that intragroup competition is an important parameter to measure in group demographic studies.

Rubenstein & Lovette (2007) suggested that cooperative breeding is an adaptation to habitats with temporally variable environments, since it allows for successful reproduction during harsh years. This hypothesis was further developed by Jetz & Rubenstein (2011) and was supported empirically (Covas *et al.* 2008; Ebensperger *et al.* 2014). Our results, however, did not support the predictions of Rubenstein & Lovette (2007). In Arabian babblers, we found that larger groups have higher survival rates of young than smaller groups only in non-drought years, i.e. when ecological conditions are good. Nevertheless, our finding that adult group size buffers against group extinction, leads us to suggest that group-living buffers against environmental uncertainty not only through load lightening, but also in the form of enhanced benefits to adults, via mechanisms such as defending high quality territories (Golabek, Ridley & Radford 2012; Mares, Young & Clutton-Brock 2012) and protection against predators (Beauchamp 2014). This is in line with the findings of (Angulo *et al.* 2013) who found that pack size in wild dogs (*Lycaon pictus*) acts as a buffer against group extinction, with larger packs less likely to go extinct.

Our long-term database and extensive analysis has enabled us to consider the relative influence of several environmental and social factors on group dynamics in cooperatively breeding Arabian babblers. Our findings lead us to suggest that a greater consideration of

social factors, and in particular how they affect group dynamics in comparison to environmental factors, is an important consideration in studies aiming to understand the factors influencing group dynamics in cooperative breeders. In addition, we suggest that a consideration of group size relative to the size of other groups in the population is an important consideration, not simply absolute group size. This is because the size of neighbouring groups, and thus their ability to appropriate a territory from the focal group, may be an important factor influencing reproductive success, and should be considered alongside other parameters potentially influencing group dynamics.

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## 7. Long-term population analysis reveals the presence of group and demographic Allee effects on a cooperatively breeding bird species.

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Co- authored by: Amanda R. Ridley

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## 7.1 Abstract

In population dynamics, inverse density dependence can be manifested by individual fitness traits (component Allee effects), and population-level traits (demographic Allee effects). Cooperatively breeding species are an excellent model for investigating the relative importance of component and demographic Allee effects, because populations are structured into groups of varying sizes. Allee effects in these societies can arise because there is a disproportionately larger benefit to an individual of being part of a large group, due to effects such as greater survival, cooperative hunting, effective territory defence, and lower parental investment costs. Although small populations of cooperative breeders may be particularly prone to Allee effects, empirical evidence for the existence of Allee effects are scarce. In order to determine the extent to which Allee effects are present in a cooperatively breeding species, we used a 35-year comprehensive life history database for cooperatively breeding Arabian babblers (*Turdoides squamiceps*). Firstly, we confirmed the existence of a component Allee effect by showing that individuals in large groups receive greater benefits than those in small groups, and that smaller groups are more prone to extinction. Secondly, we identified a demographic Allee effect by showing that population growth is affected by population density. Surprisingly, population growth rate was more influenced by group density at the study site than by individual density. This suggests that while individuals are vulnerable to component Allee effects, the group could act as a buffer against population fluctuations, since individual fitness and group fate depend on group size but not on population size. By presenting population dynamics over time, we suggest causes for the observed demographic Allee effect, and how it may eventually lead to group and component Allee effects.



## 7.2 Introduction

A positive increase in individual fitness with population size or density is known as *inverse density dependence*, or an Allee effect (named after the pioneering American ecologist Warder Clyde Allee who was the first to describe them; [1]. According to this effect, more individuals in a population will result in higher fitness per individual, until negative density dependence effects (such as competition over reproduction or resources) will take place. An Allee effect could influence small populations by several mechanisms (reviewed by [2–5]. These mechanisms include mate limitation [6], inbreeding depression [7], higher per capita risk of predation [8] and higher vulnerability to both environmental stochasticity and genetic drift [7]. The relative strength of the Allee effects affecting individual fitness components will determine the overall influence of Allee effects on the population [4]. Therefore, Stephens & Sutherland [3] suggested that in order to better study Allee effects in animal populations, it would be useful to distinguish between component Allee effects, which are manifested by individual fitness traits (increased individual fitness with population size), and demographic Allee effects, which are manifested by the level of total fitness represented by population growth rate in relation to population size.

Cooperatively breeding species, where more than two individuals help care for the young raised from a single brood (reviewed in [9–11]) may be particularly sensitive to Allee effects [12,13]. This is because in cooperatively breeding species, and particularly in obligate cooperative breeders, individual survival and reproduction are strongly affected by group size, with larger groups providing increased benefits to individuals such as lower costs of parental care [14–17], increased predator vigilance [18–21], better access to food resources [22] and better access to dispersal opportunities [23]. A group that decreases in size may therefore be more likely to suffer a further decrease, or even become extinct [12,24]. Courchamp et al. [12] have suggested that these high extinction rates for small cooperatively breeding groups are due to the existence of a lower threshold of group size,

beneath which the benefits of group-living will be reduced to a point that will generate a component Allee effect, (leading to lower individual survival and reproductive success), from which a group may no longer be able to recover.

Although the presence of component Allee effects has previously been demonstrated in several cooperative breeders, there has thus far been very little evidence for demographic Allee effects [25,26], and none in cooperatively breeding birds. One explanation for the scarcity of evidence may be because Allee effects in one component of fitness (such as reproductive success) may be offset by increases in other components of fitness (such as an increase in group size through immigration events), thus creating a weak Allee effect that doesn't reach the population threshold [25,26]. For example, Bateman et al [27] suggested that in cooperative breeders, component Allee effects may not translate to an effect at the population level because group growth rates are asynchronous with population growth rates, resulting in different factors influencing group and population dynamics. Similarly, Angulo et al [24] suggested that since individual fitness is more dependent on group dynamics than overall population size, the group should be considered an independent level of organization, and therefore the concept of a 'group Allee effect' should be considered in order to better understand inverse density dependence in cooperative breeders.

In this paper we use an extensive long-term dataset covering 35 years of continuous research on cooperative Arabian babbler groups (*Turdoides squamiceps*) to test for evidence of demographic, group and component Allee effects. We aim to (1) investigate the existence of component Allee effects by testing whether individual annual reproductive success (ARS) is influenced by group or population size, (2) determine the existence of a group Allee effect by testing whether group dynamics (i.e. group lifespan and extinction probability) are affected by group or population size, and (3) test for evidence of a

demographic Allee effect by examining whether population per capita growth rate is affected by population or group density. If inverse density dependence does occur in the population, we expect that reproductive success, group lifespan and population growth rate should increase with either group or population size or density.

In the past two decades there has been a considerable increase in human activity around our study site, resulting in extensive development of roads, farmland and human settlement. This has led to considerable habitat loss for Arabian babblers [28,29]. We believe that identifying the factors causing Allee effects in the study population may have important implications for future conservation decisions regarding habitat loss and human development in the region.

### **7.3 Materials & methods**

#### *Study site and population:*

Our study was conducted in the Negev desert, south-east Israel (30°48'N, 35°13'E), at the Shezaf Nature Reserve, a 40 km<sup>2</sup> protected wildlife area in the Arava region surrounded by approximately 20 km<sup>2</sup> of farmland. The habitat is defined as hyper-arid desert (rainfall <50mm per annum, UNESCO 1977). A long-term research project on the ecology of the cooperatively breeding Arabian Babbler has been continuously conducted in the area since 1971 by Profs Amotz & Avishag Zahavi [30–32]. Each individual in the population is ringed with a unique combination of one metal and three coloured rings, and all individuals are habituated to human presence (for a description of habituation, see [17,32,33], allowing close-range observations.

Arabian babblers are a group-territorial, cooperatively breeding bird species with age-related linear dominance hierarchies within each sex class [30,31], Chapters 5 and 6 in this thesis). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to the dominant pair may gain reproductive

success on rare occasions (less than 5% of breeding attempts, [34]). Groups differ in their size (ranging from three -20 adults). Groups are highly territorial year-round. The breeding season usually starts around the end of February and continues until July [30,31]. Only one nest is incubated at a time, and usually all adult group members help in raising young [33]. Juveniles are considered adults when they reach 12 months old. At about this age it is possible to discriminate between the sexes through sexual dimorphism in beak shape and sexual dichromatism in eye colour [33,35]

### *Data collection*

We used data that was continuously collected on cooperative groups of Arabian babblers between 1978 and 2013. During this period, all groups were visited at least once every month outside the breeding season, and at least once a week during the breeding season to monitor group size and composition. We extracted and cross-examined the data from different sources (a Microsoft Access database, field notes and large cardboard datasheets). This resulted in a data set comprising 79 different groups and totalling 908 group-years. For the analysis of group extinction and annual reproductive success we only used groups that had a complete group history in all three sources, resulting in data set comprising 43 groups. We extracted the size of each group at the last observation in December of each year: we chose this date because breeding activity is typically absent in December [30,31], but the juveniles from the previous breeding season have reached nutritional independence and participate in all group activities. Weather data was collected from the long-term databases of the Israeli Meteorological Service (IMS) using the weather stations based close to the study site (within 10 km) in the villages of Hazeva, Ein Yahav and Sappir. We measured annual rainfall between the months of August of consecutive years to encompass all rainfall events prior to and during the breeding season (since no rainfall occurs during the summer months). We followed the IMS definition of drought as any year where the

rainfall was 75% or less than the average annual rainfall. The average annual rainfall for the study site is 30.6 mm (calculated from local weather station data for the past 35 years).

### *Data analysis*

Statistical analyses were conducted using IBM SPSS statistics version 22 and R version 2.15.3 [36]

We calculated the geographical area that the entire study population occupied for every year (defined as the areas in which established groups were present and regularly observed), using Google Earth version 7.1.2 and GEPATH 1.4.6). We determined group and population density by dividing total area by group number and total population size. To test for demographic Allee effects, we calculated the population per capita growth rate (PCG) which is the number of individuals per km<sup>2</sup> in year t+1 divided by the number of individuals per km<sup>2</sup> in year t, this factor was calculated as the natural logarithm ( $[\ln(n_{t+1} / n_t)]$ , *sensu* [37]). We then used Generalized Linear Models (GLMs) to measure PCG against population density (number of groups and individuals per km<sup>2</sup>). We compared candidate models using Akaike's Information Criterion corrected for small sample size (AICc, [38]). We considered that the model with the lowest AICc value provided the best fit to the data; models with an AICc value of 5 or more than this best model were considered an insufficient fit for further interpretation. Candidate models were compared to the AIC basic model (with no predictors). If candidate models did not have AICc values > 5 lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data. When models scored within 5 AICc units of the best model, multi-model averaging was employed to determine significant variables (*sensu* [39]). The best terms were checked for significance using 95% confidence intervals (CI). A term was not considered a good predictor of data patterns if its CIs did intersect zero [38]

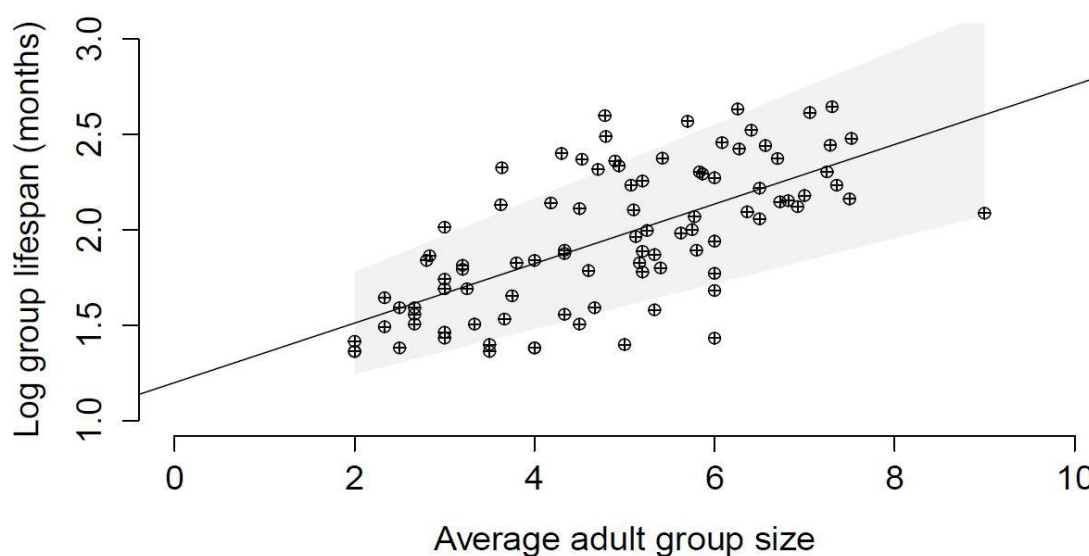
To test for component Allee effects we first plotted the effect of group size on group lifespan (log transformed to achieve normality) using linear regression. We then measured the effect of group size and group and population density on annual reproductive success (ARS) for breeding individuals, and the probability of group extinction. To do that we used General Estimating Equations (GEEs) with a binomial or Poisson distribution. We compared candidate models using Corrected Quasi Likelihood under independence model criterion (QICc, [40]). We considered that the model with the lowest QICc value provided the best fit to the data; and that all models with a QICc value that was 5 or more units higher than the 'best model' were considered an insufficient fit for further interpretation. All candidate models were compared to the QICc basic model (with no predictors). If candidate models did not have QICc values  $> 5$  lower than the basic, we concluded that none of the terms tested had a significant influence on the distribution of data. A trait was considered to be influenced by a group Allee effect when it was positively influenced by an increase in group size and influenced by demographic Allee effect if it was positively influenced by an increase in group or population density (*sensu* [13,24]).

To test our assumption that habitat loss and climate change has resulted in a decline in individual reproductive success and population distribution in the region over the past 35 years (1978-2013), we plotted environmental variables (rainfall), individual and group variables (dominant individual ARS, average group size) and population variables (number. of groups per km<sup>2</sup>) against the years of research. We used linear regressions to test for any significant decrease in these variables over time (*sensu* [41]).

## 7.4 Results

### *Population and group characteristics*

Group size ranged from 3-17 individuals with an average ( $\pm$ SE) of  $5.54 \pm 0.3$  adult individuals per group. Group lifespan ranged from 3-35 years with an average  $7.3 \pm 0.71$  years and was significantly affected by group size ( $F=68.22$ ,  $R^2=0.43$ ,  $p<0.0001$ ; Figure 7.1). Yearly group density per  $\text{km}^2$  ranged from a minimum of 0.31 groups/ $\text{km}^2$  in 2012 to a maximum 0.73 groups/ $\text{km}^2$  in 1988, with an average of  $0.54 \pm 0.02$  groups/ $\text{km}^2$ . Yearly population size ranged from a minimum of 1.25 individuals/ $\text{km}^2$  in 2012 to a maximum of 5.62 individuals/ $\text{km}^2$  in 1986, with an average  $3.09 \pm 0.21$  individuals/ $\text{km}^2$ .



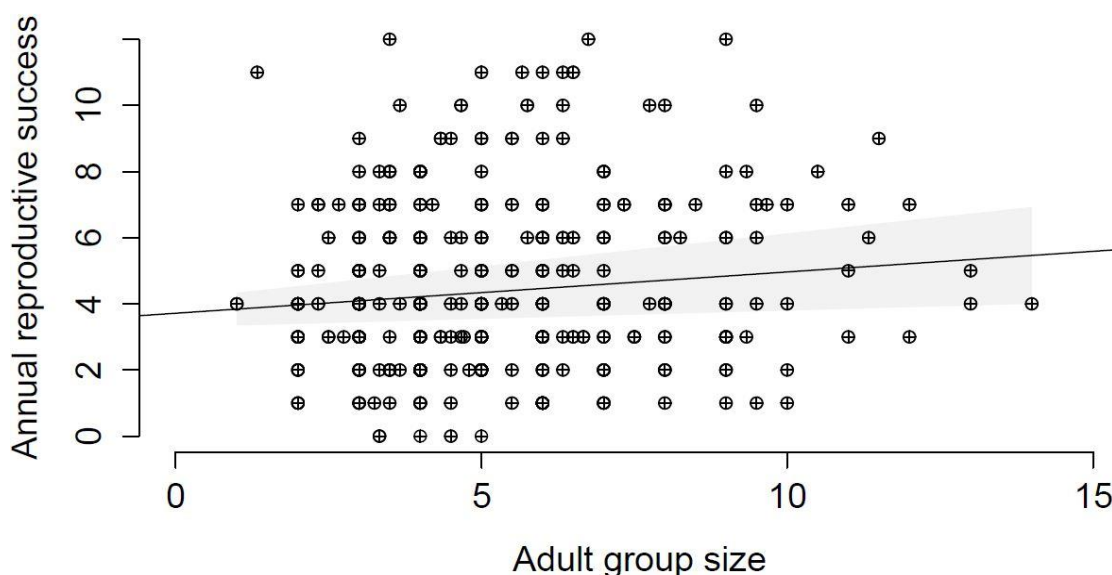
**Figure 7.1:** The relationship between adult group size and group lifespan (log-transformed; months)  $n=908$  group years from 79 groups. Grey area represents confidence intervals (Ci)

### Allee effects

We found that group size, but not population size or group density, had a positive influence on individual ARS in both drought and non-drought years, although ARS was lower during drought years for all group sizes (Table 7.1, Figure 7.2). There was no effect of group or population density on ARS. The likelihood of a group going extinct in a given year decreased with group size (Table 7.2, Figure 7.3). Population PCG rate increased with group density but not with individual density (Table 7.3, Figure 7.4).

**Table 7.1:** Model selection (QICc) of the terms influencing annual reproductive success (ARS). Group identity, individual identity and breeding year were included as random terms. Data is based on 309 individuals who were dominant for at least 365 days.

Term	QICc	B (effect size)	SE	Confidence intervals
Basic	1106.48	1.47	0.02	1.43, 1.51
<b>Group size</b>	<b>1094.27</b>	<b>0.03</b>	<b>0.01</b>	<b>0.01, 0.04</b>
No. of ind'/km <sup>2</sup>	1105.97	0.03	0.01	-0.01, 0.06
No. of groups/km <sup>2</sup>	1099.3	0.43	0.13	0.17, 0.69

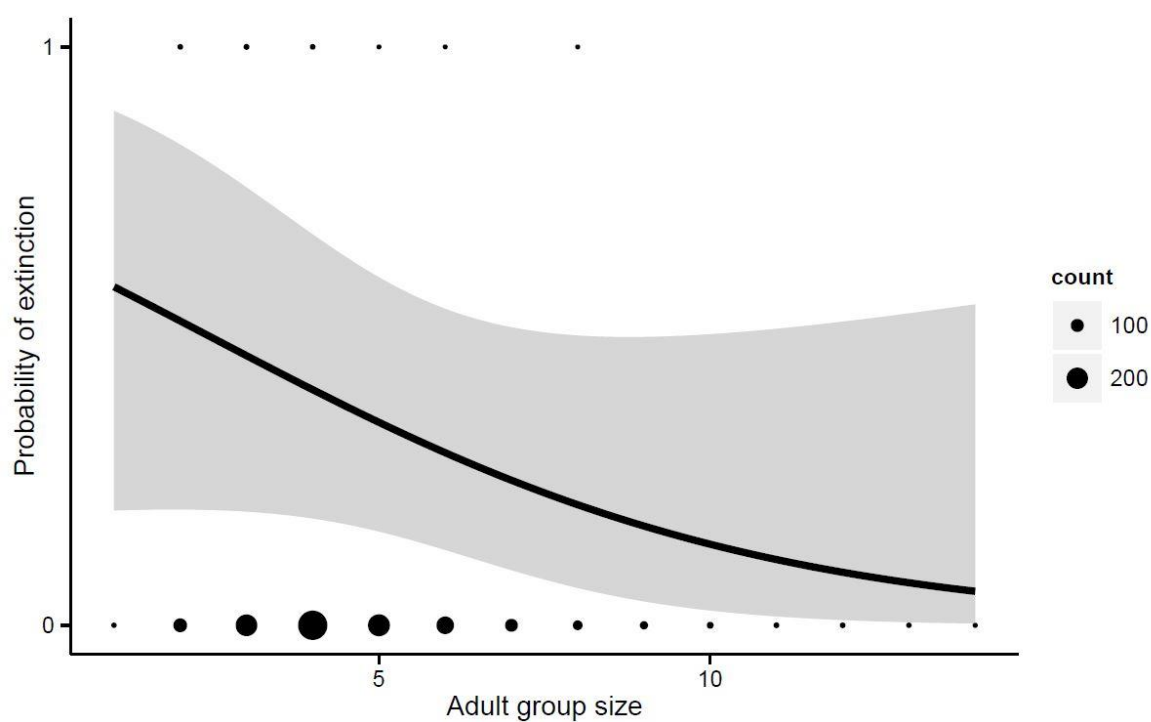


**Figure 7.2:** The relationship between adult group size and annual reproductive success (number of fledglings per year). N=504 successful breeding attempts (attempts that hatched successfully) from 43 groups. Grey area represents confidence intervals (Ci)



**Table 7.2:** Model selection (QICc) of the terms influencing the likelihood of group extinction on an annual basis. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold. Data is based on 660 group-years for 43 groups and 36 extinction events over the time period spanning 1978-2013.

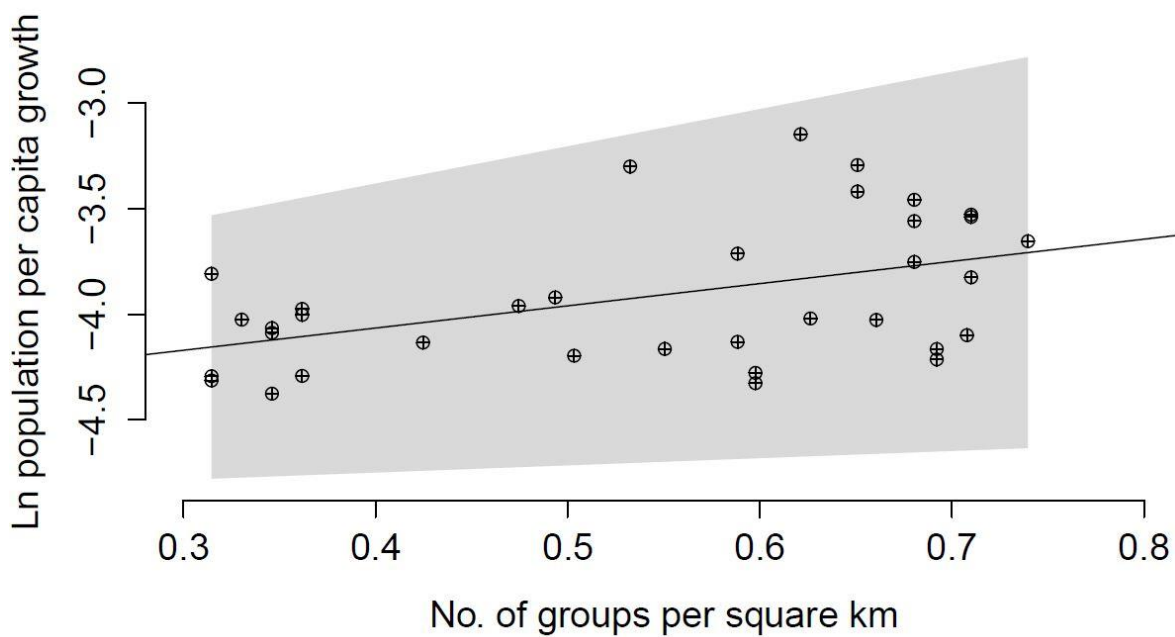
Term	QICc	B (effect size)	SE	Confidence interval
Basic	101.93	3.14	0.29	2.56, 3.52
<b>Group size</b>	<b>94.7</b>	<b>0.6</b>	<b>0.26</b>	<b>0.08, 1.11</b>
No. of ind <sup>9</sup> / km <sup>2</sup>	102.29	0.38	0.3	-0.22, 0.98
No. of groups/ km <sup>2</sup>	100.87	3.54	1.8	-0.04, 7.14



**Figure 7.3:** The relationship between adult group size and extinction events (0=no, 1=yes). N= 36 extinction events from 660 group-years for 43 groups.), thickness of dots represents the number of observations. . Grey area represents confidence intervals (Ci)

**Table 3:** Model selection (AICc) of the terms influencing population per capita growth rate. The model of greatest parsimony is highlighted in bold. Data is based on 908 group years, covering 79 groups over the time period spanning 1978-2013.

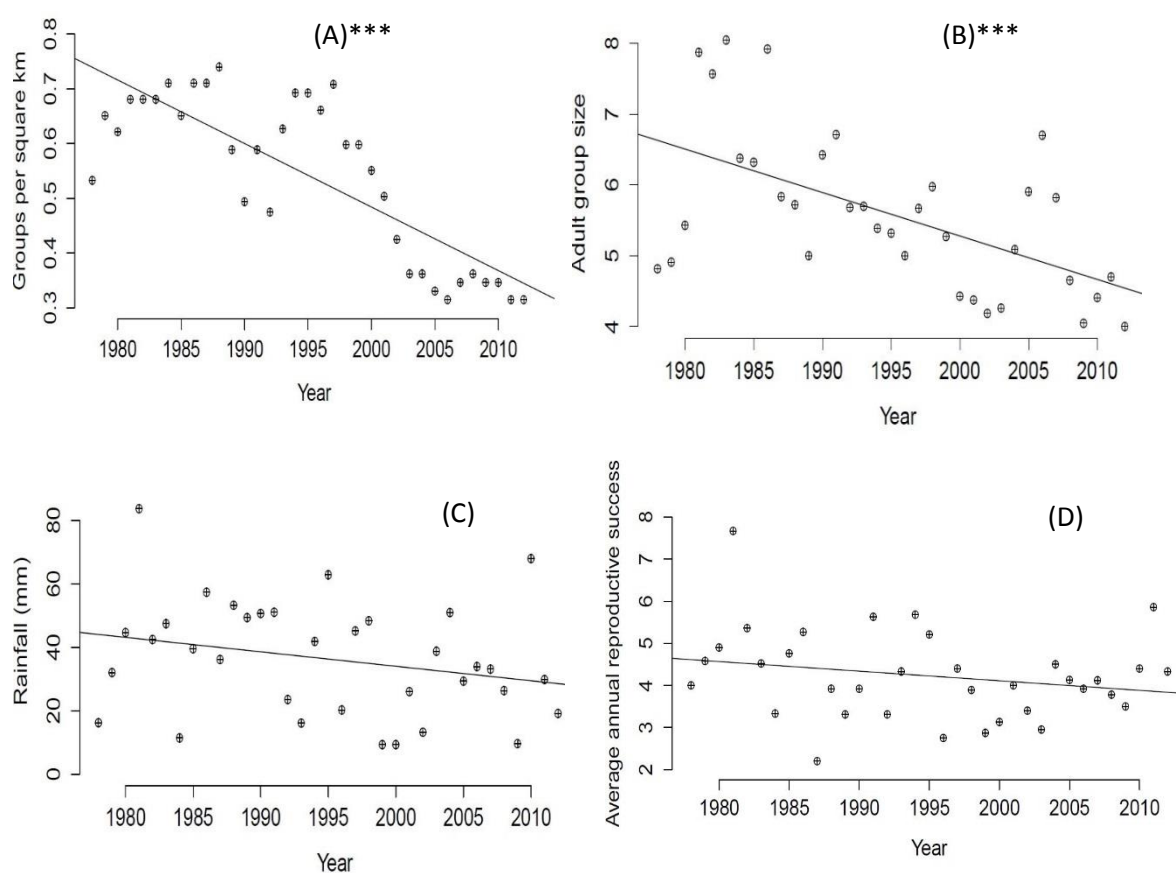
Term	QICC	B (effect size)	SE	Confidence interval	Weight
Basic	-31.94	-1.7	0.02	-1.75, -1.65	
No. of ind'/km <sup>2</sup>	-37.01	0.05	0.02	0.02, 0.08	0.36
<b>No. of groups/km<sup>2</sup></b>	<b>-38.02</b>	<b>0.45</b>	<b>0.15</b>	<b>0.17, 0.74</b>	<b>0.61</b>



**Figure 7.4:** The relationship between population per capita growth rate (number of individuals in the population in year t+1/ number of individuals in year t, log-transformed) and the number of groups per km<sup>2</sup> in year t. N=908 group years from 79 groups. Grey area represents confidence intervals (Ci)

*Changes in the population throughout the years:*

The numbers of groups per km<sup>2</sup> significantly declined over time ( $F=59.96$   $R^2=0.64$ ,  $p<0.0001$ , Figure 4a), as did average group size ( $F=15.49$ ,  $R^2=0.32$ ,  $p<0.0001$  Figure 4b). However, there was no change in average dominant ARS, ( $F=1.679$   $R^2=0.05$ ,  $p=0.2$ , Figure 4c) or rainfall over time ( $F=2.35$ ,  $R^2=0.066$ ,  $p=0.135$ , Figure 4d).



**Figure 7.4:** Yearly changes in (A) the number of groups of Arabian babblers per km<sup>2</sup>, (B) adult group size, (C) dominant individuals ARS (average number of fledglings) and (D) rainfall, between the years 1978-2013. Variables with a significant decrease over time are marked with \*\*\*.

## 7.5 Discussion

Our long-term analyses of density dependence in a cooperative breeder enabled us to explore the presence of group and demographic Allee effects. We found that group size, but not population size, affected both annual reproductive success and group extinction, and we also found group size to significantly influence group lifespan, providing evidence of component Allee effects acting on the population. We also found that population per capita growth rate increased with an increase in group density, suggesting that a demographic Allee effect also affects the study population. This is the first evidence for a demographic Allee effect in a cooperatively breeding bird species.

In obligate cooperatively breeding species, the longevity and physical condition of an individual is highly dependent on group characteristics (reviewed in [9,11,42], and this may explain the strong influence of group size on reproductive success and group lifespan and extinction rates in our population. In non-cooperative species, Allee effects may reduce individual success as the number of individuals in the population decreases [4], but our results show that both individual ARS and group dynamics were not dependent on population size. This supports the recent suggestion of Angulo et al [24], that other mechanisms exist in cooperative breeders that separate individual reproductive success from overall population dynamics. Bateman et al [43] suggested that any Allee effect present in small groups may be masked by negative density dependence present in large groups (i.e. emigration from larger groups to smaller groups due to critical group size effects), and this will prevent small groups from declining further or becoming extinct - thus preventing a demographic Allee effect. Indeed, in previous analyses we found that dispersal in Arabian babblers occurs mostly from large groups, while immigration occurs mostly in small groups (Chapter five, [44]). Expanding on Bateman et al's [43] suggestion, if there are factors limiting the movement of individuals via inter-group interactions, then a

demographic Allee effect may occur, or as suggested by Courchamp et al [2,12], high extinction rates amongst groups might increase the risk of population extinction.

Although the presence of both component and group-level Allee effects have recently been described for several cooperatively breeding species (e.g.[13,24,27,43]), empirical evidence for demographic Allee effects have not yet been described for any cooperative breeder. Our results revealed an inverse density dependence in population per capita growth rate, and this was primarily influenced by the density of groups in our population rather than by the density of individuals (in contrast to the demographic Allee effects described for non-cooperative species, [2,25,45]). This finding further demonstrates the need to account for the group as a basic level of organization in cooperative breeders when considering population demographics. Courchamp et al. [12] suggested that a strong demographic Allee effect will be observed in a population once it declines below a threshold known as the ‘Allee threshold’. Our findings suggest that group size in cooperative breeders may decrease once the number of the groups in the population decrease, but individual RS will not be affected as long as group size doesn’t fall beneath the Allee threshold.

During the past two decades there has been a severe decline in local populations of avian species in the Arava valley, where the Arabian babbler population is located [46]. For example, species like the Arabian Warbler (*Sylvia leucomelanea*) Hoopoe lark (*Alemon alaudipes*), Macqueen’s Bustard (*Chlamydotis macqueenii*) and Bar-tailed desert lark (*Amommanes cincturus*), once common throughout the Arava valley, have become endangered [46]. Our data shows a similar pattern of population decline is happening in Arabian babblers, potentially leading to a demographic Allee effect that may lead to local extinction of the species. We suggest that the reason that local extinction has not yet occurred in our population is because most groups still maintain a size that is large enough

to prevent a reduction in individual reproductive success. It seems that the existence of a group Allee effect weakens the potential effect of the reduction in the number of groups in the population, thus preventing local extinction.

In this study we have presented the first evidence for a demographic Allee effect in a cooperative breeder, together with further evidence for the existence of group Allee effects. The demographic Allee effect we found was especially interesting since it showed that population growth in a cooperative breeder depends on the number of groups in the population, rather than the number of individuals. This supports previous models and studies that have highlighted the importance of the group as an additional level of organization between individual and population dynamics in cooperative breeders. Our findings of the effect of the group on both component and demographic Allee effects may have important implications on habitat management and protection of cooperatively breeding species.

## 7.6 References

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## 8. General discussion

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## 8.1 Overview

In this thesis I explored how living in cooperatively breeding groups influences variation in individual foraging and learning abilities, fitness traits and group dynamics. I further considered how individual traits and group dynamics relate to population dynamics. I have approached these questions from three different perspectives: the individual, the group and the population. I started by conducting an experiment on social foraging behaviour, in order to see whether it may serve as a benefit to individuals in the group, and whether intragroup individuals differ in their social foraging strategies. I then went on to explore the existence and causes of variation in the ability to innovate and acquire novel foraging skills, and whether such ability differs between contexts. This gave me an overview of how group-living influences individual foraging strategies and innovative behavior.

I then went on to investigate the factors that affect the costs and benefits of group living in a cooperatively breeding society with high reproductive skew, using an extensive and detailed database covering 35 years of continuous observation on a single study population. I investigated the following three questions:

1. The causes of variation in individual fitness traits, including the factors that affect the probability of attaining a breeding position (i.e. becoming dominant), maintaining dominance tenure, and overall lifetime reproductive success.
2. The influence of social and environmental factors on group dynamics, including the initiation of breeding activity, the probability of young surviving to adulthood, the frequency of immigration and emigration events, and the probability of group extinction.
3. The variation in population dynamics over the long-term, and the presence of component, group and demographic Allee effects.

By addressing these questions I have provided a comprehensive overview of the costs and benefits of group-living, the causes of fluctuations in growth at both the group and population level, and the presence of Allee effects, the latter providing an insight into ways to address effective population management in cooperatively breeding species.

## **8.2 Social foraging, acquisition of novel skills and innovation**

While an understanding of how long-term processes influence individuals living in cooperatively breeding groups are of great importance, the everyday social activities that individuals are involved in may help to specify the actual costs and benefits of cooperation. An important consequence of sociality is the complexity of interactions among individuals (Hatchwell & Komdeur 2000). Some examples of such interactions include social play (Diamond & Bond 2003; Pozis-Francois et al. 2004), allopreening (Radford & Du Plessis 2006) and allofeeding among adults (Woolfenden 1984; Carlisle & Zahavi 1986). Social foraging strategies, and their connection to the spread of novel behavior and innovation, are relatively unexplored in cooperative breeders (but see Chiarati et al. 2012; Thornton & Samson 2012). In chapters three and four I conducted a set of three experiments in order to look at the social context of foraging, innovation and the spread of foraging skills in Arabian babblers.

My finding that subordinates and dominants differ in their foraging strategies, and that innovation is task-dependent was a result I did not predict. The fact that subordinates tend to scrounge more than dominant individuals is in contrast to the results of similar cognitive experiments conducted on non-cooperatively breeding species (Stahl et al. 2001; Liker & Barta 2002; Beauchamp 2006; Belmaker et al. 2012), where individuals with higher competitive ability tended to scrounge more. In addition, the finding that the individuals who scrounged (subordinates) were better at acquiring a novel foraging skill was also in contrast to previous studies, who found the tendency to produce (rather than scrounge) is

associated with better learning of a novel skill (Coolen 2002; Beauchamp 2006; Arbilly et al. 2010; Katsnelson et al. 2011). I suggest that the reason for my contrasting result is that in cooperative breeders, scrounging may be adaptive for subordinates since it can facilitate social learning of foraging behaviour (as suggested by Giraldeau 1997; Laland 2004; Arbilly et al. 2011).

In Chapter 4, I used cognitive experiments to test a different novel skill from that in Chapter 3, and I found that innovation was task-dependent: dominants were better than subordinates at a different task. This finding is in line with the recent idea that cognitive abilities in general, and learning abilities specifically, are context-dependent (Griffin et al. 2013; Rowe & Healy 2014). My findings suggest that there are different cognitive strategies between subordinates and dominants. While subordinates seem to explore a wider range of foraging opportunities, including scrounging and the exploration of novel objects, dominants seem to be better in generalizing from familiar tasks to similar ones, making them more sensitive to refined cues. This variability in innovation abilities may generate a ‘skill pool effect’ or ‘pool of competence effect’ (Giraldeau 1984; Morand-Ferron & Quinn 2011), that allows social foragers to exploit a greater variety of food resources (Giraldeau & Lefebvre 1986; Ilan et al. 2013).

The finding that an innovative behaviour was quickly transmitted among group members (when one learned the novel skill in a group, the new skill was passed to all group members) may present another important benefit of group-living. However, the fact that I didn’t find group size to affect social foraging, learning or innovation in groups of Arabian babblers is in contrast to studies conducted on non-cooperatively breeding species (Liker & Bókony 2009; Morand-Ferron & Quinn 2011). Although it could be that our sample size was too small to detect the effect of group size, it is also feasible that once a group reaches

a certain size, social foraging behavior depends mostly on the interactions between dominants and subordinates, and less on group size.

This study was one of the first to explore social foraging, acquisition of novel skills and differences in innovative abilities in a wild cooperatively breeding bird species, highlighting the ways that foraging in a group may benefit individuals, and presenting unique evidence for task-dependent differences in innovative behavior in a cooperatively breeding bird

### **8.3 The effect of social and environmental factors on individual fitness traits and group dynamics.**

Individuals in cooperatively breeding species characterised by high reproductive skew, gain access to breeding almost exclusively through attaining a dominant breeding position in a group, with reproductive success for subordinates extremely low (Lundy, Parker & Zahavi 1998; Hager & Jones 2009; Nelson-Flower *et al.* 2011). My finding that the probability of a subordinate attaining a dominant position is significantly higher if it disperses from the natal group supports previous studies on cooperative breeders (Koenig *et al.* 2000; Ekman *et al.* 2001; Raihani *et al.* 2010), where inbreeding is avoided and dispersal is a primary means to find unrelated mates. If social foraging provides benefits to subordinates (as suggested in chapters 3 & 4), and the group serves as a safe haven for subordinates before they disperse to find reproductive opportunities, then it could be that delayed dispersal is not only a consequence of ecological constraints, but an adaptive strategy that may enhance the probability of gaining future reproductive opportunities (the benefits of a ‘safe haven’ as suggested by Covas & Griesser 2007).

Social factors such as group size and reproductive competition were found to significantly influence individual reproductive success. It is well known that group size influences adult survival and reproductive success in cooperative breeders (Kokko *et al.* 2001; Kingma *et*

al. 2014). Recent studies that conducted more detailed analyses of the benefits of group size have revealed the important role that group size plays in buffering individuals from harsh environmental conditions (through higher survival and reproductive success in larger groups) when ecological constraints are high (Ebensperger et al. 2012, 2014; Angulo et al. 2013; Bateman et al. 2013). However, my findings did not support these trends, with dominant individuals from larger groups not displaying higher reproductive success than dominants from small groups during low rainfall years. It could be that larger groups facilitate individual survival when ecological constraints are high via other mechanisms (for example, protection of higher quality territories and hence better access to food resources, or greater anti-predator vigilance) rather than higher reproductive success, but further research is needed to better understand how variations in group size influence adult survival during extreme weather conditions.

My study found that relative group size (i.e. the size of the focal group divided by the average group size in the population) is a better predictor of individual success and group dynamics than the traditional group size measure (defined as the absolute number of adults in the group). I suggest two possible reasons for this: (1) fluctuations in group size between years is a known characteristic of many cooperatively breeding species (Bateman et al. 2013), therefore, a size that represents a ‘large group’ in absolute numbers in poor years may be a small group size in other years. (Ridley & Huyvaert 2007; Bateman et al. 2013), (2) the size of neighbouring groups, and thus their ability to appropriate territory from the focal group, may be an important factor influencing reproductive success and group dynamics (Ridley & Huyvaert 2007). By showing that relatively larger groups are more likely to initiate a breeding event and produce young that survive to adulthood, I have highlighted how group size effects are caused not only by mechanisms such as increased levels of care received by offspring and a lower load of reproductive investment per adult



(load lightening, Crick 1992), but also by the ability of groups to retain better territories and defend against intruders (Kokko et al. 2001; Kingma et al. 2014).

How social and environmental factors influence group dynamics may play an important role in shaping the costs and benefits of cooperative breeding. Changes in group size are known to influence emigration and immigration rates, with more subordinates leaving large groups in order to achieve reproductive success (the social queue effect, Kokko & Johnstone 1999; Cant & English 2006), while smaller groups are more vulnerable to invasion from neighbouring groups (Ridley 2012, Korb & Roux 2012). My findings support these studies and further highlights the importance of group size in influencing group dynamics. The fact that the probability of group extinction was influenced by group size (with larger groups less likely to become extinct), and that I found no direct influence of environmental factors on group extinction, suggests that social factors are relatively more important than environmental factors in determining group extinction and hence individual survival and reproductive success.

The presence of intragroup female reproductive competition was an important influence on both individual and group dynamics. This supports an increasing body of research identifying the important influence that reproductive competition may have on individual fitness and group dynamics (Clutton-Brock et al. 2006; Lardy et al. 2012; Nelson-Flower 2013; Bell et al. 2014). In this study I have found that female competition over reproduction caused a decline in annual reproductive success, (Chapter five), even when environmental conditions were favourable. The reason for this strong influence is probably because competing females were infanticidal, destroying one another's eggs. I have personally observed this behavior in Arabian babblers, and it is also documented in other species of cooperatively breeding birds (Koenig et al. 1995; Nelson-Flower 2013). My

findings provide further support for the idea that intragroup competition is an important parameter to measure in studies measuring influences on group dynamics.

#### **8.4 Inverse density dependence and Allee effects.**

Inverse density dependence (Allee effects) have recently been recognised as more important in shaping population dynamics than previously supposed, particularly in cooperatively breeding species (Courchamp et al. 2008; Bateman et al. 2011). Furthermore, Allee effects have been found to have important consequences for the stability and regulation of populations. In this study I have presented the first evidence for a demographic Allee effect in a cooperative breeder, together with further evidence for the existence of group Allee effects. I found that individual reproductive success and group dynamics are affected by group size but not population size, supporting the existence of a group Allee effect in cooperative breeders (as originally suggested by Angulo et al. 2013). However, this study also found that population growth is primarily influenced by the number of groups in the population, thus being the first to show a demographic Allee effect in cooperative breeders. Bateman et al. (2011) suggested that the reason for the difficulty in finding demographic Allee effects in cooperatively breeding species is due to their population structure, which is formed by groups of varying size. Therefore, an Allee effect that affected small groups will be masked by dispersal from large groups, or by the formation of new groups. The recent habitat loss around the Shezaf Nature Reserve (where my study population is based) may create conditions that limit dispersal between groups, or the formation of new groups, and thus the “masking” mechanism described by Bateman et al (2011) will cease to exist, leading to a demographic Allee effect in the population. My findings of both group and demographic Allee effects in the population may contribute to the understanding of inverse density dependence in cooperative breeders, and to the development of management and nature conservation tools.

## 8.5 Conclusion

The ways in which group-living benefits individuals in cooperatively breeding species has been demonstrated in many previous studies (reviewed in Koenig & Dickinson 2004; Cockburn 2013), but the relative influence of social and environmental factors on variation in individual fitness traits, group dynamics, and population dynamics, have only recently begun to be considered (Clutton-Brock et al. 2006; Hodge et al. 2008; Koenig et al. 2011; Lardy et al. 2012; Bateman et al. 2013). In this thesis I investigated the effect of social and environmental factors on the costs and benefits of group-living in a cooperatively breeding bird species, the Arabian babbler, from three different perspectives: the individual, the group and the population. Firstly, I have been able to identify how subordinate and dominant individuals differ in their social foraging strategies, enabling them to acquire different types of novel foraging skills. To my knowledge, this is the first time that task-dependent innovation and different cognitive strategies have been described in a cooperative breeder. Secondly, I analysed an extensive long-term dataset, covering 35 years of observations, enabling me to look at the causes of variation in reproductive success between individuals and groups, and to connect that to long-term population dynamics. My analyses revealed that some factors that are not commonly measured in studies of individual and group dynamics are important influences. Relative group size, rather than absolute group size, was an important predictor of individual fitness traits and group dynamics. In addition, reproductive competition played an important role on reproductive success. This was the first study to directly measure both these traits on a long-term dataset, and I suggest that these measures be considered in further studies on individual fitness and group dynamics in cooperative breeders. Finally, this study was the first to show the existence of component and group Allee effects in a cooperatively breeding bird, and the first to identify the existence of a demographic Allee effect in a cooperatively breeding species. By doing so I found supporting evidence for previous

models and studies (Courchamp et al. 1999; Bateman et al. 2011, 2012) demonstrating the existence of a group Allee effect in cooperative breeders, and suggesting how habitat loss may facilitate a demographic Allee effect through a reduction in the number of groups in the population.

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## For general chapters

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## Appendices

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## Appendix 1- complete model sets for chapter 3: Social foraging strategies and

**Table S3.1:** Complete model set of the terms influencing the amount of time spent on the grid per individual during the producer-scrounger game using model selection (AICc). Individual and group identity were included as random terms. Data is based on 152 trials of 85 individuals from 16 groups.

Term	AICC	B (effect size)	SE	Confidence interval
Basic	63.524	20.09	0.05	1.98,2.20
Sex	76.17	-0.19	0.17	-0.53, 0.14
Dominance	55.49	-0.18	0.05	-0.29, -0.08
Group size	77.66	-0.01	0.02	-0.06, 0.04
Age	74.09	-9.9E-5	3.35E-5	-0.001, 3.2E-5
Trial number	68.14	-0.009	0.04	-0.08, 0.06
Time to step on grid	73.7	-0.0005	0.0002	-0.00009, -6.6E-5
Sex* Age	85.5	-0.0001	4.2E-5	-0.0002, -4.6E-5
Dominance* Group size	63.53	-0.04	-0.02	-0.09, 0.01
Dominance* time to step on grid	77.5	-0.0008	0.0003	-0.001, -0.00025

acquisition of novel foraging skills in cooperatively- breeding Arabian babblers.



**Table S3.2:** Complete model set of the terms of the terms influencing the number of rewarded foraging steps/second for each individual in the producer-scrourer game using model selection (AICc). Individual and group identity were included as random terms. Data is based on 152 trials of 85 individuals from 16 groups.

<b>Term</b>	<b>AICC</b>	<b>B (effect size)</b>	<b>SE</b>	<b>Confidence interval</b>
Basic	-467.2	0.132	0.008	0.12,0.15
Dominance	-471.9	-0.03	0.008	-0.05, -0.02
Sex	-464.6	-0.02	0.007	-0.04, -0.007
Group Size	-464.43	-0.002	0.003	-0.009, 0.005
Age	-454.305	-9.8E-6	5.8E-6	-1.9E-5, 1.6E-7
Trial number	-465.620	-0.0007	0.007	-0.01, 0.01
Dominance* Group size	-465.86	-0.007	0.003	-0.02, 0.0005
Dominance* Age	-436.27	-8.8E-6	5.12E-6	-1.9E-5, 1.27E-6

**Table S3.3:** Complete model set of the terms influencing the proportion of individuals joining (scrounging) during the producer-scrounger game using model selection (AICc). Individual and group identity were included as random terms. Data is based on 152 trials of 85 individuals from 16 groups.

Term	AICC	B (effect size)	SE	Confidence interval
Basic	27.581	0.27	0.03	0.21, 0.33
Dominance	20.045	-0.16	0.05	-0.25, -0.06
Sex	31.11	-0.04	0.05	-0.13, 0.05
Group size	33.171	0.015	0.012	-0.01, 0.04
Age	37.622	-9.4E-5	3.1E-5	-0.0001, -3.1E-5
Trial number	31.39	0.03	0.03	-0.03, 0.1
Time to approach the grid	40.32	-0.0003	0.0002	-0.0008, 0.0001
Number of individuals on the grid	23.98	0.08	0.027	0.02, 0.13
Ind. grid time	35.472	0.0006	0.0002	-0.0001, 0.001
Dominance +	18.21	-0.16	0.05	-0.25, -0.06
Number on the grid		0.07	0.03	0.01, 0.13
Dominance *Number on grid	23.553	0.09	0.03	0.04, 0.15

**Table S3.4:** Complete model set of the terms influencing whether an individual learnt the novel foraging task (0 = didn't learn, 1 = learned) using Generalized Estimating Equations (QICc). Individual and group identity were included as random terms. Data is based on 227 trials of 66 individuals from 14 groups.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	274.157	0.77	0.28	0.28, 1.25
Dominance	260.433	1.86	0.68	0.51, 3.2
Sex	276.122	0.34	0.49	-0.64, 1.32
Group size	276.048	-0.07	0.09	-0.27, 0.12
Age	268.025	0.001	0.0004	0, 0.002
Trial number	273.369	0.4	0.26	-0.12, 0.92
Individual grid time	273.018	-0.003	0.002	-0.006, 0
Dominance+	267.01	1.08	0.87	-0.6, 2.79
Age		0	0.0005	-0.001, 0.001
Dominance (dom)*Age	269.46	0.001	0.0004	0, 0.002
Dominance (sub)*age		0	0.0009	-0.002, 0.002

**Table S5:** Complete model set of the terms influencing the time that it took each individual to remove its first lid (for learners) or its total time on the grid (for non-learners) using model selection (AICc). Individual and group identity were included as random terms. Data is based on 227 trials of 66 individuals from 14 groups.

<b>Term</b>	<b>AICC</b>	<b>B (effect size)</b>	<b>SE</b>	<b>Confidence interval</b>
Basic	1253.347	8.16	0.48	7.22, 9.09
Dominance	1251.602	0.54	0.77	-0.95, 2.03
Sex	1251.908	-0.37	0.73	-1.8, 1.08
Group size	1254.661	-0.05	0.21	-0.54, 0.44
Age	1266.782	0.0002	0.0005	-0.0007, 0.001
Trial number	1227.419	-1.24	0.23	-0.17, -0.79
Learning (y/n)	1199.642	4.68	0.56	3.57, 5.79
Trial Number + Learning	1182.320	-0.99 4.68	0.22 0.56	-1.4, -0.55 3.56, 5.79

**Appendix 2- complete model sets for chapter 4. Task-dependent differences in innovation abilities by subordinates and dominant wild Arabian babblers**

**Table S4.1:** Complete model set of the terms influencing the probability to be the first to remove white lid (innovator) using Generalized Estimating Equations (QICc). Individual and group identity were included as random terms. Data were based on 16 individuals from 6 mixed groups that had both dominant and subordinate who knew how to remove black lids.

<b>Term</b>	<b>QICC</b>	<b>B (effect size)</b>	<b>SE</b>	<b>Confidence interval</b>
Basic	51.9	-0.38	0.32	-1, 0.25
Sex	53.3	0.57	0.52	-0.44, 1.6
Dominance	45.05	-2.25	0.59	-3.4, -1.1
Group size	53.9	0.13	0.6	-1.05, 1.3
Age	52.65	0.0	0.0004	-0.001, 0.00
Trial number	53.9	0.44	0.96	-1.4, 2.36
Steps/sec (until first individual removed a white lid)	49.3	-2.1	1.09	-4.3, 0.02
Time to step on grid	51.73	0.003	0.003	-0.002, 0.008
Time to remove first black	53.8	0.18	0.4	-0.6, 0.9
Dominance* steps/sec	47.94	-2.8	1.7	-6.1, 0.5
Subordinate* steps/sec		-0.15	1.5	-3.07, 2.8

**Table S4.2:** Detailed information on group construction in the study, on the numbers of dominant and subordinates who knew already how to remove black lids and on which individual was the first to remove whit lid in each trial. For each first remover of a white lid we present whether it was a dominant, subordinate, male or female, numbers of subordinates do not represent their rank.

Group name	Group size	knew to remove black		first in trial 1	first in trial 2	first in trial 3	first in trial 4
		Sub	Dom				
AR1	7	3	0	Subordinate1 female	Subordinate1 female	Subordinate1 female	Subordinate1 female
ARU	5	1	2	no	Dominant male	Dominant female	Dominant male
ADR	4	2	1	no	no	no	no
BSZ	2	0	1	Dominant male	Dominant male	Dominant male	Dominant male
ELU	2	0	2	no	no	no	no
HIL	5	1	2	Subordinate1 Male	Subordinate1 Male	Dominant female	Subordinate1 Male
HOR	6	3	0	Subordinate1 female	Subordinate1 female	Subordinate2 female	Subordinate3 female
KOT	4	1	1	Dominant male	Dominant male	Dominant male	Dominant male
LIR	4	1	2	Dominant female	Dominant male	Dominant male	Dominant male
NEK	3	0	1	Dominant female	Dominant female	Dominant female	Dominant female
NIS	3	1	1	no	no	no	no
POL	4	1	0	Subordinate male	Subordinate male	Subordinate male	Subordinate1 male
TLM	5	2	1	Dominant male	Dominant male	Dominant male	Dominant male
TMR	3	1	1	Dominant male	Subordinate male	Dominant male	Dominant male

**Table S4.3:** Complete model set of the terms influencing the probability to be the first to remove black lid (innovator) in the current study, using Generalized Estimating Equations (QICc). Individual and group identity were included as random terms. Data were based on 16 individuals from 6 mixed groups that had both dominant and subordinate who knew how to remove black lids.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	76.56	0.15	0.3	-0.45, 0.75
Sex	77.34	0.66	0.64	-0.59, 1.9
Dominance	77.7	0.5	0.65	-0.78, 1.79
Group size	77.8	0.32	0.34	-0.34, 0.98
Trial number	80.9	-0.8	0.79	-2.4, 0.74

**Table S4.4:** Complete model set of the terms influencing the probability to learn to remove white lid.

Individual and group identity were included as random terms. Data were based on 36 individuals from 14 groups.

<b>Term</b>	<b>QICC</b>	<b>B (effect size)</b>	<b>SE</b>	<b>Confidence interval</b>
Basic	115.27	-1.34	0.4	-2.1, -0.55
Sex	117.27	0.02	0.8	-1.6, 1.6
Dominance	112.9	-1	0.9	-2.8, 0.77
Group size	117.05	0.16	0.48	-0.8, 1.1
Age	117.23	5.1E-5	0.0004	-0.001, 0.001
Trial number	114.45	-0.39	0.13	-0.65, -0.13
Time on grid	111.44	0.008	0.003	0.002, 0.01
Steps on grid	108.33	0.07	0.02	0.02, 0.12
<b>Others learned in the group</b>	<b>93.9</b>	<b>2.4</b>	<b>0.9</b>	<b>0.63, 4.3</b>
Others learned* steps	107.8	0.04	0.04	-0.03, 0.12
No others learned* steps		0.1	0.07	-0.04, 0.25
Others learned* time	108.78	0.005	0.004	-0.003, 0.01
No others learned* time		0.02	0.01	-0.007, 0.04

**Table S4.5:** Complete model set of the terms influencing the probability to prefer white lids using

Generalized Estimating Equations (QICc). Individual and group identity were included as random terms.

Data were based on 21 individuals from 11 groups who learned to remove white lids.

<b>Term</b>	<b>QICC</b>	<b>B (effect size)</b>	<b>SE</b>	<b>Confidence interval</b>
Basic	103.18	0.93	0.26	0.43, 1.44
Sex	102.38	0.86	0.55	-0.23, 1.96
Dominance	102.67	-0.77	0.5	-1.7, 0.22
First to remove white	102.87	0.74	0.51	-0.26, 1.75
Group size	105.15	0.05	0.37	-0.68, 0.79
Age	104.76	0.0	0.0002	-0.001, 0.0
<b>Trial number</b>	<b>75.2</b>	<b>-1.6</b>	<b>0.34</b>	<b>-2.2, -0.89</b>
Time on grid	97.05	0.009	0.005	0.02, 4.1
Steps on grid	102.22	0.03	0.02	-0.02, 0.07
Trial number + Time on the grid	76.23	-1.45 0.005	0.38 0.006	-2.2, -0.7 -0.006, 0.02

### Appendix 3- complete model sets for chapter 5. Causes of variation in dominance acquisition, tenure, and lifetime reproductive success in a cooperatively breeding bird

**Table S5.1:** Model selection (QICc) to determine the potential influence of early body mass on attainment of dominance rank as an adult. Data is based on 118 individuals from 43 groups over the time period spanning 1978-2013 whose body mass at time of ringing (9-11 days post hatching) was recorded

Term	QICC	B (effect size)	SE	Confidence interval
Basic	1490.75	0.35	0.06	0.24, 0.48
Mass rank in brood	1492.17	0.04	0.05	-0.07, 0.16

**Table S5.2:** Complete model selection (QICc) of the terms the probability of attaining a dominant breeding position per year of life. Group and individual identity were included as random terms. Data is based on 192 dominant and 238 subordinate individuals from 43 groups over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	2100.79	0.29	0.09	0.1, 0.5
Sex	2102	0.022	0.2	-0.37, 0.42
Dispersal	1447.37	3.2	0.27	2.68, 3.73
Drought	2093.7	0.31	0.1	0.1, 0.52
Rainfall	2094.3	0.009	0.003	0.003, 0.01
Female ratio	2094.2	3.67	2.57	-1.3, 8.7
<b>Dispersal + Drought</b>	<b>1437.48</b>	<b>3.23 -0.26</b>	<b>0.06 0.08</b>	<b>0.21, 0.46 -0.41, -0.11</b>

**Table S5.3:** Complete model selection (QICc) of the main terms influencing dominance tenure. Group and individual identity were included as random terms. Data is based on 343 individuals from 43 groups over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	2739.7	31.5	0.82	29.8, 33.1
Sex	2736.58	1.09	1.4	-1.6, 3.8
Dispersal	2736.95	0.5	1.4	-2.4, 3.4
<b>Relative group size</b>	<b>2720.66</b>	<b>9.78</b>	<b>2.6</b>	<b>4.7, 14.8</b>
Absolute group size	2722	1.19	0.26	0.7, 1.7
Average ARS	2738.85	0.19	0.58	-0.9, 1.3

**Table S5.4:** Model selection (QICc) to determine the potential influence of Age on dominant individual annual reproductive success (ARS) Data is based on 193 individuals from 43 groups over the time period spanning 1978-2013 who hatched in the study population.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	756.01	1.5	0.23	1.45, 1.54
Age	757.4	1.56E-5	2.26E-5	-2.9E-5, 6E-5

**Table S5.5:** Complete model selection (QICc) of the terms influencing annual reproductive success (ARS). Group identity, individual identity and breeding year were included as random terms. Data is based on 309 individuals who were dominant for at least 365 days.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	1106.5	1.47	0.02	1.4, 1.5
Sex	1108.4	-0.001	0.4	-0.08, 0.07
Female competition	1079.67	0.18	0.04	0.1, 0.26
Male competition	1086.9	0.16	0.04	0.08, 0.23
Dispersal	1104.3	0.07	0.04	-0.009, 0.15
Drought	1043.87	0.4	0.05	0.3, 0.5
Absolute group size	1094.3	0.03	0.008	0.01, 0.04
Relative group size	1085.2	0.2	0.05	0.11, 0.3
Relative group size* competition present	1061.7	0.06	0.05	-0.04, 0.17
Relative group size* competition absent		0.22	0.04	0.13, 0.3
Relative group size* drought	1012.83	-0.08	0.06	-0.19, 0.03
Relative group size* no drought		0.27	0.04	0.19, 0.04
<b>Competition+</b>	<b>994.24</b>	<b>0.16</b>	<b>0.04</b>	<b>0.08, 0.23</b>
<b>Drought+</b>		<b>0.42</b>	<b>0.05</b>	<b>0.3, 0.53</b>
<b>Relative group size</b>		<b>0.2</b>	<b>0.04</b>	<b>0.12, 0.3</b>



**Table S5.6:** Model selection (QICc) to determine the potential influence of age on dominant individual lifetime reproductive success (ARS) Data is based on 193 individuals from 43 groups over the time period spanning 1978-2013 who hatched in the study population.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	1799.5	6.97	0.05	6.8, 7.07
Age	1560.26	0.00	8.6E-5	0.0, 2.3E-5
Tenure	714.2	0.001	3.1E-5	0.001, 0.001

**Table S5.7:** Complete model selection (QICc) of the terms influencing individual variation in lifetime reproductive success. Group and individual identity were included as random terms Data is based on 309 individuals who were dominant for at least 365 days

Term	QICC	B (effect size)	SE	Confidence interval
Basic	1604.06	1.7	0.06	1.6, 1.8
Sex	1606.05	0.001	0.12	-0.23, 0.24
Dispersal	1605.9	0.01	0.12	-0.23, 0.26
Average relative group size	1472.08	1.5	0.3	0.87, 2.1
Longest pair bond	1177.7	0.001	7.4E-5	0.0, 0.001
Dominant tenure	849.55	0.001	3.7E-5	0.001, 0.001
Average ARS	1128	0.28	0.02	0.23, 0.32
<b>Dominance tenure+</b>	<b>450.5</b>	<b>0.001</b>	<b>3.5E-5</b>	<b>0.001, 0.001</b>
<b>Ars+</b>		<b>0.26</b>	<b>0.01</b>	<b>0.23, 0.29</b>
<b>Relative group size</b>		<b>0.38</b>	<b>0.38</b>	<b>0.09, 0.66</b>

#### Appendix 4- complete model sets for chapter 6. Long-term analysis of social and environmental influences on group dynamics in a cooperative breeder

**Table S6.1:** Complete model selection (QICc) of the terms influencing initiation of breeding. Group identity and breeding year were included as random terms. Data is based on 660 breeding years of 43 groups over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	663.034	-1.37	0.97	-1.56,-1.18
Drought	617.104	-1.42	0.2	-1.8,-1.02
Rainfall	570.5	-0.06	0.007	-0.08, -0.05
Reproductive competition	664.336	-0.17	0.2	-0.56, 0.22
Female competition	664.22	-0.18	0.2	-0.59, 0.2
Male competition	665.02	-0.02	0.19	-0.4, 0.36
Group size	659.5	-0.12	0.47	-0.2, -0.02
Relative group size	659.2	-0.6	0.26	-1.1, -0.08
Group size <sup>2</sup>	660.17	-0.02	0.02	-0.05, 1.16
Female ratio	664.86	-0.26	0.68	-1.6,1.07
reproductive competition	664.336	-0.17	0.2	-0.56, 0.22
Rainfall+	565.6	-0.06	0.007	-0.08, -0.05
Group size		-0.14	0.05	-0.2, -0.03
<b>Rainfall+</b>		<b>-0.06</b>	<b>0.007</b>	<b>-0.08, -0.05</b>
<b>Relative Group size</b>	<b>563.1</b>	<b>-0.8</b>	<b>0.28</b>	<b>-1.3,-0.2</b>
Rainfall*competition	572.5	-0.06	0.008	-0.08,-0.05
Drought*Group size	618.02	0.02	0.05	-0.08, 0.12

**Table S6.2:** Complete model set (QICc) of the main terms influencing hatching success. Group identity and breeding year were included as random terms. Data is based on 684 breeding attempts from 43 groups over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	8664.98	0.76	0.07	0.63,0.89
Brood overlap	8674.45	-0.26	0.14	-0.55,0.03
Drought	8641.42	0.35	0.16	0.05,0.66
Female competition	8614.03	0.48	0.15	0.18,0.78
Male competition	8625.047	0.32	0.13	0.06,0.58
Reproductive competition (total)	8641.23	-0.12	0.13	-0.37,0.12
Breeding attempt	8666.99	0.1	0.08	-0.5, 0.27
Group size	8667.32	-0.003	0.03	-0.06,0.5
Relative group size	8666.92	-0.02	0.17	-0.36,0.32
Rainfall	8653.003	0.007	0.003	0.0, 0.02
Heatwaves	8584.87	0.13	0.04	0.06,0.2
Drought+	8383.5	0.36	0.16	0.05, 0.7
Female competition		0.48	0.15	0.18, 0.8
Heatwaves +	8337.3	0.13	0.03	0.06, 0.2
Female competition		0.48	0.15	0.18, 0.78
Rainfall+	8395.5	0.007	0.003	0.001, 0.01
Female competition		0.48	0.15	0.18,0.78
Heatwaves* female competition (yes)	8481.7	0.008	0.06	-0.1, 0.1
Heatwaves* female competition (no)		0.2	0.04	0.11,0.28
<b>Rainfall*female competition (yes)</b>	<b>8302.43</b>	<b>-0.002</b>	<b>0.004</b>	<b>-0.009, 0.006</b>
<b>Rainfall*female competition (no)</b>		<b>0.01</b>	<b>0.003</b>	<b>0.18,0.73</b>

**Table S6.3:** Complete model set (QICc) of the terms influencing survival of young to first year. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold. Data is based on 504 breeding attempts from 42 groups over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	3210.08	0.41	0.06	-0.54,-0.29
Drought	3164.76	0.62	0.21	0.2,1.04
Brood overlap	3211.65	-0.02	0.13	-0.27, 0.24
Female reproductive competition	3207.88	-0.1	0.14	-0.38,0.17
Male reproductive competition	3212.33	-0.04	0.12	-0.29,0.2
Breeding attempt	3210.13	-0.07	0.09	-0.26, 0.12
Group size	3197	0.04	0.03	-0.01,0.09
Relative group size	3196	0.21	0.14	-0.06, 0.49
Female ratio	3207.05	-0.28	0.2	-1.09, 0.52
Group size + group size <sup>2</sup>	3182	0.233 -0.02	0.11 0.008	0.01,0.45 -0.03,0.001
Rainfall	3159.74	0.01	0.003	0.006,0.02
Group size+	3148.7	0.04	0.03	-0.1, 0.09
Rainfall		0.01	0.003	0.006, 0.02
Rainfall* Female competition	3156.77	0.01	0.004	0.007, 0.02
<b>Relative group size* Drought (yes)</b>	<b>3135.76</b>	<b>-0.05</b>	<b>0.14</b>	<b>-0.34,0.23</b>
<b>Relative group size* Drought (no)</b>		<b>0.45</b>	<b>0.14</b>	<b>0.17,0.72</b>

**Table S6.4:** Complete model selection (QICc) of the main terms influencing emigration. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold. Data is based on 618 breeding years from 43 groups over the time period spanning 1978-2013

Term	QICC	B (effect size)	SE	Confidence interval
Basic	1181.73	-0.38	0.06	-0.5, -0.26
Group size	881.5	0.21	0.01	0.19, 0.24
relative Group size	901.18	1.3	0.09	1.13, 1.5
Group size + Group size <sup>2</sup>	883.16	0.25 -0.002	0.06 0.003	0.12, 0.37 -0.009, 0.005
Drought	1181.92	0.13	0.15	-0.15, 0.42
Number of fledglings	1161.14	0.07	0.02	0.03,0.11
<b>group size+</b>	<b>883.32</b>	<b>0.2</b>	<b>0.01</b>	<b>0.19, 0.24</b>
<b>Number of fledglings</b>		<b>-0.006</b>	<b>0.02</b>	<b>-0.04, 0.03</b>

**Table S6.5:** Complete model selection (QICc) of the main terms influencing immigration. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold. Data is based on 618 breeding years from 43 groups over the time period spanning 1978-2013

Term	QICC	B (effect size)	SE	Confidence interval
Basic	893.4	-0.8	0.009	-0.98, -0.06
Group size	800.28	-0.26	0.05	-0.36, -0.17
<b>relative Group size</b>	<b>798.06</b>	<b>-1.6</b>	<b>0.28</b>	<b>-2.1, -1.05</b>
Group size + Group size <sup>2</sup>	795.35	-0.52 0.02	0.12 0.009	-0.76, -0.28 0.004, 0.04
Drought	892.42	0.24	0.19	-0.14, 0.63
Number of fledglings	884.98	-0.07	0.03	-0.13, -0.02
Relative group size+ Number of fledglings	799.09	-1.6 -0.02	0.28 0.03	-2.1, -1.01 -0.08, 0.03

**Table S6:** Complete model selection (QICc) of the terms influencing the likelihood of group extinction on an annual basis. Group identity and breeding year were included as random terms. The models of greatest parsimony are highlighted in bold.

Data is based on 660 group-years for 43 groups and 36 extinction events over the time period spanning 1978-2013.

Term	QICC	B (effect size)	SE	Confidence interval
Basic	101.93	3.14	0.29	2.56, 3.52
Brood overlap	103.85	-0.23	0.79	-1.79, 1.3
Drought	103.7	0.340	0.69	-1.0, 1.7
Competition (total)	102.38	-0.61	0.6	-1.7, 0.57
Female competition	103.5	0.42	0.64	-0.84, 1.7
Male competition	103.4	-0.4	0.61	-1.6, 0.68
Group size	94.7	0.6	0.26	0.08, 1.11
Relative group size	97	2.59	1.33	-0.02, 5.2
Female ratio	101.002	-3.2	1.53	-6.21, -0.21
Rainfall	103.9	0.003	0.02	-0.32, 0.38
Number of individuals in the population per km <sup>2</sup>	102.29	0.384	0.3	-0.22, 0.98
Number of groups in the population per km <sup>2</sup>	100.87	3.54	1.8	-0.04, 7.14
Number of fledglings	96.8	0.35	0.14	0.07, 0.64
<b>Group size+ Number of fledglings</b>	<b>90.86</b>	<b>0.56 0.335</b>	<b>0.27 0.14</b>	<b>0.038, 1.08 0.067, 0.602</b>

## Appendix 5- Final ethics approval letter

Dear A/Professor Ridley,

2011/038	A/Professor Amanda Ridley (Biological Sciences)	Effect of group size and composition on individual behaviour, group dynamics and population regulation in the Arabian Babbler ( <i>Turdoides squamiceps</i> )
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### Decision

The Committee accepted the final report.

Your Final Report for the above project was considered and accepted at the Animal Ethics Committee meeting of 20 March 2014.

Thank you and all the best for your future research endeavours.

This email serves as official notification of the AEC decision. Please keep a copy for your records. Should you have any queries or require clarification, please contact the AEC Secretariat.

Regards,

**Professor Mark Connor**  
Chair, AEC

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CRICOS Provider Number 00002J



## ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2011/038-2

Date of Expiry: 30 September 2013

**Full Approval Duration: 1 October 2011 to 30 September 2014 (36 months)**

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry / is contingent upon receipt of a Final Report at the end of this period (see Approval email for submission details).

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**INPA director: Eli Amitay, Tel: 02-500-5403/4; Fax: 02-500-5409**

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

**Title of the project:** Effect of group size and composition on individual behaviour, group dynamics and population regulation in the Arabian Babbler (*Turdoides squamiceps*)

**Purpose:** 7 – Research: environmental study

**Aims:** To investigate how the impact of climatic and anthropogenic environmental changes on animal populations may be explained through their direct impact on individual development and group size.

**Surgical Procedure Category:** 1. Observation Involving Minor Interference

**All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.**

**Maximum numbers approved:**

Species	Strain	Age/Sex/Weight	Total	Supplier/Source
Birds	Arabian Babbler ( <i>Turdoides squamiceps</i> )	M/F	300	Field
		<b>TOTAL</b>	<b>300</b>	

**Location of research:**  
Shezaf Nature Reserve, Arava Region, Negev Desert, Israel

**Conditions of Approval:**

*All Permits/Licenses (to obtain and use fauna; to conduct research at interstate/overseas locations; to house animals, etc.) must be obtained prior to work commencing, and copies forwarded to the Animal Ethics Secretariat.*

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal supplier's license.

Prof Michael Gillings (Chair, Animal Ethics Committee)

Approval Date: 18 October 2012