

**An experimental approach to assess the role of nest  
predation in the population dynamics of the sociable weaver**

***(Philetairus socius)***

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## DEDICATION

I dedicate this dissertation to the glory of Jesus Christ, the Lord God Almighty, for His creation, provision and strength.

*“O LORD, You are my God;  
I will exalt You, I will give thanks to Your name;  
for You have worked wonders,  
plans formed long ago,  
with perfect faithfulness.”*

**Isaiah 25:1**

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## PLAGIARISM DECLARATION

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2. I will not allow anyone to plagiarise my work.
3. I have used a referencing and formatting style similar to the journal *African Entomology*.

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## ABSTRACT

Predation is a widespread population process that has been shown to affect the distribution, abundance and dynamics of populations in ecosystems. This is the first study that used an experimental approach to assess the effect of nest predation on the population dynamics of the sociable weaver (*Philetairus socius*), a keystone species in the semi-arid savannas of the Kalahari and Namib regions. Snakes were excluded from five colonies for five breeding seasons and two colonies for three breeding seasons, with another eight colonies acting as the controls. Reproductive output, colony size, dispersal events and several environmental variables were measured between 2010 and 2015. This was done to determine (1) what effect nest predator exclusion had on reproductive output; (2) how this related to colony and population size trends by using a matrix-projection metapopulation model; (3) how protected colonies influence movement patterns; and (4) if nest predation had a compensatory or positive effect by reducing the intraspecific competition of a colony. The fourth aim was investigated by tracking the foraging paths of eight colonies of varying sizes, with foraging distance acting as a proxy for intraspecific competition. Colonies that were protected from snake predation produced, on average, more than double the number of fledglings per female per breeding season that were produced in unprotected colonies. However, the magnitude of this effect decreased with increasing colony size of protected colonies, most likely due to the negative effects that large colony sizes have on reproductive output. Increasing aridity was found to have a negative effect on reproductive output and warmer winter minimum temperatures were found to have a positive effect. My results suggested that protecting a subset of colonies in the metapopulation may be sufficient in preventing population declines under climate change conditions. The protected colonies played an important role in structuring and connecting the movement network of the metapopulation, whilst colony size explained the migration rates of colonies. However, predation was not found to have a compensatory effect in reducing the intraspecific competition (measured as foraging distance) of a colony. Instead, foraging distance was probably determined by the ability to thermoregulate under hot and humid conditions. To fully understand the effects of nest predation on sociable weaver population dynamics, future studies need to investigate the response of snake predators to sociable weaver behaviour and environmental conditions.

**Key words:** coloniality, snake predation, reproductive output, metapopulation model, network analysis, connectivity, dispersal, compensatory effects, intraspecific competition, foraging distance, predator control, conservation and management

## INTRODUCTION

A main aim of conservation ecology is to describe, explain and understand the distribution and abundance of organisms (Begon *et al.* 1996). Population trends are determined by gains through reproduction and immigration and losses through death and emigration (Altwegg *et al.* 2014). Therefore, we are interested in how birth, death and migration cause variation in population size and the ways in which these demographic parameters are themselves influenced by social and environmental factors (Begon *et al.* 1996; Gaillard *et al.* 1998). Predation is a widespread population process that has been shown to affect the distribution, abundance and dynamics of populations in ecosystems (Bonsall & Hassell 2007). Predation affects prey species directly by removing individuals from the population (lethal effects) and indirectly by changing prey behavior (non-lethal effects; Lima & Dill 1990).

For birds in particular, the lethal effects of predation are thought to have a greater influence on pre-fledgling mortality than post-fledgling mortality (Côté & Sutherland 1997). This is because the egg and nestling stage of altricial or semiprecocial species are constrained to the nest site once the egg is laid, which limits options for predator evasion (Lima 2009). Reviews have found that over a third of nests are lost to predation in many bird species (O'Connor 1991; Martin 1993; Côté & Sutherland 1995). Several countries have controlled native predators for the purpose of increasing the population size of game birds (Potts 1986). For example, after six years of removing several predator species during the breeding season of the grey partridge (*Perdix perdix*), there was a significant increase in average brood size and fledgling numbers; which contributed to increasing the population size of protected sites (Tapper *et al.* 1996). The tradition of removing predators for game management has extended itself into conservation management, where practitioners control predators for the purpose of increasing the breeding population of a threatened prey species (Côté & Sutherland 1997). A meta-analysis looking at the effect of predator removal on the breeding performance and population size of prey species included studies that covered a variety of life-history traits and habitats (Smith *et al.* 2010). On average, the effect of predator removal resulted in a 77% increase in hatching success, a 79% increase in fledging success and a 71% increase in long-term breeding populations (Smith *et al.* 2010). This suggests that nest predation is an important limiting factor to the population growth of birds (Newton 1998).

The mere presence of a predator can influence prey demographics through changes in prey behaviour (Lima 2009). Calls, olfactory cues and direct sightings of predators are used by prey species to determine the perceived risk of an area (Lima 2009). In an experimental study where direct predation was removed, the calls and sounds of predators were played back to female song sparrows (*Melospiza melodia*) to manipulate perceived risk (Zanette *et al.* 2011). Females exposed to predator playbacks produced 40% fewer offspring per year than females that were not exposed as a result of changes in nest site selection, vigilance, nest attendance and foraging (Zanette *et al.* 2011). A particular non-lethal effect of predation on birds is a change in movement patterns so as to avoid nest predators (Cresswell 2008). This is because birds are flexible in their movements due to their ability to fly (Cresswell 2008). For example, female black kites (*Milvus migrans*) that moved between breeding seasons to territories with lower risk of nest predation had a significantly higher breeding success than when they bred in territories with a high predation risk (Forero *et al.* 1999). Male Tengmalm's owls (*Aegolius funereus*) that were exposed to simulated nest predation risk by pine marten (*Martes martes*) increased nest-hole shift and breeding dispersal distance compared to control males (Hakkarainen *et al.* 2001). Adult birds may also select sites that have a lower risk of post-fledgling predation. A community-based study on a farmland area in western Finland found that the breeding density of migratory birds was higher on sites that were more than 1 km from the nearest European kestrel (*Falco tinnunculus*) nest, which is outside the hunting range of the raptor (Suhonen *et al.* 1994). However, the avoidance of predators carries a fitness cost in that the breeding density of prey species is higher in areas without predators, thus increasing competition for shared resources (Hernandez & Laundre 2005; Cresswell 2008). In addition, the energetic costs of anti-predator behaviour may also divert resources away from reproduction (Thomson *et al.* 2006; Cresswell 2008).

The effects of predation are not always so predictable. Predators that target young age classes may have less of an effect than predators that target older age classes, because young individuals may not be contributing to the reproductive output of the prey population (FitzGibbon 1990; Begon *et al.* 1996; Cresswell 2011). Predation may not contribute to the overall mortality rate of the prey species, because of compensatory effects (Cresswell 2011). For example, populations of blue tit (*Cyanistes caeruleus*) at Wytham Wood, Oxford, have remained constant regardless of the presence or absence of sparrowhawks (*Accipiter nisus*; Perrins & Geer 1980). Newly fledged blue tits already have a low chance of survival as they

compete with adults for food during winter. When fewer sparrowhawks are present, density-dependent intraspecific competition is intensified as a result of increasing blue tit numbers; resulting in a greater mortality rate of blue tits. In fact, the effect of predation is often nullified by the positive effect that it has on intraspecific competition (Begon *et al.* 1996). For example, in an experiment in which a large number of woodpigeons (*Columba palumbus*) were shot, the overall winter mortality rate did not increase, nor did pigeon abundance increase when shooting ceased (Murton *et al.* 1974). By reducing the density of pigeons, intraspecific competition for food was reduced and there was an increase in the immigration rate of pigeons to take advantage of the unexploited resources. Thus, the number of pigeons surviving locally was ultimately determined by competition (food availability), not predation. Extreme weather events can also have an overriding effect on pre-fledgling and post-fledgling mortality, regardless of prey and predator density (Newton 1998). This is because weather acts in a density-independent manner and normally affects birds indirectly by acting through habitat quality and resource availability (Olsen & Olsen 1989; Newton 1998). For example, the number of fledglings produced by the western kingbird (*Tyrannus verticalis*) in North America was correlated to insect abundance, which was dependent on the amount of rain that fell during the preceding year (Blancher & Robertson 1987).

Sociable weavers (*Philetairus socius*) are facultative colonial breeders that build large communal haystack-like nests, with separate breeding chambers (Maclean 1973b; Covas *et al.* 2008). Local populations often consist of several nest masses or breeding colonies that make up a metapopulation (Altwegg *et al.* 2014). This system provides an ideal opportunity to study the effects of social and environmental factors on population dynamics. The weavers are considered a keystone species in the semi-arid savannas of the Kalahari and Namib regions of southern Africa (Maclean 1973a; Mendelsohn & Anderson 1997). The nest chambers are inhabited by several communalistic symbionts, including a diverse community of invertebrates, lizards and birds (Maclean 1973c; Craig 2010). Predators, such as snakes and African pygmy-falcons (*Polihierax semitorquatus*), may also take up residence and consume eggs and nestlings (Maclean 1973c; Covas *et al.* 2004a; Covas *et al.* 2008). However, the vital role that sociable weavers play in this semi-arid ecosystem is uncertain given future climate change predictions. The conditions of the southwestern regions of southern Africa are predicted to become drier and warmer, with maximum increases in temperature focused over the Kalahari Desert (Moise & Hudson 2008). Already, populations

of sociable weaver have been observed to be declining as a result of increasing aridity (Altwegg *et al.* 2014). Although changes in habitat quality and resource availability may be the primary cause of population decline, predation can act as a secondary exacerbating factor that keeps prey numbers below carrying capacity (Côté & Sutherland 1997). To determine if predation acts as a secondary exacerbating factor requires an understanding of how predation affects the parameters that determine population trends and how predation interacts with other social and environmental factors (Evans 2004).

Previous studies have found that the survival and reproductive output of sociable weavers are strongly affected by social and environmental factors. The survival of adult sociable weavers increases with increasing rainfall and minimum temperature and decreases with increasing maximum temperature (Altwegg *et al.* 2014). Reproductive output, measured as clutch size and fledgling success, is also influenced by rainfall (Covas *et al.* 2008; Altwegg *et al.* 2014). Rainfall is an important driver of population dynamics in semi-arid environments, because it is related to food availability (Noy-Meir 1973; Altwegg *et al.* 2014). Increasing colony size has a positive effect on juvenile (yearling) and adult survival and a negative effect on reproductive output (Brown *et al.* 2003; Covas *et al.* 2008). Fewer eggs and nestlings successfully hatch and fledge in large colonies for pairs breeding alone, but this effect is ameliorated when helpers are present (Covas *et al.* 2008). Coloniality can have potential foraging-related costs, because all of the birds in the colony are conspecifics with similar food requirements (Wittenberger & Hunt 1985). A larger colony may deplete local resources and have to travel further in search of food or spend more time and energy searching nearby areas than a smaller colony (Brown & Brown 1996). The more time away from the nest may reduce breeding success, due to deficient incubation or nestling malnutrition (Brown & Brown 1996). Foraging further away from the colony may also reduce survival by increasing the chances of being caught by a predator, as a greater distance needs to be covered to reach the safety of the colony (K. Lloyd pers. obs). Sociable weavers may disperse to other colonies when the colony size is below the long-term mean and close to extinction (Altwegg *et al.* 2014). Dispersing individuals are more likely to immigrate into colonies that are in close proximity and relatively small in size (Altwegg *et al.* 2014). One potentially important environmental factor that affects reproduction and may affect survival and dispersal, but has not been studied experimentally, is the role of nest predation.

Snake predation, primarily by Cape cobras (*Naja nivea*) and boomslangs (*Dyspholidus typus*), is responsible for 70% of sociable weaver nesting failures in the southern part of the bird's distributional range (Covas *et al.* 2008). To determine the role of snake predation as a driver of population growth of sociable weavers, snakes were excluded from five colonies for five breeding seasons and two colonies for three breeding seasons, with another eight colonies acting as the controls. The metapopulation that was studied has been declining in size over the past two decades, most likely due to increasing aridity (Altwegg *et al.* 2014). Specifically, I wanted to determine how the impact of predation scales up to the metapopulation level by asking the following:

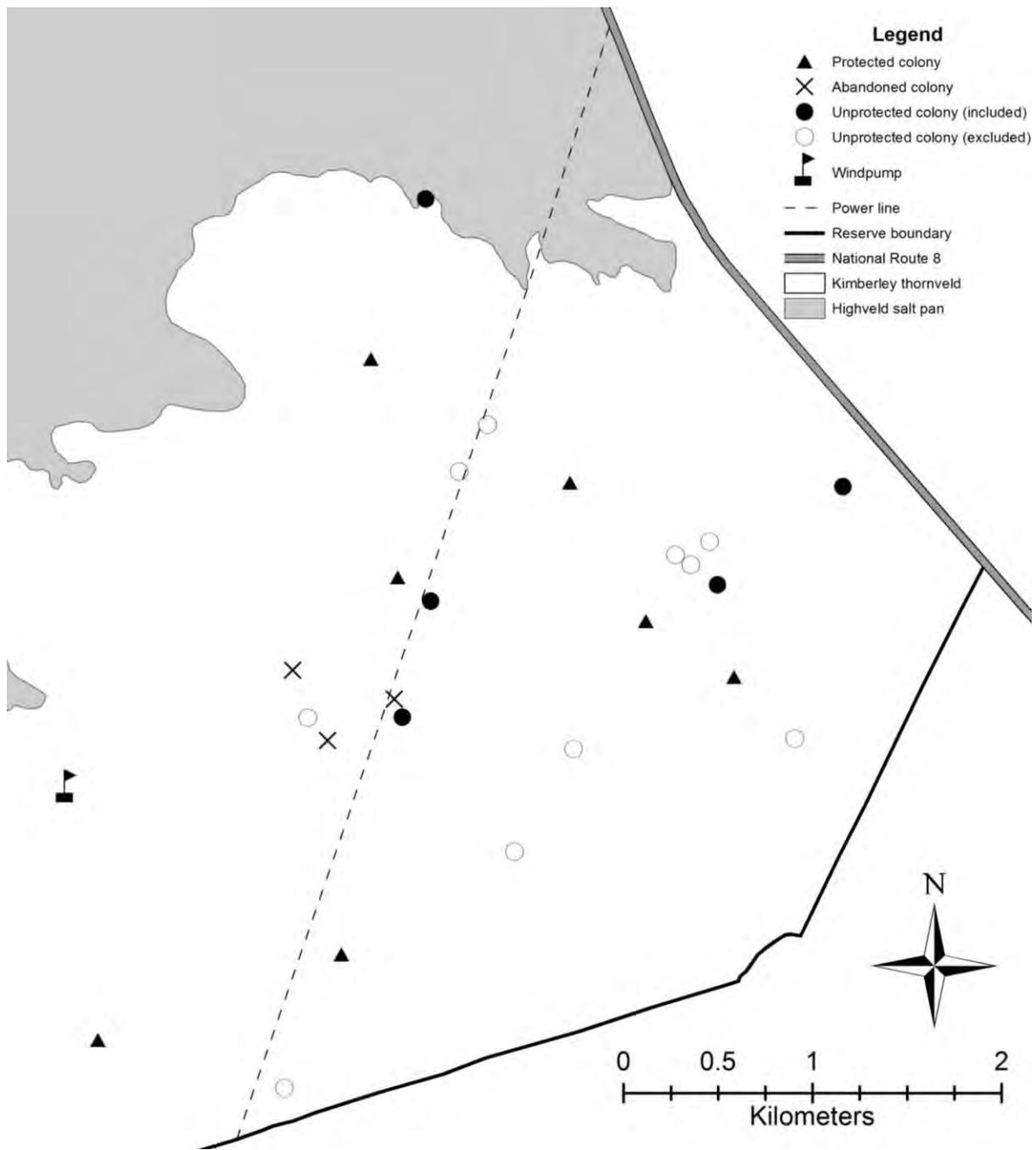
1. What effect does nest predator exclusion have on reproductive output and what combination of social and environmental factors best explains reproductive output? Does nest predation have a greater effect than colony size (intraspecific competition) or do both factors play an important role in determining reproductive output? Does the effect of low rainfall in a semi-arid environment negate the effect of nest predation?
2. How does this relate to colony and population size trends? Can nest predator exclusion be used as a conservation management tool to prevent the current and future decline of the sociable weaver population as a result of increasing aridity?
3. How does nest predator exclusion influence the movement patterns of dispersing birds and the migration rate of a colony? What is the importance of protected colonies in structuring and connecting the sociable weaver movement network?
4. Could nest predation have compensatory effects by reducing the intraspecific competition of a colony? Do birds from larger colonies have to travel further in search of food, because resources in the immediate vicinity of the colony are depleted?

## METHODS

### Study area & species

The study took place at Benfontein Nature Reserve near Kimberley, South Africa (28°53'S, 24°89'E). The reserve is situated in the southernmost end of the Kalahari Basin. The study area covers *ca.* 15 km<sup>2</sup> and contains a total of 22 sociable weaver colonies (Covas *et al.* 2008; Figure 1). The vegetation is classified as Kimberley thornveld, which comprises open savanna dominated by *Stipagrostis* grasses and the camelthorn tree *Vachellia erioloba* (Rutherford *et al.* 2006; Covas *et al.* 2008; Figure 2a). The mean monthly temperature for January and July is 37.5 °C and -4.1°C, respectively (Rutherford *et al.* 2006). Rainfall in the area is low (mean±SD 431±127 mm/year) and unpredictable, though usually falls during the summer months when breeding takes place (Covas *et al.* 2008).

The sociable weaver is endemic to southern Africa, with a range that closely follows the distribution of southern Kalahari savanna (Maclean 1973a; Mendelsohn & Anderson 1997). The duration of the breeding season (0-10 months), number of broods (1-4 broods) and clutch size (2-4 eggs) at the study site is dependent on rainfall, which is irregular in this area (Covas 2002; Covas *et al.* 2008; R. Covas unpubl. data). Juveniles often remain with their natal colony during their first year to help raise the offspring of their parents (Covas *et al.* 2006). The nest masses buffer the sociable weavers, symbionts and predators inhabiting the nest chambers from the extreme air temperatures of summer days and winter nights (Maclean 1973d; White *et al.* 1975; Bartholomew *et al.* 1976). Cooperation within each colony is maintained through dominance hierarchy, which is determined by a number of individual characteristics such as the bib patch size below the bill (Rat *et al.* 2015). Movement habits are regarded as sedentary, with the dispersal of individuals being confined to the metapopulation, thus forming a relatively closed system (Maclean 1973a). They forage primarily on insects (mainly termites) and seeds, the proportions of which vary seasonally (Maclean 1973d; Craig 2010). Sociable weavers forage in flocks on the ground, usually within 1.6 km of the colony (Maclean 1973d). Foraging occurs between sunrise and sunset, with the main feeding times taking place during early morning and late afternoon (Maclean 1973d).



**Figure 1:** A map of the study site showing the position of the sampled and active colonies of the 2015 census. Protected and abandoned colonies (unprotected) were included in the study, but not all of the active unprotected colonies were included. All colonies were built in the canopies of *Vachellia erioloba*. (esri, ArcGIS v.10.0)



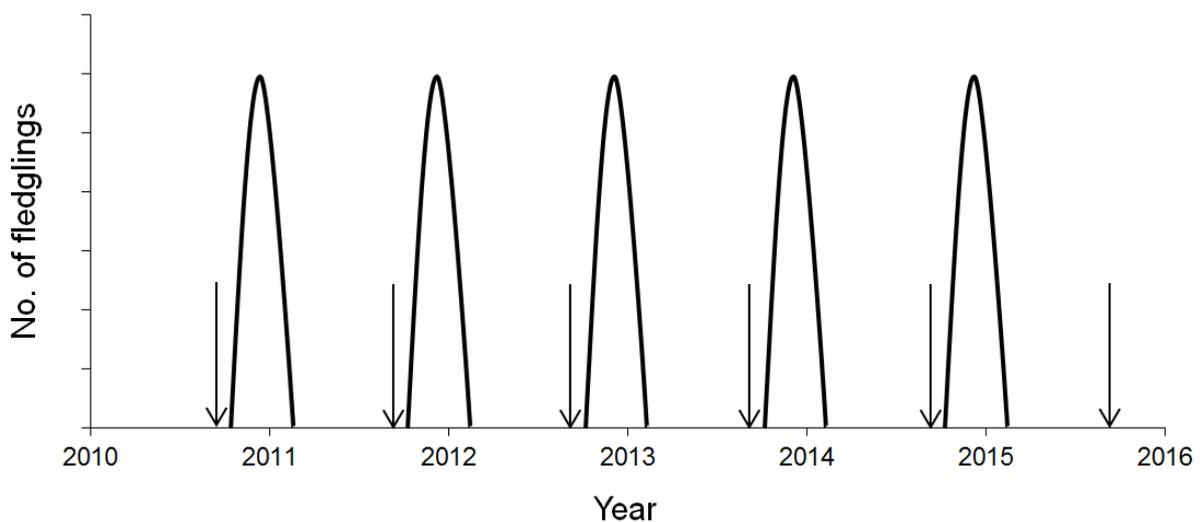
**Figure 2:** (a) The landscape of the study site consists of a continuous herbaceous layer of *Stipagrostis* grasses and a discontinuous arborescent layer of camelthorn tree *Vachellia erioloba*. The sociable weaver colony in the foreground has been protected from snakes by wrapping cling wrap around the trunk of the tree. (b) Nests inhabited by sociable weavers were identified with a numbered plastic tag that was screwed into the nest mass with a wire spiral.

## Study design

### 1. Response of reproductive output to predator exclusion and other social & environmental factors

#### *Predator exclusion*

Snakes were excluded from seven randomly selected colonies during breeding seasons by wrapping cling wrap around the main trunk of the trees housing the colonies before the start of the breeding season (Figures 1, 2a & 3). Trees that were in close proximity to neighbouring canopies, had low reaching branches and/or had many bushes below which could provide snakes with access to the colony were excluded from the selection pool. The smooth surface of the cling wrap prevented snakes from gaining traction when they attempted to climb the tree. The protection proved to be extremely effective in excluding snakes and only on four occasions were snakes seen entering through damaged cling wrap (R. Covas pers. obs.). Five of the seven colonies were protected for five consecutive breeding seasons between 2010 and 2014. The remaining two colonies were protected for three consecutive breeding seasons between 2012 and 2014. Eight colonies were randomly selected from the remaining trees and acted as the controls.



**Figure 3:** A hypothetical timeline showing the dates when sampling took place. Arrows indicate when colonies were captured for annual census data and cling wrap was applied to trees to exclude nest predators before the breeding season. The humps indicate the breeding season when breeding data was collected. The breeding season of a particular year ranged from the date the first egg was laid near the end of the year until the date the last nestling fledged the following year.

### *Reproductive output*

To estimate reproductive output, all nest chambers in each colony were identified with a numbered plastic tag before the start of the breeding seasons between 2010 and 2014 (Figures 2b & 3). During a breeding season, all nest chambers were inspected at five day intervals to detect the initiation of new clutches. Nest chambers were accessed from the roof of a pick-up truck or ladder and the inside of a nest chamber was checked by carefully extending a small mirror fitted with LED lights through the chamber entrance. Female sociable weavers lay the eggs of a clutch at one-day intervals (Covas *et al.* 2008). Therefore, a nest chamber was visited for at least four consecutive days after the supposed laying date of the first egg. Each egg in a clutch was marked with a pencil and weighed. Clutches were checked daily near the hatching date (15 days after being laid), until all of the remaining eggs in the clutch had hatched. The nestling period is 21-24 days (Maclean 1973e). Nestlings were marked on the 4<sup>th</sup> and 9<sup>th</sup> day by plucking specific feathers from the body and attaching a uniquely numbered SAFRING aluminium band, respectively. If disturbed from the 18<sup>th</sup> day onwards, the nestlings will usually fledge prematurely (Covas *et al.* 2008). Therefore, the nest chamber was visited for the last time when the oldest nestling was 17 days old and it was assumed that the number of nestlings present was the number of young that fledged from that clutch. The number and fate of the eggs and nestlings in a brood were recorded upon each visit to the nest chamber.

### *Colony size*

In addition to protection status (i.e. nest predator exclusion), several social and environmental variables were measured to explain reproductive output. Colony size was determined by capturing the resident birds in each colony at the beginning of the breeding season by placing mist nets around the colony before sunrise (Figure 3). As the sun rose, birds were flushed from their nest chambers and were caught in the nets. Birds that escaped were counted to estimate the total colony size. For birds that were caught, each bird was marked with a uniquely numbered SAFRING aluminium band and a unique plastic colour band combination. Marked individuals from previous sampling attempts were recorded, along with the identity of their resident colony. Blood samples (*c.* 10  $\mu$ l) were also taken to determine the sex of each individual.

## *Rainfall*

I used weather data collected by the South African Weather Service at Kimberley airport, approximately 12 km northwest of the study site (Altwegg *et al.* 2014). I used the literature and observations at Benfontein Nature Reserve to determine the window period over which to record rainfall data. Sociable weavers in more arid parts of the Kalahari were found to respond almost immediately to rainfall by breeding only six days after rain had fallen (Maclean 1969). Over 20 mm of rain had to fall within one month to induce a response (Maclean 1969; Maclean 1973e). The sociable weavers bred almost all-year round as they tracked rainfall events with breeding attempts. However, the sociable weavers at Benfontein Nature Reserve, which is situated in a more mesic part of the Kalahari, have a more predictable breeding season starting normally at the end of September (Covas 2002; K. Lloyd pers. obs.). In addition, the rainfall at Benfontein Nature Reserve normally falls between October and April (Rutherford *et al.* 2006). A study investigating the breeding times of several bird species in the Kalahari found that insectivorous birds have predictable breeding times, because they breed before the rains have fallen with the expectation that rain will eventually fall and there will be a peak in insect abundance when grasses grow green tissue and produce seeds (Maclean 1969). Insects have also been observed to breed in spring and summer in the absence of rain (Lloyd 1999; K. Lloyd pers. obs.) Insectivorous birds have a longer breeding season than granivorous birds, because insects are more difficult to find than the abundance of seeds available after rain has fallen (Maclean 1969). As the diet of adult sociable weavers consists of ~80% insects (Maclean 1973d), the nestlings are fed only insects (Maclean 1973e) and the breeding season at Benfontein starts predictably at the end of September, I think that the sociable weavers at Benfontein Nature Reserve respond in a similar way to the insectivorous birds described above.

I decided that the window period for recording rainfall for each breeding season would be 100 days after the first egg was laid. If sociable weavers at Benfontein Nature Reserve lay their first clutch of eggs independent of rainfall, then recording rainfall before this date would be pointless. The mean ( $\pm$ SD) number of broods laid during 2013 (the longest breeding season) and 2014 were  $2.8 \pm 1.9$  and  $2.0 \pm 1.1$ , respectively. It takes approximately 35 days to develop from egg to fledgling and 32 days to recover between successful broods (Covas *et al.* 2008). The decision to lay a second clutch of eggs would depend on whether there is a sufficient amount of insects to raise the brood. If it did not rain between the time of the first

brood and the time to lay a second clutch of eggs, there would not be enough food to support a large number of insects. Therefore, the decision to lay a second clutch of eggs and successfully raise it would be indirectly dependent on rainfall. Hence, a 100-day period is enough time to raise the first brood, make the decision to lay a second clutch of eggs and successfully raise it to fledgling stage.

### *Temperature*

Minimum temperature during winter has been found to influence the number of individuals breeding, fledgling success and the number of fledglings produced during the following breeding season (Mares *et al.* unpubl. data). The mean minimum temperature was recorded between June and July before each breeding season (Mares *et al.* unpubl. data). I did not record the maximum temperature for the duration of the breeding season, because breeding seasons varied between 5 and 9 months. The mean maximum temperatures of breeding seasons of long duration were found to be much lower than breeding seasons of short duration, because autumn and winter months were included in the breeding seasons of long duration. Instead, I recorded the number of days above 35 °C; the temperature above which the resting metabolic rate of sociable weavers increases linearly and significantly (Whitfield *et al.* 2015).

### *Statistical analysis*

One of the aims of this study was to determine which social and environmental variables affect reproductive output and which variable(s) was the best predictor of reproductive output with a focus on nest predator exclusion. Therefore, analyses involved statistical tests and model selection.

Reproductive output was compared between protected and unprotected colonies and correlated to social and environmental variables using generalised linear mixed models. Reproductive output was measured as the number of fledglings produced in a particular year (or breeding season) by each colony. The number of fledglings followed a Poisson distribution, which was confirmed by plotting the residuals of each model. Fixed effects included protection status, colony size, rainfall, mean winter minimum temperature and the

number of hot days ( $>35$  °C). A correlation analysis was conducted to determine if there was collinearity among the variables being treated as fixed effects (Zuur *et al.* 2010).

Collinearity between protection status and colony size was checked by calculating the mean and 5<sup>th</sup> & 95<sup>th</sup> percentile of colony size of protected and unprotected colonies. Colony identity and year were treated as random effects to account for variation in reproductive output among colonies and years that were not explained by the fixed effects. A constant model, which only allowed for a random colony identity and year effect, was also included to determine if the models with fixed effects explained more variation in reproductive output than some other variable. In addition, the logarithm of the total number of adult females in each colony was used as an offset to control for differences in the number of reproductive females among colonies and years; as a larger number of reproductive females would inherently produce more fledglings. Effectively, the unit of reproductive output of a colony was the number of fledglings per female per breeding season. The number of females was determined by calculating the sex ratios of each colony between 2010 and 2014 from the census data. The average sex ratio was calculated only for colonies that had 20 or more birds sexed as a small sample size would skew the data substantially. The average sex ratio of females to males was 1:1.1, so I assumed that 50% of the birds in a colony were female. Additive models and interactions between protection status and the social and environmental variables were also investigated, along with the interaction between rainfall and mean winter minimum temperature.

The second-order Akaike's information criterion ( $AIC_c$ ) was used to determine which variables or combination of variables best explained reproductive output (Akaike 1973; Anderson *et al.* 2001). The estimated  $AIC_c$  differences (the model  $AIC_c$  minus the smallest  $AIC_c$  across all candidate models,  $\Delta AIC_c$ ), the weights (the relative support a model has from the data compared to other models,  $w_i$ ), number of parameters ( $K$ ) and maximised log likelihoods (logLik) were calculated for each model. All statistical analyses were performed with the statistical software R, v.3.2.1 (R Development Core Team 2015, *lme4* package).

## 2. Simulating the effect of nest predator exclusion and climate change on population trends

A matrix-projection metapopulation model was developed by Altwegg *et al.* (2014) to examine how external and internal drivers affect the population dynamics of the sociable weaver population at Benfontein Nature Reserve. The model takes into consideration the survival and reproduction rates of each colony (or sub-population) and the movement of individuals among them. The drivers that were investigated by Altwegg *et al.* (2014) included weather, year, research-induced disturbance, colony size and colony identity. Similarly, I used the model to determine if nest predator exclusion could be used as a conservation management tool to prevent the current and future decline of the sociable weaver population as a result of climate change. This was done by projecting colony growth under different climatic scenarios with and without nest predator exclusion from the 2010 census until the end of the study period. As nest predator exclusion would have the greatest and most direct effect on reproductive output, I manipulated the number of fledglings produced per female per breeding season based on the predictions from the models that were developed to determine reproductive output in my previous analysis. The projections of the various climatic scenarios allowed me to calculate an overall population growth rate ( $\lambda$ ) to determine if nest predator exclusion can offset the detrimental effect of aridity.

Of the seventeen colonies studied by Altwegg *et al.* (2014), eight were monitored from 2010 onwards and were included in the metapopulation model: four colonies were unprotected for five years, three colonies were protected for five years and one colony was unprotected for two years and then protected for three years. To calculate colony size in year  $t$ , the colony size in the previous year ( $n_{t-1}$ ) is multiplied by the projection matrix  $A$ , where  $n_t$  is a vector holding the colony sizes in year  $t$ .

$$n_t = A n_{t-1}$$

$$\text{where, } A = \begin{bmatrix} R^{11} & \dots & R^{p1} \\ \vdots & \ddots & \vdots \\ R^{1p} & \dots & R^{pp} \end{bmatrix}$$

and  $p$  = number of colonies

Each element in the matrix can be represented as  $R^{rs}$ , the contribution of colony  $r$  to colony  $s$ . If  $r = s$ ,  $R$  is the rate of self-recruitment and self-retention.

$$R^{rs} = \phi_A^{rs} + \beta^r \phi_J^{rs}$$

where,

$\phi_A^{rs}$  is the probability of an adult bird in colony  $r$  surviving and moving to colony  $s$ ,  
 $\phi_J^{rs}$  is the probability of a juvenile bird in colony  $r$  surviving and moving to colony  $s$ ,  
and  $\beta^r$  is the number of fledglings produced per female in colony  $r$ .

The survival estimates calculated by Altwegg *et al.* (2014) for colonies between 1993 and 2009 were used in this study due to lack of time to calculate more recent estimates. Juvenile (yearling) survival estimates were assumed to be half of adult survival in the model used by Altwegg *et al.* (2014). I increased juvenile survival to 70% of adult survival, because juvenile sociable weavers at Benfontein Nature Reserve have been found to have high survival rates once they have fledged (above 0.92, Covas *et al.* 2011). The benefits of prolonged parental care and delayed dispersal result in survival rates that are similar to those of adults (Covas *et al.* 2004b). Movement estimates were calculated using the model developed by Altwegg *et al.* (2014). The model predicts the probability of adult sociable weaver movement ( $m$ ), using measurements of distance and colony size as the explanatory variables:

$$\text{logit}(m) = -3.67 - 0.0016 \times a - 0.013 \times b - 0.0021 \times c + 0.0003 \times c^2 - 0.0115 \times d - 0.00004 \times d^2$$

$a$  = distance (m) between colony of origin and destination

$b$  = delta colony size (origin – destination)

$c$  = colony size of origin relative to its mean

$d$  = colony size of destination relative to its mean

The models that were used to predict reproductive output were (1) the AIC<sub>c</sub> best model (interaction between protection status and colony size) to simulate current conditions; (2) the interaction between protection status and rainfall to simulate future aridity; (3) the interaction between protection status and mean winter minimum temperature to simulate future warmer winter temperatures; and (4) the interaction among protection status, rainfall and mean winter minimum temperature to simulate both aridity and warmer winter temperatures. I investigated rainfall and mean winter minimum temperature separately to determine the effect that each has on colony size trends before considering both factors together. The protection status of

the colonies for each of the four models or scenarios was: no protection for any of the colonies, actual protection conditions and protection for all of the colonies. The values used to simulate aridity and warm winter temperatures were one standard deviation below the mean rainfall ( $82.7 \pm 46.85$  mm) and above the mean winter minimum temperature ( $0.22 \pm 0.81$  °C) observed between 2010 and 2015, respectively. This was done so that changes in rainfall and winter minimum temperature were comparable. The fit of the models for each colony was compared to observed changes in colony size. The overall population growth rate ( $\lambda$ ) was used to project population size trends with a starting value of 100 individuals in the population of each scenario.

### **3. Response of movement to nest predator exclusion and other social & environmental factors**

#### *Movement patterns & migration rate*

The movement of individuals among colonies between 2011 and 2015 was examined using descriptive and statistical methods to determine if protected colonies influenced the movement patterns and migration rates of dispersing birds. A social network analysis was used to visualise movement over the entire metapopulation and to assess the level of connectivity and centrality. Connectivity refers to the movement of individuals through the metapopulation and centrality refers to the structural importance of each colony in the network (Janssen *et al.* 2006). Model building was used to determine which factors determined the number of immigrants per capita that entered a colony and the number of emigrants per capita that left a colony for a subset of the colonies in the metapopulation. The subset consisted of the same colonies that were analysed for reproductive output, because annual census data were collected for these colonies before the breeding season between 2011 and 2015. Colony 21 was excluded from the statistical analysis, because birds recolonised the nest after it had been previously abandoned. This behaviour is generally unusual for dispersing individuals and was regarded as an anomalous case. The identity and resident colony of each bird sampled from the annual censuses were used to detect the movement of individuals between sampling events (or years). If an individual was found to have moved between colonies during the study period, the earliest year that gave evidence of this transition was assumed to be the year that the bird emigrated from its previous colony and immigrated into its new colony.

### *Network analysis*

A network analysis consists of nodes (sub-populations) connected by edges (movement paths). Colonies represented the nodes and recapture data defined the edges that linked the nodes. One-thousand random networks were generated in R (*igraph* package) using the Erdős-Rényi algorithm and the same number of nodes and edges as the observed network to determine if the observed connectivity scores differed from the average connectivity scores of the random networks (Erdős & Rényi 1959; Calder *et al.* 2015). If the observed connectivity scores are different from the average scores of the random networks, there would be some factor(s) controlling sociable weaver movement. The connectivity scores that were used were the network's diameter (indicates how easily and far an individual can move across the network) and average path length (indicates how many edges have to be travelled to reach any other node in the network; Boccaletti *et al.* 2006).

The community structure (or modularity) of the network was assessed using two different methods, with the results of each method visualised in a different layout. The first method used to identify communities was the Louvain Method in Gephi v.0.8.2 (Blondel *et al.* 2008), with colonies being displayed in their spatial context using global positioning system (GPS) co-ordinates (Geolayout plugin; Bastian 2012). The second method used the Walktrap algorithm in R (Pons & Latapy 2006), with colonies being positioned according to the Fruchterman-Reingold algorithm; a force-directed layout algorithm where the sum of the edges between nodes uses a spring action to determine in which direction a node should move (Maciejewski & Cumming 2015). This layout overcomes the problem that nodes connected by an edge should be drawn close to one another, but not too close, with the distance between nodes dependent on the number of nodes and space available in the network (Fruchterman & Reingold 1991). The Louvain Method and Walktrap algorithm differ in that the former is faster and more accurate in identifying communities (Aynaoud & Guillaume 2010).

Measurements of centrality were calculated for each colony in Gephi. These included betweenness centrality (indicates the importance of a node in connecting various different parts of the network together), closeness centrality (indicates how close a node is to all of the

other nodes in the network) and eigenvector centrality (indicates how well-connected a node is to other highly connected nodes in the network; Valente *et al.* 2008). I intended to determine the centrality scores of protected colonies before snakes were excluded; however, there were not enough individual movements between 2008 and 2010 to construct a network.

### *Statistical analysis*

The immigration and emigration rates (number of immigrants and emigrants per resident individual in the focal colony) were correlated to colony size and compared between colonies with and without protection and African pygmy-falcons using generalised linear mixed models. It is thought that African pygmy-falcons inhabiting a colony cause sociable weavers to emigrate from the colony (Covas *et al.* 2004a). Collinearity among fixed effects was checked by calculating the mean and 5<sup>th</sup> & 95<sup>th</sup> percentile of colony size of colonies with and without protection and African pygmy-falcons. The number of immigrants and emigrants followed a Poisson distribution, which was confirmed by plotting the residuals of each model. Colony identity and year were treated as random effects to account for variation in movement among colonies and years that was not explained by the fixed effects. In addition, the logarithm of the colony size was used as an offset, as a larger colony would naturally have more immigrants and a greater nest size to receive more emigrants than a smaller colony.

## **4. Foraging distances & behaviour of sociable weavers (the effect of colony size on intraspecific competition)**

### *Tracking foraging paths*

Predation may have an indirect positive effect on survival and reproduction by reducing intraspecific competition within a colony. Foraging distance was used as a proxy for intraspecific competition, because of the reproductive and survival costs associated with travelling further away from the colony (Brown & Brown 1996). In addition, the foraging behaviour of sociable weavers in this system had never been described before. The association between foraging distance and colony size was determined from daily tracking sessions. Eight colonies of varying sizes were selected and followed before the start of the breeding season (before eggs were laid) from mid-September to mid-October 2015. Flocks

were followed when the birds left their colony just after sunrise, so that the colony identity of the flock was known. The flock was then followed from a distance that did not disturb the birds' behaviour using binoculars (UltraOptec, S1–10x50 WA). The GPS co-ordinates (Garmin eTrex) were recorded at the center of each feeding station as the foraging trajectory of the flock was followed. A feeding station qualified as the area that the flock flew to and landed in. The distance covered by the flock whilst on the ground was not recorded, because the birds were hidden by the grass canopy. Therefore, the flock was only visible when flying between feeding stations. If the flock divided, the larger portion was followed. The flock was followed for at least 2 hours, unless the flock returned to its colony after tracking it for at least 1.5 hours. The start and end time of each tracking session was recorded. At the end of each tracking session, observations of the foraging behaviour of the birds that were noted whilst tracking were recorded. This was done twice for each of the eight selected colonies. No further replicates could be collected as there was a sudden peak in insect abundance and activity after the second replicate was completed, which altered the foraging behaviour of the birds.

Several social and environmental variables were measured to explain foraging distance. Census data for 2015 were used to determine colony size. Tree density was included because most of the feeding stations were underneath tree canopies, which may affect foraging distance. Tree density was estimated by counting the number of trees in a 500 m radius around each colony on Google Earth (AfriGIS 2015) and expressed as the number of trees per km<sup>2</sup>. Weather data were also collected from the weather station at the Kimberley airport. Temperature and humidity data were recorded at five-minute intervals and the mean temperature and relative humidity were calculated for the duration of each tracking session. The minimum and maximum temperatures of each tracking session were also recorded.

### *Statistical analysis*

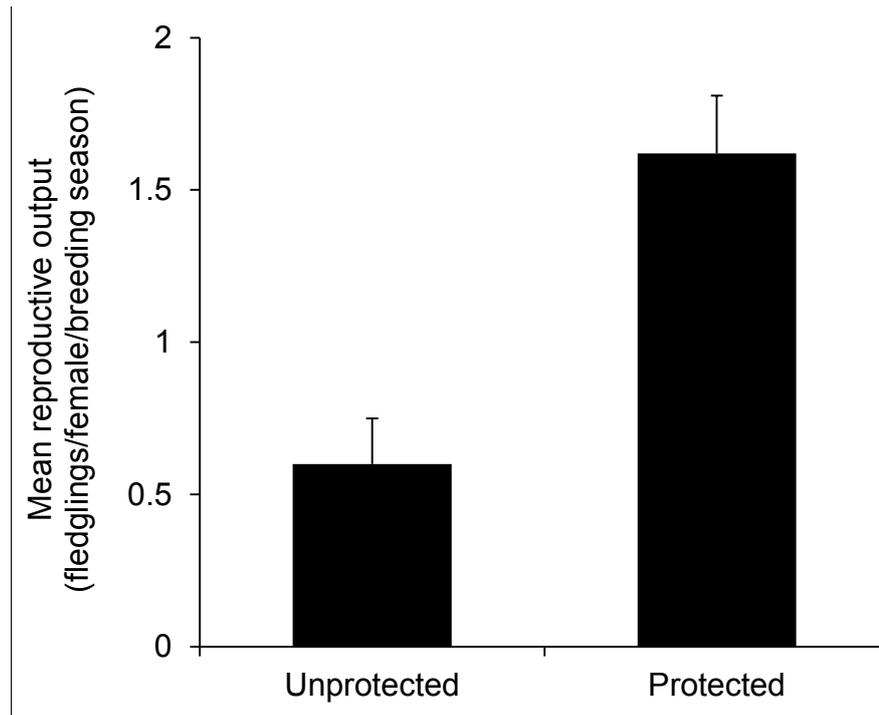
Statistical tests and model building were used to determine which variable best explained foraging distance. Foraging distance was correlated to social and environmental variables using linear mixed-effects models. The foraging distance of each colony was measured as the sum of distances between feeding stations. The sum distance travelled followed a normal distribution and the assumptions of normality (Shapiro-Wilk W-test) were confirmed

(Shapiro & Wilk 1965). A correlation analysis was conducted to determine if there was collinearity among fixed effects. Fixed effects included colony size, tree density, mean temperature, minimum temperature, maximum temperature and mean relative humidity. Colony identity was treated as a random effect to account for variation in foraging distance among colonies that was not explained by the fixed effects. A constant model, which only allows for a random colony identity effect, was also included to determine if the models with fixed effects explained more variation in foraging distance than some other variable. The interaction between maximum temperature and humidity was also investigated, because the ability of sociable weavers to dissipate heat was found to be inhibited during high ambient temperature and humidity (Gerson *et al.* 2014). The AIC<sub>c</sub> values were used to determine which combination of explanatory variables best explained foraging distance.

## RESULTS

### 1. Response of reproductive output to predator exclusion and other social & environmental factors

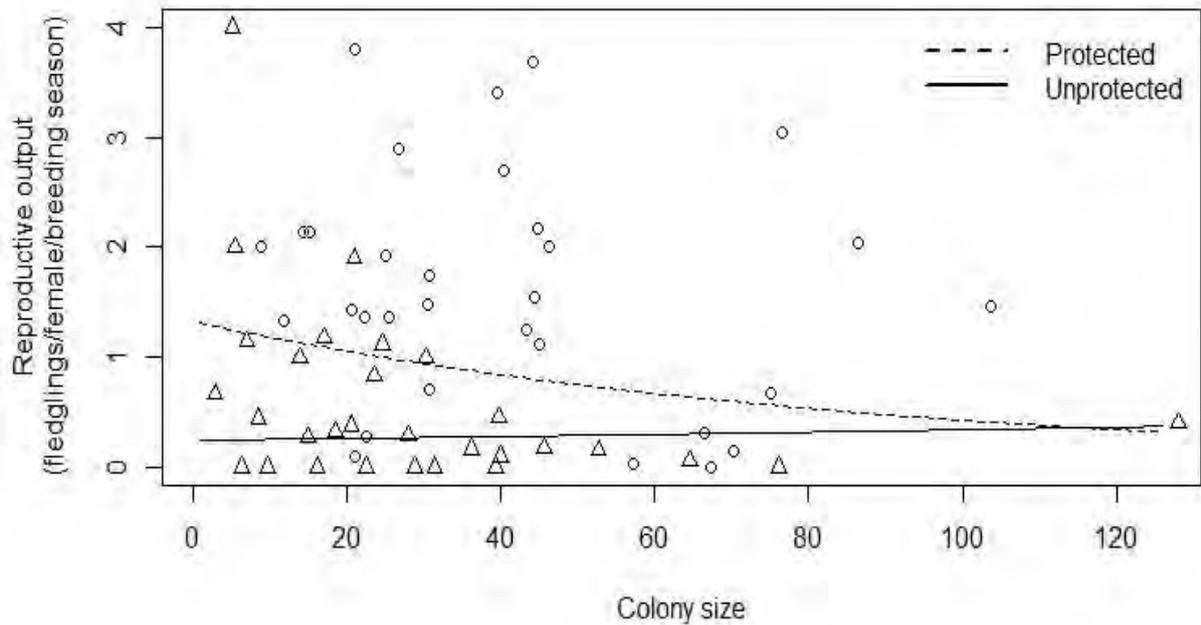
There was no strong correlation (all  $-0.5 < r < 0.5$ ) among the variables treated as fixed effects, other than the correlation between rainfall and the number of hot days ( $r=0.84$ ). The mean colony size of protected colonies (41.16 birds) was greater than unprotected colonies (26.43 birds) between 2010 and 2014, but there was an overlap between the 5<sup>th</sup> & 95<sup>th</sup> percentiles of protected (40 & 81.5 birds) and unprotected (21 & 68.3 birds) colonies. Colonies that were protected from snakes produced significantly more fledglings per female per breeding season than colonies without protection ( $\chi^2=95.59$ ,  $df=1$ ,  $P<0.001$ ), with protected colonies producing more than twice as many fledglings as unprotected colonies (mean $\pm$ SE of  $1.62\pm 0.19$  fledglings/female/breeding season for protected colonies and  $0.6\pm 0.15$  fledglings/female/breeding season for unprotected colonies; Figure 4). There was also a significant negative correlation between the number of fledglings per female per breeding season and colony size ( $\chi^2=13.64$ ,  $df=1$ ,  $P<0.001$ ); and a significant positive correlation between the number of fledglings per female per breeding season and mean winter minimum temperature ( $\chi^2=4.01$ ,  $df=1$ ,  $P=0.045$ ). The  $\Delta AIC_c$  values showed that the best three models explaining reproductive output included interactions between protection and colony size, rainfall and mean winter minimum temperature (models 6, 11 & 8; Table 1). The interaction model of protection and colony size predicted that the effects of nest predator exclusion were greatest in small colonies, but this difference became less pronounced as colony size increased (Figure 5). Rainfall and mean winter minimum temperature had an overriding influence on reproductive output. The model predicted that under low rainfall and cold winter minimum temperature conditions, protection had little to no effect on the number of fledglings produced per female per breeding season (Figure 6). Only as conditions become more favourable (wetter and warmer) did the effect of protection become increasingly apparent.



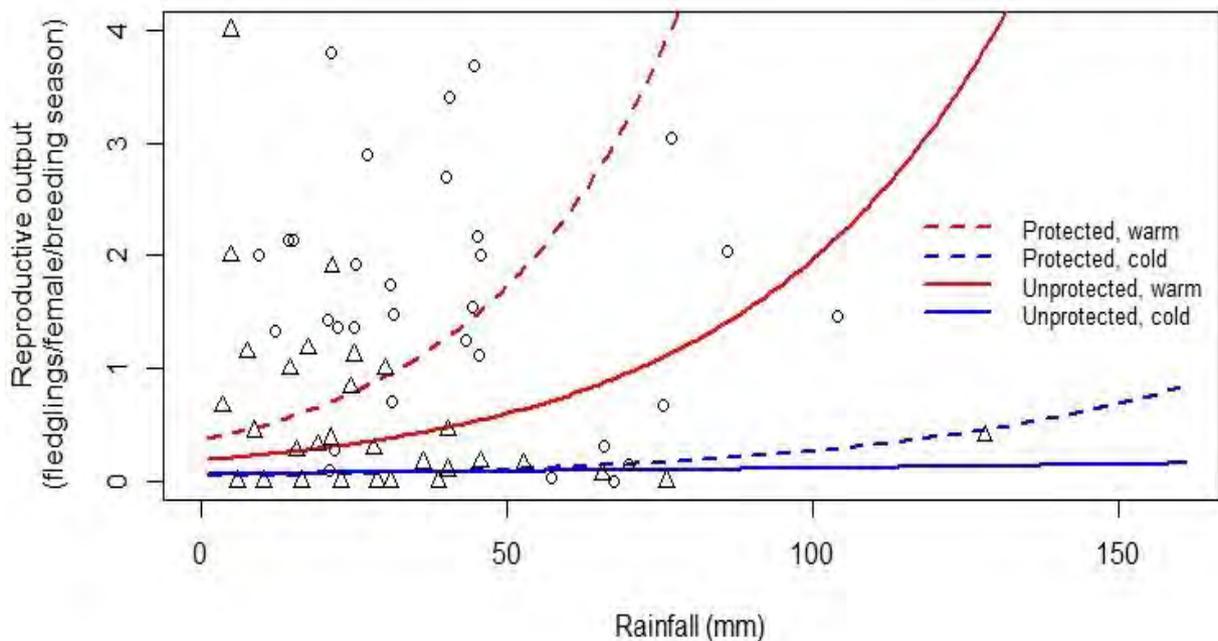
**Figure 4:** The mean reproductive output (fledglings/female/season) calculated from the raw data of 15 sociable weaver colonies that were protected from snake nest predation (n=7) and left exposed to snake nest predation (n=8) between 2010 and 2014 on Benfontein Reserve, South Africa. Error bars represent standard errors.

**Table 1:** Summary of the  $AIC_c$ -based model selection for factors explaining the reproductive output (fledglings/female/season) of 15 sociable weaver colonies on Benfontein Reserve, South Africa.  $\Delta AIC_c$  the model  $AIC_c$  minus the smallest  $AIC_c$ ,  $w_i$  Akaike weight,  $K$  number of parameters,  $\log Lik$  maximised log likelihood.

Model	$\Delta AIC_c$	$w_i$	$K$	$\log Lik$
1 Protection	17.58	0.00013	4	-239.80
2 Colony size	37.23	7.21E-09	4	-249.63
3 Rainfall	50.15	1.13E-11	4	-256.09
4 Winter min temp.	47.66	3.93E-11	4	-254.84
5 Hot days	50.33	1.03E-11	4	-256.18
6 Protection $\times$ colony size	0	0.88	6	-229.02
7 Protection + colony size	10.50	0.0046	5	-235.26
8 Protection $\times$ rain days	10.11	0.0056	6	-234.07
9 Protection $\times$ winter min temp.	16.55	0.00022	6	-237.29
10 Rainfall $\times$ winter min temp.	43.40	3.29E-10	6	-250.72
11 Protection $\times$ rainfall $\times$ winter min temp.	4.18	0.11	10	-227.10
12 Protection + rainfall + winter min temp.	10.27	0.0052	6	-234.15
13 Constant	48.68	2.36E-11	3	-256.35



**Figure 5:** The observed (protected= $\circ$ , unprotected= $\Delta$ ) and predicted relationship between the reproductive output (fledglings/female/season), protection status (protected=1, unprotected=0) and colony size of 15 sociable weaver colonies on Benfontein Reserve, South Africa (model 6, Table 1):  $\log(\text{fledglings/female/season}) = -1.41 + 1.72 \times \text{protection status} + 0.0033 \times \text{colony size} - 0.015 \times (\text{protection status} \times \text{colony size})$ .



**Figure 6:** The observed (protected= $\circ$ , unprotected= $\Delta$ ) and predicted relationship between the reproductive output (fledglings/female/season), protection status (protected=1, unprotected=0), rainfall (mm) and mean winter minimum temperature ( $^{\circ}\text{C}$ , winter temp.) of 15 sociable weaver colonies on Benfontein Reserve, South Africa (model 11, Table 1):  $\log(\text{fledglings/female/season}) = -1.37 + 0.86 \times \text{protection status} + 0.012 \times (\text{rainfall} - \text{mean rainfall}) + 1.55 \times \text{winter temp.} + 0.011 \times (\text{protection status} \times (\text{rainfall} - \text{mean rainfall})) + 0.42 \times (\text{protection status} \times \text{mean winter minimum temperature}) + 0.011 \times ((\text{rainfall} - \text{mean rainfall}) \times \text{winter temp.}) - 0.0036 \times (\text{protection status} \times (\text{rainfall} - \text{mean rainfall}) \times \text{winter temp.})$ . The graph shows predictions for warm ( $1.03^{\circ}\text{C}$ ) and cold ( $-0.59^{\circ}\text{C}$ ) conditions, which correspond to one standard deviation from the observed mean.

## **2. Simulating the effect of nest predator exclusion and climate change on population trends**

The metapopulation model was first parametrised using the predicted reproductive output from the AIC<sub>c</sub> best model (model 6, Table 1). The projected colony size of individual colonies followed observed trends closely when actual protection status was modelled (Figure 7). The major deviants were Colony 7, which was predicted to have a declining colony size trend, but was observed to be growing; and Colony 11, which had a predicted growth rate that was substantially underestimated. Because demographic rates were kept constant for each time step, the metapopulation model was only able to predict linear (on a log scale) growth trajectories. Thus, the predicted estimates were crude and were only meant to represent colony size trends in a coarse way. The model predicted that the actual protection status of the colonies that were modelled was insufficient in preventing a decline in the overall population size (-7%/yr, Figure 8a). However, this was much less than the predicted population decline without any protection (-22%/yr). If all of the colonies that were modelled were protected, the population would grow at a rate of 10%/yr.

Under arid conditions (one standard deviation less than mean rainfall), all of the colonies were predicted to decline in size, regardless of protection status (Figure 7). There was a difference in the population growth rates of the three different protection scenarios; but even if all of the colonies were protected, the population size would decline at a rate of -11%/yr (Figure 8b). However, warmer winter minimum temperatures (one standard deviation more than mean winter minimum temperature) had a positive effect on colony size trends, with all colonies either growing in size or remaining stable in the absence of protection, except for Colony 25 (Figure 7). This positive effect would result in the growth of the population at a rate of 3%/yr if no colonies were protected (Figure 8c). The effect of both protection and warmer winter temperatures would have a dramatic, but unrealistic, effect on population growth, with increases of 33%/yr and 69%/yr for actual and full protection scenarios, respectively.

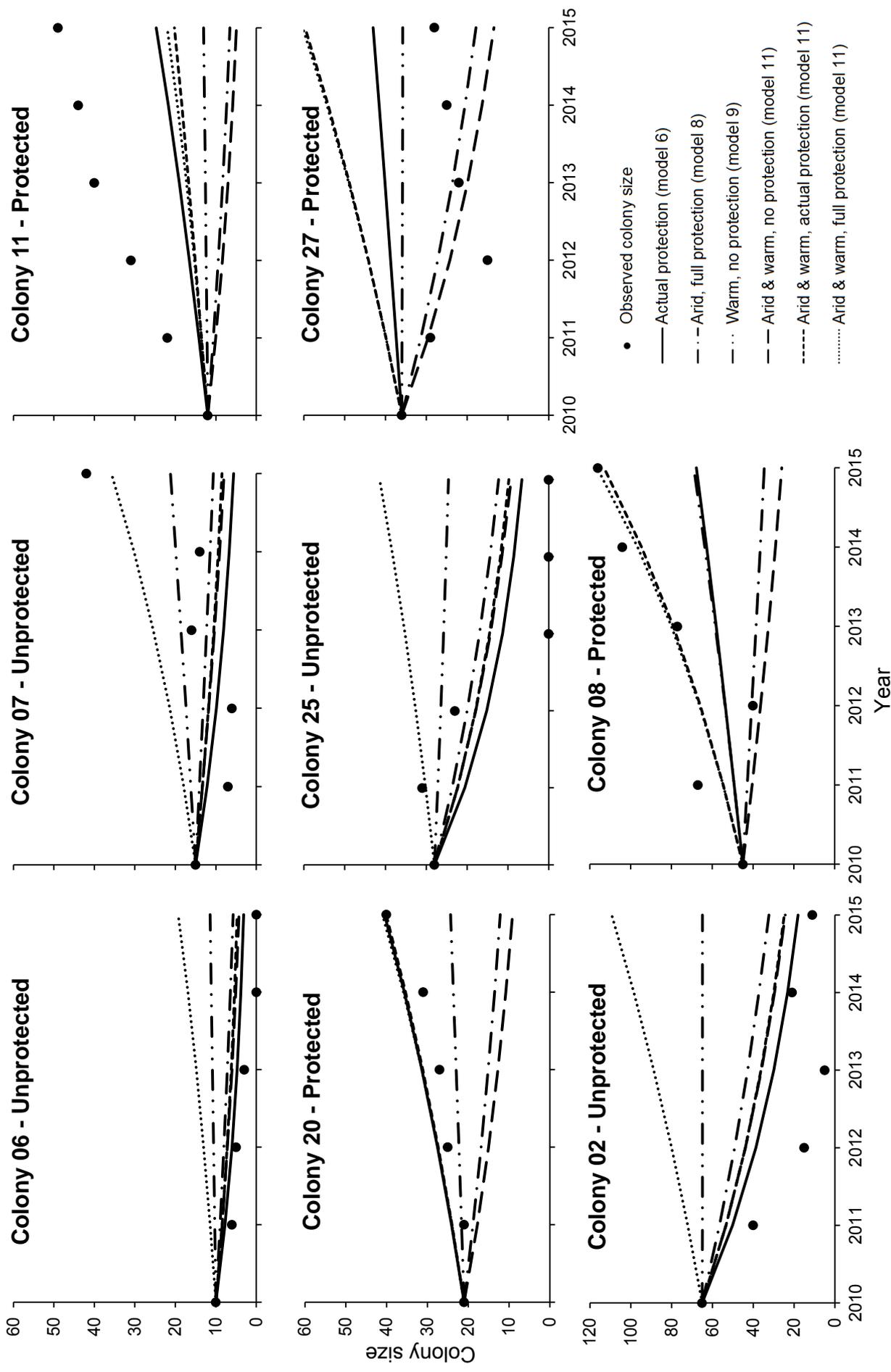
When both rainfall and winter temperature were used to predict reproductive output, the positive effect of warmer winter temperatures alone did not prevent colonies and the population as a whole from declining in size, with a predicted population decline of -16%/yr (Figures 7 & 8d). If the actual protection status of the modelled colonies were maintained, the

metapopulation model predicted that protected colonies would grow in size, whilst unprotected colonies would decrease in size (Figure 7). Despite the growth of protected colonies, it would not be sufficient to prevent an overall population decline under arid and warmer winter temperature conditions, with the population size declining slightly at a rate of -2%/yr (Figure 8d). If all of the colonies were protected under arid and warmer winter temperature conditions, all of the colonies would grow in size and would contribute to a population growth rate of 14%/yr.

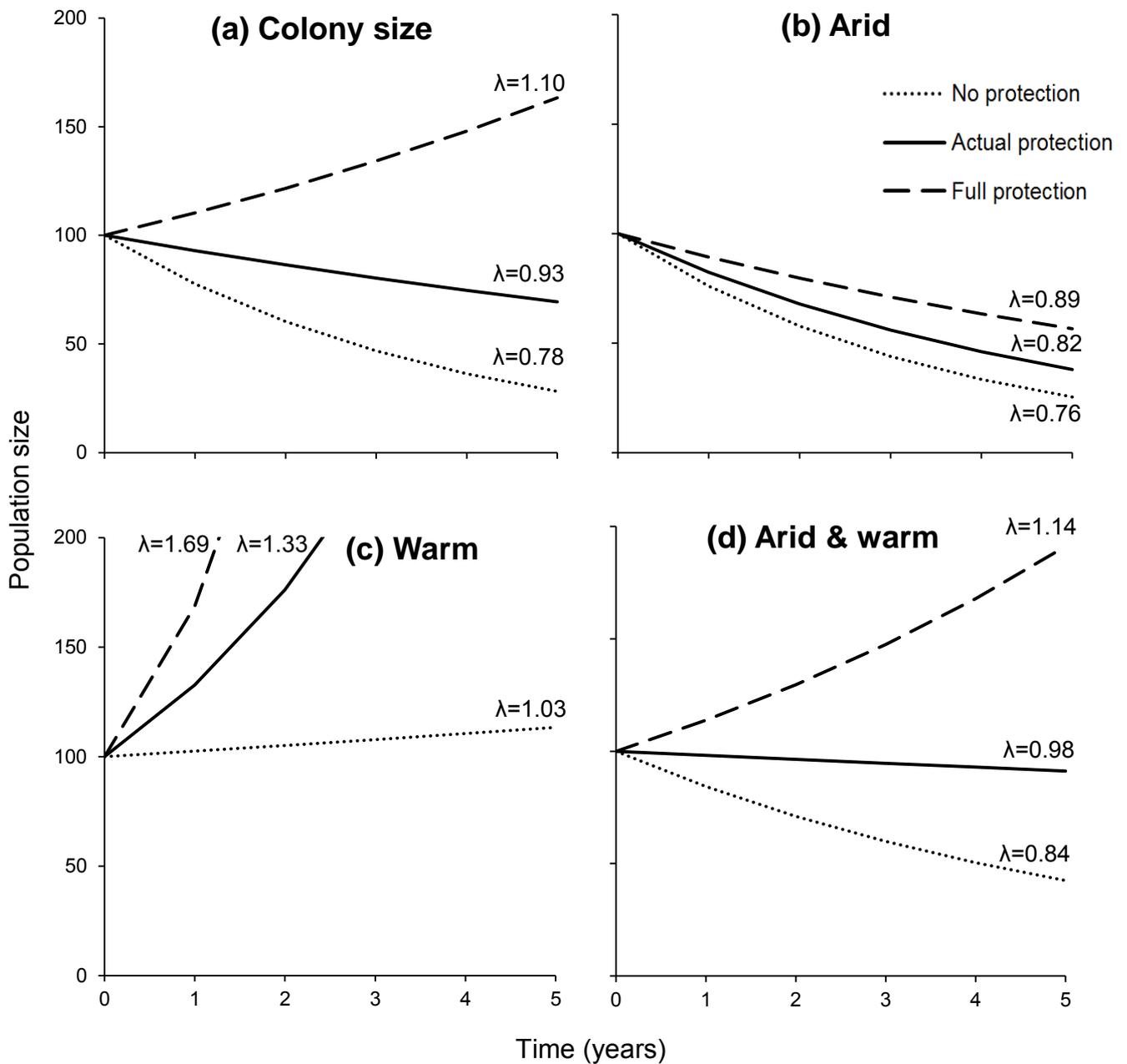
### **3. Response of movement to nest predator exclusion and other social & environmental factors**

The network analysis dataset consisted of 239 movement events, capturing the movement of 215 individual birds. A total of 28 colonies (nodes) and 116 unique individual weaver movements (edges) formed the sociable weaver network. The observed network diameter (6) and average path length (2.52) were greater than the random network mean $\pm$ SD diameter (3.32 $\pm$ 0.47) and average path length (1.87 $\pm$ 0.017); suggesting that factors were controlling the movement of sociable weavers. The greater-than-expected diameter of the observed network is indicative of low reachability, suggesting a high clustering of colonies (distinct communities) with few weavers moving between colonies that were distant from one another (Janssen *et al.* 2006). This, along with the longer-than-expected average path length, suggested a slow movement of weavers through the metapopulation, which could be interpreted as high colony fidelity (Janssen *et al.* 2006).

Both the Louvain Method and Walktrap algorithm displayed six different communities. By displaying communities in their spatial context, it was evident that proximity between colonies played an important role in the movement of weavers and the establishment of communities (Figure 9). In addition, both community structures identified pairs of colonies that formed their own community: Colony 21 & 25, Colony 33 & New, and Colony 28 & 36 (Figures 9 & 10). All three paired communities included one abandoned colony, where migrating birds left their colony en masse to join the other colony together. In one case, birds abandoned Colony 33 to build a new colony in 2013 (Colony New, R. Covas pers. comm.). Each community that had more than two colonies had at least two protected colonies, except for one community which had none.



**Figure 7:** Colony size trends of eight sociable weaver colonies on Benfontein Reserve, South Africa. Graph titles refer to colony identity and actual protection status. Lines show the projection of colony size from the first census in 2010 using the metapopulation model developed by Altwegg *et al.* (2014). Reproductive output was estimated using the models in Table 1 and are specified after each scenario in the legend.

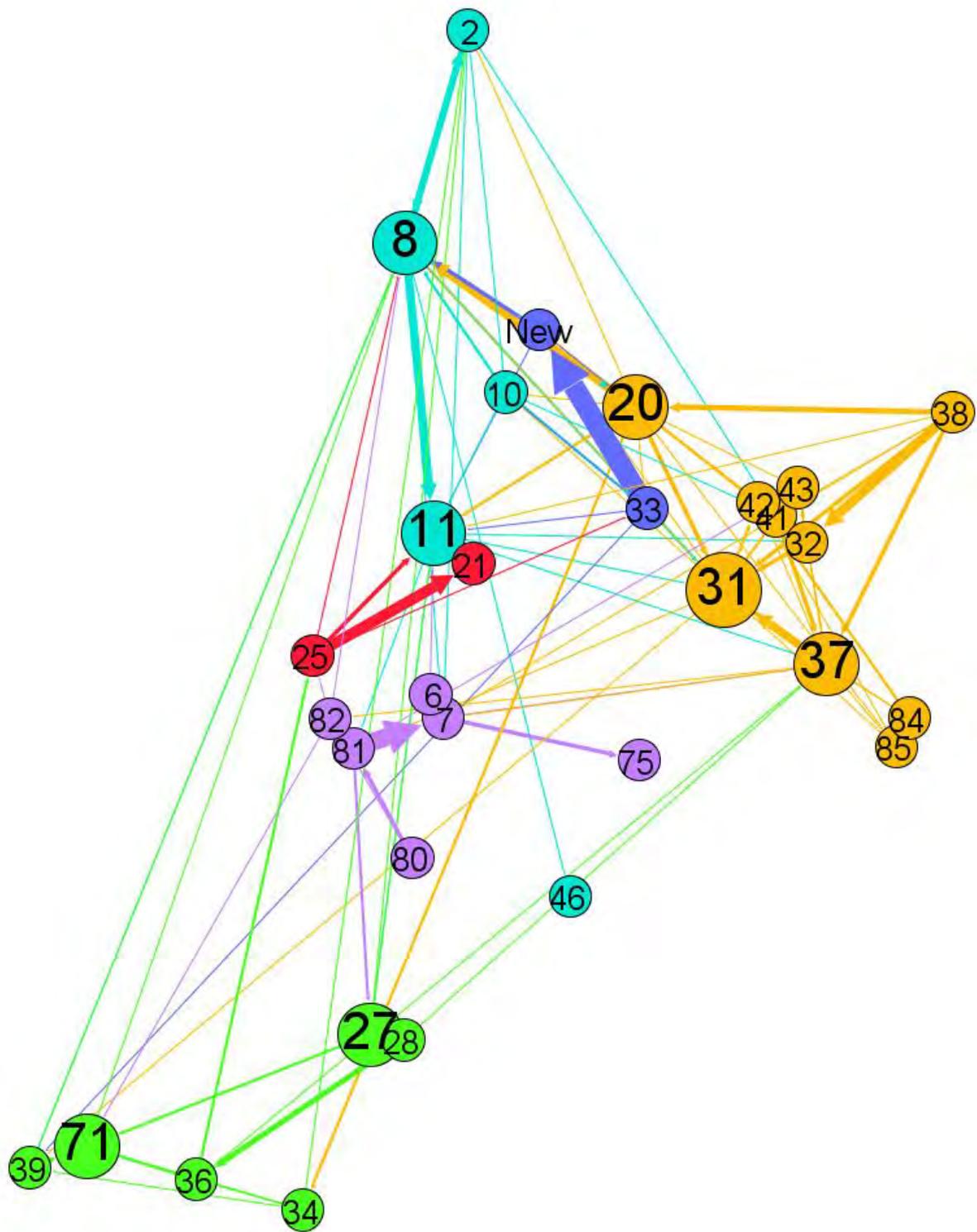


**Figure 8:** Projected population trends based on the metapopulation model developed by Altwegg *et al.* (2014). The effect of nest predator exclusion (protection status) on reproductive output was manipulated using the models in Table 1. (a) Model 6 to simulate current conditions ( $AIC_c$  best model) and the effect of colony size; (b) model 8 to simulate future aridity (35.85 mm, one standard deviation less than mean rainfall); (c) model 9 to simulate future warmer winter temperatures (1.03 °C, one standard deviation more than mean winter minimum temperature); and (d) model 11 to simulate both aridity and warmer winter temperatures.

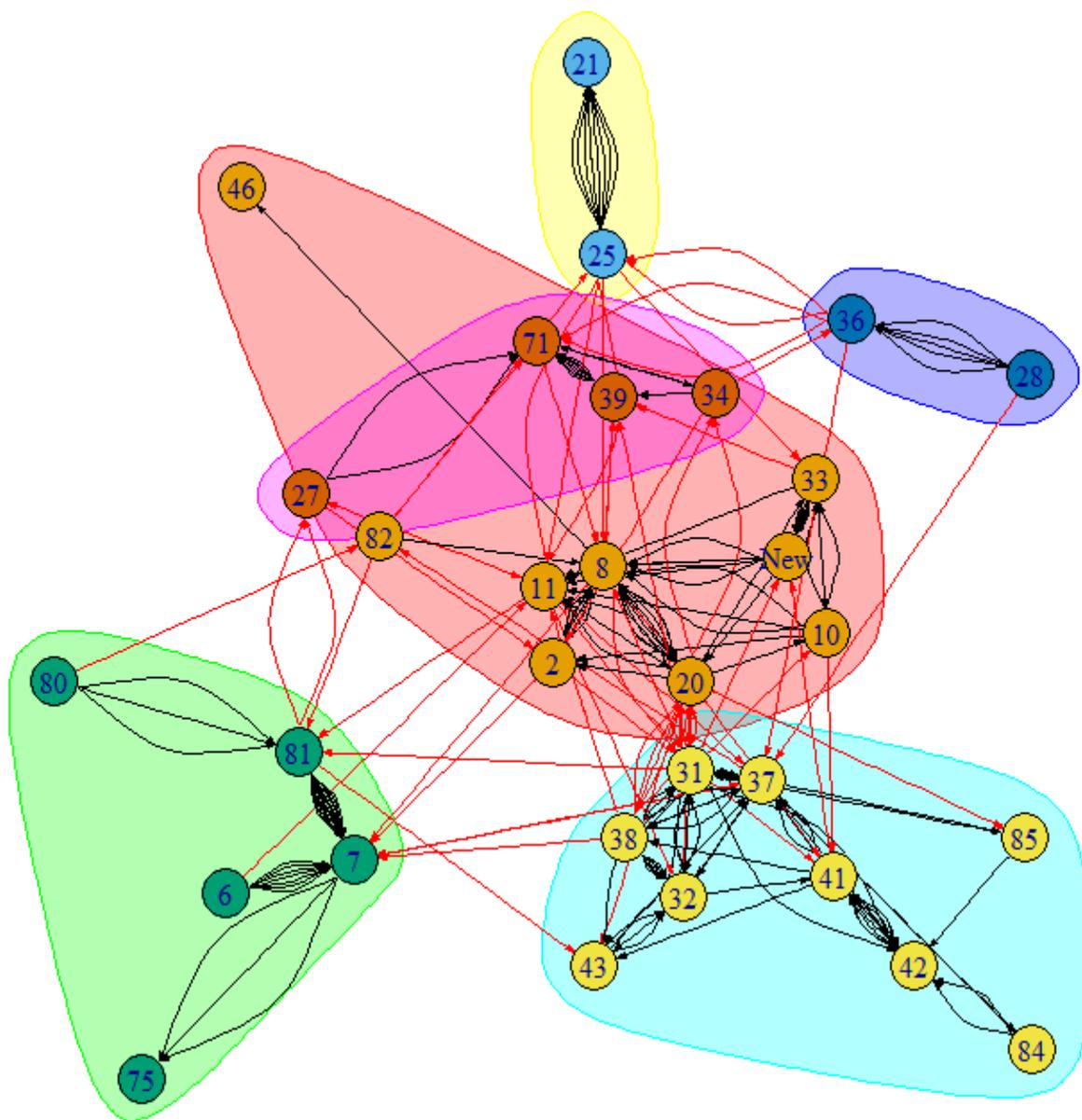
All of the colonies protected for five years (Colony 8, 11, 20, 31 & 37) played a central role in structuring the sociable weaver network (Figure 10). This was confirmed by the high betweenness centrality scores and low closeness centrality scores of protected colonies (Table 2). The scores suggested that birds from across the metapopulation immigrated into protected colonies, whereas birds only immigrated into unprotected colonies that were in close proximity to the colony from which they were emigrating. The effect of nest predator exclusion also seemed to be related to the duration of protection, because colonies that were protected for only three years had similar centrality scores to unprotected colonies and did not play as much of an important role in structuring the network (Colony 27 & 71; Table 2). However, these two colonies were also located near the edge of the metapopulation and may be too far to exchange birds with protected colonies of other communities (Figure 9). Apart from unprotected Colony 32, most of the protected colonies had high eigenvector centrality scores, suggesting that birds leaving protected colonies also immigrated into other protected colonies (Table 2). In other words, dispersing birds from both unprotected and protected colonies immigrated into protected colonies.

**Table 2:** Centrality scores of 15 sociable weaver colonies on Benfontein Reserve, South Africa, which were sampled annually between 2011 and 2015.

<b>Protection status</b>	<b>Colony ID</b>	<b>Betweenness centrality</b>	<b>Closeness centrality</b>	<b>Eigenvector centrality</b>
Unprotected	2	20.1	2.61	0.48
	6	0	2.86	0
	7	44.08	3	0.61
	21	0	0	0.015
	25	42.13	2.39	0.053
	32	27.4	2.18	0.89
	38	25.52	2.07	0.47
	81	23.5	2.96	0.36
Protected (3 years)	27	16.49	2.61	0.21
	71	32.09	2.64	0.22
Protected (5 years)	8	133.06	2.07	0.8
	11	103.24	2.07	0.69
	20	124.98	1.82	0.83
	31	102.91	1.89	0.97
	37	202.69	2.11	1



**Figure 9:** The sociable weaver movement network of Benfontein Reserve, South Africa, between 2011 and 2015 generated using the Geolayout plugin in Gephi v.0.8.2. Nodes are positioned and numbered according to colony geographic position and study identification, respectively. Nodes were sized according to protection status with large nodes representing protected colonies. Edges represent individual movement of weavers between colonies weighted by number of individuals. Different colours represent different communities identified using the Louvain Method.



**Figure 10:** The sociable weaver movement network of Benfontein Reserve, South Africa, between 2011 and 2015 generated using the Fruchterman-Reingold algorithm in R v.3.1.2. Nodes are positioned and numbered according to a force-directed layout (Fruchterman & Reingold 1991) and study identification, respectively. Edges represent individual movement of weavers between colonies of the same community (black) and different communities (red). Different colours represent different communities identified using the Walktrap algorithm.

Despite the indication that protected colonies were important in structuring and connecting the sociable weaver movement network, there was no significant difference in the rate of immigrants and emigrants between protected and unprotected colonies (Table 3). This is because the centrality scores of a node are based not only on the number of links with other nodes, but also the number of links with nodes beyond their local community (Janssen *et al.* 2006). In other words, the centrality scores of a node are a measure of how well connected the node is to other particular nodes in the network. Rather, it was colony size that explained migration rates, with both immigration and emigration rates decreasing significantly (or nearly) with increasing colony size (Table 3). The mean colony size of protected colonies (47.06 birds) was greater than unprotected colonies (22.97 birds) between 2011 and 2015, but there was an overlap between the 5<sup>th</sup> & 95<sup>th</sup> percentiles of protected (43 & 98 birds) and unprotected (19 & 48.5 birds) colonies. Emigration rates were also significantly higher in colonies with resident African pygmy-falcons (Table 3). The mean colony size of colonies with (37.44 birds) and without (34.60 birds) African pygmy falcons were similar.

**Table 3:** Summary of the generalised linear mixed model results for the immigration and emigration rates (number of immigrant/emigrants per capita) of 14 sociable weaver colonies on Benfontein Reserve, South Africa, between 2011 and 2015.

Response variable	Explanatory variable	Estimate	$\chi^2$	df	P
Immigration rate	Colony size	-0.0097	3.64	1	0.056
	Protection status	-0.40	1.48	1	0.22
	Pygmy falcon presence	-0.31	1.10	1	0.29
Emigration rate	Colony size	-0.012	5.63	1	0.018
	Protection status	-0.14	0.14	1	0.70
	Pygmy falcon presence	0.72	5.83	1	0.016

#### 4. Foraging distances & behaviour of sociable weavers (the effect of colony size on intraspecific competition)

##### *Foraging behaviour*

The birds became active shortly after sunrise, with earlier activity being observed on warmer mornings. The first signs of activity involved much chattering and individuals flying in and out of several different nest chambers. This was accompanied by flying to the ground below the colony and foraging on the floor for a few seconds before returning to a nest chamber. In

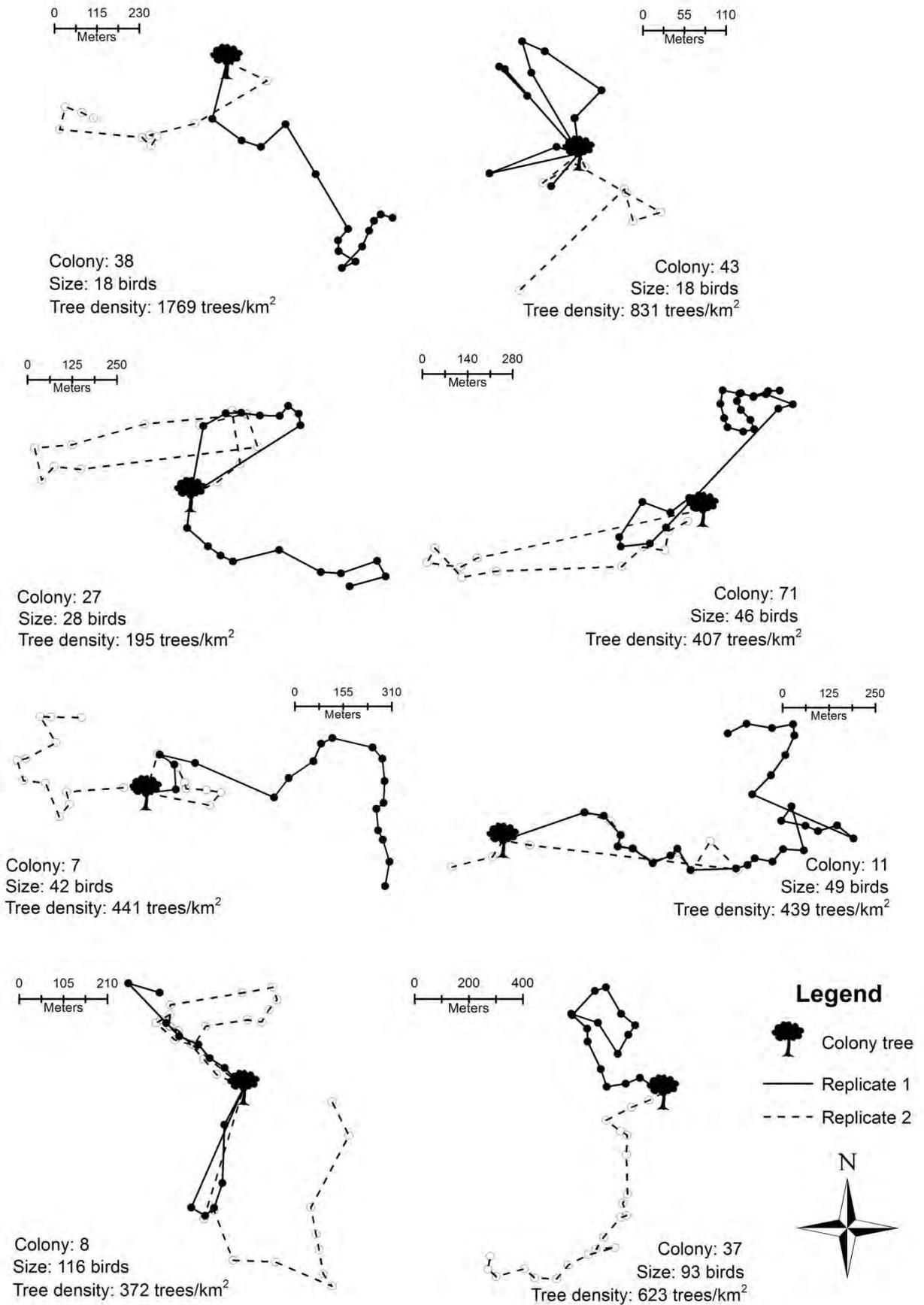
some cases, several individual birds flew to the branches of the colony tree or trees surrounding the colony, where they called to the rest of the colony. If the colony did not go to the calling birds, the calling birds returned to the colony and flew in and out of nest chambers. At some point, a large group of birds flew together to a nearby tree and started to forage on the ground underneath the tree canopy (sub-canopy). The initial group was followed shortly afterwards by more groups of birds. These subsequent groups perched on the same tree as the initial group or on an adjacent tree. As soon as one of the groups flew to the next feeding station, the other groups followed and the flock moved as a single unit from then onwards. Flocks were seen feeding more often on the ground in the sub-canopy than on the ground in the inter-canopy (the open space between tree canopies). This qualitative finding was based on the observations made whilst flocks were tracked and could not be quantified. In some cases, the flock was led by one or two birds to the next feeding station and the transition was accompanied by a distinct call from most of the birds in the flock (Supplementary material 1). It could not be confirmed if the same individuals led the flock on each occasion. The flock often landed on one side of the sub-canopy and foraged on the ground to the opposite side of the sub-canopy before moving to the next tree. Individuals at the back of the flock glided over the flock to get to the front. Some birds were chased away from the food they had found by other birds in the flock. Flocks rarely split or joined other flocks whilst foraging. The foraging trajectory of the flock was often sickle shaped, with birds circling back to the colony near the end of a foraging bout (Figure 11). When the flock had finished feeding, the birds made a lot of noise and some birds perched on the branches of the tree underneath which they were feeding. The flock then flew back to the colony, approximately 2 hours after leaving the colony. In some cases, the flock perched in a tree on route to the colony, but then flew to the colony shortly afterwards. Subsequent activities involved foraging in small groups and nest building.

The flock was always accompanied by one or more forked-tailed drongos (*Dicrurus adsimilis*), with larger flocks attracting more drongos. Drongos were quick to join the flock after they had left the colony. The drongos waited for the flock to leave the colony by perching on trees surrounding the colony. Once the sociable weavers had started to feed, the drongos perched on the lower branches above the flock. From this vantage point, the drongos chased the sociable weavers away from their food. This even involved several seconds of aerial pursuit. The drongos also served as sentries as they were seen and heard giving distinct

alarm calls when gabar goshawks (*Micronisus gabar*) attacked the flock. Drongos also gave false alarm calls to steal food from the flock. In some cases, drongos “led” the flock by haphazardly flying to a tree of their choice and the flock followed the drongo to the tree. When the flock did not follow, the drongo returned to the flock. Drongos often fought one another for possession of the flock. Other birds were seen feeding with the sociable weaver flock for reasons that are not known. The species included: ant-eating chat (*Myrmecocichla formicivora*), glossy starling (*Lamprotornis nitens*), yellow-billed hornbill (*Tockus leucomelas*), African hoopoe (*Upupa epops*), common scimitarbill (*Rhinopomastus cyanomelas*) and doves (*Streptopelia* spp.). These species followed the flock for only part of the foraging trajectory. Red-headed finches (*Amadina erythrocephala*) were chased away by the sociable weavers. When the flock was attacked by a gabar goshawk, the drongos gave the alarm call and the flock either flew directly to the colony or flew to the branches of the tree underneath which they were feeding and then flew to the colony. If the goshawk was unsuccessful, it followed the flock to the colony and waited in the tree of the colony.

#### *Foraging distance*

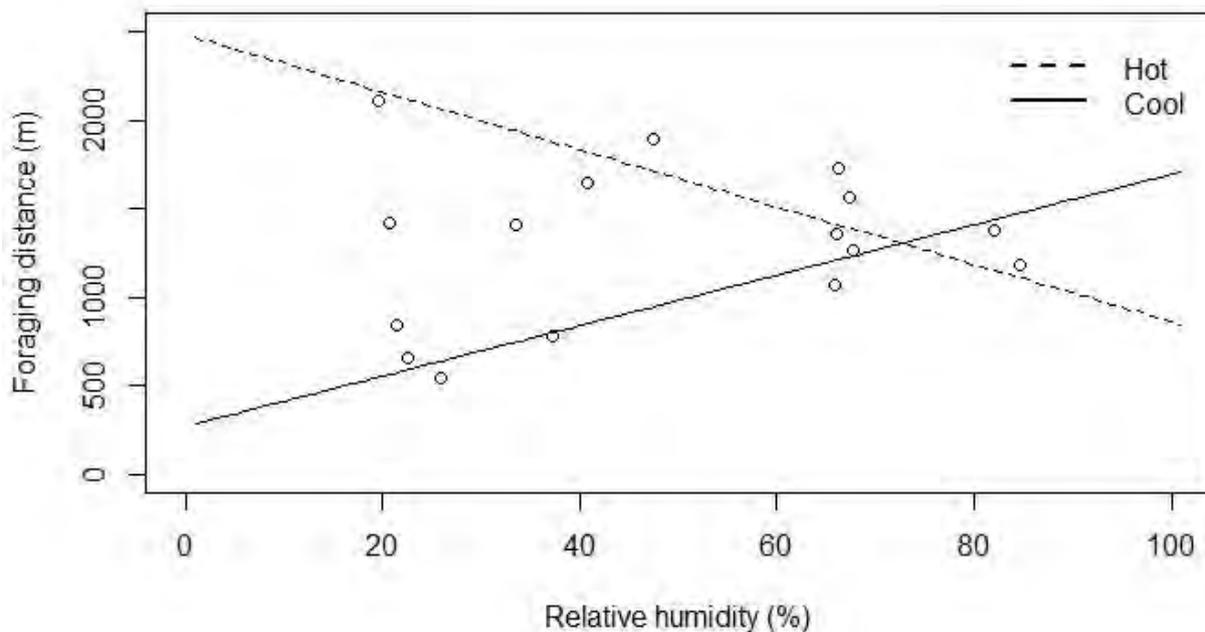
Foraging distance was not correlated to colony size ( $\chi^2=1.11$ ,  $df=1$ ,  $P=0.29$ ). Instead, there was a significant negative correlation between foraging distance and tree density ( $\chi^2=4.50$ ,  $df=1$ ,  $P<0.05$ ). However, the  $\Delta AIC_c$  best model for explaining foraging distance was the interaction between maximum temperature and humidity (Table 4). The model predicted that during hot (30 °C) and low relative humidity conditions, the birds travelled further than during high relative humidity conditions (Figure 12). Conversely, when conditions were cool (13 °C) and relative humidity was high, the foraging distance travelled by the birds increased. There were strong correlations ( $r>\pm 0.8$ ) among the various temperature measurements, but correlations with relative humidity were weak, including the correlation between maximum temperature and relative humidity ( $r=-0.58$ ).



**Figure 11:** The foraging trajectories of eight sociable weaver colonies on Benfontein Reserve, South Africa, before the 2015 breeding season. Lines show the path taken during a foraging bout and dots indicate feeding stations.

**Table 4:** Summary of the AIC<sub>c</sub>-based model selection for factors explaining the foraging distance (m) of eight sociable weaver colonies on Benfontein Reserve, South Africa.  $\Delta AIC_c$  the model AIC<sub>c</sub> minus the smallest AIC<sub>c</sub>,  $w_i$  Akaike weight,  $K$  number of parameters, logLik maximised log likelihood.

	<b>Model</b>	$\Delta AIC_c$	$w_i$	$K$	<b>logLik</b>
1	Colony size	11.06	0	4	-110.95
2	Tree density	13.99	0	4	-112.41
3	Mean temperature	7.28	0	4	-109.06
4	Minimum temperature	7.77	0	4	-109.30
5	Maximum temperature	6.67	0	4	-108.75
6	Relative humidity	11.44	0	4	-111.14
7	Max temp $\times$ rel. humidity	0	1	6	-103.42
8	Constant	14.66	0	3	-113.75



**Figure 12:** The observed ( $\circ$ ) and predicted relationship between the foraging distance (m), maximum temperature ( $^{\circ}C$ , max temp.) and relative humidity (%) of eight sociable weaver colonies on Benfontein Reserve, South Africa (model 7, Table 4):  $\log(\text{foraging distance}) = -1369.03 + 125.31 \times \text{max temp.} + 37.31 \times \text{relative humidity} - 1.75 \times (\text{max temp.} \times \text{relative humidity})$ . The lines show predictions for hot and cool conditions using the highest ( $30^{\circ}C$ ) and lowest ( $13^{\circ}C$ ) maximum temperatures recorded during tracking, respectively.

## DISCUSSION

The results of this study showed that predation played an important role in the population dynamics of the sociable weaver metapopulation on Benfontein Nature Reserve, South Africa. Colonies that were protected from snake predation produced, on average, more than double the number of fledglings per female per breeding season that were produced in unprotected colonies. The resulting increase in reproductive output may be sufficient in countering the negative effects of increasing aridity on population trends when the positive effect of warmer winter temperatures was taken into account. Protected colonies played an important role in structuring and connecting the movement network of the metapopulation and colony size explained the migration rates of each colony. It is unlikely that nest predation, through its effects on colony size, reduces the intraspecific competition (measured as foraging distance) of a colony.

### **1. Response of reproductive output to predator exclusion and other social & environmental factors**

By controlling nest predation, this study has shown that the lethal effects of predation add to the total mortality of eggs and nestlings as opposed to substituting for some other cause of mortality (Korpimäki & Krebs 1996). Snakes consume all of the eggs or nestlings when they enter a nest chamber and have been seen consuming the entire contents of a colony in one foraging bout, usually over several days (Maclean 1973c; Marsden 1999; Spottiswoode 2007). This high nest predation rate has probably been a strong selective force in evolving the ability to lay several clutches in short succession of one another (9.2-13.5 days if the previous brood failed; Maclean 1973c; Martin 1995; Covas *et al.* 2008). This is supported by the finding that the inter-nesting interval (number of days between the end of a nesting attempt and the initiation of the next clutch) was found to be dependent on the fate of the previous brood, with no effect of helpers, rainfall or colony size (Covas *et al.* 2008).

Although predation was found to have a clear and significant influence on the number of fledglings produced per female per breeding season, it was not the only factor that determined reproductive output. Colonies that were protected from snake predation produced more fledglings per female per breeding season than unprotected colonies at low colony sizes. However, the difference in reproductive output between protected and unprotected

colonies decreased with increasing colony size. This may be due to density-dependence effects. A previous study found that fewer eggs successfully hatched and fewer hatchlings fledged in large colonies for pairs breeding alone (Covas *et al.* 2008). It was thought that this was due to the high parasite loads (which affect immune response), high levels of intraspecific competition for food and high levels of conflict that are associated with large colonies (Spottiswoode 2007; Covas *et al.* 2008; Rat *et al.* 2015). However, the results of this study suggested that colony size did not influence the distance that birds needed to travel from the colony to search for food. Perhaps competition for food is experienced at the individual level rather than at the colony level when birds are foraging as a flock (see discussion on foraging distances). Foraging distances may also be greater during the breeding season when food requirements are more important and weavers fly back and forth from the colony to feed nestlings (Maclean 1973e).

Ecological events in arid and semi-arid ecosystems are controlled more by abiotic factors, such as weather, than by biotic factors (Noy-Meir 1973). This was found to be the case when dry breeding seasons and cold winters resulted in low reproductive output throughout the sociable weaver metapopulation, regardless of protection status. Only when conditions were wetter during the breeding season and warmer during the preceding winter was there a marked difference in the reproductive output of protected and unprotected colonies. Rainfall and temperature are likely to determine reproductive output by influencing food availability and the breeding response of sociable weavers (Covas *et al.* 2008; Altwegg *et al.* 2014). Rainfall in arid and semi-arid ecosystems is discontinuous, variable and unpredictable (Schwinning & Sala 2004). Many primary producers have adapted to this by coinciding growth and reproduction with the first rains (Maclean 1973e; Veenendaal *et al.* 1996; Archibald & Scholes 2007). Thus, rainfall triggers pulses in productivity such that it occurs in discrete events (Noy-Meir 1973). The magnitude of the pulse event and the subsequent magnitude and extent of the ecological response can be organised in a hierarchical manner (Schwinning & Sala 2004). A small rainfall event may only trigger a small number of ecological events, such as soil microbe activity; whilst a high rainfall event may trigger larger ecological events, such as plant productivity and recruitment (Schwinning & Sala 2004). Therefore, the amount of rain that falls during the breeding season will determine the amount of food available to feed adults and nestlings. Mean annual precipitation accounts for more than 75% of the variation in herbaceous biomass (Oosterheld *et al.* 1999) and determines the

abundance and foraging activity of insects, such as termites, in savannas (Buxton 1981). However, rainfall is but one of the necessary requirements to induce a physiological response. Temperature also plays an important role in plant productivity and insect phenology and may limit the effects of rainfall (Lloyd 1999; Bale *et al.* 2002; Schwinning & Sala 2004). Cold temperatures have been found to retard the growth of *Stipagrostis* grasses, the dominant grass genus at the study site (Lloyd 1999). There is evidence that winter temperature in temperate zones also influences the rate of alate production and growth potential of termites (Nutting 1969).

Sociable weavers are likely to use rainfall and cold winter temperatures as cues to make breeding decisions, as they can be used to predict food availability during the breeding season. This is supported by several studies that have found that rainfall influences the timing of breeding (Maclean 1969; Maclean 1973e); the number of breeding attempts and clutch size (Covas *et al.* 2008; Mares *et al.* unpubl. data); and fledgling success of sociable weavers (Altwegg *et al.* 2014). Temperature maxima have been shown to determine the duration of the breeding season (Maclean 1973e) and influence adult survival (Altwegg *et al.* 2014). However, much less is known about the role of cold winter temperatures on the reproductive output of birds in arid and semi-arid ecosystems. Some studies have shown that cold temperatures during early spring delay the start of the breeding season of birds in arid and semi-arid ecosystems by limiting plant growth (Lloyd 1999; Barrientos *et al.* 2007). Other studies suggest a physiological effect in that cold temperatures put an energetic strain on female birds due to the costs of thermoregulation and could influence the gonadal growth and maturation of male birds (Dunn 2004). Arid and semi-arid ecosystem studies often attract questions regarding the limiting effects of rainfall. However, this study and others highlight the importance of also understanding how cold temperatures affect the reproductive output of birds (Barrientos *et al.* 2007).

## **2. Simulating the effect of nest predator exclusion and climate change on population trends**

I examined how nest predation influenced colony and population size trends through its effects on reproductive output. The baseline metapopulation model (interaction between protection status and colony size to predict reproductive output) predicted the observed

colony trends of unprotected colonies well. This suggests that high nest predation rates were having an exacerbating effect on the observed decline of unprotected colonies. Two of the four unprotected colonies that were modelled were observed to go extinct, with the models also predicting low numbers for these two colonies (<7 individuals). Colony abandonment is an Allee effect, which is a demographic change triggered at very small population sizes such that the population is more likely to become extinct (Stephens *et al.* 1999; Altwegg *et al.* 2014). The apparent increase in population growth of one of the unprotected colonies (Colony 7) was due to the influx of immigrants from one of the abandoned colonies (Colony 6) and others. However, the effect of nest predator exclusion was underestimated by the metapopulation model for two of the three colonies that were protected for five years; most likely due to the negative effect that colony size had on reproductive output. Colony 27 was an exception in that it was protected for only three years from 2012 onwards. Whilst increasing colony size has a negative effect on reproductive output, it has a positive effect on the survival rates of juveniles and adults, which may outweigh the costs on reproductive output (Brown *et al.* 2003; Altwegg *et al.* 2014). The survival and movement estimates used in the metapopulation model were kept constant across years, when in reality they would change as colony size changes. However, my simple model was suited to my goals, which was to obtain a rough estimate of the expected population level effects of colony protection.

The metapopulation models have shown that changing the protection status of colonies under constant environmental conditions resulted in a change in population growth rates. By controlling rainfall and winter minimum temperature, the effect of food availability on reproductive output was kept constant, whilst only protection status varied. Under arid and warm winter conditions, the population growth rate changed among the three different protection status scenarios (i.e. no protection, actual protection and full protection). However, this difference was smallest under arid conditions, further emphasising the importance of rainfall in determining population trends (Altwegg *et al.* 2014). Therefore, population size was limited not only by weather conditions (food availability), but also, to a lesser degree, by nest predation rates. Previous studies have found that food availability and nest predation rates interact in a number of ways to determine the reproductive output of the prey species (see Newton 1998). For example, some studies have found that when food resources are low, parents have to travel further from the nest and leave nestlings exposed to predators for longer periods of time (Jansson *et al.* 1981). However, our lack of understanding of how nest

predators respond to changes in environmental factors and sociable weaver behaviour limits interpretation of the results.

My results predicted that climate change would reduce colony and population size trends under arid conditions and increase colony and population size trends under warmer winter conditions by acting through reproductive output. However, the positive effect of warmer winters would not be enough to outweigh the negative effect of drier breeding seasons. Nest predation acted as a secondary exacerbating factor under future climate change conditions, as population growth rates were lower when no colonies were protected from snakes. By removing snake predation from half of the studied colonies, reproductive output was high enough in protected colonies to keep population size trends nearly stable (~-2% decline). Even though there was a positive growth rate when all of the colonies were protected under climate change conditions; it would be better to only protect a subset of colonies if snake exclusion was used as a conservation management tool to prevent population declines. From an ecological point of view, maintaining the source-sink dynamics of the metapopulation would ensure that birds move among colonies, which promotes genetic mixing (Mech & Hallett 2001), balancing of sex ratios (Gundersen *et al.* 2001) and possibly immigration rescue effect as observed in Colony 7 (Hanski 1991). From a management point of view, it would be more costly and time consuming to protect all of the colonies in a metapopulation from snake predation. Predator control has been used to prevent the population decline of many prey species, particularly when changes in habitat quality and resource availability could not be addressed directly (Green 1995; Reynolds & Tapper 1996; Smith *et al.* 2010). The method used to exclude snakes in this study was not lethal to snakes and did not appear to harm any other organisms. However, the effect of nest predator exclusion would be short-lived if protection was not continuously applied. Several studies have found that high predation rates quickly resumed once control had ceased (Duebbert & Lokemoen 1980; Tapper *et al.* 1982; Armstrong *et al.* 2006). In addition, the results of this study may not apply to populations located in more arid regions of the sociable weaver distributional range.

### **3. Response of movement to nest predator exclusion and other social & environmental factors**

The movement of individuals among subpopulations is fundamental to the structure and functioning of a metapopulation (Hanski 1999). The network analysis provided a measure of the flow of individuals through the metapopulation (connectivity) and the importance of subpopulations (or colonies) in connecting the metapopulation (centrality); not migration rates (Janssen *et al.* 2006). The longer diameter and higher average path length of the observed network signified low reachability and high levels of clustering and colony fidelity (Janseen *et al.* 2006). In other words, there was a higher exchange of birds among colonies in close proximity to one another than among colonies further away, which was also found in another study (Altwegg *et al.* 2014). This was illustrated when communities were identified within the metapopulation when colonies were plotted in their spatial context. There may be a high cost when moving between colonies and this cost most likely increases with increasing distance between colonies (Hanski 1999). Foraging observations revealed that attacks from raptors were common and that the shelter provided by the nest mass was crucial to escaping attack. It has been noted that gabar goshawks were more likely to capture sociable weavers that were released alone from mist nets than weavers released in groups (R. Covas pers. comm.). Therefore, sociable weavers are unlikely to venture far from the location of a known colony alone. The centrality scores indicated that dispersing individuals from unprotected colonies immigrated into protected colonies of the same community; whilst dispersing individuals from protected colonies immigrated into protected colonies of the same and different communities. Therefore, protected colonies acted as the hubs that connected the communities of the metapopulation. It is not clear why individuals specifically dispersing from distant communities were more likely to select protected colonies over unprotected colonies, but it may have to do with nest predation risk. Many studies have shown that birds actively seek low predation risk areas to breed using visual and olfactory cues that indicate predator presence and activity (Forero *et al.* 1999; Hakkarainen *et al.* 2001; Wesolowski 2002; Roos & Pärt 2004; Morosinotto *et al.* 2010; Forsman *et al.* 2013). For example, some species use the reproductive performance of conspecifics to locate nesting sites, as this provides information on habitat quality (Doligez *et al.* 2004).

This study investigated migration rates at the metapopulation level rather than at the individual level. A previous study that investigated movement at the individual level found

that individuals were more likely to immigrate into colonies that were larger in size than the colony from which they were emigrating (Altwegg *et al.* 2014). In addition, individuals were more likely to emigrate from relatively small and relatively large colonies as opposed to those colonies close to their long-term mean; and immigrate into colonies that were below their long-term mean (Altwegg *et al.* 2014). The present study found that small colonies had higher immigration and emigration rates than large colonies. Because this study investigated movement data at the metapopulation level, the characteristics of each colony can be used to explain movement patterns. The higher immigration rates of smaller colonies were most likely due to the reproductive costs associated with larger colonies. The findings of this and other studies have shown that colony size has a negative effect on reproductive output, probably due to the higher parasite loads and higher levels of intraspecific competition (Covas *et al.* 2008). In addition, it may be more difficult for dispersing individuals (particularly younger birds) to establish themselves into the social structure of large colonies. Large colonies have been found to have more aggressive interactions than small colonies, because they have more birds of the same social status (Rat *et al.* 2015). Therefore, large colonies carry a fitness cost in terms of reproductive output and access to resources (social status). There was no significant difference in immigration rates between protected and unprotected colonies, because protected colonies grew in size with the duration of nest predator exclusion and would have received fewer immigrants over time.

The higher emigration rate of small colonies was most likely a consequence of Allee effects (Altwegg *et al.* 2014). Allee effects refer to the fitness benefits associated with being in the presence of conspecifics, such as collective modification of the environment and antipredator vigilance (Allee 1938; Stephens *et al.* 1999). In social species, such as the sociable weaver, there is often a minimum group size required for survival and reproduction (Stephens & Sutherland 1999). The thermoregulatory benefit of the communal nest mass is a strong positive consequence of group living (Van Dijk *et al.* 2013). The nest mass buffers against extreme temperatures during cold winter nights and hot summer days (White *et al.* 1975; Bartholomew *et al.* 1976). However, to build and maintain the nest requires a group effort. When numbers are too low to do so, the birds leave the colony to immigrate into an active colony, recolonise an abandoned colony or start building a new colony. It has been suggested that larger colony sizes provide protection benefits from aerial predators when foraging as a group, because there are more birds to spot predators (Brown *et al.* 2003). However, the

probability of detecting a predator would increase only up to a point with increasing flock size (Kenward 1978; Stephens *et al.* 1999). Foraging observations have shown that forked-tailed drongos were mostly responsible for vigilance, whilst the weavers were more preoccupied with looking for food on the ground. However, what was noted was that larger colonies attracted more forked-tailed drongos than smaller colonies, which would increase vigilance. It was also interesting to find that colonies with resident African-pygmy falcons had higher emigration rates than colonies without African-pygmy falcons. This supports the observations of Covas *et al.* (2004a) who found that a large portion of a colony emigrated after a pair of African pygmy-falcons took up residence. African-pygmy falcons are known to occasionally consume sociable weaver nestlings and adults (De Swardt 1990; Covas *et al.* 2004a). This finding further highlights the need to evaluate the benefits African pygmy-falcons provide to their sociable weaver hosts in order to fully understand their relationship (Covas *et al.* 2004a).

#### **4. Foraging distances & behaviour of sociable weavers (the effect of colony size on intraspecific competition)**

There was no significant correlation between foraging distance and colony size. Rather, it was abiotic factors in the form of landscape features (tree density) and extreme weather conditions (maximum temperature and humidity) that explained foraging distance. Foraging observations showed that sociable weaver flocks preferred to feed under the sub-canopy of a tree rather than in the inter-canopy. Birds can sift through the soil of the sub-canopy more easily, because the soil is less compact as a result of grass exclusion and the activity of animals that take refuge from the heat of the day (Scholes & Archer 1997). In addition, the search effort of the birds is reduced in the sub-canopy, because the sub-canopy microhabitat attracts a diversity of animal dispersed plants and insects (Scholes & Archer 1997). The tree itself also provides the birds with shade and a quick escape from the ground should they feel threatened (K. Lloyd pers. obs). Therefore, it was not surprising to find that flocks foraging in areas with a high tree density had shorter foraging distances than flocks foraging in areas with a low tree density. The greater distance between trees (or feeding stations) in areas with a low tree density would mean that flocks would need to travel greater distances in order to feed at enough feeding stations before returning to the colony nest. The foraging trajectory of sociable weaver flocks was sickle shaped, so that birds did not travel too far from the colony in a straight direction. Foraging observations showed that the primary response to an aerial

attack was to fly in a straight direction to the colony, where they could take shelter. By circling back to the colony in the latter half of the feeding bout, the flock reduced the distance that needed to be covered if they were attacked by a raptor.

However, it was the interaction between maximum air temperature and relative humidity that best explained foraging distance, which was likely to be related to thermoregulation. Birds living in hot environments cool their body temperature down through behavioural and physiological responses (Gerson *et al.* 2014). Passeriformes, such as sociable weavers, dissipate heat loads primarily through panting, which involves increasing ventilation rates so that more air can pass through the evaporative surfaces of the lungs, air sacs and nasal mucosa (Wolf & Walsberg 1995). However, the ability to do so is inhibited if the water gradient that drives the rate of diffusion of water vapour across the evaporative membranes is low (Gerson *et al.* 2014). Therefore, the rate of diffusion of water vapour (and heat dissipation) across the evaporative membranes is dependent on ambient humidity (Powers 1992).

High ambient humidity imposes a thermoregulatory challenge to sociable weavers when they try to dissipate heat by panting (Gerson *et al.* 2014). A laboratory study found that the ability of sociable weavers to dissipate heat was inhibited by as much as 36% when ambient humidity was high at 48 °C, but ambient humidity had little effect at lower ambient temperatures of 40-44 °C (Gerson *et al.* 2014). These ambient temperatures of the laboratory environment were much higher than the maximum air temperature that was observed when flocks were tracked in the field (30.6 °C). However, unlike the laboratory experiment in which birds were kept calm in a controlled environment, sociable weavers are active when foraging and would have higher metabolic rates (Bennettand & Harvey 1987; Gerson *et al.* 2014). Sociable weaver resting metabolic rates are also considerably variable between 25 °C and 35 °C ambient temperature in the laboratory (Whitfield *et al.* 2015). In addition, the weather station only recorded air temperature (temperature of the air column), whereas the environmental temperatures experienced by foraging weavers would additionally be dependent on conduction, convection and radiation among other factors, and therefore quite different from air temperature alone (Walsberg 1988). Birds often dissipate heat through changes in behaviour before physiologically responding to high environmental temperatures. This is because behavioural responses are quicker and cost less energy than most

physiological responses (Lustick 1983). Thus, to avoid having to pant to cool down, sociable weavers may have responded behaviourally by reducing the foraging distance from the colony under hot and humid conditions. Flocks may have done this by travelling shorter distances between feeding stations or by reducing the time spent foraging (which varied between 1.5 and 2 hours). The nest mass maintains a cooler temperature inside and provides the birds with shelter from the hot temperatures outside of the nest (Van Dijk *et al.* 2013).

Flocks forage as a unit and thus all of the birds in a flock travel the same distance from the colony during a morning foraging bout. Therefore, if intraspecific competition was present, the study would only be able to detect costs on flock fitness, not individual fitness.

Intraspecific competition may be present at the individual level (within the flock), which would be related to colony size. The members of a colony do not have egalitarian access to food resources (Rat *et al.* 2015). Instead, food access is determined by dominance hierarchies, with dominance being determined by status, sex, and relatedness (Rat *et al.* 2015). In terms of food, this involves a low ranking individual giving up their food to a higher ranking individual (avoidance behaviour; Rat *et al.* 2015). Larger colonies have more aggressive interactions among birds than smaller colonies because they have more birds of similar social status (intermediate status, male and unrelated; Rat *et al.* 2015). Foraging observations revealed that individuals were often chased away from the food that they had found by other birds in the flock. In addition, the decision to fly back to the colony appeared to be made by several individuals in the flock, not the flock as a whole. Therefore, lower ranking individuals in the flock may not have consumed as much food as higher ranking individuals when it came time to fly back to the colony. Competition for food may also be greater during the breeding season when food requirements are more important and weavers fly back and forth from the colony to feed nestlings (Maclean 1973e)

## CONCLUSION

This was the first study that used an experimental approach to exclude snakes from several colonies within a sociable weaver metapopulation. Using an experimental approach allowed me to quantify the magnitude of the nest predation effect on population dynamics and understand how nest predation interacted with other social and environmental factors that were known to affect sociable weavers. Nest predation had a substantial effect on reproductive output. However, the magnitude of the nest predation effect was dependent on social and environmental factors. The magnitude of the effect was reduced with increasing colony size (density-dependence) and increased as environmental conditions (which are related to food availability) became more favourable to initiate reproductive events (density-independence). The effect of nest predation on reproductive output transcended into colony and population size trends. Nest predation limited growth rates, but to a lesser degree when compared to environmental factors. Under future climate change conditions, controlling the exacerbating effect of nest predation on reproductive output may assist in keeping populations stable. Colonies that excluded snakes played an important role in structuring and connecting the sociable weaver movement network, with protected colonies acting as the hubs that connected colonies that were far apart from one another. However, it was colony size more than protection status that determined the migration rates of a colony; with smaller colonies having higher per capita immigration and emigration rates. Foraging distance was not explained by colony size and therefore is unlikely to be related to the level of nest predation. Rather, it was probably the ability to thermoregulate under hot and humid conditions that determined foraging distance, which would be expected of a species inhabiting a semi-arid environment. But given the relatively small number of colonies studied, these results should be seen as preliminary.

This study has also identified knowledge gaps in our understanding of sociable weaver population dynamics. The most obvious study that needs to follow is one which investigates the behaviour of the nest predators, namely Cape cobras and boomslangs. Snakes have been found to be the most important group of nest predators in several studies, accounting for up to 90% of nest failures (Weatherhead & Blouin-Demers 2004). Changes in snake activity patterns have also been found to cause variation in the reproductive output of some bird species (Sperry *et al.* 2008). By understanding how snakes behave and react to the behaviour of sociable weavers and environmental factors, we will know what determines the level of

nest predation of a colony. There is evidence from observational studies that snakes preferentially select colonies based on colony size (Marsden 1999; Spottiswoode 2007). We also do not know if coloniality of sociable weavers reduces nest predation rates through predator satiation and communal mobbing of predators (Götmark & Andersson 1984). Another important social factor that was not included in this study, because it operates at the individual level, is the number birds that help raise the nestlings (Covas *et al.* 2008). In addition, the metapopulation model could be improved by determining how nest predation interacts with other factors to determine survival and movement estimates. An improved metapopulation model would allow for a more precise identification of the causes of population decline and evaluation of potential remedies. For example, managers may need to know at what colony size snakes should no longer be excluded. The cues used by dispersing birds to select colonies still need to be investigated. This study has also shown that using a network analysis provided information on the importance of protected colonies in structuring and connecting the metapopulation, which the statistical analysis of migration rates could not. Lastly, the foraging observations and results of this study have generated a suite of questions regarding the social structure of the foraging flock (who initiates foraging, who leads the flock, what kind of interactions occur within the flock), predator avoidance (is there a mortality cost to foraging too far from the colony and is there a correlation between colony size and the number of forked-tailed drongos that keep watch), and the relationship with other foraging species (parasitic or mutualistic).

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