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UNIVERSITY OF MIAMI

THE EVOLUTIONARY MAINTENANCE OF COOPERATIVE NEST CONSTRUCTION IN SOCIABLE WEAVERS (*PHILETAIRUS SOCIUS*)

By

Gavin McLean Leighton

A DISSERTATION

Submitted to the Faculty of the
University of Miami
in partial fulfillment of the requirements for the
degree of Doctor of Philosophy

Coral Gables, Florida

May 2015

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THE EVOLUTIONARY MAINTENANCE OF COOPERATIVE NEST CONSTRUCTION IN SOCIABLE WEAVERS (*PHILETAIRUS SOCIUS*)

Gavin M. Leighton

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The Evolutionary Maintenance of Cooperative Nest (May 2015)
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The evolutionary maintenance of cooperative behaviors, i.e. those behaviors that increase the fitness of other individuals, is difficult to explain because natural selection should eliminate behaviors that reduce an individual's fitness. Despite this seeming disadvantage, cooperative behaviors permeate nature; indeed, many of the major evolutionary transitions require cooperation. The prevalence of cooperative behaviors suggests that mechanisms exist that allow for the evolution and maintenance of cooperation. In this dissertation I investigated the cooperative nest construction of sociable weavers *Philetairus socius*. Sociable weavers are colonial birds that roost and breed in large, communal nests; the communal nests provide thermal buffering, and thus fitness benefits, to colony members. The communal nest therefore represents a public good, and as such should be susceptible to exploitation. Given the potential risk of exploitation, I tested whether certain evolutionary mechanisms are responsible for limiting the exploitation of public good and thus for maintaining cooperation; specifically, I tested both kin selection and punishment as potential forces for maintaining cooperative nest construction. Observations of nest building combined with next-generation sequencing data on relatedness demonstrate that the relatedness of an individual to its colony of residence is positively associated with cooperative investment in the public good. This result supports the importance of kin selection in maintaining cooperative building. Other results support

a role for punishment in maintaining cooperation. Sociable weavers that focus their nest construction efforts on interior nest chambers (a less cooperative behavior) suffer aggression from weavers that focus their construction efforts on the nest exterior (a more cooperative behavior). The individuals that suffer aggression subsequently increase their cooperative investment in exterior construction. The totality of the evidence thus suggests that both kin selection and punishment contribute to the evolutionary maintenance of cooperation in this system.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Page

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 1

Introduction

Current biological diversity is explained in part by major transitions in evolution (Maynard Smith and Szathmáry 1997). The transitions are often characterized by previously independent individuals coalescing around a new, communal resource (Bourke 2011a). For instance, complex multicellular forms arose from the transition from free-living, single-celled organisms to multicellular forms that often maintain a communal somatic tissue (Fisher et al. 2013). Thus, the stability and maintenance of certain major transitions relies on cooperative behaviors that produce the communal resource. However, communal resources, i.e. public goods (Hardin 1968), are susceptible to exploitation because the benefits of a public good cannot be monopolized by individuals that maintain the good. Selfish individuals can exploit the public good without contributing to it, selecting for strategies of non-investment in the communal resource. The exhaustion of the public good by selfish individuals leads to a collapse of the good, or a 'tragedy of the commons' (Hardin 1968). The stable existence of public goods such as burrows (Sherman 1981, Lacey and Sherman 1991), webs (Jackson 2007), and nests (Hölldobler and Wilson 1990, Queller and Strassmann 1998) implies that evolutionary mechanisms maintain the cooperative behavior that supports public goods.

For cooperative behaviors to resist invasion by selfish strategies, the individuals performing the cooperative behaviors must receive relatively more fitness benefits. Importantly, individuals can accrue fitness via two types of reproduction: personal reproduction, i.e. direct fitness benefits, and the reproduction of related individuals, i.e.

indirect fitness benefits (Brown et al. 1980). Hamilton (1964) demonstrated that cooperative behaviors can evolve even if they reduce the focal individual's direct benefits, so long as the behavior provides sufficient indirect benefits to compensate for the loss of direct benefits. The evolutionary mechanism of selecting for a cooperative behavior because it benefits relatives was termed "kin selection" (Maynard Smith and Wynne-Edwards 1964) and is summarized by Hamilton's inequality:

$$r \times B > C \tag{1}$$

In inequality [1], the "B" term represents the fitness benefit the recipient receives as a result of the cooperative act, which levies a fitness cost "C" that the focal individual suffers. The term "r" is the relatedness between the focal individual and the recipient. If a behavior meets the requirements of inequality [1], then selection will favor the behavior. The combination of direct and indirect benefits is known as inclusive fitness, and individuals are selected to maximize their inclusive fitness (West and Gardner 2010).

In certain circumstances, individuals can increase their inclusive fitness benefits by cooperating to produce a public good (Rankin et al. 2007) necessitating a change to the original inequality (Connor 2010, Leigh 2010). Hamilton's equation can be modified to sum the benefit across recipients weighted by relatedness:

$$\sum_{i}^{n} r_i \times B_i > C \tag{2}$$

Individuals maintaining public goods can therefore benefit multiple relatives simultaneously and more easily satisfy Hamilton's inequality.

Although indirect benefits can lead to selection for cooperative behaviors, unrelated individuals within the group could exploit the cooperative behaviors of group mates. The opposing selective interests of individuals within a group often lead to conflict; indeed, conflict is present in many societies, including societies composed of microbes (Gilbert et al. 2007), mammals (Bell et al. 2014, Cant et al. 2014), insects (Trivers and Hare 1976, Bourke 1999), and birds (Emlen and Wrege 1992). Excessive conflict can lead to group dissolution if the costs of conflict exceed the benefits of sociality; therefore mechanisms to modulate conflict within the group are often necessary for group stability (Frank 1995).

One option to reduce conflict is for cooperative individuals to coerce selfish individuals into performing cooperative behaviors. If cooperative individuals induce cooperative behavior in group mates they can prevent free-riding individuals, thus stabilizing the cooperative behaviors that maintain the public goods the group relies on for group persistence.

Punishment of selfish behavior can render selfish behavior more costly than cooperative behavior, leading to selection for cooperation. The evolutionary mechanism of punishment was first described and explored theoretically by Clutton-Brock and Parker (1995), and is described by a cascade of behaviors. First, an individual performs a cooperative behavior that is exploited by a second individual. Subsequently, the cooperative individual acts reduce the fitness of the exploitative individual, suffering a fitness cost for doing so. Finally, the exploitative individual switches to performing cooperative behavior that returns fitness gains to the aggressive, cooperative individual.

Alternatively, some argue that cooperative behaviors can be used as a sexual signal and sexual selection for cooperation can sustain cooperative output (Zahavi 1995). Although the signal hypothesis has not received general support, recent work provides evidence that individuals use cooperative behaviors as signals (Doutrelant and Covas 2007). Sexual selection therefore provides an alternative hypothesis for the maintenance of cooperative behavior that sustains public goods.

While the combination of inclusive fitness benefits and coercive mechanisms are thought to stabilize societies, recent theoretical work argues that kin selection is not a predictive framework for describing social behaviors and that cooperation can evolve in the absence of any coercive mechanism (Nowak et al. 2010). Arguments between opponents (Nowak et al. 2010) and proponents (Emlen 1996, Clutton-Brock 2002, West et al. 2007a, Strassmann et al. 2011) of kin selection explanations for cooperation have focused primarily on eusocial insects, which are often highly cooperative and strongly related to fellow group members (Queller and Strassmann 1998). To resolve the disagreement regarding the evolutionary maintenance of cooperative behaviors that maintain public goods, tests of these evolutionary mechanisms are needed in in novel systems. A useful system for testing these mechanisms is the sociable weaver (*Phileatairus socius*).

Sociable weavers build and maintain a communal nest, and therefore represent an ideal system for understanding the evolutionary maintenance of public goods.

Study System

Sociable weavers are small passerines (26-32 g) that feed on seeds and insects. Sociable weavers live in perennial colonies of up to 400 individuals and are endemic to southwestern Africa (Maclean 1973). In South Africa, Namibia, and Botswana, colonies of sociable weavers construct communal nests in *Acacia spp.* trees using dry *Stipograstis spp.* grasses (Maclean 1973). In the communal nests, pairs breed on an annual cycle or opportunistically after significant rainfall (Maclean 1973). Sociable weavers are cooperative breeders with a mean of roughly one alloparent (Covas et al. 2006) per breeding pair. The alloparents are often related to a member of the breeding pair and provide survival advantages for the offspring (Covas et al. 2008).

The individuals within a colony both build and maintain the communal nest. The nest contains multiple chambers where individuals roost during the night and often reside during parts of the day (White et al. 1975). Sociable weavers often spend time constructing various parts of the nest, including the superstructure (i.e. the roof and walls), the underside of the nest, and the nest chambers (Collias and Collias 1978). The communal nest likely provides increased survival via thermal benefits during the winter (White et al. 1975, Brown et al. 2003). Sociable weavers also enhance thermoregulation by roosting with more birds per chamber in the winter compared to the summer (White et al. 1975, Batholomew et al. 1976).

An individual that contributes to nest construction bestows benefits upon itself and the other individuals in the colony. In this regard, the communal nest can be thought of as a potentially non-excludable public good from which the members of a colony all derive benefits (Rankin et al. 2007, Frank 2010). Even though benefits are extended to every individual in the colony, it is likely beneficial to individuals to cheat and "free ride" on the cooperative efforts of others. The selfishness of weavers within a colony would lead to conflict, and evolutionary mechanisms are necessary to minimize conflict so that the colony can exist stably (Rankin et al. 2007).

Research Aims

Since sociable weavers avoid a tragedy of the commons with respect to the communal nest, I tested several hypotheses regarding the evolutionary maintenance of cooperative nest construction. I examined the following questions: 1) are there differences in cooperative output based on age, sex, or body size? 2) are populations of sociable weavers structured, and if so, does population structure generate increased relatedness between individuals within a nest? 3) does kin selection sustain cooperative nest construction, and in particular, do individuals modulate their cooperative output based on how related they are to their colony of residence? 4) could sociable weavers use nest construction as a sexual signal, and if so, would it be effective as a sexual signal? 5) do sociable weavers punish selfish individuals, and if aggression is directed at selfish individuals, how do they respond to aggression?

This dissertation research was performed using a suite of techniques, including behavioral observations, population genomics, and individual-based modeling. Behavioral observations were performed at two field sites in central Namibia, Windhoek region. I employed next-generation sequencing techniques to quantify the population genomics of sociable weavers. I built individual-based models in Java to assess the effectiveness of using cooperative nest construction as a signal. I then synthesized the results to discuss the evolutionary maintenance of cooperative nest construction.

Chapter 2

Sex and individual differences in cooperative nest construction of sociable weavers (*Philetairus socius*)

Summary

Complex animal societies often rely on communal resources from which all individuals in the group derive benefits. Selection should favor individuals that diminish their contribution towards these communal resources, and to increase their consumption of the resource, thus compromising the stability of these "public goods". To begin to understand how public goods are maintained, it is useful to describe the cooperative behaviors that maintain the public good. One such public good is the communal nest in sociable weavers (*Philetairus socius*), which is constructed and maintained cooperatively by individual weavers in a colony. A captive colony of sociable weavers was observed for six weeks and each individuals' level of cooperative nest construction was recorded. Individuals in the colony lived in one of six possible nests and each individual focused their nest construction behavior on their respective nest of residence. Sociable weaver males cooperated at a higher level than females, with measures of cooperation being consistent over time. These results provide the first description of cooperative nest construction in an entire colony and suggest potential mechanisms that may maintain cooperation.

Background

The maintenance of animal societies often requires that individuals perform group-beneficial cooperative behaviors such as territory defense or nest maintenance (Bourke 2011b); however, the stability of such cooperative behaviors can be undermined by individuals that forego cooperation, i.e. cheaters (Maynard Smith and Szathmáry 1997, Queller and Strassmann 1998, Clutton-Brock 2009). Cooperative behaviors that are especially susceptible to cheating are those behaviors that maintain public goods (Rankin et al. 2007). Cooperative individuals that maintain public goods often do not have options that limit cheating, e.g. partner choice (Clutton-Brock and Parker 1995, Sachs et al. 2004). Therefore, it is necessary to delimit the ecological conditions (Korb and Heinze 2008) and inclusive fitness benefits that allow for the maintenance of public goods through cooperative behaviors.

Recent theoretical studies (Foster 2004, Rankin et al. 2007, Frank 2010, Raihani and Bshary 2011) have delineated mechanisms that can maintain cooperative behaviors that maintain public goods. Evolutionary mechanisms that can maintain public goods include indirect reciprocity (Nowak and Sigmund 1998), generalized reciprocity (Barta et al. 2011), punishment (Frank 1995), and kin selection (Hamilton 1964). Both indirect reciprocity and generalized reciprocity use the previous behaviors of interactants to dictate behavioral response. Specifically, the future behaviors that recipient individuals are subject to is based on either the behavioral history of the recipient (Raihani et al. 2012), or the recent behavioral interactions with individuals (Barta et al. 2011). Similarly, punishment also relies on reputation to guide the behavior of conspecifics. Individuals that have not cooperated in the past suffer the aggression of other individuals within the group, thus rendering cooperation less costly than defection (Clutton-Brock and Parker 1995). Finally, kin selection can maintain cooperation if the benefits of cooperative behaviors are directed to relatives that share genes with the individuals performing the cooperative behavior (West et al. 2007b). These mechanisms have received variable support in empirical systems, with punishment and kin selection argued as the most prevalent mechanisms for maintaining public goods (Rankin et al. 2007)

Public goods are not homogeneous and can be organized into categories according to specific criteria (Rankin et al. 2007). The most familiar category is a common resource that is actively produced by individual cooperation (in contrast to a resource that may regenerate over time, e.g. a communal pasture), labeled “Type 2 Social Goods” (Rankin et al. 2007). One salient example of this type of public good is an actively maintained communal nest. Many Hymenopteran species reside in nests that are constructed via large-scale cooperation (Hölldobler and Wilson 1990, Queller and Strassmann 1998). These types of public goods represent useful systems for testing the social evolutionary theory. To test the generality of certain mechanisms that can maintain cooperation, previously unstudied systems can be assayed and implemented in comparative analyses (Lehmann and Keller 2006).

One novel system is the sociable weaver (*Philetairus socius*) of southwestern Africa. Sociable weavers construct and maintain a large communal nest that they inhabit for the entirety of the year. The nest requires maintenance because it loses nest material over time (Leighton, unpublished data) but also provides thermal benefits to the individuals in the colony (van Dijk et al. 2013); and therefore represents an appropriate system to test which mechanisms are maintaining cooperative nest construction behavior. Sociable weavers cooperatively construct and maintain the communal nest which they inhabit for multiple years (Maclean 1973). The nest is constructed in *Acacia spp*. trees and is built piece-by-piece using *Stipagrostis spp.* grass. The overarching superstructure of the nest supports many discrete, individual chambers where one to several weavers roost at night (Maclean 1973). During winter nights the nests provide a thermal buffer from the outside temperatures, which likely helps individual weavers maintain thermal homeostasis (White et al. 1975, van Dijk et al. 2013). Nest construction is considered cooperative because temperature measurements in the wild suggest that thermal benefits are received by nest-mates by simply roosting in the same nest. Similarly, evidence suggests that larger nests bestow higher survival rates compared to small nests (Brown et al. 2003). Through nest construction, individuals may accrue both direct and indirect benefits; interestingly, the indirect benefits may be important since they could simultaneously benefit multiple relatives (Leigh 2010) and potentially benefit individuals into the future (Lehmann 2007).

Since *P. socius* represents a potential system that can be used to understand social evolution there may be salient characteristics of the system that would suggest whether certain mechanisms are more likely to be maintaining cooperative nest construction (Sundstrom 1994, Gardner et al. 2012). Indeed, other studies have found sexual dimorphism in cooperative behavior that suggests certain evolutionary mechanisms maintain cooperation. For instance, the female-biased cooperation in Belding's ground squirrels (*Spermophilus beldingi*) was a component of the system that suggested indirect benefits were important for the maintenance of certain alarm calls (Sherman 1985). Additionally, any effect of age may be informative for delimiting the evolutionary mechanisms maintaining the behavior (Koenig and Walters 2011). For instance, if juveniles are the individuals performing the majority of cooperative nest construction, this may suggest coercion or some pay-to-stay mechanism (Emlen and Wrege 1992). While some previous work has examined the cooperative output of sociable weavers, the individuals in that study were in social groups smaller than those experienced in natural contexts and were observed in the beginning stages of nest construction (Collias and Collias 1978). To make an estimate of behavior while individuals already have stable nests, individuals should be observed in nests that are within the range of nest sizes in the wild and in groups that are more similar to a natural context.

Materials and Methods

Ethics Statement

This study was carried out in accordance with the University of Miami's Institutional Animal Care Use Committee's (IACUC) guidelines for animal research. This study's protocol (#10-087) was approved by the University of Miami's IACUC committee. The study, conducted at the San Diego Zoo, was approved by Mr. David Rimlinger, curator of birds.

Behavioral Observations

Sociable weavers are a small passerine endemic to Southwestern Africa that live in semi-arid habitats with variable rainfall (Maclean 1973). Sociable weavers are one of the uncommon instances of genetically monogamous species of bird (Covas et al. 2006), and the sex ratio of birds in the wild is not significantly different from the expected 50:50

ratio (Doutrelant et al. 2004). In this study I observed a 15 year old captive colony of sociable weavers at the San Diego Zoo, San Diego, California, during two three week periods: December 17, 2010, to January 6, 2011, and June 19, 2011 to July 9, 2011. Given the climate and availability of food, there is no defined breeding season for the sociable weavers in the enclosure and during the second time period there was at least one set of chicks audibly begging. While there could have been eggs in other chambers the majority of birds were not breeding.

The sociable weaver enclosure housed six nests and ~60 sociable weavers. The nests contained between ~5-20 individuals each, with 2-10 chambers per nest, and are therefore on the smaller side of the nest size spectrum. Each nest contains smaller nest chambers where individuals roost at night; unless otherwise specified, I will use the term nest to refer to the entire nest and will use the term chamber to refer to nest chambers. Inside the enclosure the nests were in close proximity, often being ~1-2 meters from each other. The weavers were fed a diet consisting of crickets (*Acheta domesticus*), mealworms (*Tenebrio molitor*), and fly larvae (*Calliphora vomitoria*) *ad libitum*. Within the enclosure were several small trees and several *Aloe vera* plants on the ground. Birds were provided with a daily supply of dry grass, dry pine needles, and small twigs as nest construction materials.

To begin observations, birds were chosen randomly and observed in 1-hour time blocks (n = 104 observation blocks) and a majority of the birds (67.4%) were observed for more than one time-block. The modal number of times observed for individuals was three, one-hour time blocks. All observations were conducted outside of the enclosure so as to avoid direct interference with behavior. The identity of birds was confirmed by unique color leg band combinations.

During an observation time block, the proportion of time a bird spent constructing any part of the exterior of the nest was recorded as well as the number of pieces of nest material the bird inserted into the nest per hour. From here on, referring to "nest construction" means construction of the exterior of the nest. A bird was considered constructing the nest if it was placing new material on the outside of the nest or if it was re-weaving part of the superstructure of the nest (ethogram placed in Ethosearch repository under "Sociable Weaver 1"). The time a bird spent searching for nest material was *not* scored as cooperative because in several instances, the individual would grasp nest material and subsequently drop the material without inserting it into the nest. In these cases, the bird may have been foraging. If a bird's behavior was obscured by one of the trees or if a bird entered a nest chamber, then the time it was not in view was scored as non-cooperative. Therefore, the measurement of nest construction only reflected the maintenance of the outside architecture of the nest. Given these conditions, the proportion of time a bird was scored as cooperative is a conservative estimate. All individuals were included in the analysis even if they were never recorded cooperating.

The zoo continually places individual-specific ID bands on weavers within the enclosure so as to document the age of individuals within the colony. The zoo provided me with the age of all sociable weavers in the enclosure (range 1 to 11 years old), which allowed me to test for any effects of age on cooperative nest construction. For the analysis, I also classified birds as young (< 2 years of age) versus adults (≥ 2 years of age).

There were 12 individuals (7 males and 5 females) that were measured during both observation periods; six of these 12 individuals had switched nests after being observed during the first observation period (December 2010/January 2011). These individuals allowed me to estimate the effect of changing nests on cooperative output.

Sex Determination

An individual's sex was determined genetically by extracting genomic DNA and assigning sex using three avian primers (P0, P2, and P8). To begin, several contour feathers were plucked from the bird and shipped to the University of Miami where DNA extractions were performed by slightly modifying the protocol developed by Bush et al (2005). To maximize genomic DNA yield, the proteinase K wash was extended from 24 hours to 48 hours. The genomic DNA was exposed to the P2 and P8 primers developed by Griffiths et al (1998) and the new P0 primer developed Han et al (2009) via a multiplex PCR; all of the PCR specifications listed by Han (Han et al. 2009) were followed with one exception: during the PCR, the number of cycles was increased by five so as to increase the targeted DNA product. The sex of the sociable weavers was determined genetically because the sexes are indistinguishable using size and plumage characteristics (Maclean 1973).

Statistical Analysis

Two dependent measures of cooperation were used: the proportion of time spent cooperating and the number of pieces of grass/twigs inserted into the nest per hour. I used two measures because each bout of nest construction could differ in time between individuals. The number of items inserted into the nest was analyzed as a rate because some “hour” time blocks had to be shortened by 1-3 minutes if individuals were being fed. Neither measure of cooperation was normally distributed, so the distribution of the data was inspected to select the appropriate test. While both variables show a superficial similarity to a Poisson-distributed variable, both measures are continuous. Therefore, typical analyses such as Poisson, generalized-linear mixed models (GLMM) are inappropriate for analyzing these data. Instead, the cplm package in R (Team 2014) was used because it utilizes the Tweedie distribution. The Tweedie distribution allows one to fit continuous data to a distribution that has positive mass at 0 with a continuous distribution extending from 0 in the positive direction (Dunn and Smyth 2005). This distribution was used with a logarithmic link in a GLMM as in some other studies of cooperative behavior (Browning et al. 2012). Parameter values were generated using a Laplace approximation as this method produces more accurate estimates compared to the penalized quasilikelihood approximation (Bolker et al. 2009).

Two models were built: a model with a proportion of time as the dependent variable and a model with items added to the nest per hour as a dependent variable. In both models the independent factors entered into the model were age (either the continuous set of ages or the young versus adult categorization), sex, and whether an individual moved to a new nest, while the random factor of “individual” was included to improve estimates of fixed factors (Bell et al. 2009). To select the best model, i.e. the model that loses the least information, I compared the AIC values of each respective model after dropping terms from the full model sequentially (Burnham and Anderson 2004). Similarly, I performed log-likelihood tests comparing the full model to nested models. The residuals were plotted against the final explanatory variables and assessed for heterogeneity visually (Zuur et al. 2009).

Since division of labor is common in communal systems where nests are constructed (Seeley 1982, Hölldobler and Wilson 1990), I built a model that predicted the number of twigs added to the nest using the amount of time devoted to cooperation. After removing the variation associated with the amount of time devoted to cooperative nest construction, I used the same predictive factors as above (age, sex, and moving to a new nest) to explain any remaining variation. All these factors were entered into a GLMM with a Tweedie distribution and log-link due to the heterogeneity associated with the dependent variable across multiple levels of each factor.

Within the enclosure there were six active nests. For a subset of hour-long observations I recorded the specific nest individuals added items to. Using these data I was able to perform a multinomial test to determine if individuals were adding items to one nest in particular, or if individuals were adding items to several nests indiscriminately.

While some GLMMs allow for repeatability estimates, there is no way to calculate repeatability for GLMM's built with the Tweedie distribution (Nakagawa and Schielzeth 2010). Given this problem, repeatability was calculated following the traditional formulation (Lessells and Boag 1987); because of the potential for bias in the repeatability estimates, they are interpreted with caution in the results.

Results

The best predictor for both dependent variables, the proportion of time devoted to cooperative nest construction and items inserted into the nest, was the sex of the individual (Tables 2.1 & 2.2). Specifically, males contributed significantly more than females to both cooperative dependent variables (Figures 2.1 & 2.2).

Log-likelihood tests of nested models demonstrated that sex of the individual was the only significant predictor of cooperative variables ($p < 0.01$ in both models). The log-likelihood tests agreed largely with the best models as specified by AIC values; though ΔAIC values also suggest that whether an individual moved to a new nest may have a weak effect on cooperative output (Supplementary tables 2.1 & 2.2; (Burnham et al. 2011)). Both age and age x sex effects were non-informative ($p > 0.05$) and dropped from the best model. Additionally, neither age metric was a significant predictor of cooperative output. Neither the continuous measure or age nor the classification of individuals into young (< 2 years old) versus adult (≥ 2 years old) predicted cooperative output, though the three individuals of age 0 appeared to cooperate less (Figure 2.3). The best model for both dependent variables contained sex as a fixed factor and individual as a random factor.

The standard repeatability for these behaviors was calculated following Lessells and Boag (1987). Repeatability was 0.630 for the proportion of time devoted to cooperative nest construction and the repeatability for the number of materials inserted into the nest was 0.589. These values should be interpreted with some caution as they may be slightly biased due to heterogeneity. Importantly, these repeatability values indicate that, even with minor bias assumed, individuals were consistent in cooperative behaviors across time.

I built a GLMM that predicted the number of items inserted into the nest from the amount of time devoted to cooperative nest construction. The amount of time devoted to cooperative nest construction was a significant predictor of the number of items added to the nest ($p < 0.001$; Table 2.3, Supplementary Table 2.3). Though much of the variation associated with the number of items added to the nest was explained by the amount of time an individual spent cooperating, other factors explained the residual variation in the number of items added to the nest (Table 2.3). Specifically, whether an individual moved to a new nest and the sex of an individual were both predictive of residual variation in the cooperative variable model. Males inserted more items into the nest than would be predicted based on the time devoted to cooperative nest construction and individuals that moved to a new nest inserted more items into the nest than would be expected based on the amount of time devoted to cooperative nest construction (Table 2.3).

For the subset of individuals whose cooperative behavior was recorded as well as the specific nest the individual inserted items, a multinomial test was performed on whether an individual built at the same nest. Individuals consistently built at one of the six nests, rather than building for a fraction of the time at all of the six nests ($p < 0.001$, multinomial test).

Finally, the sex ratio of individuals in this population was tested to determine if the ratio deviated from an expected 50:50 ratio. There were 42 individuals total, of which 22 were males. A binomial test indicated that the ratio was not significantly different than 50:50 ($p > 0.05$). There was also no difference in the average age between males and females ($p > 0.05$).

Discussion

The sex discrepancy in output of cooperative nest construction suggests that certain evolutionary mechanisms are more likely than others in terms of maintaining cooperative nest construction. Since female sociable weavers disperse to non-natal nests more than males (Doutrelant et al. 2004) the population-wide relatedness to the nest of residence is likely higher in males than in females. Indeed, male sociable weavers within colonies show genetic structuring amongst themselves compared to males in other colonies compared to females that do not show such structuring (Covas et al. 2006). Since relatedness to the nest inhabitants is higher in males, it may be possible for males to accrue more indirect benefits from cooperative nest construction than females. The pattern observed in sociable weavers can be explained by a recent inclusive fitness model by Johnstone & Cant (2008) and thus comports with some theoretical expectations.

While individuals that construct the superstructure of the nest are likely obtaining direct benefits from the behavior, direct benefits alone do not represent a likely explanation for the sexual dimorphism in cooperative output. If direct benefits were stabilizing the behavior, then female sociable weavers should be expected to show similar levels of cooperative nest construction since females show high nest fidelity after dispersal (Brown et al. 2003). While females perform some cooperative nest construction, they perform less than males, suggesting that both sexes may be accruing direct benefits via cooperative nest construction. Additionally, female sociable weavers tend to build more inside the nest chamber than on the superstructure of the nest (Collias and Collias 1978), though the result from the previous study was non-significant as it was based on four females. If females do focus on nest construction behavior within their chamber, females may be doing so because the lack of potential indirect benefits leads them to maximize direct benefits by maintaining their individual chamber. While it is technically challenging to measure maintenance of nest chambers, future studies could monitor the number of items individuals bring into the nest chambers as a proxy for chamber maintenance. A full analysis of chamber maintenance vs. nest construction would likely provide insight into the maintenance of this behavior.

An alternative explanation for the sex difference in cooperation is sexual selection for increased nest construction in males. This explanation is possible but relatively less likely because of the demography of *P. socius*. Sociable weavers are a genetically monogamous cooperative breeder (Covas et al. 2006), and recent work has demonstrated that in cooperative groups where reproductive skew is high in both sexes, the strength of sexual selection is comparable in males and females (Rubenstein and Lovette 2009). Therefore, morphological traits and behavioral traits such as cooperation between sexes will not diverge due to sexual selection. Instead, sexual selection will lead to sexually selected traits that are comparable between the sexes (Rubenstein and Lovette 2009). Since the sex ratio of sociable weavers is even in both the wild and this study ($p > 0.05$), and considering that sociable weavers are genetically monogamous (Doutrelant et al. 2004), reproductive skew should be high in both sexes and resultant sexual selection should drive similar sexually selected traits in both sexes. Indeed, in a system where nest building is used as a signal (*Euplectes orix*), there is high reproductive skew in males and high sexual dimorphism (Lawes et al. 2002), unlike the plumage monomorphism observed in sociable weavers. Whether all species of weavers actually use nest-building behavior and nests as a signal is unclear and in some cases empirical evidence demonstrates that nests and nest building are not being used as a signal (Quader 2005b).

Sociable weaver nests and the nests of other weavers differ in ways that are pertinent to the requirements for sexual selection. In contrast to the large nest mass of sociable weavers, other weaver species build discrete, individual nests and females assess the nest-building output of males by inspecting the discrete nests of individual males (Da Camara-Smeets 1982, Quader 2006). In contrast, female sociable weavers cannot sequentially sample the nest building output of individual males. Instead, to accurately gauge the nest construction of male sociable weavers, females would necessarily have to observe male cooperative output over time, as there is temporal variation in male cooperative output. Females would not only have to assess multiple males, but would also have to accurately update the output of male nest construction daily, thus necessitating a sophisticated memory. While possible, the neural machinery required for ranking male output seems implausible. Indeed, monitoring multiple individuals and their cooperative output is now recognized as particularly demanding of time and neural machinery, thus potentially explaining the paucity of punishment behaviors in nature (Raihani et al. 2012).

Previous work has shown that allofeeding may be used as a signal by sociable weavers (Doutrelant and Covas 2007); however these results are ambiguous as individuals are less likely to display with food items in front of large flocks, failing to maximize the benefits of display (Leighton, unpublished modeling data). The data presented here also conflict with the idea of using items to signal quality. Males placed more items into the nest than expected given a certain amount of time whereas individuals displaying food items in the wild perch with the items (Doutrelant and Covas 2007). If male sociable weavers were signaling with nest construction behavior, they should insert fewer items than expected given a certain amount of time, which was not observed in this population. Importantly, helpers are predominantly male and help kin more than expected by chance, suggesting that male helpers are acquiring indirect benefits by helping to raise siblings (Covas et al. 2006). With respect to alloparenting in sociable weavers, kin identification is critical to directing cooperation towards a sibling or half-sibling (Gilbert et al. 2007, Ostrowski et al. 2008).

Several other mechanisms that maintain cooperation could maintain cooperative nest construction, but these mechanisms do not readily predict the sex discrepancy in cooperative output. However, one other potential mechanism for the maintenance of cooperative nest construction is group augmentation (Kokko et al. 2001). Group augmentation selects for cooperation to increase the group-size because larger groups confer fitness benefits to all group members. Indeed, general behaviors in other species have been interpreted as being maintained via group augmentation. For example, in meerkats (*Suricata suricata*), individual female helpers perform more vigilance behaviors when pups are nearby (Santema and Clutton-Brock 2013). As vigilance is a general helping behavior, the interpretation that female meerkats are performing the behavior due to the benefits of group augmentation comports well with previous findings in meerkats (Clutton-Brock et al. 2002). In sociable weavers group augmentation may explain the sex discrepancy in cooperative nest construction. Group augmentation may benefit male sociable weavers more as these individuals are likely more exposed to predation due to increased parental effort and the fact that alloparents are predominantly male (Doutrelant et al. 2004, Doutrelant and Covas 2007). Future studies of cooperative nest construction in nature could examine whether individual sociable weavers targeted specific areas of the superstructure of the nest for construction, or if individuals were performing general nest-wide construction.

Recent theoretical and empirical research has found that reciprocity can maintain cooperative behaviors (Rutte and Taborsky 2007, Barta et al. 2011); however, reciprocity requires that individuals experience cooperation in previous social interactions. In sociable weavers, there is a large class of individuals that performed no cooperative nest construction, suggesting that reciprocity would break down in sociable weavers. Reciprocity also does not provide a mechanism for the discrepancy in cooperative output between sexes if inclusive fitness benefits were comparable between the sexes, suggesting that reciprocity does not maintain cooperative nest construction in sociable weavers.

Finally, punishment has been argued as a potential mechanism in the maintenance of cooperative behaviors that maintain public goods (Frank 1995, Raihani et al. 2012). While punishment is suspected to maintain public goods in some systems, the evolution of punishment creates a second-order public goods dilemma where punishers should be selected to refrain from punishment when other individuals will do the punishing, thus compromising the stability of the public good (Dreber et al. 2008). Similarly, the memory requirements for punishment are cumbersome and recent reviews suggest that the neural requirements for punishment explain the general dearth of punishment behavior that maintains cooperative behaviors (Raihani et al. 2012). Similar to the other evolutionary mechanisms, punishment does not readily provide a reason for the sexual discrepancy in cooperative output.

The sex difference in cooperative nest construction is at least superficially similar to some sex differences in cooperative behavior in other species with sex-biased dispersal. For example, female Belding’s ground squirrels (*Spermophilus beldingi*) are more philopatric than males and perform various cooperative behaviors more than males (Sherman 1981, 1985). Specifically, related females often cooperatively defend nearby nest burrows and the likelihood that females will give a “trill” alarm call is highly contingent upon the proximity of kin (Sherman 1985). Despite the difference in which sex is philopatric, the philopatric sex in sociable weavers and Belding’s ground squirrels are more cooperative than the dispersing sex, emphasizing the potential generality of the phenomena.

Some instances of large-scale cooperation such as communal nests may evolve primarily due to kin selection, and subsequent behavioral mechanisms such as punishment can evolve secondarily and maintain the cooperative behavior (Okasha 2006, West et al. 2011). In sociable weavers, the reconstructed level of promiscuity was low (Cornwallis et al. 2010), suggesting that relatedness in ancestral groups of sociable weavers was high. The elevated relatedness within males in sociable weaver groups could have allowed for the evolution of cooperative nest construction, thus facilitating the transition from smaller nests, comparable with other weaver species (Collias and Collias 1977), to the larger, communal nests of sociable weavers.

While this study has expanded on previous observational work in sociable weavers (Collias and Collias 1978), future tests of competing hypotheses will need to be completed in field populations of sociable weavers. A strong test of whether cooperative nest construction is maintained, at least in part, by indirect benefits will be a high-resolution assessment of relatedness and whether relatedness predicts cooperative output.

Figure 2.1: Box and whisker plot comparing the proportion of time the sexes devoted to cooperative nest construction. The sample size for each sex is represented below their respective distribution. The central tendency of the male distribution is significantly higher than that of females. The box represents the interquartile range while the line represents the median of the data. The whiskers extend to the maximum point that is no more than 1.5 x the inter-quartile range in either direction. Any individuals beyond that range are indicated by circles.

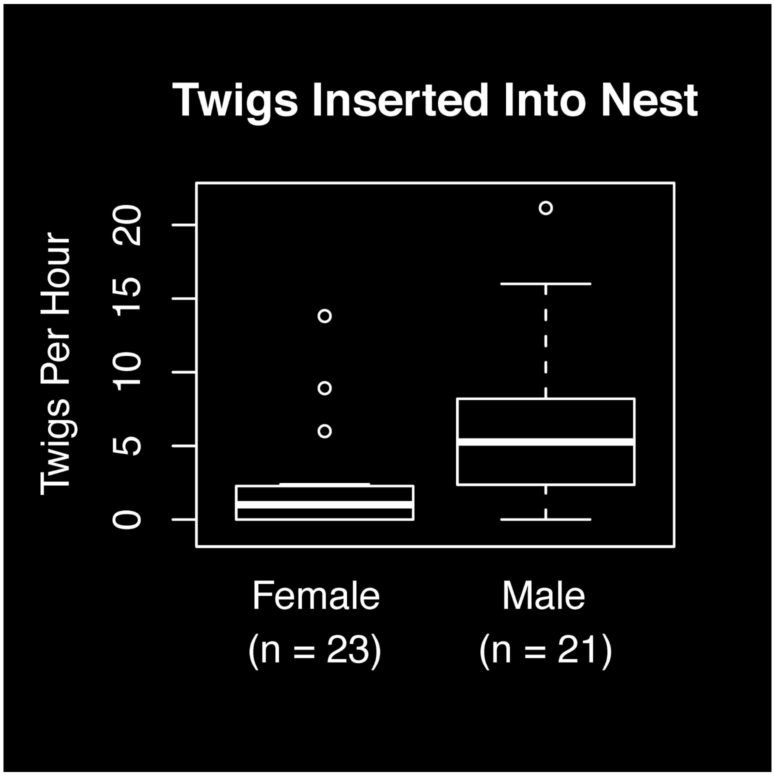


Figure 2.2: Box and whisker plot comparing the number of twigs the sexes inserted into the nest. The sample size for each sex is represented below their respective distribution. The central tendency of the male distribution is significantly higher than that of females. The box represents the interquartile range while the line represents the median of the data. The whiskers extend to the maximum point that is no more than 1.5 x the inter-quartile range in either direction. Any individuals beyond that range are indicated by circles.

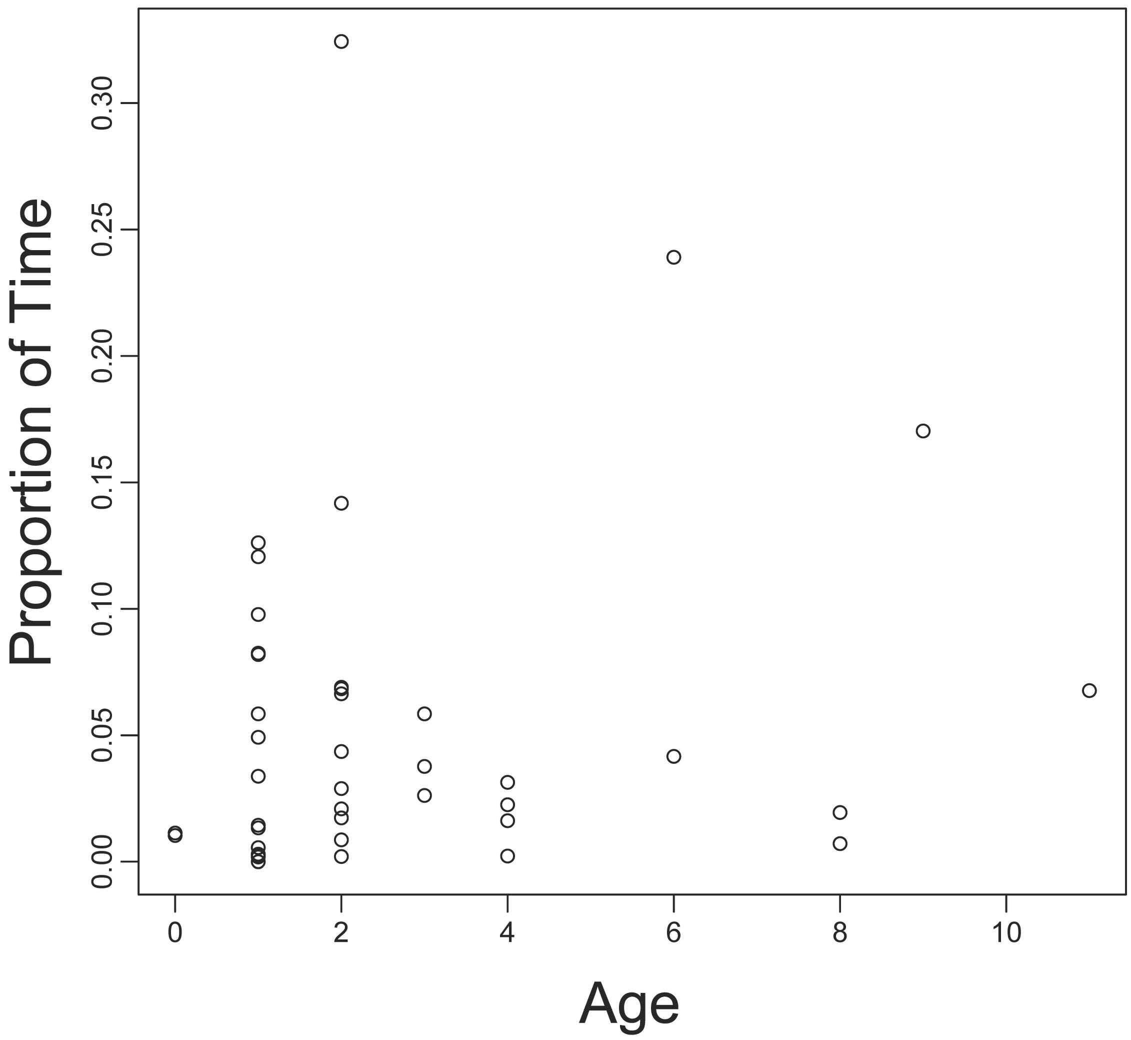


Figure 2.3: Scatterplot of the proportion of time individuals spent cooperating plotted on their age. For individuals that were measured more than once, their average proportion of time was used as a single point. No bivariate linear trend was significant and age was not a significant predictor of either cooperative variable in the models.

Table 2.1: Explanatory variables in GLMM predicting proportion of time devoted to cooperative nest construction. The proportion of time an individual dedicated to cooperative nest construction was best predicted by the sex of the individual ($p < 0.001$; 1.56 ± 0.50). All estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 0.83 ± 0.91) were included in all models.

Predictor	Estimate	s.e.	df	p-value
Intercept	-0.04	0.04		
Sex (m > f)	1.56	0.50	1	<0.001
Moved (no > yes)	0.06	0.24	1	0.79
Age	0.04	0.13	1	0.88
Sex x Age	-0.000039	0.15	1	0.99

Table 2.2: Explanatory variables in GLMM predicting number of items inserted into communal nest. The number of items an individual inserted into the nest was best predicted by the sex of the individual (p = 0.002; 1.26 ± 0.52). All estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 0.82 ± 0.90) were included in all models.

Predictor	Estimate	s.e.	df	p-value
Intercept	0.36	0.38		
Sex (m > f)	1.26	0.52	1	0.002
Moved (no > yes)	-0.24	0.24	1	0.30
Age	-0.10	0.15	1	0.70
Sex x Age	0.06	0.18	1	0.72

Table 2.3: Explanatory variables in GLMM predicting number of items inserted into communal nest after controlling for the amount of time dedicated to cooperative nest construction. To assess an individual's contribution of items to nest construction after controlling for time devoted to nest construction, a GLMM was built that predicted the number of items inserted into the nest with time as a predictor. The amount of time devoted to nest construction was a significant predictor ($p < 0.001$). Similarly, both sex ($p = 0.003$) and whether an individual moved ($p = 0.004$) were predictor of items added to the nest after controlling for the time devoted to nest construction. All estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 0.36 ± 0.60) were included in all models.

Predictor	Estimate	s.e.	df	p-value
Intercept	0.09	0.24		
Time	0.14	0.02	1	<0.001
Sex (m > f)	0.86	0.28	1	0.003
Age	-0.08	0.06	1	0.18
Moved (yes > no)	0.61	0.20	1	0.004

Chapter 3

Sociality likely drives genomic structuring over microspatial scales in sociable weavers

Summary

The evolution of sociality often leads to genetic structuring among groups, and alters the evolutionary forces the groups experience. Describing the genomic structuring of social species is therefore necessary to understand the selective forces that act on a species. While some recent work have used genomic methods to investigate population structure in eusocial insects, relatively little genomic work has examined population structure in the largest non-human mammal and avian clades. We delimited genomic structuring in sociable weavers (*Philetairus socius*), a passerine bird that lives in stable, perennial colonies, using the genotype-by-sequencing approach to generate a dataset of several thousand SNP's to estimate genetic structuring within and among eight nests. While we discovered relatively low levels of genomic structuring among nests, the structuring was not explained by distance between nests. We also found significantly higher structuring among male sociable weavers compared to female weavers, suggesting that female sociable weavers are more prone to dispersal in this species. The nests represent distinct genomic groups according to Bayesian clustering analysis, though the differentiation among nests is relatively low compared to other social species.

Background

The causes and consequences of genetic structure are of fundamental importance for understanding evolution because the influence of population subdivision on genetic structuring dictates the strength of selection acting on individuals within those groups

(Charlesworth 2003). Genetic structuring among groups can therefore alter the evolutionary trajectory of populations and species. For instance, theory demonstrates the evolution of sociality and genetic structuring can lead to biological scenarios that violate basic assumptions in population genetic models (Fisher 1930, Wilson et al. 1992, Neel et al. 2013), or scenarios that require fundamental changes when modeling the evolution of certain traits (Hamilton 1964). In empirical systems populations can become divided and structured due to the evolution of sociality, and in some circumstances sociality leads to inbreeding and the potential extinction of the species (Agnarsson et al. 2013). To understand how selection acts on groups of individuals, it is therefore necessary to understand the genetic structuring among groups.

A critical population genetics parameter than influences genetic structure is the effective population size. The effective population size is different than the census population size in that effective population size incorporates information about the sex ratio of the population and the proportion of individuals that actually breed in a population. Recent work on certain species of eusocial Hymenoptera demonstrates that the evolution of sociality, and the subsequent evolution of division of reproductive labor has reduced the effective population size of several species of social insects (Romiguier et al. 2014). Given the relatively long-lived queens and major reproductive skew in these societies, some species of eusocial insects have effective population sizes that mirror certain solitary mammal and avian species. The evolution of sociality and division of reproductive labor in eusocial insects therefore reduced the effective population size and increased structuring among groups (Romiguier et al. 2014). Indeed, the reduced effective population size may lead to increased homozygosity and reduced fitness in certain colonies (Haag-Liautard et al. 2009).

Similarly, social mammals and birds may also experience reduced effective population size and increased genetic structuring relative to solitary congeners (Nichols et al. 2014). Indeed, the evolution of sociality often generates considerable genetic structure (genetic variation found among groups rather than within groups) among groups due to unequal sharing of reproduction within groups, i.e. reproductive skew, and sometimes increased relatedness between breeding individuals (Ross 2001). Genetic structure is often estimated using F statistics, with F_{ST} representing an estimate of the proportion of genetic structure found among groups. Banded mongoose (*Mungo mungo*), grey-crowned babblers (*Pomatostomus temporalis*), and white-browed sparrow weavers (*Plocepasser mahali*) display considerable genetic structuring with $F_{ST} > 0.1$ (Blackmore et al. 2011, Nichols et al. 2012, Harrison et al. 2014).

Although considerable research has investigated the population genetics of moderately sized vertebrate societies (Blackmore et al. 2011, Nichols et al. 2012), relatively less work has investigated the population genetics of the largest non-human mammal and avian societies. With respect to non-human mammals, early research using DNA fingerprinting techniques found high levels of inbreeding and population structure in naked mole rats (*Heterocephalus glaber*) (Reeve et al. 1990), though see (Braude 2000) for an interpretation that suggests high inbreeding is an artifact of study design. Similarly, average relatedness within a colony of Damaraland mole rats (*Cryptomys damarensis*) was high and averaged slightly under ~0.5 (Burland et al. 2002). To provide a comparative insight into the population genetics of large vertebrate societies we investigated the influence of sociality on genomic structuring in colonies of sociable weavers (*Philetairus socius*).

Sociable weavers live in perennial groups in a large communal nest and group size can reach 500 individuals (Maclean 1973), and therefore represent one of the largest avian societies. Although sociable weaver group size is similar to group size in mole rats, mole rats are eusocial (Reeve et al. 1990) and may therefore lead to differences in genetic structure. Previous work on sociable weavers suggests that there is limited dispersal away from the natal colony (Brown et al. 2003), and that females are more likely to disperse than males (Covas et al. 2006). Importantly, there is high reproductive skew in breeding groups within nests (Covas et al. 2006) which can depress heterozygosity and increase structuring among groups (Hedrick 2010). Similarly, van Dijk et al. (2014) found low levels of relatedness (~0.05 in males and ~0.01 in females) within colonies of sociable weavers, though these authors argue for population-wide estimates of relatedness that show no relatedness among individuals. To resolve relationships among groups of sociable weavers we build on this previous research by investigating whether there is genomic structuring among populations, and whether factors such distance between nests and group size can be used as potential predictors of genomic diversity. We compared the genomic structuring between the sexes because recent evidence in white-browed sparrow weavers (*Plocerpasser mahali*), one of the sociable weavers closest living relative, have reversed the typical avian sex-biased dispersal (Harrison et al. 2014).

We used genome-wide sampling using genotyping-by-sequencing (GBS) to estimate genomic structuring among groups and to determine whether social or spatial variables influence genomic structuring in sociable weavers. Next-generation sequencing (NGS) technologies are useful for delimiting both inter and intra-specific genomic structuring (Davey et al. 2011, Ellegren et al. 2012). Given the coloniality of weavers, the low dispersal of sociable weavers, and the genetic structuring in a close living relative (Harrison et al. 2014), we predicted significant genomic structuring among groups potentially leading to low heterozygosity within groups. In addition, we compared genomic structuring among males and females to determine if sociable weavers follow the typical avian pattern of female-biased dispersal or if sociable weavers share reversed sex-biased dispersal with white-browed sparrow weavers.

Materials and Methods

Study Species and Site

Sociable weavers are small passerines (25 – 30 g) endemic to the semi-arid savannahs of South Africa and Namibia. Sociable weavers roost communally in massive nests that are constructed using twigs, *Stipagrostis spp.* grass, and softer materials for nest lining (Maclean 1973). The nest provides thermal benefits to the weavers (Leighton and Echeverri 2014), and within the massive nest smaller groups of individuals roost in disparate chambers. Sociable weavers are sexually monomorphic as adults so we identified the sex of individuals using primers that anneal to avian sex chromosomes (Han et al. 2009).

To examine the population structuring of sociable weaver colonies, we mist-netted individuals from eight colonies (range of individuals sampled per colony = 4 – 26, mean = 12 ± 7, supplemental table 3.2) resulting in 95 total individuals. After removing individuals from mist nets we collected one capillary tube of blood (~80 µL) from the brachial vein and stored the blood in lysis buffer. Genomic DNA was extracted from the blood using Qiagen© DNeasy Blood and Tissue kits following the protocol adapted by Bush et al. (2005).

The colonies we sampled varied in both size and isolation from the other colonies (see below). We collected GPS locations of nests to estimate the effect of isolation on genetic diversity. For each of the eight nests we recorded the GPS coordinates using a Garmin Nuvi© and plotted these coordinates using the "RgoogleMaps" package in R. The GPS locations are listed in supplementary table 1. Distances between nests were estimated as a straight-line distance using R (2014) To estimate nest size, we followed the protocols for estimating nest sizes used in Leighton and Echeverri (2014). We sampled 8 nests in total, with nest size ranging from n = 4 to n > 300 individuals.

Next-Generation Sequencing

Between 0.3 – 3.0 µg of genomic DNA from each sample was sent in a 96-well PCR plate to Cornell University's Institute for Genomic Diversity (IGD) for analysis. IGD used EcoT22I as the restriction enzyme after performing Experion© traces on digested genomic DNA. The institute then followed the single-digest, genotype-by-sequencing

(GBS) protocol described by Elshire et al (2011). Under this protocol genomic DNA is digested using EcoT22I, individual-specific adapters and general adapters are ligated to the digested DNA fragments, and the DNA is amplified by PCR and sequenced on Illumina© Hi-Seq machines. Samples were run on a full lane of 100-bp single-end Illumina HiSeq 2000 at the Cornell Core Laboratories Center.

Bioinformatic Analysis

The Cornell Institute of Genomic Diversity processed the raw sequence reads using the UNEAK pipeline, a component of the TASSEL software (Glaubitz et al. 2014). The UNEAK pipeline retains all reads with a barcode, cut site and confidence in base pair calls up to the 64th base pair. The retained reads are then clustered by identity and any reads differing by a single base-pair are called as tentative SNPs. To reduce the influence of sequencing error on the analysis we removed any alleles that are represented by five or fewer reads or are at a minor allele frequency of less than 5%. We reduced the influence of paralogs by filtering SNPs with heterozygosity greater than 75%.

Filtering Steps

The original UNEAK pipeline identified 9495 variable SNPs where there was < 5% of missing values, and a minor allele frequency > 5%. To remove all missing data we further filtered the SNP dataset to 1333 variable SNPs and thus the final dataset contained SNPs that had a called SNP value for each individual in the population, and a minor allele frequency > 10%. We used this filtered dataset to compute pairwise F_{ST} values between populations and for all the following results.

Statistics

We estimated pairwise F_{ST} values between each of the colonies using Genepop Version 4.2 (Rousset 2008), which computes F_{ST} based on Weir and Cockerham (1984). Since recent work in the closest relative of sociable weavers, the white-browed sparrow weaver, shows evidence of male-biased dispersal (Harrison et al. 2014), we also divided the dataset into male and female individuals and compared overall F_{ST} values between the sexes to determine if male-biased dispersal is ancestral in this group. We computed expected heterozygosity and observed heterozygosity using Genepop for each locus and used exact tests (Rousset 2008) to detect heterozygote excess or deficiency in the in the sampled nests.

To determine if there was a correlation between genetic distance and spatial distance, we performed a Mantel test using the R package 'ade4'. We estimated genomic distance as $F_{ST}/(1-F_{ST})$ using the entire set of SNPs to calculate F_{ST}. The Mantel test compares two distance matrices and compares the correlation coefficient to a set of randomized correlation coefficients calculated after randomizing the values in each matrix (Sokal and Rohlf 1995).

Structure Analysis

We used the program STRUCTURE (Pritchard et al. 2000) to gauge the most likely number of genomic groups. We used a burn-in of 100,000 steps and then ran each model for 25,000 steps after the burn in. We performed this analysis for $K = 2$ through $K = 8$

and compared the posterior probability of each K value. We used the LOCPRIOR setting as the model can incorporate data about sampling location that facilitate the detection of subtle population structure; however, using LOCPRIOR does not facilitate the detection of population structure if the structure does not exist (Hubisz et al. 2009). The rest of the settings were set to the default settings suggested by Pritchard (http://pritchardlab.stanford.edu/structure_software/; 2010). We employed all SNPs in this analysis regardless of F_{ST} value and argue that this presents an accurate picture of admixture among groups. We used the software 'distruct' (Rosenberg 2004) to display the output STRUCTURE.

Results

F_{ST} and Isolation by Distance

We found considerable genomic structuring among colonies over these spatial scales (Table 3.1). We estimated F_{ST} values for each of the SNPs in the main dataset (> 9,000) loci and found that while the majority of SNPs show no structure, several thousand SNPs do indicate genomic structuring among the populations. While we did find genomic structuring among colonies, the Mantel test demonstrated that distance did not explain pairwise F_{ST} comparisons (15,000 Monte Carlo steps, $r = 0.06$, $p = 0.37$, Supplemental Figure 3.1). We found that when we split the dataset by sex and compared the global F_{ST} values, males show higher genomic structuring than females (Figure 3.2, $p = 0.001$, $t = 3.28$, S.E.M. = 0.002).

Structure

The SNP data strongly favor a population structure of 7 clusters (Table 3.2) according to the program STRUCTURE. Indeed, no other clustering (K) value received support when computing the posterior probabilities. Using the full dataset we see that there is indeed admixture among all populations (Figure 3.2) though the software still suggests that subpopulations are almost always defined by the physical colony.

Heterozygosity

We used the 1333 SNPs to test for heterozygote excess or deficiency in each of the colonies. We performed multilocus U-tests using the Genepop software. We found one colony with heterozygote deficiency ($p < 0.001$; Table 3.3) and we found four colonies with an excess of heterozygotes across the genome ($p < 0.001$ for each of the four nests; Table 3.3).

Discussion

We identified between ~1000 and ~9000 variable loci depending on the stringency of the filtering steps, allowing us to assess the fine-scale population structure in sociable weavers (Backström et al. 2007). The number of loci used here is roughly two orders of magnitude larger than previous studies on sociable weavers using genetic markers (van Dijk et al. 2014). We used these loci to document the existence of genomic structuring among nests (Table 3.1), and of significantly higher genomic structuring in males compared to females (Figure 3.1). Along with banding records (G.M. Leighton, pers. obs.) and previous work with a limited set microsatellites (Covas et al. 2006), our results strongly suggest that female sociable weavers disperse significantly more than males. Sociable weavers therefore follow the typical sex-biased dispersal in avian clades, and the reversed sex-biased dispersal in white-browed sparrow weavers (*Plocepasser mahali*) is likely of recent and independent origin (Harrison et al. 2014). Future research on the population genetics of other *Plocepasser* species will be able to define the extent of male-biased dispersal in that genus.

With respect to GBS and RAD-tag data sets, it is not uncommon to select loci with elevated F_{ST} values for subsequent estimates of genomic structuring. In contrast to previous research (Baldassarre et al. 2014, Taylor et al. 2014), we did not isolate SNPs with high F_{ST} values to perform the genomic structuring analyses. We argue that employing all loci regardless of F_{ST} value presents a more accurate view of genomic structuring between groups. The structure analysis suggests that there are low, but consistent, levels of genomic structuring among nests (Figure 3.2, Table 3.3). The structure analysis also suggests a clustering coefficient that is one unit away from the number of nests samples, arguing that nests do represent distinct groups, in contrast to the findings of van Dijk et al. (2014). While there is a large background of genomic variation that is shared among all nests (green in Figure 3.2), many nests have distinct familial units that are genomically distinct from other nests (e.g. yellow and purple colors in Blue nest in Figure 3.2A). When nests are considered in sum, we argue that the presence of distinct familial units leads to significant genomic structuring among nests. We contend that in our nests where we do not see a familial unit that our sample size did not detect enough individuals from a family to form a cluster.

While we find genomic structuring among nests, we find no evidence of isolation by distance in this population (Supplemental Figure 3.1). One explanation for the absence of isolation by distance is that typical genetic estimators require minimum distances between populations (Rousset 1997) and consequently do not detect isolation by distance over spatial scales as small as those measured in this study. We do not consider this explanation as likely because recent evidence in African forest elephants (*Loxodonta cyclotis*) used fewer loci to detect spatial structuring between 1 – 5 km (Schuttler et al. 2014). Alternatively, previous work on sociable weavers demonstrates that individuals preferentially disperse to nests that are of similar size to the nest they leave (Brown et al. 2003). Sociable weavers may therefore have a specific search image when dispersing, and dispersing individuals may bypass spatially proximate nests for nests of similar size that are farther away. This preference for nests of similar size could lead to genomic structuring among nests that is not explained by simple distance measurements. Indeed, recent research on banded mongoose (*Mungo mungo*) demonstrates that genetic differentiation may be more associated with social factors such as group fission than distance (Nichols et al. 2012).

Only one of the colonies, the white colony, had significantly less heterozygosity than expected (Table 3.3). The white nest is one of the nests in this population that have been monitored over multiple years, and interestingly, this population has shown no population growth or reduced population size over time. The white nest is relatively small compared to the other nests in the population, suggesting that inbreeding depression may be hindering colony growth, though ecological factors could also explain population growth in sociable weavers (Leighton, *in review*). Of the eight nests, half show significant heterozygote excess (Table 3.3). The preponderance of heterozygotes is surprising as colonial species are often expected to have low heterozygosity due to population structure and reduced gene admixture (Haag-Liautard et al. 2009). While our results suggest female-biased dispersal (Figure 3.1), the heterozygote excess in multiple colonies could indicate that sociable weavers are also able to select breeding partners that are significantly dissimilar to themselves, as seen in other avian species (Juola and Dearborn 2012). Finally, in our global analysis of heterozygosity there is a heterozygote deficiency (Table 3). We attribute this to the Wahlund effect (Wahlund 1928), a phenomenon wherein population substructure and differences in allele frequencies between subpopulations increases homozygosity (Figure 3.2).

The between-group F_{ST} values presented here are relatively high for an avian species over this small distance with no geographic barriers (Lebigre et al. 2008, Callens et al. 2011, Walsh et al. 2012, Nogueira et al. 2014), rivaling the F_{ST} values between some putative sub-species (Hoglund and Shorey 2004, Dor et al. 2012). In fact, the F_{ST} comparisons between some nests rivaled the F_{ST} found between certain sister taxa (Taylor et al. 2014). In contrast, the F_{ST} values presented here are lower than F_{ST} values reported for other cooperative societies with fewer individuals (Blackmore et al. 2011, Nichols et al. 2012). The much larger group size in sociable weavers, combined with moderate gene flow between colonies, and multiple sets of breeding pairs within a colony, may explain the the intermediate F_{ST} values in this species. Interestingly, the F_{ST} values are not associated with distance. Since geographic distance does not explain genomic structuring, limited admixture between groups is likely instead explained by high philopatry and high reproductive skew in breeding units, which are both shared in the closest living relative of sociable weavers, the white-browed sparrow weaver (*Plocepasser mahali*) (Harrison et al. 2014).

The Bayesian clustering analysis strongly supports seven distinct clusters (Table 3.2) and this suggests that sociality in sociable weavers likely leads to grouping of familial units and the build up of background genomic structure. Despite genomic structuring, however, we do not see high levels of inbreeding, as shown by expected or elevated levels of heterozygosity (Table 3.3). Unlike other species where sociality leads to inbreeding and risk of population extinction (Agnarsson et al. 2013), sociable weavers seem to avoid high levels of inbreeding despite sociality and reproductive skew. Sociable weavers may avoid inbreeding via sex-biased dispersal (Dobson 2013) and possibly by breeding with individuals that are genomically dissimilar from themselves. The latter case may be especially important for social species, and future research could investigate mechanisms that may allow for mismatching among breeding partners.

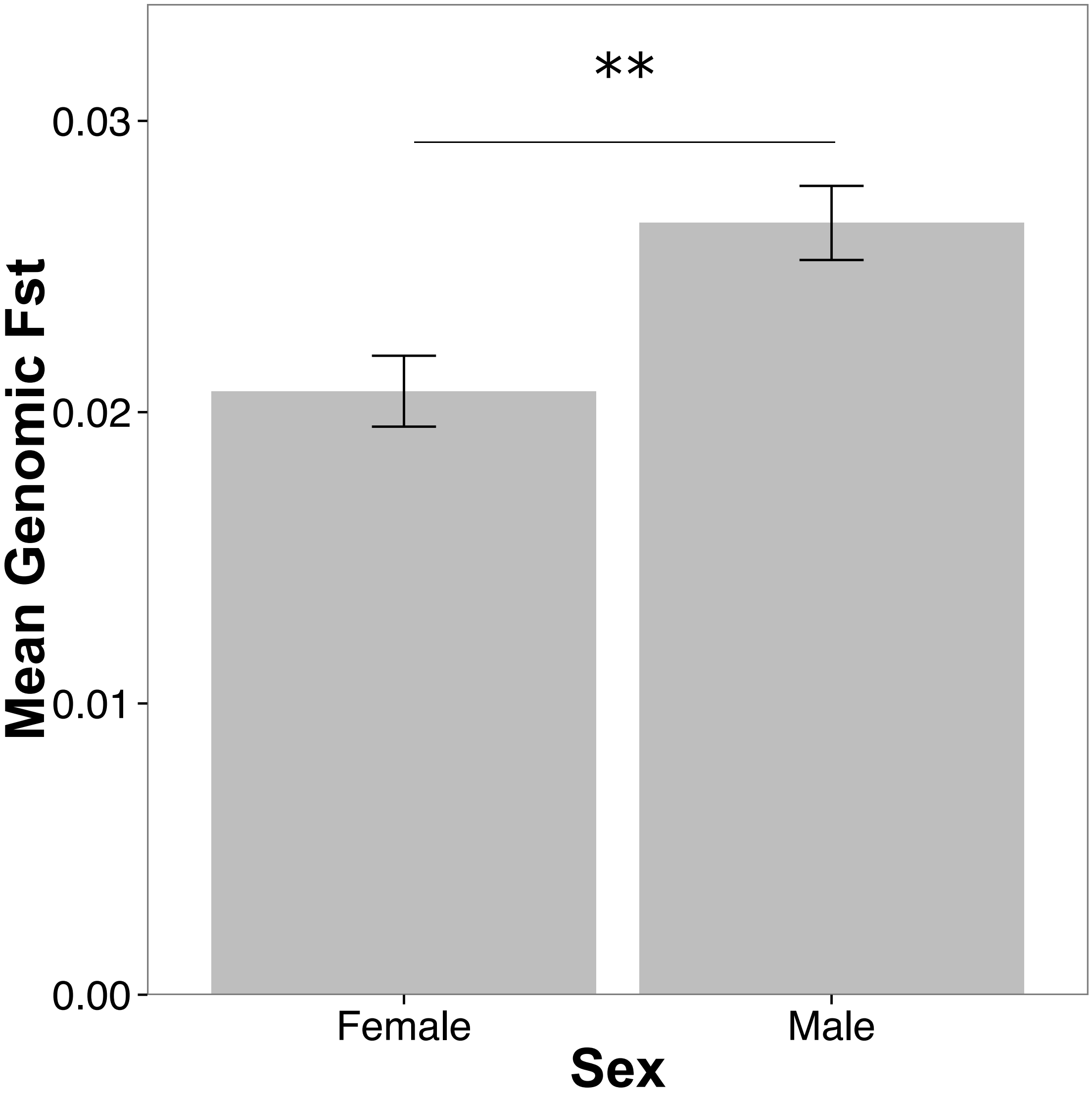


Figure 3.1: Comparison of F_{ST} values between the sexes in sociable weavers. Male weavers show a significantly higher global F_{ST} value compared to females when using loci from across the genome ($p = 0.001$).

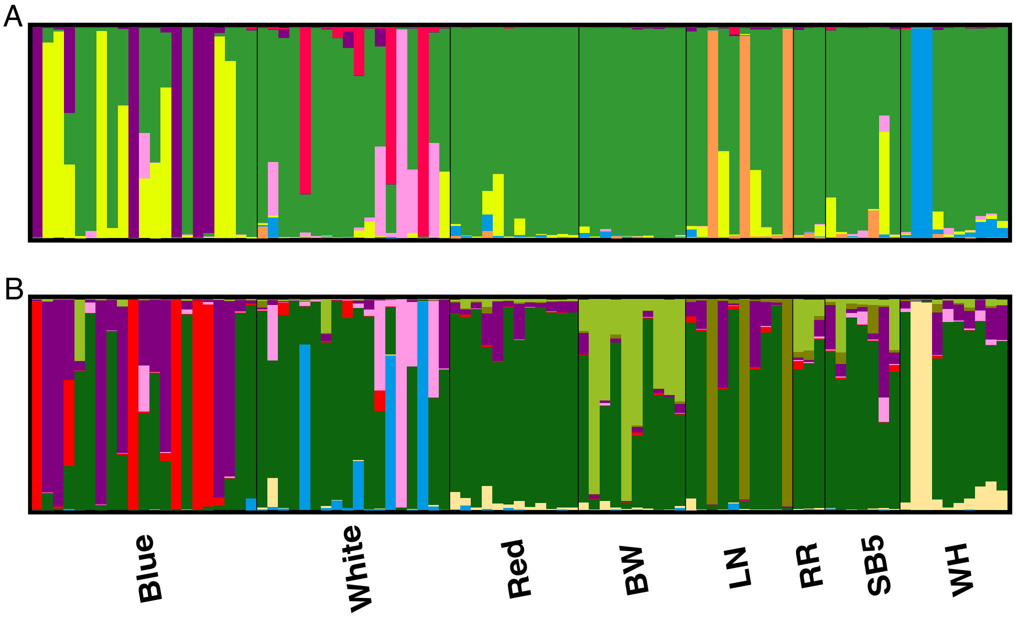


Figure 3.2: Structure plots using the SNP dataset with no missing information. (A) Structure estimated when software instructed to use seven clusters. (B) Structure estimated when software instructed to use eight clusters. The program strongly prefers seven clusters (A) and finds no support for eight clusters, although individuals were sampled from eight distinct nests. Distinct colors represent estimated clusters from Structure.

Table 3.1: Table showing the inter-colony distances (kilometers) above the diagonal and the pairwise colony F_{ST} values below the diagonal.

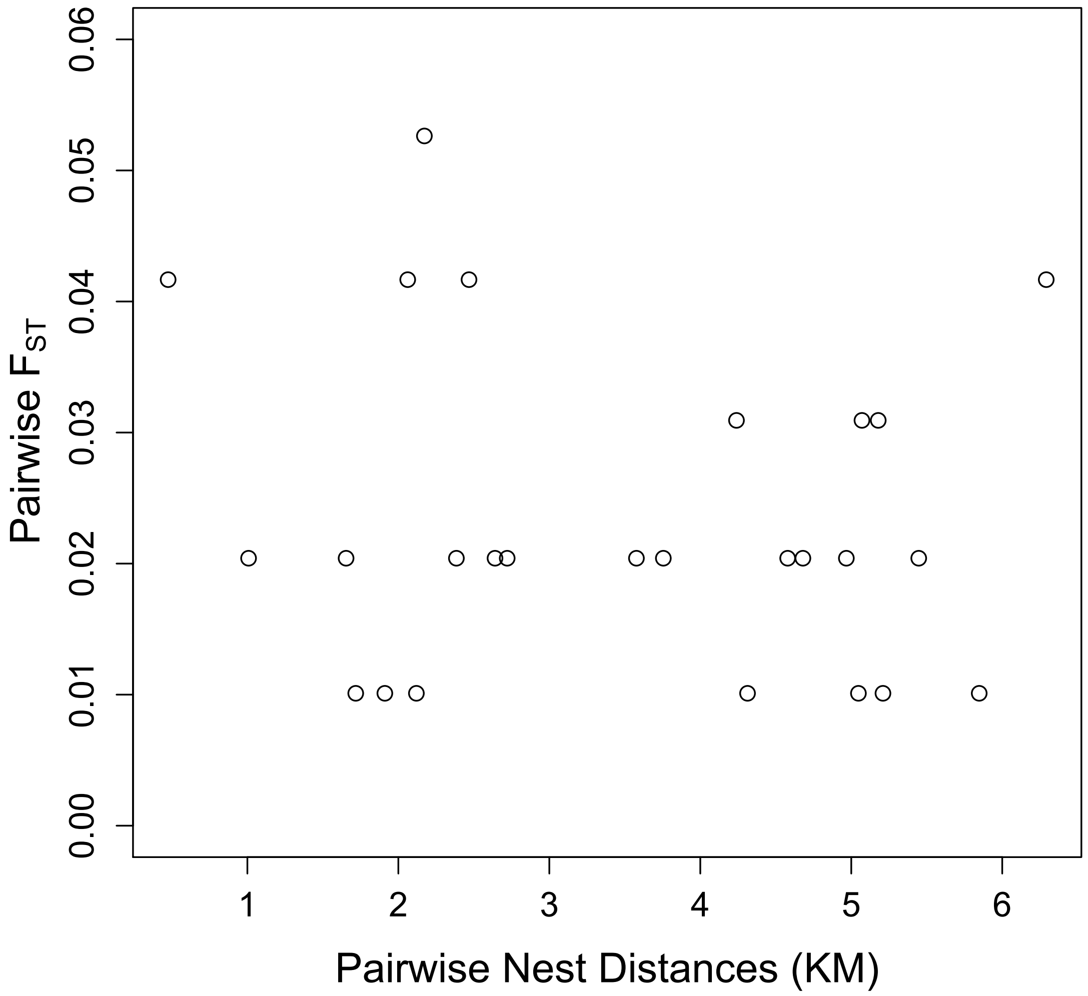
Colony	Blue	White	Red	BW	LN	RR	SB5	WH
Blue	_	1.91	2.12	5.85	0.48	1.72	4.98	4.31
White	0.02	_	3.58	5.05	2.06	2.72	3.75	5.21
Red	0.01	0.01	_	5.45	2.47	1.01	5.18	2.38
BW	0.03	0.02	0.02	_	6.30	4.68	1.65	4.58
LN	0.02	0.02	0.01	0.03	_	2.17	5.35	4.73
RR	0.04	0.04	0.04	0.06	0.05	_	4.24	2.64
SB5	0.02	0.01	0.01	0.02	0.02	0.04	_	5.07
WH	0.02	0.01	0.01	0.03	0.02	0.06	0.02	_

Table 3.2: Results from Structure analysis inferring the number of populations (K) based on the posterior likelihood.

K	ln Pr(X|K)	P(K|X)
1	-126697.0	0.0000
2	-125366.9	0.0000
3	-124910.4	0.0000
4	-124442.6	0.0000
5	-123876.3	0.0000
6	-123861.6	0.0000
7	-123173.1	1.0000
8	-123254.1	0.0000

Table 3.3: Table listing the U-test value for heterozygote deficiency or heterozygote excess in each of the colonies. The p-values represent the U-test for the combined multilocus test and the standard error (S.E.) around that p-value estimate.

	Heterozygote Deficiency		Heterozygote Excess	
Colony	p-value	S.E.	p-value	S.E.
Blue	0.10	0.0013	0.90	0.0013
White	< 0.001	0.0010	1.0	<0.001
Red	0.11	0.0013	0.89	0.0013
BW	1.0	<0.001	<0.001	<0.001
LN	1.0	<0.001	<0.001	<0.001
RR	1.0	<0.001	<0.001	<0.001
SB5	0.33	0.0022	0.67	0.002
WH	0.99	0.0001	0.003	<0.001
Global	0.02	0.005	0.98	0.005



Supplemental Figure 3.1: Correlation between pairwise F_{ST} values between nests and pairwise distances between the nests.

Supplemental Table 3.1: GPS Coordinates for the nests that were sampled in this study.

Nest	GPS Coordinates	
Blue	S23°20.486	E017°33.230
White	S23°19.894	E017°32.307
Red	S23°21.628	E017°33.225
BW	S23°21.632	E017°30.031
LN	S23°20.311	E017°33.431
RR	S23°21.303	E017°32.754
SB5	S23°20.784	E017°30.331
WH	S23°22.699	E017°32.453

Supplemental Table 3.2: Number of individuals sampled from the nests in this study.

Nest	Number of individuals sampled
Blue	24
White	19
Red	12
BW	10
LN	10
RR	3
SB5	7
WH	10

Chapter 4

Relatedness predicts multiple measures of investment in cooperative nest construction in sociable weavers

Summary

Although communal goods are often critical to society, they are simultaneously susceptible to exploitation, and are evolutionarily stable only if mechanisms exist to curtail exploitation. Mechanisms such as punishment and kin selection have been offered as general explanations for how communal resources can be maintained. Evidence for these mechanisms comes largely from humans and social insects, leaving their generality in question. To assess how communal resources are maintained we observed cooperative nest construction in sociable weavers (*Philetairus socius*). The communal nest of sociable weavers provides thermal benefits for all individuals but requires continual maintenance. We[1] observed cooperative nest construction and also recorded basic morphological characteristics. We also collected blood samples, performed next-generation sequencing, and isolated 2,358 variable SNPs to estimate relatedness. We find that relatedness predicts investment in cooperative nest construction, while no other morphological characters significantly explain cooperative output. We argue that indirect benefits are a critical fitness component for maintaining the cooperative behavior that maintains the communal good.

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[1] Note: The research was performed with Sebastian Echeverri, Dirk Heinrich, and Holger Kolberg.

Background

The major transitions (Maynard Smith and Szathmáry 1997) in evolution rely on two simultaneous features: first, cooperation among interacting individuals and second, minimal conflict between individuals (Strassmann and Queller 2010). For many of the transitions, e.g. the transition from individuals to societies, the cooperative group relies on a communal resource that benefits all of the individuals in the group and coalesces the group around a single resource. For instance, burrows (Sherman 1981, Lacey and Sherman 1991), webs (Jackson 2007), and nests (Hölldobler and Wilson 1990, Queller and Strassmann 1998) can be communal resources that are necessary for the maintenance of certain groups (Rankin et al. 2007). However, communal resources (i.e. public goods) are susceptible to exploitation and can lead to conflict within the group, thus leading to intra-group conflict that compromises group stability (Pruitt and Riechert 2009). In cases where exploitation cannot be avoided a communal resource may be exhausted leading to a collapse of the public good, i.e. a tragedy of the commons (Hardin 1968). Despite the inherent instability of public goods many natural systems are able to maintain them, and the maintenance of these public goods suggests evolutionary mechanisms that promote cooperation and minimize conflict (Queller and Strassmann 2009).

One potential mechanism that can select for cooperative behaviors in general is kin selection (Hamilton 1964). Kin selection models of public goods demonstrate that elevated relatedness within groups can select for cooperative behaviors that maintain public goods (Frank 1995, 2010). Indeed, kin selection may be especially effective at maintaining public goods because the benefit provided by the public good can simultaneously benefit multiple relatives (Leigh 2010). Similarly, the extended lifespan of some communal resources may allow individuals to attain considerable indirect benefits; specifically, since communal resources may overlap multiple generations, individuals in earlier generations can benefit future relatives with contemporary cooperation (Lehmann 2007). These two aspects of communal resources, extending benefits to multiple relatives simultaneously and extending benefits to future kin, may allow kin selection to drive the evolution and maintenance of behaviors that stabilize public goods.

However, the validity of kin selection (Nowak et al. 2010) and certain methods used to model kin selection (Allen et al. 2013) have been questioned. In particular, Nowak et al. (2010) argue that relatedness is often a byproduct of sociality and that inclusive fitness models apply to few biological situations, though see (Rousset and Lion 2011). To assess the generality of kin selection as an evolutionary mechanism, tests of predictions from inclusive fitness models are needed. When investigating natural systems, however, correct estimates of relatedness are necessary in these empirical tests so that kin selection can be assessed properly as an evolutionary mechanism (West et al. 2002).

A novel system to test mechanisms that maintain public goods is the communal nest of sociable weavers (*Philetairus socius*). Sociable weavers are genetically monogamous passerines that live in stable groups from four up to 500 individuals, with the median group size near 75 individuals (Maclean 1973). The communal nest is a perennial structure that sociable weavers maintain by adding new material to the nest as well as re-weaving material that is already present in the nest. The nest is composed of a superstructure that houses multiple, disparate chambers where groups of individuals roost at night (Maclean 1973). The chambers in the nest provide thermal benefits to individuals within the chamber simply as a result of being a part of the communal nest (van Dijk et al. 2013) and therefore the nest qualifies as a public good (Frank 2010). The cooperative nest construction of sociable weavers can be exploited by selfish individuals that live in the nest without contributing to nest construction. Selfish individuals that do not contribute to the public good expose the nest to the tragedy of the commons (Hardin 1968).

To investigate the mechanisms that maintain cooperative nest construction we measured morphological characteristics, cooperative nest construction behavior, and the relatedness of individuals to their nest of origin. We set out to test specific hypotheses of cooperative nest construction generated from inclusive fitness models and kin selection (Johnstone and Cant 2008). Specifically, sociable weavers follow the typical avian pattern of female-biased dispersal (Covas et al. 2006), where the sex-biased dispersal likely leads to elevated relatedness in males (Leighton 2014b) that would allow males to acquire relatively more indirect benefits via cooperation. We therefore predicted that males will show elevated cooperative nest construction due to higher relatedness to their colony of residence, and that in general more related individuals would perform more cooperative nest construction.

Methods and Materials

Study Species and Field Site

Sociable weavers are small passerines (25 – 30 g) endemic to semi-arid savannahs of South Africa and Namibia. Sociable weavers roost communally in massive nests that are constructed using various materials. Most items inserted into the nest are twigs, *Stipagrostis spp.* grass, and softer materials for chamber lining (Maclean 1973). Within the larger nest superstructure subsets of individuals roost in separate chambers and individuals maintain these chambers over time (Leighton 2014b). Sociable weavers are sexually monomorphic so we identified the sex of individuals genetically (see below). Importantly, the sex of individuals was determined after the field season was completed, and therefore all behavioral observations were conducted blind with respect to the sex of individuals.

Two colonies of sociable weavers were observed at a field site (Wiese property) 150 kilometers southeast of Windhoek, Namibia. We observed individuals in the colonies from May 2012 to July 2012; during this time the area experiences little rainfall (< 10 millimeters) and is often cold at night (< 0°C). These conditions are relatively unsuitable for reproduction and the majority of the reproduction for sociable weavers takes place in the warmer, wet season between November and March (Maclean 1973).

Behavioral Observations

We measured the behavior of individuals at two nests (the white nest and the blue nest) that are ~2.5 kilometers apart. We trapped sociable weavers at the two nests using mist nets and applied individual-specific color leg bands so that we could assign nest construction to specific individuals. In total, we banded 127 individuals (33 individuals from the white nest and 94 individuals from the blue nest) for which we also had information on age, sex, and wing length. Most of the individuals were banded before the field season began, however; ~30 individuals were banded in June 2012. We did not perform observations within seven days of capture and we standardize cooperative measures based on potential time observed to allow for comparison among all individuals.

To record behaviors, we placed two hunting blinds ~5 meters away from the nest and at a 180° angle from each other. The hunting blinds were left for at least 72 hours at the nest of interest so that individuals at the nest could habituate to their presence. After acclimation we recorded behavior in 3-hour time blocks in the morning (between 08:30 and 11:30) and afternoon (between 13:30 and 16:30) at the focal nest. Since sociable weavers from the same colony leave in multiple foraging flocks over the course of the day (G.M. Leighton pers. obs.), we recorded the behavior of all individuals constructing the nest during time blocks instead of attempting to follow a single individual. We recorded two measures of cooperation: 1) the proportion of time individuals devoted to cooperative nest construction; 2) the total number of items individuals inserted into the nest superstructure. These behaviors have been described previously by Leighton (2014b). While these measurements are associated, they are not perfectly correlated, suggesting that individuals may specialize in different aspects of cooperative nest construction. Specifically, many individuals devote considerable effort into re-weaving materials that are already present in the nest, and the re-weaving component of cooperative nest construction is not entirely captured by the number of items inserted into the nest.

Sex Determination

Sex was determined genetically by extracting genomic DNA from 50 microliters of blood. To maximize genomic DNA yield, the proteinase K wash was extended from 24 hours to 48 hours. The genomic DNA was exposed to the P2 and P8 primers developed by Griffiths et al (1998) and the new P0 primer developed Han et al (2009) via a multiplex PCR. The sex of the sociable weavers was determined genetically because the sexes are indistinguishable using size and plumage characteristics (Maclean 1973).

Relatedness

Of these 127 individuals, 40 (23 from the blue nest and 17 from white nest) were genotyped using Genotype-by-sequencing (Elshire et al. 2011), which was performed at the Cornell Institute for Genomic Diversity. We employed the TASSEL pipeline to filter out DNA reads with errors and invariable sites using the default parameters (Glaubitz et al. 2014). From the ~10,000 variable single nucleotide polymorphisms (SNPs), we isolated a subset of 2,358 SNPs that were successfully genotyped for each of the 40 individuals. The subset of SNPs was exported into VCF files and then read into R (version 3.0.1) and analyzed using the SNPRelate package (Zheng et al. 2012). The SNPRelate package accepts the VCF file and estimates the k coefficients (k_0, k_1, and kinship) from the SNP data. We used the k coefficients provided by SNPRelate to calculate average relatedness (Thompson 1975) of individuals to the members of their colony. In contrast to van Dijk et al. (2014), we estimated pairwise relatedness of an individual to their colony of residence because estimates of relatedness should reflect the competitive environment of the individual (West et al. 2002). Population-wide estimates of relatedness do not therefore properly account for competition. Since sociable weavers do not compete with weavers from distant nests (West et al. 2002), and since foraging flocks are almost entirely composed of individuals from the same nest, the relatedness values presented here represent a more accurate estimate of relatedness.

Statistical Analysis

The two cooperative variables, time devoted to cooperative nest construction and the number of items inserted into the nest, were standardized to allow for comparisons amongst all individuals. Specifically, we analyzed the amount of time devoted to cooperative nest construction and we analyzed the number of items inserted as twigs per hour. Both variables were non-normally distributed and contained multiple zeroes in the data set. These characteristics of the data set thus necessitated the use of generalized linear mixed models (GLMMs). Since the variables are continuous a Poisson GLMM would be inappropriate. We therefore employed the Tweedie distribution, which is a compound-Poisson distribution that is continuous and has positive mass at 0 (Zhang 2013). Indeed, this statistical method has been used to analyze other behaviors with multiple measurements of 0 (Browning et al. 2012, Zhang 2013, Leighton 2014b). In addition to the multiple measures of 0 in the dependent variables, there was also considerable variance in the dependent variable. We therefore performed a square-root transformation on the dependent variables to improve the fit of the models.

For the entire set of individuals, we predicted both cooperative variables with the following set of independent variables: sex, age, wing length, nest, part of the day, and temperature of the previous night. For individuals with genetic data (31% of the individuals) we used the SNP data to calculate relatedness for the subset of individuals, and we included relatedness as a predictive variable in a second analysis. We fit GLMMs with individual as a random factor, and retained variables that significantly improved the fit of the model. Variables were assessed using both model selection criteria (Burnham et al. 2011) and chi-square tests (Zuur et al. 2009). With respect to model selection, we compared the AIC values of the full model with the model with a focal variable removed, and variables that improved the fit of the model by ΔAIC > 2 were retained (Richards et al. 2011). Variable parameters were estimated using a Laplace approximation because this method produces more accurate estimates relative to other approximations (Bolker et al. 2009).

Finally, we calculated intra-individual repeatability following Lessells and Boag (1987) because calculating repeatability using the Tweedie distribution is not currently possible (Nakagawa and Schielzeth 2010). Specifically, we calculate repeatability as among-group variance divided by the sum of within-group variance and among-group variance. Due to the non-normally distributed data we expect some bias in the estimates of repeatability, and therefore interpret these results with caution.

Permits

The University of Miami IACUC (permit number: 12-098) and the Ministry of Environment and Tourism (permit number: 1866) provided permits that allowed for this work. The work was performed on private land.

Results

Full Dataset

Cooperative nest construction was observed for 299 hours, yielding 2741 observations of 129 individuals. Following the standard calculations for repeatability (Lessells and Boag 1987) we found that the repeatability for the amount of time devoted to cooperative nest construction between observation blocks was $r = 0.33$, while the repeatability for the number of items inserted into the nest was $r = 0.69$. For both variables there was significantly more variation among individuals than within individuals ($F > 10$ and $p < 0.001$ for both measures).

Consistent with observations from a captive population (Leighton 2014b), males devoted significantly more time to cooperative nest construction than females (Figure 4.1a; Supplementary Table 4.1). Similarly, we found that males insert significantly more items into the nest superstructure relative to females (Figure 4.1b; Table 4.2). For both variables, sociable weavers perform more cooperative nest construction in the morning than in the afternoon (Supplementary Tables 4.1 and 4.2). None of the other predictive variables, i.e. wing length, age, nest of residence, or temperature, were significantly associated cooperative output.

Subset of Individuals with Relatedness Estimates

We used the 2,358 variable SNPs to calculate the average pairwise relatedness of each individual to its colony of residence. Relatedness should be estimated by including only the conspecifics the focal individual competes with (Grafen 1985), and since weavers most often forage in flocks composed only of individuals from their colony, we calculated relatedness with respect to the colony of residence. The average pairwise relatedness of all individuals to their colony of residence was 0.09 ± 0.004 (S.E.M). For the individual sexes, males had a marginally higher relatedness to their colony (0.092 ± 0.01) than females (0.079 ± 0.009), though the estimates were similar ($t = 1.53$, d.f. = 35.3, $p = 0.13$, Figure 4.2). However, if we remove the most extreme female outlier (see upper circle in Figure 4.2 in females) then males did have significantly higher relatedness (new female mean = 0.073 ± 0.004, $p < 0.05$).

When relatedness was included as a predictor variable for the subset of individuals ($n = 40$ individuals), we found that relatedness significantly and positively predicted both the amount of time an individual devoted to cooperative nest construction and the number of items inserted into the nest (Figure 4.3; Supplementary Tables 4.3 & 4.4). Similar to the previous model fitted to the full data set, sociable weavers devoted more time to cooperative nest construction in the morning than in the afternoon (Supplementary Table 4.3). In contrast, after accounting for relatedness and part of the day, none of the remaining variables significantly explained variation in the data for the amount of time individuals spent cooperatively constructing the nest (Supplementary Table 4.3). With respect to the number of items inserted into the nest, both part of the day and relatedness predicted investment; additionally, male sociable weavers inserted significantly more items into the nest than females after controlling for other variables (Supplementary Table 4.4).

Discussion

That relatedness positively predicts both the time invested in cooperative nest construction and the number of items inserted into the nest suggests that indirect benefits are a necessary fitness component of the behaviors (Figure 3). Indeed, since the nest loses material over time (G.M. Leighton, pers. obs.) and individuals gain thermal benefits (van Dijk et al. 2013, Leighton and Echeverri 2014), the nest is a public good that is susceptible to exploitation. The results suggest that kin selection is important for the maintenance of the public good in sociable weavers. While van Dijk et al. (2014) found local effects of relatedness, we find a significant, group-wide relationship between genomic relatedness and nest construction. We find this relationship because our relatedness estimates reflect the appropriate reference group (West et al. 2002, West et al. 2006) and because we have more detailed behavioral measurements. When considering results from both studies it appears that sociable weavers spatially direct cooperative nest construction toward kin (van Dijk et al. 2014) within the nest, and that individuals adjust their entire cooperative output based on the extent of their relatedness to individuals in the nest (Figure 4.2).

The low overall relatedness values suggest that while sociable weavers maintain complex societies, they do so with considerable conflict and competition within the groups, in contrast to some other complex societies (Hughes et al. 2008, Cornwallis et al. 2010, Lukas and Clutton-Brock 2012, Fisher et al. 2013). The insect and multicellular societies harbor more cooperation because both monogamy and single-cell bottlenecks result in relatively higher relatedness among interacting individuals, and thus allow for the evolution of cooperation via the acquisition of indirect benefits (Boomsma 2009). In contrast, there are multiple breeding pairs in sociable weaver nests (Covas et al. 2006) that likely depresses relatedness compared to other, more cooperative, societies.

While the significant relationship between relatedness and cooperation suggests indirect benefits are necessary for the maintenance of the behavior, there could be alternative explanations. For example, cooperative nest construction could be used as a signal by individuals, as has been suggested for cooperative feeding as a signal in sociable weavers (Doutrelant and Covas 2007). Using cooperative nest construction as a signal, however, seems untenable. First, similar sexually selected traits are expected to evolve in both sexes in avian lineages where there is reproductive skew in both males and females (Rubenstein and Lovette 2009). Sociable weavers are genetically monogamous (Covas et al. 2006) and breeding is limited due to ecological constraints (Covas et al. 2004), suggesting little if any difference in reproductive skew between the sexes. Since selection can drive rapid evolution of shared traits between the sexes (Price and Whalen 2009) we would expect a trait to be similar between the sexes if it was being used as a sexual signal based on previous research on African Starlings (Sturnidae) (Rubenstein and Lovette

2009). However, we find that the trait is strongly sex-biased (Figure 4.1), suggesting that selection is maintaining the trait of nest construction in male sociable weavers. Second, recent modeling demonstrates that using external items while signaling sharply reduces the effectiveness of signaling (Leighton 2014a), therefore reducing the power of sexual selection to maintain the trait because individuals are less able to accurately assess signaling output.

Leighton (2014b) originally suggested that the sex-biased cooperative nest construction could also be explained if the direct benefits of group augmentation were biased towards males. The argument was based on evidence that sociable weaver fathers provided more food to offspring than either mothers or helpers (Doutrelant and Covas 2007). However, male helpers did not show elevated alloparenting relative to mothers, as would be predicted if males were selected to increase group size. Additionally, offspring raised by sociable weaver parents and helpers were more likely to emigrate than offspring raised by parents alone (Covas et al. 2011), largely diminishing the benefits of group augmentation for fathers and male helpers.

Here we show that genomic relatedness likely mediates conflict in the group, with more related individuals investing more in cooperative nest construction and individuals directing cooperative nest construction towards certain areas of the nest. Thus, kin selection helps maintain cooperative investment in a vertebrate society public good. However, kin selection alone does not preclude exploitation, and therefore other mechanisms may help reduce intra-group conflict over investment in the communal nest.

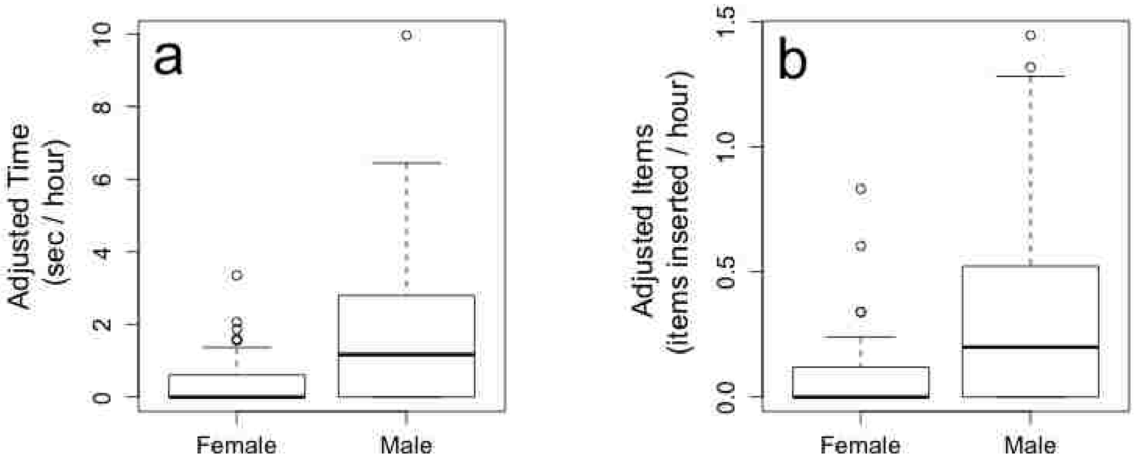

Figure 4.1: Boxplot comparing the cooperative output of sexes in sociable weavers. a. Males devote significantly more time to cooperative nest construction than females. The median is represented by the line in the box and the 25% and 75% percentiles are the lower and upper edges of the box, respectively. b. Boxplot comparing the cooperative output of sexes in sociable weavers. Males insert significantly more items into the nest superstructure than females. The median is represented by the line in the box and the 25% and 75% percentiles are the lower and upper edges of the box, respectively. Outliers (individuals that are more than 1.5 x the inter-quartile range from an edge of the box) are plotted as circles.

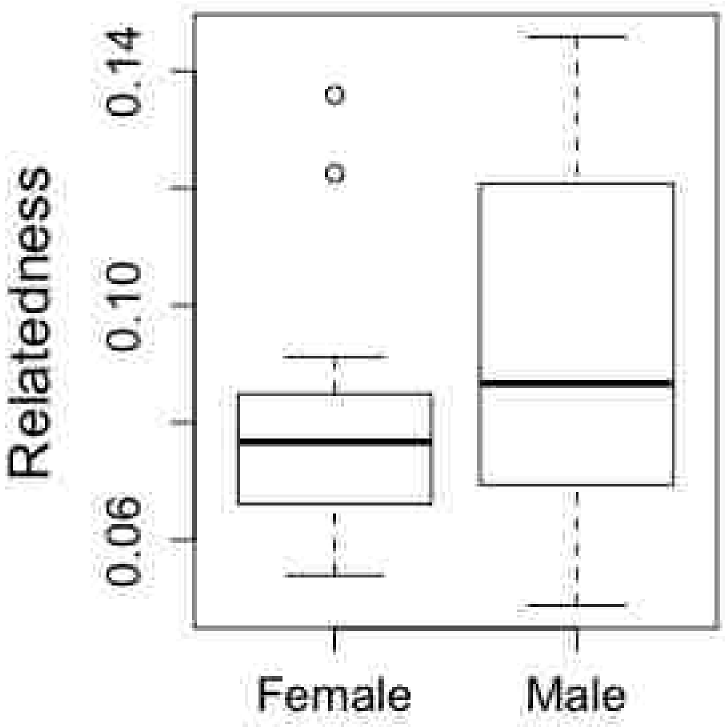

Figure 4.2: Boxplot comparing the average relatedness to colony of residence between sexes in sociable weavers. Males tend to be more related to their colony of residence than females. The median is represented by the line in the box and the 25% and 75% percentiles are the lower and upper edges of the box, respectively. Outliers (individuals that are more than 1.5 x the inter-quartile range from an edge of the box) are plotted as circle.

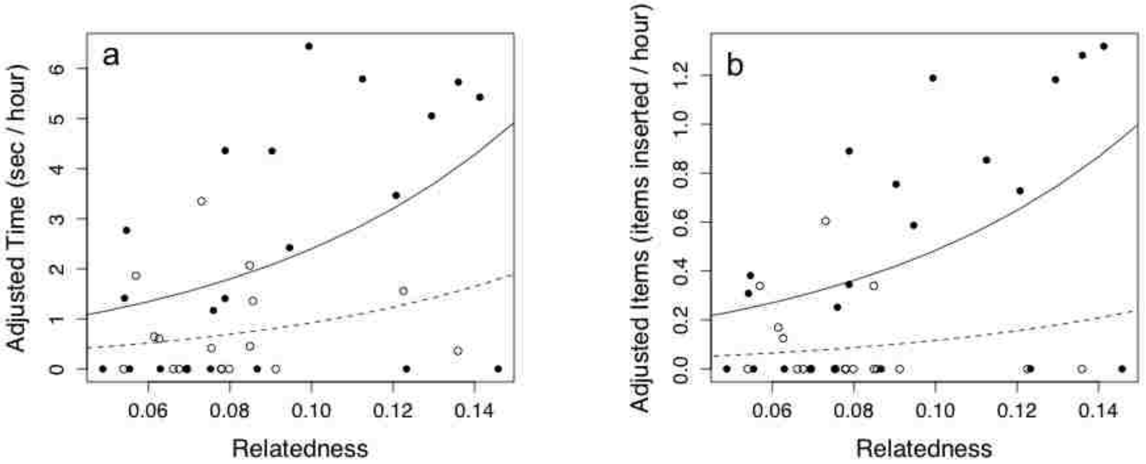

Figure 4.3: Plot of cooperative output based on relatedness to colony of residence. a. Plot of time devoted to cooperative nest construction versus the relatedness of the individual to the colony of residence. There is a significant ($p < 0.05$) positive, relationship between time spent on cooperative nest construction and relatedness. b. Regression of number of items inserted into nest superstructure on relatedness of the individual to the colony of residence. There is a significant relationship ($p < 0.05$) between number of items inserted into the nest and relatedness of the individual. For both plots, the lines represent the fitted line based on the generalized linear model, where the solid line represents the fitted values for males and the dashed line represents the fitted line for females. In both plots filled circles represent male values while open circles represent female values.

Supplemental Tables in Chapter 4

Supplemental Table 4.1: Explanatory variables in GLMM that predicts the proportion of time devoted to cooperative nest construction in the full dataset of individuals. All variable estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 2.91 ± 1.71) were included in all models. Positive ΔAIC values mean that the model fit decreased when the focal variable was removed.

Predictive Variable	Estimate	S.E.	ΔAIC compared to full model	p-value
Part of Day	0.62	0.10	40.9	< 0.001
Sex	2.09	0.39	25.2	< 0.001
Temp	-0.01	0.01	-1.9	0.38
Age	0.75	0.12	-1.6	0.52
Wing length	0.06	0.09	-1.6	0.54
Nest	0.32	0.73	-0.4	0.21

Supplemental Table 4.2: Explanatory variables in GLMM that predicts the number of items inserted into the communal nest using the full dataset of individuals. All variable estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 3.32 ± 1.82) were included in all models. Positive ΔAIC values mean that the model fit decreased when the focal variable was removed.

Predictive Variable	Estimate	S.E.	ΔAIC compared to full model	p-value
Part of Day	0.77	0.12	46.1	< 0.001
Sex	2.41	0.47	25.5	< 0.001
Temp	-0.02	0.02	-0.6	0.23
Age	0.09	0.13	-1.5	0.46
Wing length	0.17	0.11	-0.4	0.12
Nest	0.40	0.45	-1.2	0.38

Supplemental Table 4.3: Explanatory variables in GLMM that predicts the proportion of time devoted to cooperative nest construction in the subset of individuals that have relatedness information. Both relatedness and the time of the day predicted the proportion of time devoted to cooperative nest construction. All variable estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercept for individual (variance ± s.e. = 2.98 ± 1.73) were included in all models. Positive ΔAIC values mean that the model fit decreased when the focal variable was removed.

Predictive Variable	Estimate	S.E.	ΔAIC compared to full model	p-value
Part of Day	0.8	0.15	29.1	< 0.001
Relatedness	41.7	14.0	5.8	0.005
Sex	0.64	0.73	-1.4	0.41
Age	0.23	0.18	-0.4	0.20
Wing length	0.15	0.20	-1.6	0.50
Nest	0.44	0.63	-1.8	0.67
Temperature	-0.005	0.02	-2.0	0.84

Supplemental Table 4.4: Explanatory variables in GLMM that predicts the number of items inserted into the communal nest. Time of day, relatedness, and sex, predicted the number of items inserted into the communal nest. All variable estimates of effects are on the latent, logarithmic scale. P-values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individual (variance ± s.e. = 2.98 ± 1.73) were included in all models. Positive ΔAIC values mean that the model fit decreased when the focal variable was removed.

Predictive Variable	Estimate	S.E.	ΔAIC compared to full model	p-value
Part of Day	0.83	0.18	21.0	< 0.001
Relatedness	35.75	14.6	3.8	0.02
Sex	1.90	0.81	3.0	0.03
Age	0.12	0.18	1.5	0.5
Wing length	0.31	0.23	0.2	0.18
Nest	0.26	0.67	-1.8	0.70
Temperature	-0.002	0.02	-2.0	0.95

Chapter 5

The relative effectiveness of signaling systems: relying on external items reduces signaling accuracy while leks increase accuracy

Summary

Multiple evolutionary phenomena require individual animals to assess conspecifics based on behaviors, morphology, or both. Both behavior and morphology can provide information about individuals and are often used as signals to convey information about quality, motivation, or energetic output. In certain cases, conspecific receivers of this information must rank these signaling individuals based on specific traits. The efficacy of information transfer associated within a signal is likely related to the type of trait used to signal, though few studies have investigated the relative effectiveness of contrasting signaling systems. I present a set of models that represent a large portion of signaling systems and compare them in terms of the ability of receivers to rank signalers accurately. Receivers more accurately assess signalers if the signalers use traits that do not require non-food resources; similarly, receivers more accurately ranked signalers if all the signalers could be observed simultaneously, similar to leks. Surprisingly, I also found that receivers are only slightly better at ranking signaler effort if the effort results in a cumulative structure. This series of findings suggests that receivers may attend to specific traits because the traits provide more information relative to others; and similarly, these results may explain the preponderance of morphological and behavioral display signals.

Background

The social environment presents situations where alternative behavioral decisions can result in considerably different returns in inclusive fitness for the individual making the decision. To maximize fitness individuals often must observe other conspecifics and the conspecific's set of characteristics in order to respond appropriately towards the individual being observed (Székely et al. 2010, Taborsky and Oliveira 2012). For instance, individuals observe characteristics that indicate sex, dominance, or viability of conspecifics that then dictate behavioral decisions (Smith et al. 2010). In many cases, individuals readily signal their condition (Candolin 2000) or morphological characteristics to conspecifics because it maximizes fitness (Searcy and Nowicki 2005). Therefore, assessing conspecifics is a fundamental requirement for individual organisms and a fundamental assumption of several biological phenomena, such as direct and indirect reciprocity (Trivers 1971), punishment (Clutton-Brock and Parker 1995), and sexual selection (Grafen 1990, Andersson 1994).

In some empirical systems ranking and remembering individuals is critical for the maintenance of sexually selected traits (Jennions et al. 2001); whether the traits are morphological features or behavioral displays, individuals are often required to sample partners and select mates based on individual characteristics (Fiske et al. 1998). While individuals that advertise their characteristics should be selected to exaggerate quality to acquire more partners, the individuals assessing potential partners should be selected to ignore uninformative traits that exploit the receiver's sensory system (Searcy and Nowicki 2005). The maintenance of some sexually selected traits therefore relies on the following two criteria: first, individuals signal traits that convey potential direct or indirect benefits of the individual bearing the trait; and second, individuals assessing potential mates can remember and reliably rank individuals based on trait values (Andersson 1994). For example, female satin bowerbirds (*Ptilonorhynchus violaceus*) visit a set of males and then re-visit a subset of original sample (Uy et al. 2001). After sampling males, female satin bowerbirds base their mating decision on the size of the male and certain decorations in the bower (Robson et al. 2005). As demonstrated by female bowerbirds, individuals assessing potential partners can base their behavioral decisions on some intrinsic property of a signaler such as body size (Fiske et al. 1998), on some sort of external structure, such as a nest (Moreno et al. 1994, Moller et al. 1995), or both (Searcy 1992, Buchanan and Catchpole 1997).

In addition to sexual selection, signaling is also critical to other evolutionary mechanisms; for instance, the assessment of an individual's behavioral output is critical to certain evolutionary mechanisms suggested to maintain cooperative behaviors (Trivers 1971, Raihani et al. 2012). In direct reciprocity, an individual's past history of behaviors must be observable so that the individuals that were previously cooperative can receive cooperation from others (Nowak and Sigmund 1998). While definitive cases of reciprocity are uncommon, evidence suggests reciprocity could occur: e.g. in chimpanzees (*Pan troglodytes*) (Melis et al. 2008), pied flycatchers (*Ficedula hypoleuca*) (Krams et al. 2008), and vampire bats (Wilkinson 1984). A second mechanism that can maintain cooperation is punishment (Clutton-Brock and Parker 1995); for punishment to maintain cooperation certain individuals must quantify behavioral output of the individual that might be subject to punishment. If an individual is not cooperating, or not cooperating at a sufficient level, the individual will be attacked or evicted by others, thus rendering defection more costly than cooperation (Clutton-Brock and Parker 1995). Recent concerns regarding requirements associated with tracking both the identity and behavioral output of individuals suggest punishment would be rare in nature (Raihani et al. 2012); however, punishment does seem to maintain cooperation e.g. in the cleaner wrasse (*Labroides dimidiatus*) (Bshary and Grutter 2002).

The neural machinery necessary for identifying and observing conspecific morphology, behavior, or both (Andersson 1994), may be too costly for many organisms (Raihani et al. 2012). In addition to neural constraints, other characteristics of signaling systems may reduce an individual's ability to assess conspecifics; for instance, certain traits may contain too little information to be distinguished among conspecifics. A recent study on poison frogs (*Oophaga pumilio*) found that females chose to mate with the closest male, irrespective of the male's other traits (Meuche et al. 2013). Meuche et al. (2013) argued that female poison frogs chose males based on proximity because the low variance in certain male traits prevented females from effectively identifying preferable males.

While low variation may reduce the utility of a signal, several other ecological factors could potentially reduce the efficacy of image-based mechanisms (since image-based mechanisms are important in both cooperation and sexual selection, I will use the terms "signaler" and "receiver" from here on). For example, opportunities for signaling to receivers may be limited if resources are especially scarce and survival necessitates increased foraging effort. These limitations could be especially severe in species where signalers attempt to convey quality through behavior, or by acquiring objects for a display (Doutrelant and Covas 2007, Schaedelin and Taborsky 2010). In these systems, receivers are unable to assess certain morphological traits quickly; instead, individual receivers must observe signalers, and then remember the behavioral output of signalers to compare to other potential partners. In contrast, systems where signalers can build a structure that represents a cumulative effort may provide more robust and accurate estimates of an individual's behavioral output (Soler et al. 1998, Schaedelin and Taborsky 2009). For example, the bowers of several bowerbird species (Borgia 1995) and the individual nests constructed by males in village weavers (Collias and Victoria 1978) represent the effort of males (the signaler) over time, while the time it takes females (the receiver) to assess the cumulative effort of males is a fraction of the time required for the males to build the structures.

If some traits provide more accurate information for image scoring and can be assessed in shorter time periods, receivers will be selected to use those traits as opposed to traits with low information, low variance, or large time demands (Searcy and Nowicki 2005). These preferences can drive evolution and exploring these systems theoretically may provide insight into the evolution of certain traits. To formally investigate if specific characteristics of systems provide more accurate ranking of signalers by receivers, I designed a full factorial set of agent-based models (Table 5.1) that represents salient features of many signaling systems.

The overall set of models tested the following questions: 1) whether constructing discrete structures (or growing specific physiological structures, as in the case of morphological features) allows for more accurate ranking of signaler output; 2) whether relying on ecologically variable items diminishes the accuracy of ranking of signaler's output; and 3) if being able to observe all displaying signalers simultaneously (as in leks) increased accuracy of ranking of signaler output.

Methods and Materials

Model Design

To address these questions I built a spatially explicit agent-based model (ABM) that had signalers perform generic display behaviors. The overall model had different builds that reflected specific situations (Table 5.1). In one model build the signaler's effort did not result in a cumulative structure (as in behavioral displays), while in the second each signaler's cumulative effort could be observed by receivers (as in discrete structures such as nests). Receivers also differed in disparate model builds; in a certain build, receivers could assess all the signaling individuals in a single time step, while in another build the receivers could only assess one "territory" at a time. Finally, in one model build signalers needed non-food display items for display, while in another build signalers could display after acquiring sufficient energy. These behavioral differences resulted in a full-factorial model design for situations that are described in Table 5.1.

Agent-based modeling was selected to investigate these questions because this method is amenable to modeling the set situations described above. Agent-based models allow for straightforward modeling of space (Grimm and Railsback 2005), and consequently, agent-based models do not rely on mean-field assumptions for interactions. Specifically, agent-based models recapitulate patchiness in resources that is often a more accurate reflection of ecological conditions. Second, agent-based models allow for the development of inter-individual heterogeneity in traits (Grimm and Railsback 2011). Such heterogeneity is critical in these models because it allows individual receivers to potentially observe heterogeneity among signalers.

Model Assumptions

The model assumes that receivers are observing a display trait and the display trait is left intentionally generic due to the large number of possible display traits that can be observed by receivers (Kokko et al. 2002). The model assumes a "best-of-n-males" sampling strategy (Janetos 1980) where receivers are observing a set of signalers, as opposed to selecting the first signaler that surpasses a certain threshold (Wiegmann et al. 2013). Such an assumption is warranted given the mate searching strategies seen in several taxa (Petrie et al. 1991, Backwell and Passmore 1996, Uy et al. 2001) and that theoretical work has demonstrated that comparing a pool of signalers can be the optimal searching strategy under certain conditions (Luttbeg 1996). The model presented here also assumes a simple energy budget where individuals have a threshold level of energy (representing the energy needed for survival and maintenance) and the remaining energy is dedicated to display in the case of signalers or observing signalers in the case of receivers. While a more complex energy budget may be appropriate in specific situations (Sibly et al. 2012a), choosing any specific type of energy budget for a general model would be inappropriate as energy budgets can be highly variable between species (Sibly et al. 2012b). Finally, the model assumes perfect memory, where each receiver accurately and unambiguously records the behavior of all signalers without making mistakes or forgetting information.

Software

The agent-based model was built in Java using the compiler Eclipse © (version 1.5.1) and utilized the open-source MASON toolkit (version 16) (Luke et al. 2005). MASON implements a premier random number generator and MASON classes allow for simple construction of spatially explicit models. Data from model runs was output from Eclipse into text files and read into R (version 3.0.1) (2014) using unique scripts that read the data and performed statistical computations.

Statistical Assessment of Information Transfer

To quantify how accurately the receivers ranked displayers in terms of output (see Process overview and scheduling below) I needed summary statistics that averaged across receivers and simulation replicates. The specific lists output by the model were the rankings of signalers estimated by each specific receiver (20 in total) and the true rankings of signalers; to acquire the true rankings, the signalers each tracked their respective signaling effort so as to provide the true output of each signaler. Each receiver's ranking of signalers needed to be compared to the true rankings provided by the signalers, thus suggesting the use of correlational statistics, e.g. Pearson or Spearman correlation. Due to the heterogeneity in resource acquisition by receivers, some individual receivers were never able to assess the output of displayers due to a lack of resources, resulting in no variation when receivers estimated each male's output as 0. In these cases, traditional tests of correlation fail as they assume some sort of variation in the denominator of the test statistic. Therefore Kendall's W, a test of concordance that can accommodate zero variance in some rankings (Sokal and Rohlf 1995), was used to assess the agreement between the true rankings of displayers and the estimates of receivers.

Model Description

The model documentation is described according to the Overview, Design Concepts, and Details (ODD) process described in (Grimm et al. 2006) and updated in (Grimm et al. 2010); the ODD method of description has been adopted because agent-based models (ABMs) have been historically difficult to describe and re-implement without the source code. The ODD contains relevant model information including variables, reproduction, and implicit assumptions. The ODD process is now utilized in multiple disciplines (Grimm et al. 2010), because of its utility (Jovani and Grimm 2008, Aktipis and Fernandez-Duque 2011). The model code can be downloaded from the agent-based model repository OpenABM (http://www.openabm.org/model/4079/version/1/view) or from the supplementary material (Model Code S1). A shortened ODD protocol is reproduced below that describes the model; the full ODD protocol (Model ODD Protocol S2) and model validation (Model Validation S3) can be found in the supplementary information.

State variables and scales

All model runs were conducted on a 500 x 500 continuous space toroid; continuous space was chosen because this ABM did not rely on a lattice and the neighbor interactions that lattice designs facilitate. Time is represented using discrete time steps and advanced to time step #1440 before writing data to an external file. While slightly arbitrary, 1440 was selected because it represents the number of 15-minute time steps over the span of a month, assuming 12-hour days. In each of these time steps, the four main types of agents execute their behaviors in a random order. The four types of agents are the signalers, receivers, food items, and display items in the model builds where displayers require display items before display. Each of these agents has a specific set of variables, and there are in addition several global variables (see Table 5.2 for a list of model variables).

Process overview and scheduling

After initialization, the model is incremented in time steps in which the agents perform behaviors based on their energy reserves. In a single time step, the order of all agents is randomized to avoid order effects, and the list of randomized agents perform their specified behavior. A description of the type of agent behavior for each agent is listed below:

1. Signalers: If a signaler has sufficient energy reserves, it will return to its home territory to display. This display is dichotomous, i.e. an individual will display or it will not display regardless of the excess energy reserves. To display the signaler simply sets a Boolean display variable to “true” and the amount of energy consumed during display is the same as the amount of energy consumed in normal time steps. The model was designed this way

because the model tests different display systems while simplifying other aspects of the system. If the signaler does not have enough energy, it will search for foraging resources (food items) and if there are no food items in the preset neighborhood, then it will move in a random heading to try to find food in the next time step.

2. Receivers: If a receiver has sufficient energy, it will move to a certain location to observer signalers. In the “lek” model build, the receiver moves to the center of the arena to observe all displaying signalers. In the second build, the receiver will move from one territory to the next to observe displaying signalers; and can only inspect one territory in per time step. If the receiver does not find a signaler on its territory, the receiver will move on to the next territory in the next time step. The model assumes that the receivers know where all local territories are located. To rank signalers, the receivers performed one of two disparate behaviors. In the model builds where receivers could only observe signaling in real time, the receiver would observe the signalers in the arena or territory, and for each signaling individual, increment their internal estimate for the specific signaler by 1. In the model builds where receivers could observe the entire previous effort of signalers, the receivers would obtain the true value from each signaling individual and update their internal representation of each specific signaler using the acquired value.
3. Food items and display items: Food items and display items follow the same dynamics as follows, items age and if they reach the maximum age will die.

Otherwise, the item reproduces with a 10% chance if the item "population" is under the specified carrying capacity.

Design concepts

Basic Principles: In these models I ask how fundamental features of signaling systems influence the accuracy with which receivers rank signalers.

Emergence: The key results expected from the model are the groups of comparisons of signaler quality produced by the several model builds. Specifically, I compared estimates of signaler quality assessed by receivers in the different signaling scenarios.

Adaptation: As there is no reproduction of receivers or signalers in this model, there is no adaptation.

Objectives: The objectives of individuals vary depending on the type of the individual. The signalers' objective is to signal depending on the condition they are in while the objective of receivers is to assess each of the signaler's display effort.

Learning: There is no learning in the model.

Prediction: There is no explicit prediction in the model.

Sensing: The signalers and receivers both sense internal levels of energy resources and respond to low resources by searching for food. While searching for food, individuals can sense food items within a predefined neighborhood. Signalers perform the same sensing procedure with display items, where they will find a display item within their neighborhood or move randomly to find an item if one is not within the search radius.

The receivers sense food using the same searching behaviors as signalers. The receivers also have to sense potential signalers that are in their neighborhood. To observe displaying signalers the receivers observe all the signalers within the arena or territory; importantly, some of the signalers in the arena or individual territory may be searching for food, therefore, the signalers must also have a Boolean display variable set to true. The Boolean variable is crucial as it only registers displaying signalers and not signalers that are within the arena foraging.

Interaction: There are no direct interactions among individuals. There is indirect competition for food between all the signalers and receivers. The signalers compete indirectly for the display items.

Stochasticity: The initialization of starting energy resources for each signaler and receiver is a random process where each individual starts with a randomly chosen integer between 0-1000 energy units. While two signaling individuals in nature may never differ in energy by three orders of magnitude, the large range is a necessary and useful component of the model. The large potential range in initial energy values should facilitate accurate rankings of signaling individuals, and in any case where the rankings are relatively inaccurate the cause of the reduced accuracy can not be attributed to reduced variation within signalers. Indeed, this randomization is important as it generates heterogeneity in both groups. There is also stochasticity in the birth of food items and display items so that ~10% of the items will reproduce in each time step as long as these populations are under the carrying capacity.

Collectives: There are no collectives in this model.

Observation: The main data collected from the model are the true display values that all the signalers have and the values each receiver estimates for each signaler. In the output files, the array of signalers output their true values, and in subsequent columns each receiver prints their estimates for each signaler. Therefore, a 20 x 21 table is generated for each model run. The table represents the 20 estimates of signaler quality produced by receivers plus the true values of signaler quality. These values are then used in the assessment of concordance between signaler output and receiver rankings (see above). Finally, in model simulations where signalers require display items, a global variable was created that measured the number of time steps that a signaler had sufficient energy reserves, but could not signal because they could not locate a display item. This variable suggests whether any potential reduced accuracy in ranking is due to a lack of food or an inability to locate display items. Since this variable is only meaningful when signalers have to locate items, it was tested under the specific model builds where signalers had to locate display items before signaling.

Initialization

At time t = 0 there are 20 signalers and 20 receivers placed randomly on the continuous space landscape. The energy reserves for each individual are the result of a random integer draw between 0 and 1000. Depending on the model conditions, between 250 and 25000 instances of each item (food and display) are created; the age for each of these items is a random integer draw from 0 – 100.

Input

No external data were used as input in these models.

Statistical Analysis of Model Simulations

The data from the simulation runs yielded 5121 data points. These data were analyzed using a general linear model in R (2014). Importantly, using parametric statistics to analyze results from agent-based model simulations is somewhat artificial as significance can almost always be achieved by increasing the number of sample runs (Grimm and Railsback 2005). The analysis performed here should be used to assess the effect size of each treatment (reported in Table 5.3), rather than using the analysis to designate each variable as significant or non-significant.

Results

The results of the general linear model are presented in Table 5.3. All three factors that influenced model build significantly influenced the accuracy of receiver rankings of signalers (Table 5.3). Specifically, requiring signalers to acquire non-food items reduced the accuracy of display, requiring receivers to assess signalers sequentially reduced the accuracy of display, and requiring receivers to assess contemporary effort reduced the accuracy of display, though this last effect was extremely weak (Table 5.3).

When signalers needed non-food items for display the accuracy of receiver rankings of signalers decreased considerably (Table 5.3). This pattern held at all levels of food production (Figure 5.1), and in both cases the accuracy of receivers' rankings increased with increasing food production until Kendall's W reached an asymptote.

To investigate this result, a variable was created that tracked the number of time steps where signalers had sufficient energy reserves but could not signal due to an inability to locate a display item. Two factors influenced the number of lost signaling opportunities: with increasing food production, there was increased loss of opportunities for signaling;

similarly, reducing the number of display items on the landscape also increased the lost opportunities for signaling (Figure 5.2).

The second effect was the time it took receivers to sample signalers. When receivers had to assess individual signalers one at a time, the accuracy of their rankings of signalers decreased compared to scenarios where all the signalers could be observed simultaneously (Table 5.3). When receivers had to sample signalers sequentially, the accuracy of the receiver rankings was reduced at all resource levels (Figure 5.3).

The final condition compared scenarios where receivers were able to observe the entire history of a signaler's effort, to the scenarios where the receiver could only observe a signaler's display in real time. While observing the entirety of a signaler's effort did improve estimation, the effect was weak (Table 5.3). Indeed, at non-saturating levels of food resources, the mean estimation of receivers is indistinguishable between the two cases (Figure 5.4).

In model runs where individuals had to acquire non-food items for display, the accuracy of assessment increased with both the number of original food items and the production of display items (Figure 5.5). As evidenced by the solid points, receivers were able to more accurately rank the signalers when more display items were initialized on the landscape.

Discussion

Specific characteristics of signaling systems affect the ability of receivers to rank displaying signalers (Table 5.3). First, when signalers rely on external items for display the receivers do not rank displayers as accurately as when external items are not needed (Figure 5.1). When external items are needed for display signaling individuals lose opportunities to signal; in these situations receivers are unable to distinguish between individuals that have sufficient energy reserves to signal but can not locate a display item and those individuals that are not signaling due to inability to locate food (Figure 5.2). When signalers needed items for display, receivers were able to rank signalers with moderate accuracy when the landscape was saturated with both display items and food items (Figure 5.4), though in high food conditions the difference in accuracy between not needing and requiring display items is maximized (Figure 5.1). Therefore, the conditions necessary for receivers to accurately rank signalers who require non-food items for display are the same conditions that most strongly favor using signals that do not require items for display. These results question the utility of using certain behaviors as signals or cues; for instance, using nest-building behavior likely leads to lower accuracy when assessing signalers, though using the final structure can improve accuracy (see below). The scenario where receivers fail to reliably assess signalers is superficially similar to sexual selection dynamics in fallow deer (*Dama dama*). In this system, female yearlings often mate with low-ranking males and maintain more genetic variation relative to the scenario where all female fallow deer mate with high-ranking males (Farrell et al. 2011).

The low accuracy of signaler ranks observed under some model conditions is also not due to memory because in all simulations the model assumes perfect memory, and no ambiguity in assigning identity to certain individuals. Given that these assumptions are almost certainly not met in nature the reliability of signaling based on acquiring items is potentially further reduced; and for these systems to function rather extraordinary mechanisms must be invoked for accurate ranking of signalers.

When receivers can assess the entire history of output of a signaler there is an increase in accuracy when ranking signalers (Figure 5.3). Indeed, in natural situations where non-foraging items are required for display, receivers often observe completed structures instead of observing the construction behavior that leads to the final structure. For example both bowerbirds (*Ptilonorhynchidae*) and the wren (*Troglodytes trogolodytes*) require that the display item be placed into a structure, thus extending the lifespan of the display (Evans and Burn 1996).

An especially pertinent group where signalers may require external items is the weaver clade (*Ploceidae*). Many species of weaver construct elaborate nests that are used to attract mates, raise young, or both. In village weavers (*Ploceus cucullatus*) females are attracted to nests and inspect the nests of males, and manipulated nests lead to lower mating success (Collias and Victoria 1978), though this is confounded with lower display effort by males (Garson 1979). Across the *Ploceidae* group though, sexual selection for nest building is variable and ambiguous. In red bishops (*Euplectes orix*), evidence suggests that nest building behavior may be a signal (Lawes et al. 2002); but in baya weavers (*Ploceus philippinus*), females are more attentive to the location of nests, as opposed to the nest itself (Quader 2005a), and do not seem to consider the building behavior. In situations where individuals do use cumulative structures as signals, competition among signalers may select for destructive behaviors. Specifically, signalers may be expected to destroy the signaling structures built by rivals. Indeed, evidence from satin bowerbirds and village weavers suggest that males will destroy the structures of others (Borgia 1985), effectively erasing the record of previous effort.

When receivers can assess all of the displaying signalers at once, the accuracy of assessment is higher than when receivers had to assess signalers sequentially (Figure 5.2). Indeed, in species where signalers display in leks (Shorey 2002) females can observe a group of males in a short amount of time compared to situations where females search out males that are defending territories that are relatively far apart (Waage 1973). Interestingly, the improved accuracy of ranking males may provide an alternative explanation for the evolution of some leks. Assuming that females trade off the costs searching for mates against the benefits of choosing high quality mates (Janetos 1980, Wiegmann et al. 1996), females that select males from within aggregations may survive at higher rates than females that do not prefer aggregations. If females more accurately rank males in leks, and the most successful males acquire the majority of mating in leks (Shorey 2002), then the genes for attractive male displays may fall into linkage disequilibrium with genes for displaying in congregations; thus satisfying the requirements for run-away selection (Fisher 1930). A female preference for males that form groups before display is evolutionarily plausible. Selection could utilize pre-existing genetic architecture for pro-social tendencies (Goodson et al. 2009) in a new context (Lynch 2007b); specifically, a female preference for joining a group of individuals would be linked with other mating behaviors.

In this set of models signalers only displayed a singular, non-descript trait, despite the considerable evidence that many organisms utilize multi-modal signaling to communicate quality (Partan and Marler 2005, Uy and Safran 2013). If individuals employ multiple signals for redundancy (Krebs and Dawkins 1984) then the results presented here are still largely applicable. In cases where individuals use multiple signals to convey different information (Endler 1993) selection to communicate non-redundant information may lead to the evolution of traits that are sub-optimal in terms of information transfer.

The results presented here provide a potential explanation for the preponderance of morphological and stereotyped displays used in sexual selection (Andersson 1994). First, neither morphological structures nor stereotyped behavioral displays tend to require non-food items, allowing for increased accuracy in ranking signalers. Additionally, multiple types of these kinds of traits can be assessed in short time periods. Previous theoretical work on signaling specifies that multiple displays can evolve so long as the secondary preferences that evolve do not incur synergistic costs (Iwasa and Pomiankowski 1994, Candolin 2003). Assessing multiple morphological traits likely requires little extra cost relative to devoting considerable portions of time to observe signaling behaviors that reduce time for maintenance behaviors such as foraging and preening. In contrast, assessing behavioral traits that rely on external items could drastically increase the search cost and thus make behavioral signals that rely on external items evolutionarily untenable (Pomiankowski and Iwasa 1993). However, if receivers use traits that are not useful for ranking signalers only as threshold traits, i.e. they only assess signalers that have acquired items or are present on a territory, this may reduce search costs and facilitate the evolution of multi-component signaling (Candolin 2003). For instance, European bitterlings (*Rhodeus sericeus*) females choose to initially inspect males based on behavior and morphology, but final mating decisions are based on aspects of the male's territory (Candolin and Reynolds 2001).

In cases where individuals do build structures, observing the final product is likely more efficient because the structure represents a record of output. The distinction between observing the final structure and observing the behavior that produced the structure is important. Some nests may take hours or days of work to build and receivers likely could not observe the entire behavioral output of multiple males. By observing the completed structure, receivers can spend considerably less time at each signaler and therefore sample more potential partners while still observing a structure that represents considerable output. Similarly, receivers can more accurately assess signalers when groups of signalers can be assessed in single time steps; as is possible in lekking species. By selecting partners from groups of signaling individuals, receivers are able to increase the number of potential partners they sample. Since many signaling systems rely on the relatively efficient characteristics identified above these results suggest that ecological and social characteristics drive selection in receivers to identify and use signals that reflect the quality of signalers (Searcy and Nowicki 2005, Rubenstein 2012).

For selection to maintain any trait in a population the selection coefficient has to be sufficiently large given a specific population size (Lynch 2007b). In many animals, small population size requires a relatively large selection coefficient to maintain traits via selection (Lynch 2007a). Therefore, those traits that are unreliable in terms of ranking individuals will be harder to maintain via selection or will be subject to drift. The models described here have shown that certain traits are unlikely to be useful for ranking signalers, especially those traits that require external items for display. For traits that do require external items, future research should examine whether these traits are used to make a binary choice between assessing or not assessing other aspects of a signaler. In contrast, leks are conducive to ranking males and the benefit provided by leks may provide an explanation for the evolution of leks in certain species.

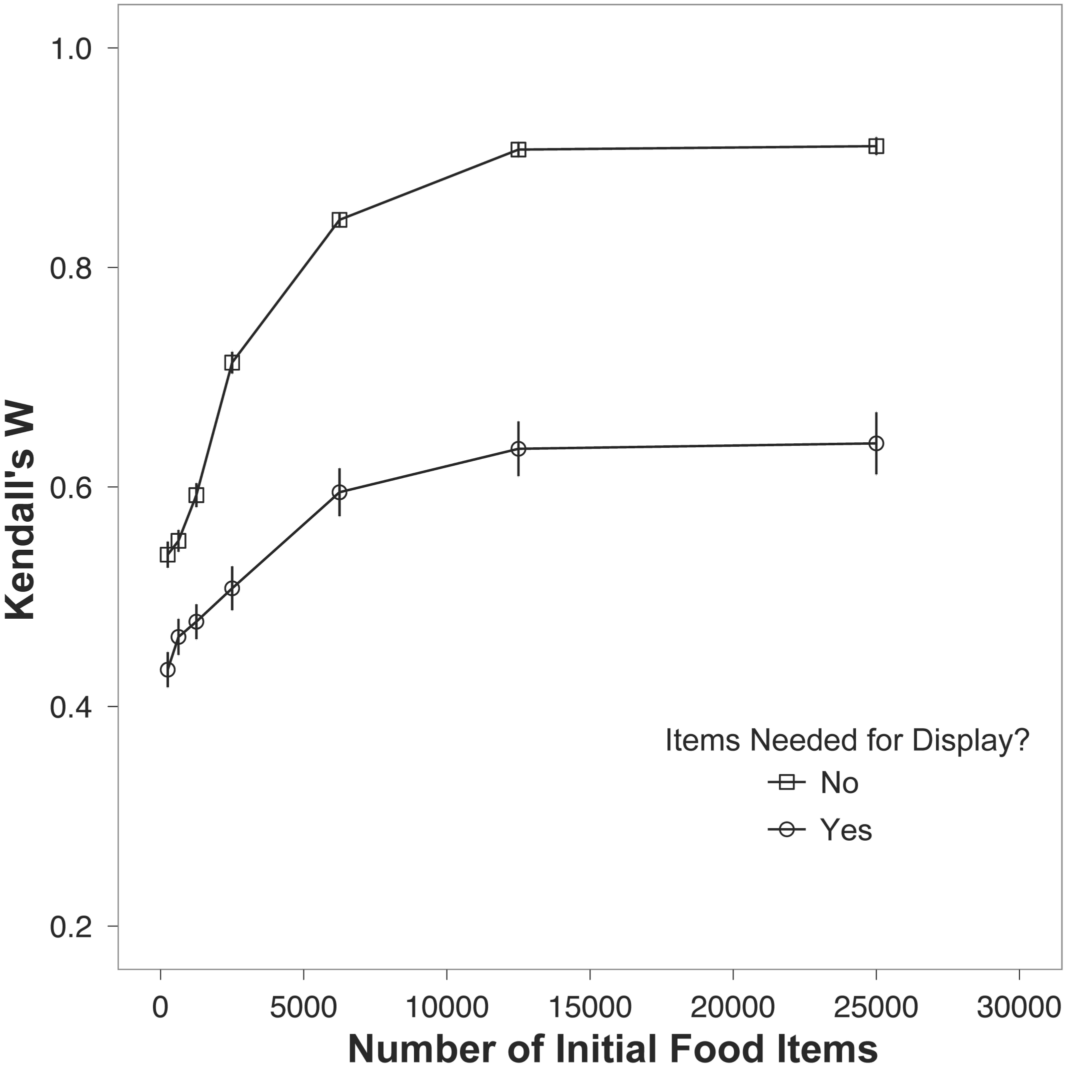

Figure 5.1: Association between ranking accuracy and the number of initial food items. Kendall’s W for the two situations where non-food items are needed for display and not needed for display (open circles and open squares, respectively) across a range of food availability. The plotted points are the means ± 1 s.e.m.

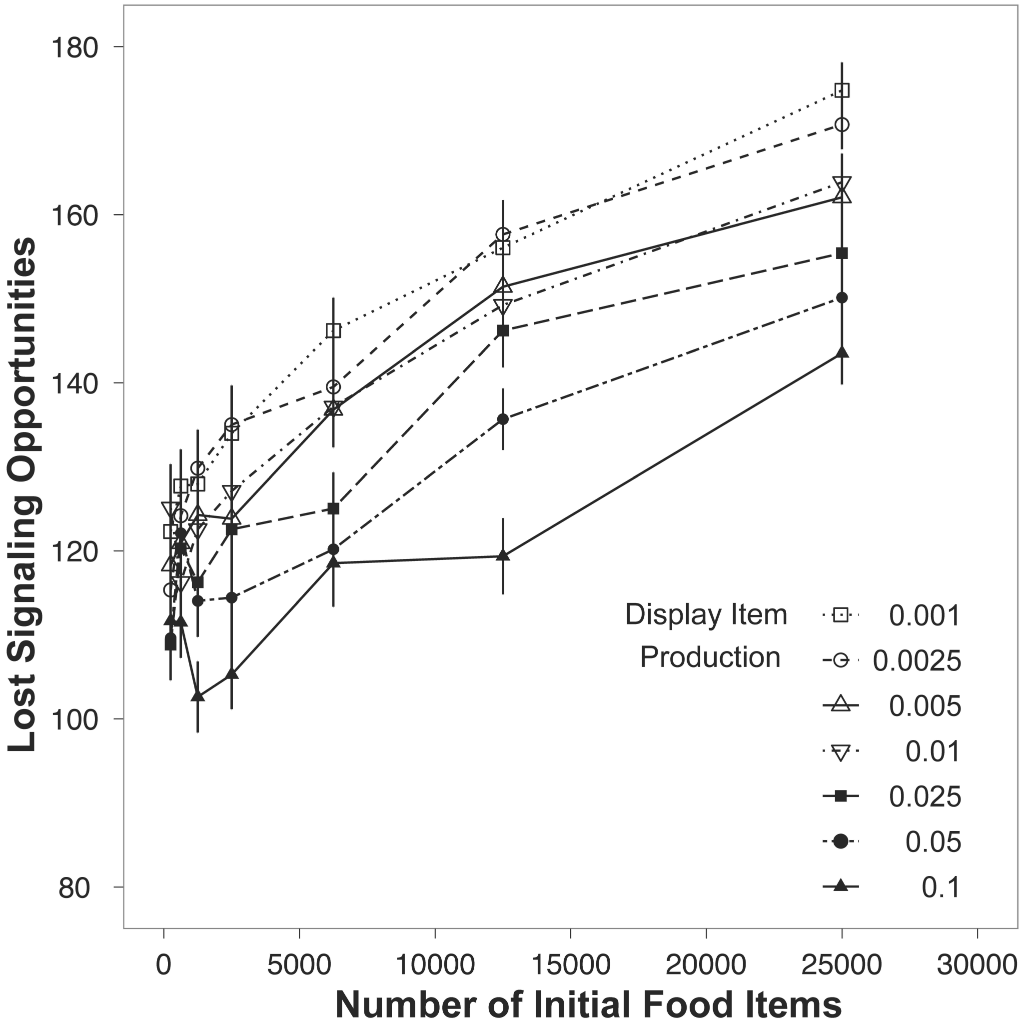

Figure 5.2: Association between the number of lost signaling opportunities and the number of initial food items. The number of lost displaying opportunities for signaling individuals in the model across food item availability and separated by the display item production. The plotted points for each display item line are the means ± 1 s.e.m.

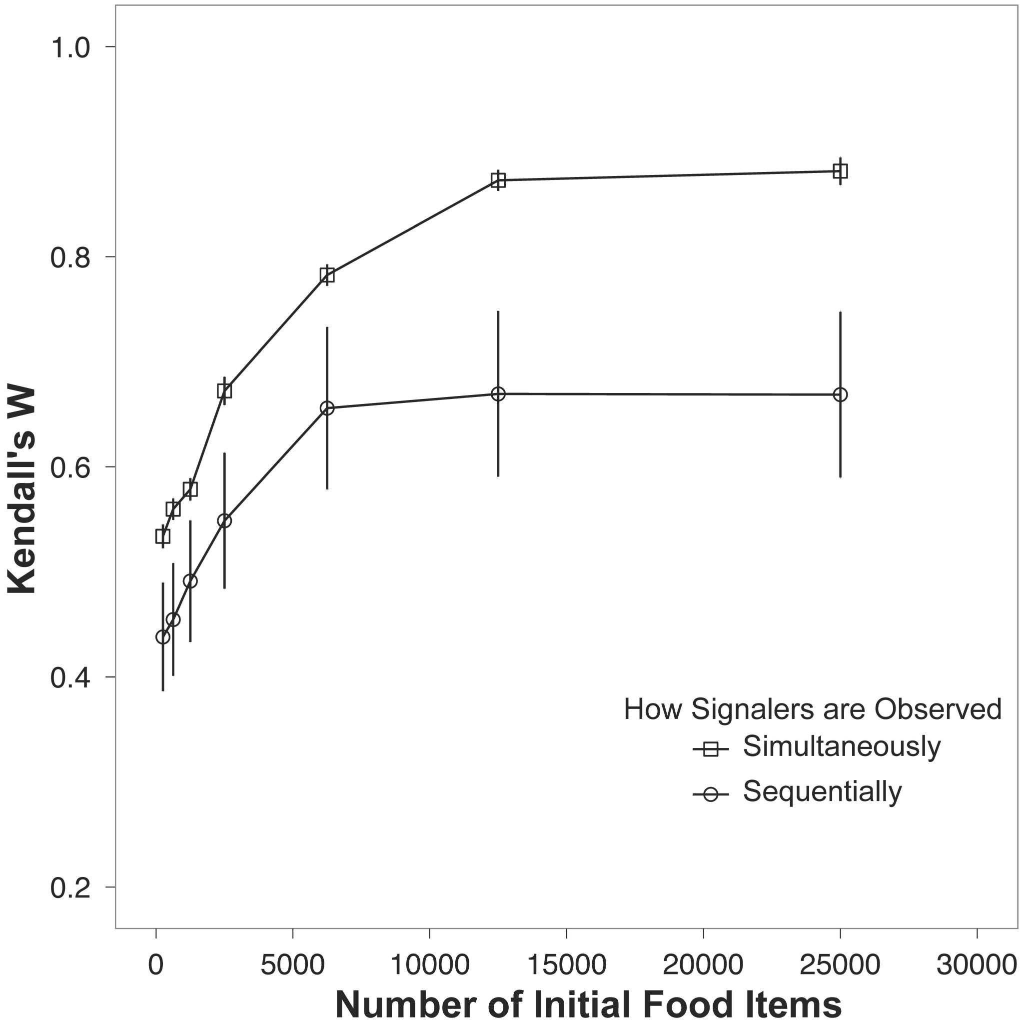

Figure 5.3: Association between ranking accuracy and number of initial food items. Kendall's W for the two situations where signalers are observed either sequentially or simultaneously (open circles and open squares, respectively) across a range of food availability. The plotted points are the means ± 1 s.e.m.

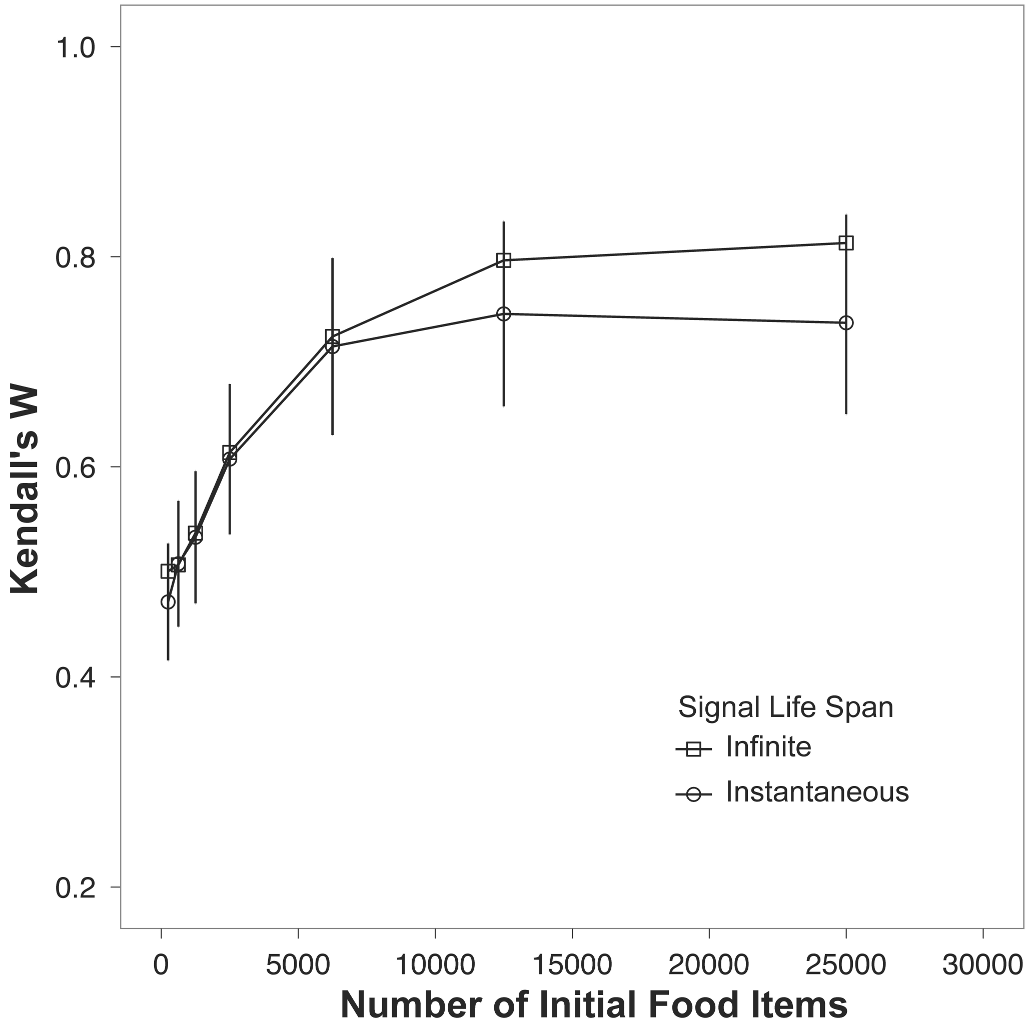

Figure 5.4: Association between ranking accuracy and the number of initial food items depending on the signal life span. Kendall's W for the two situations where signalers previous effort can be observed or effort can only be observed in real time (open squares and open circles, respectively) across a range of food availability. The plotted points are the means ± 1 s.e.m.

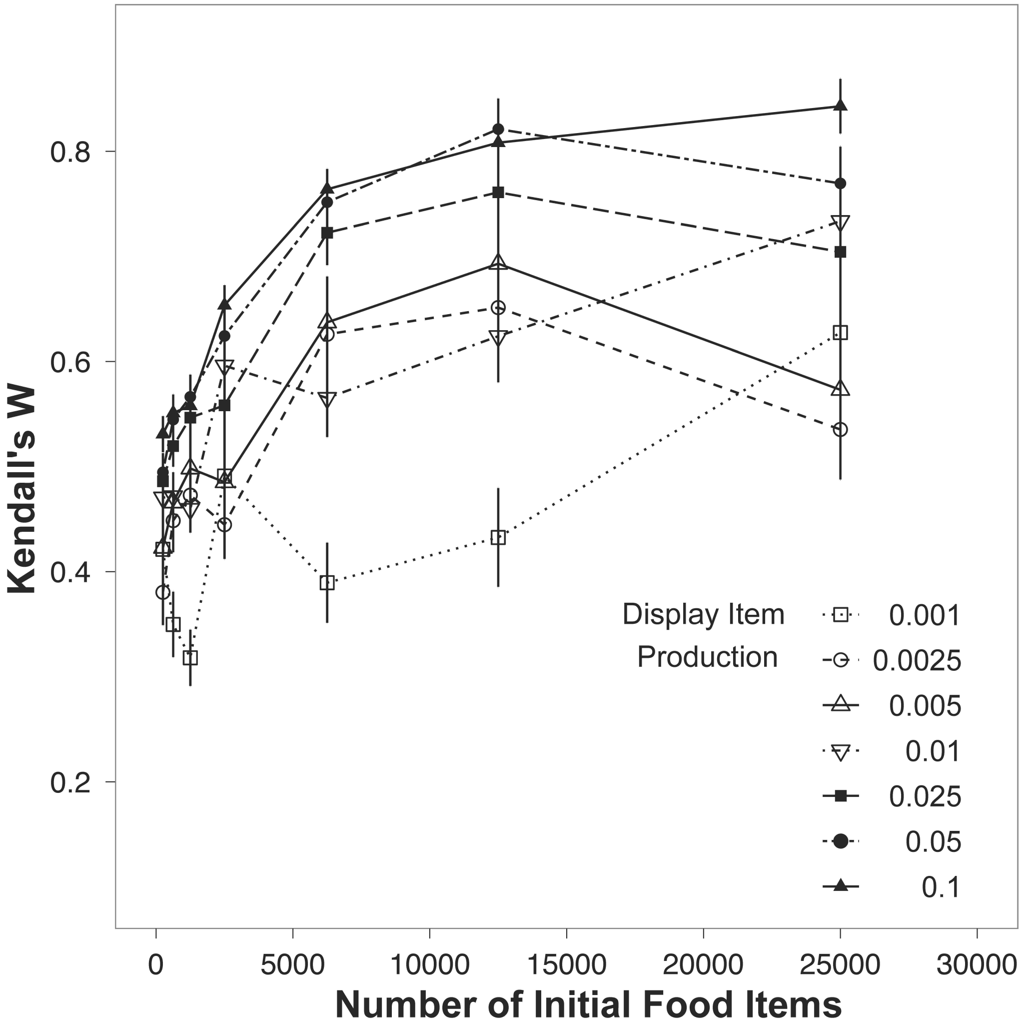

Figure 5.5: Association between ranking accuracy and the number of initial food items depending on the production of display items. Kendall's W for multiple display item production rates across a range of food availabilities (see legend). The plotted points are the means ± 1 s.e.m.

Table 5.1: Conceptual design of the model builds. In the first column, the results of signaler effort are described and whether the displayer effort results in some structure (morphological or an external structure like a nest) that persists over time. The second column describes whether the receivers can observe the entire effort of a male in a time step or can only observe the effort in the current time step. The third column specifies whether an external item, such as a twig, needs to be found before display. In the final column putative examples of these scenarios are provided. Question marks represent examples where the author could not locate unequivocal examples of this scenario. References and scientific names printed below the table.

Signaler	Receiver	Items Needed for Display?	Example
Collection of items results in cumulative structure.	Can assess all displaying signalers in a single time step.	Yes	Village weavers[1] (?)
Items used in display can only be observed in real time.	Can assess all displaying signalers in a single time step.	Yes	(?)
Collection of items results in cumulative structure.	Can assess one signaler in one time step.	Yes	Satin bowerbirds[2], Wren[3], Black Wheatear[4], Cichlid[5]
Items used display can only be observed in real time.	Can assess one signaler in one time step.	Yes	Hangingflies[6], other species with nuptial gifts

Total effort results in cumulative structure (morphological structures included)	Can assess all displaying signalers in a single time step.	No	Sage grouse morphological features[7], other species with leks
Effort can only be observed in real time.	Can assess all displaying signalers in a single time step.	No	Pied flycatchers[8]
Total effort results in cumulative structure or morphology	Can assess one signaler in one time step.	No	Peacock[9] trains, various other morphological traits
Effort can only be observed in real time.	Can assess one signaler in one time step.	No	Golden-collared manakins[10], courtship dances, Cleaner wrasse[11] partner monitoring

[1]*Ploceus phillipinus (Collias and Victoria 1978)*, [2]*Ptilonorhynchus violaceus (Uy et al. 2001)*, [3]*Troglodytes troglodytes(Evans and Burn 1996)*, [4]*Oenanthe leucura (Moreno et al. 1994)*, [5]*Lamprologus callipterus*, [6]*Bittacus apicalis(Thornhill 1976)*, [7]*Centrocerus urophasianus (Gibson and Bradbury 1985)*, [8]*Ficedula hypoleuca (Krams et al. 2008)*, [9]*Pavo cristatus (Petrie 2002)*, [10]*Manacus vitellinus(Barske et al. 2011),* [11]*Labroides dimidiatus (Soares et al. 2009)*

Table 5.2: List of variables and what they represent within the model. The Numeric Value column specifies how these variables were initialized, variables that were manipulated across a spectrum of values during simulations are indicated with a range of values.

Visibility	Variable	Description	Numeric Values
Global	Time Steps	Count of the number of time steps	Always initialized to 0 and stopped after step 1440
	Neighborhood	Spatial extent that signalers and receivers could perceive items	Initialized to 10
	Energy Threshold	Lowest amount of energy an individual could have before having to forage	Initialized to 500
Signalers	Home Location	Specific site where each signaler returned to for display	Each signaler received a unique home location
	Location	Current Location	Randomized at initialization
	Energy Reserves	Amount of energy the signaler has	Each signaler given a random value between 0 and 1000 at initialization
	Display Effort	A cumulative log of the number of time steps a signaler has displayed	Initialized to 0

	ID	Unique integer identifier for each signaler	Between 0-19 depending on the signaler
Receivers	Signaler Values	An array of values corresponding to each signaler and how much the receiver has witnessed a specific signaler display	All values in the array are initialized to 0
	Location	Current Location	Randomized at initialization
Food Items	Age	A value that increased with each time step that indicates the age of each food item.	Random values when initialized, set to 0 if born during simulation run
	Location	Current Location	Randomized at initialization
Display Items	Age	A value that increases with each time step that indicates the age of each display item.	Random values when initialized, set to 0 if born during simulation run
	Location	Current Location	Randomized at initialization

Table 5.3: General linear model coefficients for predicting Kendall’s W based on certain model characteristics. Value represents the coefficient’s value in the predicting Kendall’s W. The effect size was estimated using partial eta$_2$ (SS$_{Factor}$ / SS$_{Factor}$ + SS$_{Error}$).

Coefficients	Value	Standard Error	t-value	Effect size (η^2_P)	p-value
Intercept	0.72	0.009	83.07	na	<0.001
Food Item Production	3.02	0.126	24.02	0.250	<0.001
Items Needed for Display	-0.18	0.008	-23.13	0.261	<0.001
Signalers observed Sequentially	-0.14	0.008	-16.89	0.295	<0.001
Observe effort in real time	-0.02	0.008	-2.93	0.006	0.0034

Chapter 6

Punishment increases the cooperative nest construction behavior of sociable weavers

Summary

The major transitions in evolution rely on the formation of stable groups that are composed of previously independent units, and the stability of these groups requires both cooperation and reduced conflict. Conflict over investment in group resources may be common, though relatively little work outside of humans has investigated how societies resolve conflict over investment in group resources, i.e. public goods. We investigated whether punishment helps stabilize a public good, the communal nest of sociable weavers (*Philetairus socius*). We[2] found that the individuals that build the communal exterior of the nest, i.e. the individuals most at risk of exploitation, are the most aggressive individuals. We show that individuals that invest in interior chamber maintenance, i.e. more selfish behaviors, suffer relatively more aggression. After suffering aggression individuals significantly increase cooperative construction of the communal nest exterior. We show that cooperative individuals target aggression towards selfish individuals, and the individuals suffering aggression perform cooperative behaviors subsequent to suffering aggression, thus suggesting that punishment is used to limit exploitation in sociable weavers.

Background

The major transitions in evolution rely on the formation of stable groups that are composed of previously independent units, and the stability of these groups requires both

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[2] Note: This research was performed with Laura Nicole Vander Meiden.

cooperation and limited conflict within the group (Maynard Smith and Szathmáry 1997). Although elevated relatedness can reduce conflict within a group (Hamilton 1964), there will still be conflict in groups when the fitness of individuals is not perfectly aligned (Frank 1995, Bourke 2011a). Thus there is often conflict in insect, mammal, and bird societies (Ratnieks 1988, Emlen and Wrege 1992, Monnin et al. 2002, Stankowich and Sherman 2002, Bell et al. 2012), especially in regards to reproductive share between individuals within groups (Bell et al. 2014, Cant et al. 2014). However, there is likely also conflict over investment in cooperative behaviors that produce a resource that benefits the entire group, i.e. a public good (Hardin 1968). Despite the importance of public goods for the stability of many animal societies, relatively less work has investigated the conflict over cooperative investment in public goods compared to investment in reproduction (Bell et al. 2014, Cant et al. 2014).

While public goods often underlie the stability of a group they are simultaneously at risk of being over-exploited by selfish individuals within the group (Rankin et al. 2007), and over-exploitation can lead to a collapse of the resource, i.e. a ‘tragedy of the commons’ (Hardin 1968). To protect investment in public goods coercive behaviors such as punishment are often necessary to limit exploitation (Ratnieks and Wenseleers 2008). We therefore investigated how aggression modulates cooperative nest construction in sociable weavers (*Philetairus socius*). Sociable weavers are a useful system for studying social evolution because individuals live in communal nests with multiple chambers present within the nest (Maclean 1973). Recent evidence suggest that individuals attain indirect benefits via cooperative nest construction (van Dijk et al. 2014), and that the communal nest is a public good since individuals obtain thermal benefits simply by roosting in the nest (Leighton and Echeverri 2014). Sociable weaver nests are maintained via two disparate routes. First, individuals can maintain the chambers they roost in at night, with individuals showing fidelity to specific nest chambers (van Dijk et al. 2013). Second, individuals can insert items into the nest exterior, referred to as the communal thatch from here on, and spend time re-weaving materials already in the exterior (Leighton 2014b). The first route of maintaining individual chambers is considered relatively selfish because individuals can monopolize the benefits of the behavior (van Dijk et al. 2013). We measured both forms of nest construction as well as aggressive behaviors that have been defined for sociable weavers (Collias and Collias 1978).

We derive predictions based on the canonical definition of punishment (Clutton-Brock and Parker 1995). We assume that sociable weavers that build the communal thatch are exploited by individuals that contribute little to maintaining the communal thatch. We predict that the cooperative weavers will act aggressively towards the uncooperative individuals and that aggression will induce increased cooperative behavior in the individuals that suffer aggression.

Methods

Study Site and Species

Sociable weavers are colonial passerines (24 – 30 g) that live in the semi-arid savannahs of Southwestern Africa (primarily Namibia and South Africa). Individuals live in colonies and build a communal, perennial nest (Maclean 1973). Most items inserted into the nest are twigs, *Stipagrostis spp.* grass, and softer materials for nest chamber lining (Maclean 1973). The nest is composed of a large, exterior communal thatch, and the underside of the nest houses disparate chambers. We studied three sociable weaver nests at the Brink Research Site in central Namibia during May and June 2014. We used mist-nets to band 83 individuals at three nests (n = 31, 39, 13, for the three nests). We recorded the following morphological measurements for each individual: mass, wing length, tarsus length, beak depth, beak width, and sex. We regressed mass on tarsus to estimate body condition.

Behavioral Observations

We observed individuals for a total of 248 hours and recorded the total number of items individuals inserted into the communal thatch and the amount of time individuals spent weaving material into the communal thatch. We also recorded the number of items individuals brought into an internal nest chamber for chamber maintenance. Finally, we measured chasing behavior, a previously described behavior that is considered aggressive in sociable weavers (Collias and Collias 1978). For each chase, we recorded the individual that initiated the chase and the individual that was being chased.

Statistical Analysis

As the dependent variables in the data were count data, which displayed increased variance at higher values, we employed generalized linear mixed models with a negative binomial error structure and a log-link function (Zuur et al. 2009). We built these models in R (2014) using the package lme4 (Bates et al. 2014). In all of the models we assigned individual and nest as a random factor. We compared models using AIC criteria and compared the full model to models with a single variable removed (Burnham et al. 2011). We then used p-values to assess regression coefficients and whether they differed significantly from zero whereas we used AIC values to estimate how a variable influenced the fit of the model. These two measures are complementary and thus provide more information about the system.

Results

We found that aggression as measured by the number of times an individual chased other individuals, is significantly and positively predicted by the number of items inserted into the communal thatch by weavers ($p < 0.001$, Figure 6.1a). The number of chases an individual performs is also predicted by wing length, but no other variables (Supplemental Table 6.1). To further investigate the influence of communal thatch construction on aggression we regressed the number of items an individual inserted into the communal thatch on the number of items inserted into a nest chamber. We used the residuals from this model to predict aggressive behavior. We found that more positive residuals, i.e. individuals that devote significantly more energy to inserting items into the communal thatch relative to chamber maintenance, significantly predict aggressive behavior ($\beta = 0.06$, $t = 3.5$, $p < 0.001$, Supplemental Figure 6.1). We also find that aggressive behavior is repeatable within individuals, $r = 0.406$ (95% C.I. = 0.245 – 0.506).

The number of times an individual is chased is positively associated with the number of items that they insert into their nest chamber ($p < 0.001$, Figure 6.1b). Thus the amount of aggression an individual experiences from others is predicted by the amount of internal nest maintenance it performs. The number of times an individual is chased is also negatively correlated with beak width, while no other variables explained the variation in the aggression suffered by an individual (Supplemental Table 6.2). Suffering aggression is not repeatable within individuals (Supplemental Table 6.3).

When we combined all the time points before or after aggression, we see that sociable weavers that suffer aggression contribute significantly more to communal thatch construction after aggression compared to before being chased ($F = 8.13$, $p = 0.008$, Figure 6.2). We investigated how behaviors changed prior to an aggressive bout. There is a negative relationship between the time before suffering aggression and the number of items added to the communal thatch. In general, the time before suffering aggression approaches, individuals significantly decreased the number of items they added to the communal thatch ($\beta = -0.04$, Std. Error = 0.009, $z = -43.9$, $p < 0.001$, Supplemental Figure 6.2).

Discussion

Sociable weavers that spend more time cooperatively constructing the communal thatch are also more aggressive in terms of chasing other individuals away from the nest (Figure 6.1A). We also find that individuals at the highest risk of exploitation, i.e. individuals that preferentially build the communal thatch, are those individuals that are most aggressive (Supplemental Figure 6.1). Indeed, these cooperative individuals are at the most risk of exploitation and therefore should be selected to minimize the exploitation of the cooperative output (Clutton-Brock and Parker 1995). The chased individuals are not evicted, however, as we observe these same individuals at the nest in following observation periods (G.M. Leighton, unpublished data). Weavers with larger wings do chase significantly more, suggesting that these individuals may be dominants chasing subordinates. Even if dominant weavers do perform more chases, individuals that are chased respond by investing more in the communal thatch (Figure 6.2), which suggests that aggression induces cooperation and can still be considered punishment.

While recent work in vertebrate societies suggests that individuals attend to the behavior of conspecifics within the group, behavioral manipulations demonstrated that the threat of punishment in these groups seems to maintain cooperation in the absence of experimental manipulation (Zottl et al. 2013, Bell et al. 2014, Cant et al. 2014, Fischer et al. 2014), more so than active punishment. In contrast, sociable weavers actively and constantly use aggression to influence the cooperative behavior of group mates. Aggression is targeted towards individuals that have reduced cooperative output and the individuals that suffer aggression subsequently increase cooperative output; therefore sociable weavers are likely using punishment to limit exploitation of the communal nest.

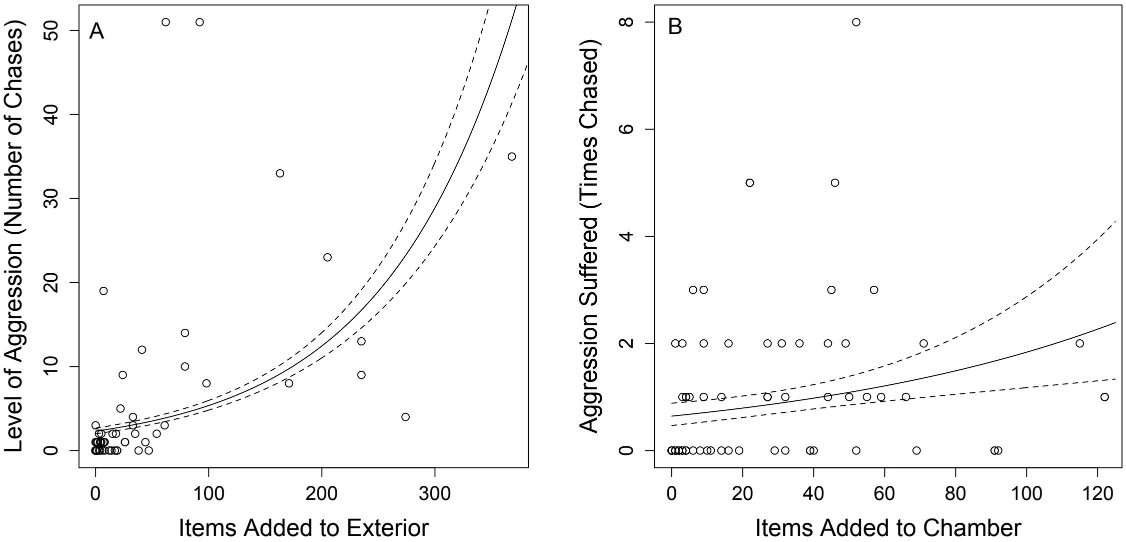


Figure 6.1: Relationships between certain behaviors and measures of nest construction. (A) Positive association between the number of items added to the exterior of the nest and the number of chases an individual performed. (B) Positive relationship between the number of items added to a nest chamber and the aggression suffered by the individual. In both plots the solid line is the predicted line from the generalized linear mixed model while the dashed lines represent the 95% confidence intervals around the line.

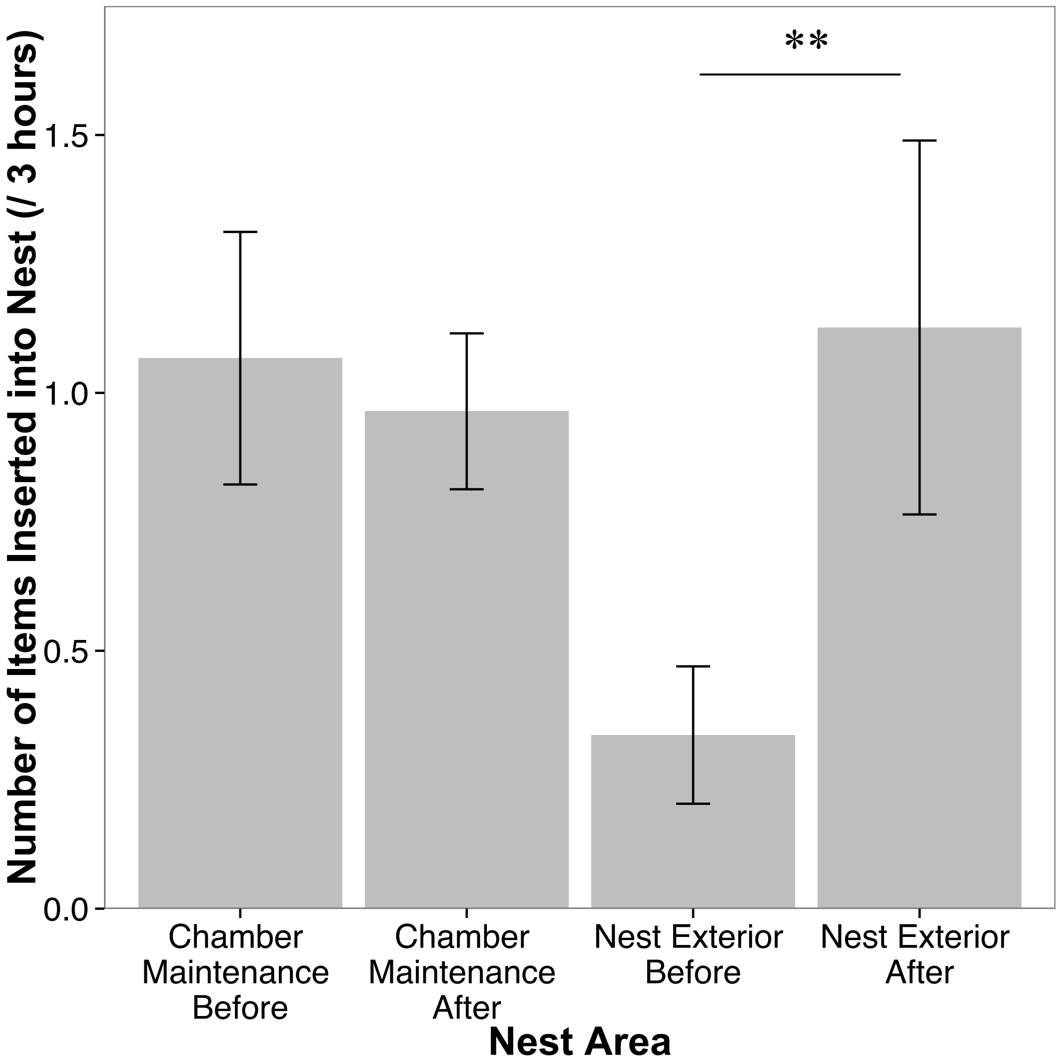
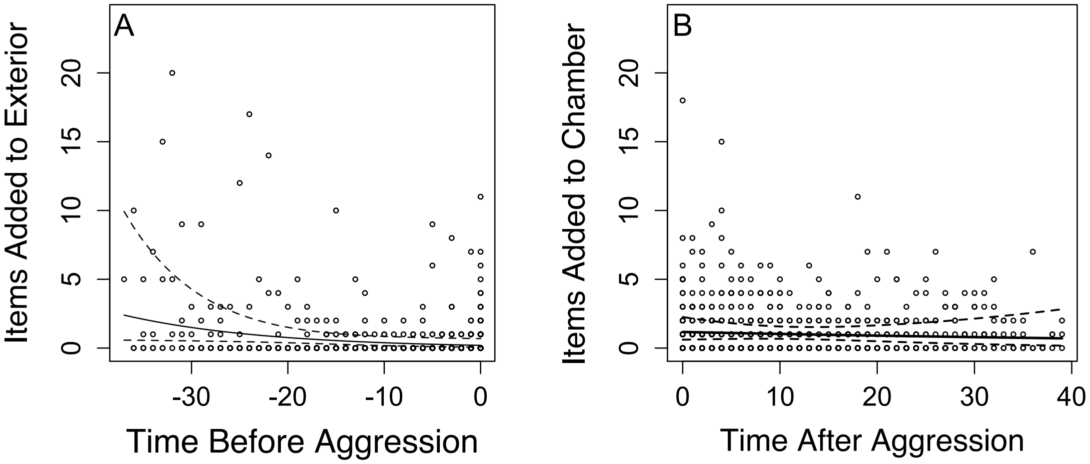
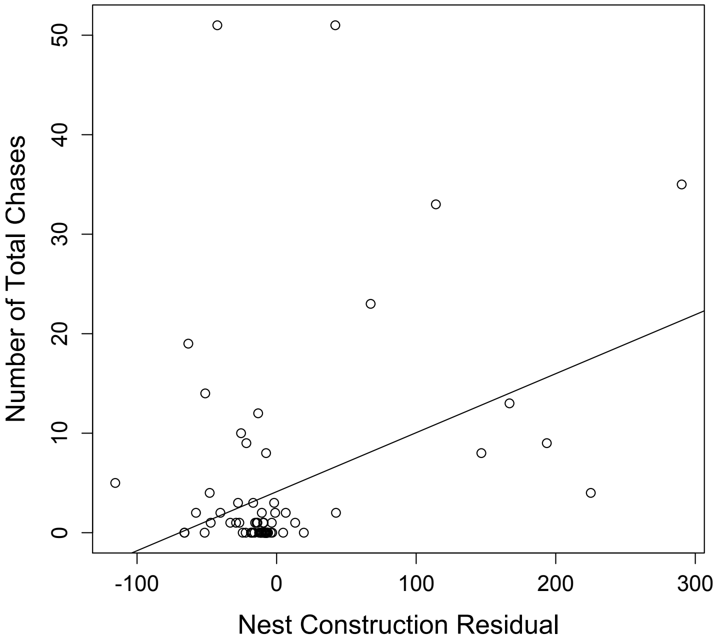


Figure 6.2: Number of items inserted into the nest where left two bars represent items inserted into the nest chamber before and after aggression, respectively. The right two bars represent the number of items inserted into the nest exterior before and after aggression, respectively. There is a significant increase in items inserted into the nest exterior after an individual suffers aggression. Error bars represent ± 1 S.E.M.



Supplemental Figure 6.1: Plots describing how items added to the nest change before and after aggression. (A) Negative relationship between the number of nest items added to the nest exterior and the time until suffering aggression. 0 represents the time point when the individual suffered the aggressive bout. (B) Negative relationship between the number of items inserted into a nest chamber and the time since suffering aggression. In both plots the solid line is the predicted line from the generalized linear mixed model while the dashed lines represent the 95% confidence intervals around the line.



Supplemental Figure 6.2: The number of total chases performed by an individual predicted by the individual's residual from the model that predicts the number of items inserted into the nest exterior by the number of items inserted into the nest chamber. Higher residual values represent individuals that inserted significantly more items into the nest exterior than the nest chamber. The line represents the predicted value from the linear model and represents a significant, positive association between the two variables, ($\beta = 0.06$, S.E. = 0.02, $t = 3.5$, $p < 0.001$).

Supplemental Table 6.1: The generalized linear mixed model with log link and negative binomial error structure with variables predicting the number of times an individual chased other nest mates. P-values represent whether regression coefficient is significantly different than zero. AIC values represent the full model except for the variable in question. ΔAIC values are the differences in AIC from the full model and positive values indicate that removing the variable increased the AIC value. Note that the variable indicating sex represents an analysis with NAs removed, and therefore does not have a comparable AIC value, though the ΔAIC can still be calculated using the reduced dataset.

Variable	Coefficient	Std. Error	t-value	P-value	AIC	ΔAIC
Mass	0.15	0.16	0.959	0.34	1578.2	-1.1
Wing Length	0.43	0.17	2.53	0.01	1584.1	4.8
Tarsus	0.04	0.27	0.15	0.89	1577.3	-2.0
Beak Depth	1.01	0.53	1.88	0.06	1580.7	1.4
Beak Width	-0.71	0.46	-1.56	0.11	1589.7	0.4
Items Inserted into Exterior	0.09	0.01	5.76	<0.001	1610.2	30.9
Predator Present	0.14	0.18	0.805	0.42	1577.9	-1.4
Sex	0.004	0.64	0.007	1	*NA	-0.2

Supplemental Table 6.2: The generalized linear mixed model with log link and negative binomial error structure with variables predicting the number of times and individual was chased by other nest mates. P-values represent whether regression coefficient is significantly different than zero. AIC values represent the full model except for the variable in question. ΔAIC values are the differences in AIC from the full model.

Variable	Coefficient	Std. Error	t-value	P-value	AIC	ΔAIC
Items inserted into chamber	0.24	0.07	3.62	<0.001	656.6	11.8
Mass	0.05	0.11	0.50	0.65	643.0	-1.8
Wing Length	-0.20	0.11	-1.85	0.06	656.1	11.3
Tarsus	-0.10	0.19	-0.54	0.59	643.1	-1.7
Beak Depth	0.29	0.38	0.75	0.45	643.3	-1.5
Beak Width	-0.88	0.32	-2.74	0.006	652.1	5.4
Age Class	-1.23	0.81	-1.52	0.12	645.6	0.8
Predator Present	-1.01	0.49	-2.04	0.04	647.8	3.0
Sex	-0.21	0.41	-0.58	0.61	NA	1.0

Supplemental Table 6.3: Repeatabilities assuming a poisson error structure and log link for behaviors. We calculated repeatability using the “rptR” package in R.

Behavior	Repeatability	95% Confidence Interval
Items Added to Chamber	0.308	0.252 – 0.377
Items Added to Nest Exterior	0.109	0.074 – 0.141
Aggressive Chases	0.406	0.245 – 0.506
Number of Times Chased	0.01	0 – 0.046

Chapter 7

Conclusion

The evolutionary maintenance of cooperative nest construction in sociable weavers is likely stabilized by a combination of mechanisms. First, I found that individuals likely gain indirect benefits from nest construction as an individual's relatedness to the colony of residence predicts cooperative output. I found that sociable weaver males spend significantly more time and insert significantly more items into the exterior of the nest than females. This is a robust finding as I documented male-biased nest construction in both a captive population and a wild population. Although male and female sociable weavers were similarly related to the colony, males that were more closely related to the colony devoted more time and energy to nest construction. The fact that highly related males cooperated at higher levels largely drives the association between relatedness and cooperative output. Importantly, male-biased nest construction is likely the ancestral state in weavers (Garson 1979, Quader 2005a), and this ancestral condition could have facilitated the evolution of cooperative nest construction in sociable weavers. The results presented here are the first to show a significant predictive relationship between relatedness and investment in a public good in a vertebrate.

One alternative hypothesis that could explain male-biased nest construction is that nest construction is a sexual signal. This hypothesis is unlikely for several reasons. First, in genetically monogamous systems with reproductive skew in both sexes the expectation for sexual signals is that both sexes develop similar sexual signals. Second, I built a model that compared the effectiveness of signaling across different ecological contexts and found that signaling with external items, such as twigs or grass, is much less effective than using morphological characteristics. Sexually selected signals cannot be maintained under any mechanism if receivers of signals cannot reliably assess signalers, and thus it is unlikely that nest construction is being used as a sexual signal for several reasons. First, since the nest is a continuous mass, individuals would have to watch others building the nest in real time. Second, individuals would have to estimate cooperative output over time. Finally, weavers would have to distinguish between dozens of individuals on the nest. In sum, it seems unlikely that weavers would attend to nest construction as a signal unless simple rules were being used to rank individuals.

Certain individuals in sociable weaver societies invest considerable time and energy in cooperative nest construction and this behavior yields inclusive fitness benefits. However, this cooperative investment by individuals could be exploited by selfish individuals. I found that the sociable weavers that contributed most to external nest construction, i.e. those individuals most at risk of exploitation, are the most aggressive individuals. These aggressive individuals targeted aggression at individuals that inserted significantly more items into the nest chambers, a putatively selfish behavior. The selfish individuals subsequently contributed significantly more time and energy towards maintaining the exterior of the nest. Investment in nest construction is therefore likely protected against exploitation by aggression in sociable weavers. Therefore sociable weavers represent one of the only systems found in non-human animals where individuals actively coerce others into cooperative investment in a public good.

Sociable weavers are one of the few vertebrate societies to maintain a communal, perennial, public good. Sociable weavers invest in the communal nest and the investment is predicted by relatedness. The association between relatedness to the colony and investment in the nest suggests that sociable weavers receive indirect benefits by investing in a nest that benefits relatives. Weavers protect this investment by directing aggression towards selfish individuals, and this aggression induces cooperative nest construction in the selfish individuals. Therefore, the combination of kin selection and punishment stabilizes cooperative nest construction in sociable weavers.

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