

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

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**Abstract** 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 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.

**Keywords** Cooperation · Public good · Kin selection · Sociable weaver · GLMM

## Zusammenfassung

### Geschlechts- und individuelle Unterschiede beim kooperativen Nestbau von Siedelwebern *Philetairus socius*

Komplexe Tiergemeinschaften sind oftmals auf kommunale Ressourcen angewiesen, von denen alle Individuen in der Gruppe profitieren. Selektion sollte Individuen begünstigen, die ihren Beitrag zu diesen kommunalen Ressourcen verringern, und ihren Verbrauch der Ressourcen erhöhen, was die Stabilität dieser „Allgemeingüter“ gefährdet. Um ein Verständnis dafür zu entwickeln, wie solche Allgemeingüter aufrechterhalten werden, ist es hilfreich, die kooperativen Verhaltensweisen zu beschreiben, die Allgemeingüter aufrechterhalten. Ein solches Allgemeingut ist das Gemeinschaftsnest von Siedelwebern (*Philetairus socius*), das kooperativ von individuellen Webern in der Kolonie gebaut und instandgehalten wird. Eine in Gefangenschaft gehaltene Siedelweberkolonie wurde sechs Wochen lang beobachtet, und es wurde erfasst, wie sehr sich einzelne Tiere am kooperativen Nestbau beteiligten. Die Individuen in der Kolonie wohnten in einem von sechs verfügbaren Nestern, und jedes Individuum konzentrierte sein Nestbauverhalten auf das jeweilige Nest, in dem es wohnte. Männliche Siedelweber kooperierten stärker als Weibchen, und die Maße der Kooperation waren gleichbleibend über die Zeit. Diese Ergebnisse liefern eine erste Beschreibung des kooperativen Nestbaus in einer ganzen Kolonie und schlagen potenzielle Mechanismen vor, die Kooperation aufrechterhalten könnten.

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## Introduction

The maintenance of animal societies often requires that individuals perform group-beneficial cooperative behaviors

such as territory defense or nest maintenance (Bourke 2011); 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 literature (Foster 2004; Rankin et al. 2007; Frank 2010; Raihani and Bshary 2011) has 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. 2007). 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 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 nestmates 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 maintain 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 ascertain 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.

## 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 small passerines endemic to southwestern Africa that live in semi-arid habitats with variable rainfall (Maclean 1973). Sociable weavers are among the uncommon instances of genetically monogamous bird species (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 3-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 and 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 m 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-h 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 1-h 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. When referring to “nest construction” in this paper, this will only apply to 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 1–11 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 ( $\geq 2$  years of age).

There were 12 individuals (seven males and five 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 each 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 to 48 h. 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 min 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 variables. Therefore, the typical analysis, a Poisson generalized-linear mixed model (GLMM), is inappropriate for analyzing these data. Instead, the *cplm* package in R (Team 2010) 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 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 quasiliikelihood 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 to which individuals added items. Using this 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' 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.

The data from this work has been deposited in the Dryad repository (doi:10.5061/dryad.312d1).

### 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 1, 2). Specifically, males contributed significantly more than females to both cooperative dependent variables (Figs. 1, 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, although  $\Delta$ AIC values also suggest that whether an individual moved to a new nest may have a weak effect on cooperative output (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

**Table 1** Explanatory variables in GLMM predicting proportion of time devoted to cooperative nest construction

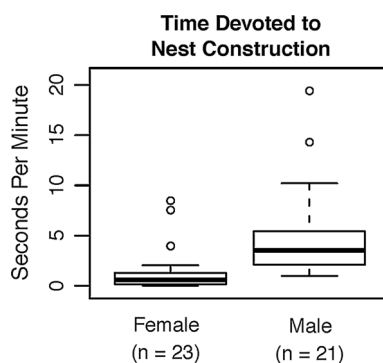
Predictor	Estimate	SE	df	p value
Intercept	-0.04	0.04		
Sex (m > f)	1.56	0.50	1	<0.001
Moved (no > yes)	0.06	0.24	1	0.79
Age	0.04	0.13	1	0.88
Sex × age	-0.000039	0.15	1	0.99

The proportion of time an individual dedicated to cooperative nest construction was best predicted by the sex of the individual ( $p < 0.001$ ;  $1.56 \pm 0.50$ ). 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 individuals (variance  $\pm$  SE =  $0.83 \pm 0.91$ ) were included in all models

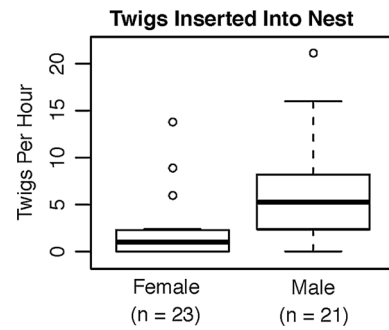
**Table 2** Explanatory variables in GLMM predicting number of items inserted into communal nest

Predictor	Estimate	SE	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 × age	0.06	0.18	1	0.72

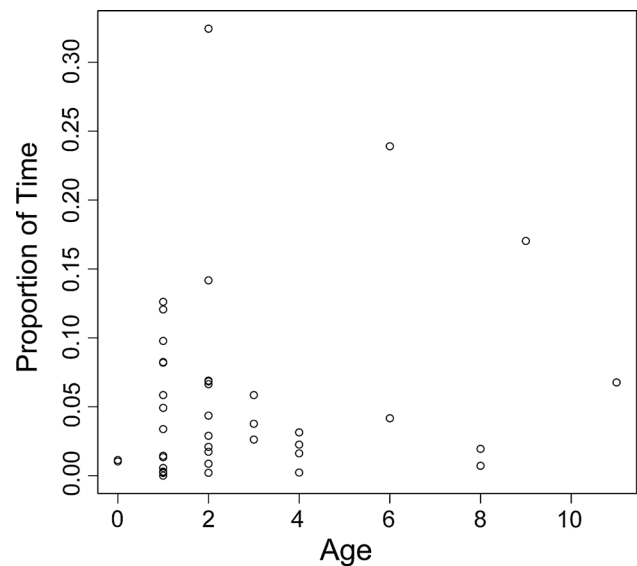
The number of items an individual inserted into the nest was best predicted by the sex of the individual ( $p = 0.002$ ;  $1.26 \pm 0.52$ ). All estimates of effects are on the latent, logarithmic scale.  $p$  values were generated for specific variables via nested model comparisons to the full model using the ANOVA command in R assuming a Chi distribution. The random intercepts for individuals (variance  $\pm$  SE =  $0.82 \pm 0.90$ ) were included in all models



**Fig. 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  $1.5 \times$  the inter-quartile range in either direction. Any individuals beyond that range are indicated by *circles*



**Fig. 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  $1.5 \times$  the inter-quartile range in either direction. Any individuals beyond that range are indicated by *circles*



**Fig. 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

cooperative output. Neither the continuous measure of age nor the classification of individuals into young ( $< 2$  years old) versus adult ( $\geq 2$  years old) predicted cooperative output, although the three individuals of age 0 appeared to cooperate less (Fig. 3). The best model for both dependent variables contained sex as a fixed factor and individual as a random factor (Tables 1 and 2).

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

**Table 3** Explanatory variables in GLMM predicting number of items inserted into a communal nest after controlling for the amount of time dedicated to cooperative nest construction

Predictor	Estimate	SE	df	<i>p</i> 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

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 predictors 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 individuals (variance  $\pm$  SE =  $0.36 \pm 0.60$ ) were included in all models

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 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 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 3).

For the subset of individuals whose cooperative behavior was recorded and it was known into which 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 the 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 and 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 and 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 only 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 the 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 2005).

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 can not 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 males were signaling in a similar way with nest material, 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 that alloparents are predominantly male (Doutrelant et al. 2004; Doutrelant and Covas 2007). Future studies of cooperative nest construction in nature could examine whether the 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 phenomenon.

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. Accurate measures

of relatedness can now be obtained using contemporary methods such as RAD-tag sequencing (Peterson et al. 2012) and could describe a potential disparity in the indirect benefits the two sexes may be able to acquire.

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