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

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Abstract

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 observed cooperative nest construction and also recorded basic morphological characteristics. We also collected blood samples, performed next-generation sequencing, and isolated 2358 variable single nucleotide polymorphisms (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.

Keywords

Sociable weavers; Kin selection; Inclusive fitness; Tragedy of the commons; Cooperation

Introduction

The major transitions (Maynard Smith and Szathmáry 1995) in evolution rely on two concurrent features: first, cooperation among interacting individuals and, second, reduced 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. The communal resource can

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Data accessibility

All data from this work will be deposited into Dryad (<http://datadryad.org/>) upon acceptance of the manuscript.

facilitate the process of a major transition because it spatially coalesces the group (Bourke 2011a). 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), and recent phylogenetic evidence suggests that nests may be an important preadaptation for eusociality (Johnson Brian et al. 2013). 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 an individual living in a group with relatives can help propagate their own genes by helping the relatives reproduce and thus selecting for genes underlying cooperation (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 generation 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, can allow kin selection to drive the evolution and maintenance of behaviors that stabilize public goods (Queller and Strassmann 1998).

Recently, some have questioned the generality of kin selection (Wilson and Wilson 2007; Nowak et al. 2010), the methods used to model kin selection (Allen et al. 2013), or argued that the two methods answer different questions (Traulsen 2010). In particular, Nowak et al. (2010) argue that relatedness is often a by-product of sociality, that inclusive fitness models apply to few biological situations, and that communal nests themselves can drive the evolution of cooperation, though see Bourke (2011b) and Rousset and Lion (2011) for an assessment of inclusive fitness criticisms. Therefore, specific tests of the predictions of inclusive fitness models in novel systems where individuals live in communal nests will help resolve the criticisms of inclusive fitness theory.

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 4 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 communal nest as well as re-weaving material that is already present in the communal nest. The nest is composed of a superstructure that houses multiple, disparate chambers where groups of individuals roost at

night and use them for breeding during the breeding season (Maclean 1973). Individuals obtain thermal benefits from the communal nest by roosting in the nest chambers (van Dijk et al. 2013; Leighton and Echeverri 2014). The thermal benefits are provided to individuals simply by being in the group therefore qualifying the communal nest as a public good (Frank 2010). The cooperative nest construction of sociable weavers can be exploited by selfish individuals, thus exposing the nest to the tragedy of the commons (Hardin 1968). Throughout the rest of the article, we use the term “nest” to refer to the communal nest and colony when referring to the sociable weavers inhabiting a nest. We use the term “nest exterior” to refer to the outer layer of nest material.

Previous observations of sociable weaver behavior have found that construction of the exterior nest is male biased (Leighton 2014b), and Leighton (2014b) suggested that kin selection may partially explain the sex bias in cooperative nest construction. Indeed, van Dijk et al. (2014) used behavioral observations to classify individuals as those that built the exterior of the nest or did not build and determined whether individuals directed their exterior nest construction towards parts of the nest that housed related individuals. van Dijk et al. (2014) found that exterior nest construction was spatially associated with where relatives live in the nest, implicating indirect benefits as an important fitness component for the maintenance of this behavior. van Dijk et al. (2014) ceased recording behavior at a nest when behavioral observations did not seemingly provide more information on nest chamber residence or whether an individual was an exterior builder. This stopping rule allows one to categorize a large number of individuals as exterior builders and determine what factors influence the decision to build. However, the stopping rule does not allow for analysis of the magnitude of contribution to the nest exterior by those weavers that do build. We therefore combine extensive and detailed behavioral observations with estimates of relatedness to test inclusive fitness theory in sociable weavers.

To generate predictions about whether kin selection maintained cooperative nest construction, we identified an inclusive fitness model that incorporated important aspects of the life history of sociable weavers. The model by Johnstone and Cant (2008) incorporates sex-biased dispersal and group-wide helping behaviors and investigates the evolution and maintenance of group-wide cooperative behaviors. We confirm predictions of the model that have been reported in previous studies and perform tests of new hypotheses. Specifically, we tested in this population whether males will show higher relatedness than females as a result of female-biased dispersal (as suggested in Covas et al. 2006). Consequently, we predict that males in this population will show elevated cooperative nest construction (as reported in Leighton 2014b and van Dijk et al. 2014) due to the higher relatedness. Males, however, may also show elevated nest construction since simply because nest construction in other weaver species is also male biased (Collias and Victoria 1978; Quader 2006). We therefore also tested the additional prediction that relatedness would predict individual levels of investment in the construction of the nest at the level of the colony. We tested these hypotheses on a population of sociable weavers in Namibia.

Methods

Study species and field site

Sociable weavers are small passerines (25–30 g) endemic to semi-arid savannahs of South Africa, Botswana, 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 km 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 mm) 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). While we did not inspect all of the nest chambers, we did not hear any begging behavior from nestlings and therefore expect that there was little to no breeding during this time. We observed individuals during this time because investment in cooperative nest construction would not compete directly with raising offspring.

Behavioral observations

We measured the behavior of individuals at two nests (nest A and nest B) that are ~2.5 km apart. Sociable weavers often forage within 1 km of their nest of residence (GML, pers. obs.) and show between-nest differences in diet (Leighton and Echeverri 2015); we thus do not suspect there was considerable interaction between individuals from the two nests. 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 from the two nests. We banded 94 individuals from the nest A (estimated number of individuals in nest A ~125) and 33 individuals from the nest B (estimated number of individuals in nest B ~45). For all 127 individuals, we also had information on age, sex, and wing length. These two colonies have been banded annually or biennially for the last 12 years, and when a bird first receives a band, it is then designated as age 0. Although this is standard ornithological practice, we may underestimate the age of some individuals. 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 7 days of capture. Since some individuals were banded during the field season, we standardize cooperative measures based on the number of hours observed to allow for comparison among all individuals.

To record behaviors, we placed two hunting blinds ~5 m away from the nest and at a 180° angle from each other. The hunting blinds were ~1.5 m tall, ~1 m wide, camouflaged, and

left for at least 72 h at the nest of interest so that individuals at the nest could habituate to their presence. After acclimation, we recorded behavior in 3-h time blocks in the morning (between 08:30 and 11:30 hours) and afternoon (between 13:30 and 16:30 hours) at the focal nest. Since sociable weavers from the same colony leave in multiple foraging flocks over the course of the day (GML, 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 (relative to total time, including off the nest) individuals devoted to cooperative nest construction and (2) the total number of items individuals inserted into the nest superstructure. These behaviors have been described previously by Leighton (2014b). Although these measurements are associated, they are not perfectly correlated ($R^2=0.76$, calculated following Nakagawa et al. 2013), 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

We used sterile needles to draw ~50 μ L of blood from the brachial vein into a sterile heparinized capillary tube as is typical for birds of similar mass (van Dijk et al. 2014) and stored the blood in lysis buffer. We used styptic powder to stop bleeding along with sterile cotton pads. An individual's sex was determined genetically by extracting genomic DNA from 50 μ L of blood; to maximize genomic DNA yield, the proteinase K wash was extended from 24 to 48 h. The genomic DNA was amplified by the P2 and P8 primers developed by Griffiths et al. (1998) and the new P0 primer developed by 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 individuals from nest A and 17 individuals from nest B) random individuals were genotyped using genotype-by-sequencing (GBS) (Elshire et al. 2011), which was performed at the Cornell Institute for Genomic Diversity. The 40 individual samples used here were part of a larger population genomics study (Leighton et al., in review). 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 2358 SNPs that were successfully genotyped for each of the 40 individuals. The subset of SNPs was exported into Variant Call Format (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 relatedness (Thompson 1975) of individuals to the other members of their colony. To begin, we subset each of the colonies and then calculated pairwise relatedness of each individual to other individuals in their colony of residence. We then computed two measures for analysis. First, we counted the number of first-order relatives by summing the number of individuals related to the focal individual between $r=0.4$ – 0.6 to account for slight deviations away from the expectation of

0.5. We also took the mean relatedness of pairwise estimates to compile a summary relatedness variable in a second analysis. In contrast to van Dijk et al. (2014), we estimated relatedness of an individual to their colony of residence; in that study, relatedness was computed relative to a spatially expansive population of sociable weaver colonies. This assumes that the behavior of one individual could influence the reproduction of any other weaver in the large population. Since sociable weavers often forage within 1–2 km of their nest, if not closer (GML, pers. obs.), most weavers will compete over resources strongly with members of their own nest, rather than with weavers in other nests. Many weavers will likely never influence the gene pool of other nests outside of this radius. The appropriate reference population for calculating relatedness is the population of individuals a focal individual competes with for resources (West et al. 2002, 2006). This is the appropriate reference because individuals can only displace alleles or behavioral strategies from those individuals they compete with for resources (Grafen 1985). We argue the relatedness values presented here represent a biologically relevant estimate of relatedness.

Statistical analysis

The two cooperative variables, proportion of time devoted to cooperative nest construction and the number of items inserted into the nest, were standardized to allow for comparisons among all individuals. Specifically, we analyzed the amount of time devoted to cooperative nest construction as seconds/hour and we analyzed the number of items inserted as twigs/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 a 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. The model controls for the effect of other fixed factors when estimating the effect of a focal fixed factor. For individuals with genetic data, we used the SNP data to estimate relatedness for the subset of individuals, and we included relatedness as a predictive variable in a second analysis. We fit GLMMs with an 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 Akaike information criterion (AIC) values of the full model with the model with a focal variable removed, and variables that improved the fit of the model by $\Delta AIC > 2$ 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 of the cooperative measures 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 in central Namibia.

Results

Full data set

Cooperative nest construction was observed for 299 h, yielding 2741 observations. One “observation” is the nest construction output of an individual over a 3-h block. We included 127 individuals in the study, and following the standard calculations for repeatability (Lessells and Boag 1987), we found that the repeatability for the proportion of time devoted to cooperative nest construction between observation blocks was $r=0.33$ and 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).

Males devoted a significantly higher proportion of time to cooperative nest construction than females (Fig. 1a; Table S1). Similarly, we find that males insert significantly more items into the nest superstructure relative to females (Fig. 1b; Table S2). For both variables, sociable weavers perform more cooperative nest construction in the morning than in the afternoon (Tables S1 and S2). None of the other predictive variables, i.e., wing length, age, nest of residence, or temperature, were significantly associated with cooperative output.

Subset of individuals with relatedness estimates

We used the 2358 variable SNPs to calculate the mean pairwise relatedness of each individual to their colony of residence. As expected, there was a distribution of relatedness values between 0 and 0.5 for each individual (Fig. S1). The average pairwise relatedness of all individuals to their colony of residence was 0.09 ± 0.004 (SE). For the individual sexes, males had a higher relatedness to their colony (0.092 ± 0.01) than females (0.079 ± 0.009), though this was not significantly higher than females ($t=1.53$, d.f.=35.3, $p=0.13$, Fig. 2). However, if we remove the most extreme female outlier (see upper circle in Fig. 2 in females), then males do have significantly higher relatedness ($t=2.06$, d.f.=31.2, $p=0.04$).

When mean relatedness was included as a predictor variable for the subset of individuals ($n=40$ individuals, 18 females and 22 males), we find that relatedness significantly and positively predicted both the proportion of time an individual devoted to cooperative nest construction and the number of items inserted into the nest (Fig. 3; Tables S3 and S4). We

also tested the number of direct relatives (to be conservative, a direct relative was an individual with a relatedness value between 0.4 and 0.55) as a predictive variable but dropped this variable from the analysis as mean pairwise relatedness explained more variance (Fig. S2). 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 (Table S3). In contrast, after accounting for relatedness and part of the day, none of the remaining variables (wing length, age, nest of residence, mass, or temperature) significantly explained variation in the data for the proportion of time individuals spent cooperatively constructing the nest (Table S3). 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 after controlling for other variables (Table S4).

Discussion

That relatedness positively predicts both the proportion of time invested in cooperative nest construction and the number of items inserted into the nest suggests indirect benefits are a necessary fitness component of the behaviors (Fig. 3). Indeed, since the nest loses material over time (GML, 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. As predicted by Johnstone and Cant (2008), and previously documented by Leighton (2014b) and van Dijk et al. (2013), we find a male bias in nest construction (Fig. 1). With respect to spatial structuring in nest construction, van Dijk et al. (2014) found that sociable weavers direct nest construction towards areas of the nest with a higher concentration of relatives, and we also find that individuals spatially direct nest building to certain parts of the nest (Fig. S3). We extend these results by testing whether relatedness predicts cooperative nest construction. We find a significant, group-wide relationship between genomic relatedness and nest construction in our population (Fig. 3). We argue that we find this trend because we collected more detailed behavioral measurements compared to previous studies in sociable weavers and because we utilize relatedness estimates that reflect the relevant reference group (West et al. 2002, 2006). In sum, sociable weavers not only direct cooperative nest construction to parts of the nest with kin (van Dijk et al. 2014) but also adjust their exterior nest construction output based on the extent of their relatedness to individuals in the nest (Fig. 2).

Leighton (2014b) suggested that sex-biased cooperative nest construction may also be partially maintained if the direct benefits of group augmentation were biased towards males. We find evidence for this hypothesis; specifically, after controlling for relatedness, there is still a male bias in the number of items inserted into the nest. Indeed, sociable weavers likely receive direct benefits from nest construction; this finding is similar to work in meerkats (*Suricata suricatta*), where females are the philopatric sex and show female-biased cooperation in behaviors that increase the recruitment of offspring to the group (Clutton-Brock et al. 2002).

The low overall relatedness values suggest that while sociable weavers maintain complex societies, they do so with considerable conflict (Rat et al. 2015) and competition within the

groups, similar to some other vertebrate societies (Clutton-Brock et al. 2001; Connor 2010; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). However, sociable weaver colonies likely harbor more competition and less cooperation than certain eusocial insects (Hölldobler and Wilson 1990) and certain multicellular societies (Strassmann and Queller 2011). Insect and multicellular societies likely harbor more cooperation because both monogamy (Hughes et al. 2008) and single-cell bottlenecks (Fisher et al. 2013) 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 colonies (Covas et al. 2006) that likely depresses relatedness compared to other, more cooperative, societies.

There are other possible explanations for the male-biased nest construction. For example, nest construction could be used as a sexual signal by individuals, as has been suggested for cooperative feeding in sociable weavers (Doutrelant and Covas 2007). Using nest construction as a signal, however, seems unlikely. First, similar 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 that many individuals from both sexes do not breed during a breeding season. The limited breeding spots would lead to selection in both sexes, and since selection can drive the evolution of shared traits between the sexes (Price and Whalen 2009), we would expect the trait to be similar between the sexes if it was being used as a sexual signal (Rubenstein and Lovette 2009). However, we find that the trait is strongly sex-biased (Fig. 1), suggesting that selection is maintaining the trait in male sociable weavers alone. 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. Though it is possible that sociable weavers use nest construction as a sexual signal, it seems unlikely given previous research on sexual selection.

There are also alternative explanations for the association between relatedness and nest construction output. First, individuals may not breed and build until they are older, possibly leading to a correlation between age and relatedness. Neither van Dijk et al. (2014) nor this study found a relationship between age and relatedness, and we therefore find this hypothesis unlikely. A second alternative explanation for the relationship between relatedness and cooperative output is that high-quality individuals can invest in both nest construction and large families. The association between relatedness and nest construction would therefore be an indirect relationship that was caused by selection for individuals to produce large families while also investing in nest construction. This explanation is plausible because of potential positive feedback; specifically, individuals that invest in nest construction can increase thermal buffering (Leighton and Echeverri 2014), leading to increased energy savings which can then be routed to both reproduction and nest construction. Increased reproduction of high-quality relatives would therefore lead to groups of high-quality individuals in central nest locations (van Dijk et al. 2013) that also invest in nest construction. Although individuals in this scenario are not adjusting cooperative output based on the number of relatives, individuals would still gain both direct and indirect benefits and would therefore be maximizing inclusive fitness (West and Gardner 2013).

Studies that find significant relationships between cooperative output and relatedness are rare. While some studies find that individuals adjust behavior based on relatedness, e.g., (Wright et al. 2010), other studies have found no relationship between relatedness and cooperative output (Canestrari et al. 2005; Napper et al. 2013) and, rarely, a negative relationship between relatedness and cooperative output (Zottl et al. 2013). However, when the results from this study are paired with the finding that nest construction is also spatially directed towards relatives (van Dijk et al. 2014), we find that the evidence strongly suggests indirect benefits are important for the evolutionary maintenance of cooperative nest construction in sociable weavers.

Here, we show that genomic relatedness significantly predicts cooperative nest construction in sociable weavers. The results suggest that 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Fig. 1.

a Boxplot comparing the cooperative output of sexes in sociable weavers. Males devote significantly more time to cooperative nest construction than females. **b** Boxplot comparing the cooperative output of sexes in sociable weavers. Males insert significantly more items into the nest exterior 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× the inter-quartile range from an edge of the box) are plotted as *circles*

Fig. 2.

Boxplot of mean pairwise relatedness to colony of residence. Pairwise relatedness estimated by computing relatedness of a focal individual to their colony of residence. 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× the inter-quartile range from an edge of the box) are plotted as *circle*

Fig. 3.

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 exterior 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