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## Original Article

# More than kin: subordinates foster strong bonds with relatives and potential mates in a social bird

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Social interactions shape relationships between individuals in complex societies. Affiliative interactions are associated with benefits and strengthen social bonds, while aggressive interactions are costly and negatively affect social bonds. Individuals may attempt to reduce aggressive encounters through submissive displays directed at higher-ranking individuals. Thus, fine-scale patterns of affiliative, aggressive, and submissive interactions may reflect costly and beneficial social relationships within groups, providing insight into the benefits of group living and the mechanisms of conflict resolution. So far, however, most studies have looked at social interactions and benefits of group living in isolation. We investigated how the strength of social bonds (affiliative vs. aggressive interactions) and submissive displays varied with kin-selected and potential mating benefits, and with reproductive conflict in the cooperatively breeding purple-crowned fairy-wren, *Malurus coronatus*. Our results revealed that subordinates formed equally strong social bonds with kin and potential mates (unrelated opposite-sex individuals) while they formed antagonistic relationships with reproductive competitors that offered no kin-selected or mating benefits (unrelated same-sex individuals). Submissive displays were directed exclusively at same-sex breeders, regardless of relatedness. Affiliation and submission were associated with reduced foraging time when food was limited, indicating a cost to maintaining positive relationships. Together, our results suggest that the strength of social bonds is determined by (potential) benefits obtained from group members, while submission likely serves to reduce conflict. Our findings highlight the importance of time-costly social interactions for maintaining relationships with group members, providing insight into how social groups of individuals with (partly) divergent interests can remain stable.

**Key words:** affiliation, cooperative breeding, group living, social interactions, submission, aggression.

## INTRODUCTION

In complex societies, like those of humans and other group-living animals, individuals establish and maintain relationships, such as pair-bonds, alliances, and dominance hierarchies, by repeated social interactions (Hinde 1976; Silk et al. 2006; Kutsukake 2009; Gill 2012). Such social interactions, and the resulting social relationships, can be beneficial or costly in nature. Affiliative interactions (e.g., allogrooming, resting in contact) can provide benefits to the individuals involved, such as hygienic or thermoregulatory benefits (Hart et al. 1992; Sanchez-Villagra et al. 1998; McKechnie

and Lovegrove 2001; Radford and Du Plessis 2006; Villa et al. 2016) and reduction of stress, for both the recipient and the actor (Aureli et al. 1999; Detillion et al. 2004; Sapolsky 2005; Lewis et al. 2007; Shutt et al. 2007; Radford 2008; Sapolsky 2011; Ueno et al. 2015). Aggressive interactions on the other hand are associated with immediate costs to both parties involved, through time and energy expenditure, risk of injury, and elevated stress (Rovero et al. 2000; Petit 2010). Together, these interactions largely determine the nature of social relationships between group members. Affiliative interactions can strengthen social bonds between particular group members (Silk et al. 2006; Silk et al. 2009; Massen et al. 2010; Petit 2010; Gill 2012; Kenny et al. 2017). Conversely, although aggression can be a tool for negotiation, and save time and energy in the long-term by establishing and maintaining dominance hierarchies

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(De Waal 2000), aggressive interactions can have a long-lasting negative effect on social relationships, especially in societies where reconciliation after aggression is uncommon (De Waal 2000; Kutsukake and Clutton-Brock 2008). In addition, individuals may strategically use a third type of interaction, namely submissive displays, in an attempt to minimize negative relationships with group members; submission conveys the nonagonistic intentions of one individual to another, and may reduce the probability—and cost—of subsequently receiving aggression from others (Deag and Scott 1999; Flack and De Waal 2007; Petit 2010). Thereby, submissive displays may contribute to the stability of groups containing competitors for vital resources like food and reproduction.

Strong social bonds themselves are ultimately often associated with fitness benefits such as improved offspring survival and earlier onset of reproduction (Silk et al. 2009; Massen et al. 2010; Charpentier et al. 2012; Seyfarth and Cheney 2012). Therefore, fine-scale patterns of social interactions may reveal costs or benefits of social relationships. Both costly and beneficial social interactions are not random but instead take place mostly between particular individuals, to protect resources or to secure benefits. For example, generally, affiliative interactions are more common and aggressive interactions less common between related compared to unrelated individuals (e.g., Sanchez-Villagra et al. 1998; Kutsukake and Clutton-Brock 2006b; Silk et al. 2006; Dickinson et al. 2009; Chiarati et al. 2011; Charpentier et al. 2012; Napper et al. 2013; Viblanc et al. 2016), and between individuals of the opposite sex compared to individuals of the same sex (Seibert and Crowell-Davis 2001; Dickinson et al. 2009; Kutsukake 2009; Mitchell et al. 2009; Dey and Quinn 2014, but see Chiarati et al. 2011).

In complex avian societies in particular (e.g., cooperative breeders), groups may consist of a mix of kin and nonkin of either sex (regularly so in 30% of species; Riehl 2013). In such species, potential benefits of group living include kin-selected benefits (e.g., indirect fitness benefits from helping relatives; Hamilton 1964; Koenig & Dickinson 2016), benefits from parental nepotism (e.g., access to food, increased survival; Ekman et al. 2000; Kraaijeveld and Dickinson 2001; Kokko and Ekman 2002; Ekman et al. 2004; Griesser et al. 2006; Kingma et al. 2016), and reproductive benefits such as inheriting a breeding position or finding a mate within the group to establish a new breeding territory (Koenig et al. 1992;

Emlen 1994; Ekman et al. 2004; Kingma 2017). Since strong social bonds can improve the fitness of individuals involved (Silk et al. 2009; Charpentier et al. 2012), bonds with kin and potential mates are expected to provide the greatest potential benefits, whereas antagonistic and submissive behaviors are predicted to mainly occur between nonkin that may additionally be competitors for reproduction.

Here, we test whether social interactions match these predictions in the purple-crowned fairy-wren, *Malurus coronatus* (Table 1). In this cooperatively breeding passerine, many groups are a mix of related and unrelated group members of both sexes (Kingma et al. 2010; Kingma et al. 2011). Subordinates may benefit from being in a group with relatives if they increase their inclusive fitness by helping to raise related offspring and improving survival of parents, or through parental nepotism (Kingma et al. 2010; Kingma et al. 2011). In addition, unrelated opposite-sex group members represent potential current or future mates, whereas competition between same-sex individuals over breeding opportunities is high. Consequently, we predict that social bonds are strongest between related opposite-sex individuals (kin-selected benefits and benefits of parental nepotism) and unrelated opposite-sex group members (mating benefits), followed by related same-sex group members (that provide benefits of kin selection and parental nepotism but may also be in competition over reproduction), and weakest among unrelated same-sex individuals (reproductive competition; Table 1). We further predict that submissive displays will be targeted most at same-sex breeders (i.e., dominants; dominance is established by the fact that only dominant breeding pairs sing duets: Hall and Peters 2008, 2009). Since aggression is expected to be more likely between unrelated compared to related same-sex group members (no kin-selected benefits or nepotism to offset reproductive conflict), we expect rates of submission to be higher between these to minimize aggression received. We tested these predictions using behavioral observations of social interactions (affiliation, aggression, submission) of subordinate individuals with their group members. Time budgets were also quantified to investigate the impact of social interaction on time available for foraging. Together, these results enhance our understanding of the role social interactions may play in establishing relationships between particular group members and potential costs and benefits associated with this, which may

**Table 1**

**Predictions of social bond strength (relative occurrence of affiliation and aggression) and submission between group members, and whether these were supported in the purple-crowned fairy-wren (pcfw)**

Type of group member	Kin-selection/ nepotism benefit? <sup>a</sup>	Mating benefit? <sup>b</sup>	Reproductive conflict?	Predictions	Sample size (# dyads)	Predictions supported in pcfw?
Related, same-sex	Yes	No	Yes	1. Medium strength social bond	52	Partially <sup>c</sup> Yes <sup>d</sup>
				2. Intermediate level of submission directed at higher-ranked individuals	26	
Related, opposite-sex	Yes	No	No	1. Strong social bond	37	Yes Yes
				2. No or low level of submission directed at higher-ranked individuals	15	
Unrelated, same-sex	No	No	Yes	1. Weak/absent social bond	20	Yes Yes <sup>d</sup>
				2. Highest level of submission directed at higher-ranked individuals	12	
Unrelated, opposite-sex	No	Yes	No	1. Strong social bond	35	Yes Yes
				2. No or low level of submission directed at higher-ranked individuals	23	

Predictions are based on the balance of benefits and costs of group living according to relatedness and sex of individuals they may interact with, assuming that reproductive conflict may (partially) negate benefits.

<sup>a</sup>Kingma et al. 2010; Kingma et al. 2011; <sup>b</sup>Kingma et al. 2011; Kingma et al. 2013; <sup>c</sup>similar affiliation index as for related and unrelated opposite-sex group members; <sup>d</sup>but note that the predicted difference in submission towards related and unrelated same-sex dominants is not significant in the analyses (see Figure 3).

ultimately provide insight into how social groups and relationships remain stable.

## METHODS

### Study site and species

Purple-crowned fairy-wrens are small insectivorous birds endemic to northern Australia, where they inhabit riparian vegetation (Rowley and Russell 1993; Skroblin and Legge 2010). Territories are aligned linearly along the rivers, and boundaries and groups are stable year-round and across years (Hall and Peters 2008; Kingma et al. 2011). Breeding can take place year-round but peaks in the monsoonal wet season (December to March) (Hall and Peters 2009; Kingma et al. 2012). A strength of our study system is that only the dominant breeding pair engages in duets (Hall and Peters 2008, 2009), providing a reliable cue to assign breeder (dominant) or subordinate status to each individual independent of submissive or aggressive interactions. Subordinate individuals of both sexes can help the breeding pair raise offspring (Kingma et al. 2010; Kingma et al. 2011). Due to breeder turnover and immigration into the group, many groups are composed of related and unrelated group members of both sexes (57% of groups with subordinates for the current study period; Kingma et al. 2010; Kingma et al. 2011). Subordinate individuals benefit from sharing a group with unrelated opposite-sex individuals (potential mates); although subordinate individuals never reproduce independently and rarely gain parentage (Kingma et al. 2009), they sometimes sire offspring if they are unrelated (7% of broods), but never if they are related, to the opposite-sex breeder (Kingma et al. 2011). Increased sperm production by such subordinates compared to related subordinates suggests that they are potential competitors for the breeding male (Kingma et al. 2012). In addition, subordinates that are unrelated to the opposite-sex breeder have higher chances of inheriting the breeding position when the same sex breeder dies or disappears (Kingma et al. 2011), and approximately 16% of subordinates gain their first breeding position this way (Hidalgo Aranzamendi et al. 2016). Subordinates may also pair with an unrelated subordinate group member of the opposite sex and bud off a new territory from their original territory (approximately 6% of subordinates gain their first breeding position this way; Hidalgo Aranzamendi et al. 2016). The benefits of acquiring a territory and an unrelated mate are substantial, as breeding vacancies are rare and the cost of inbreeding is high (Kingma et al. 2013).

We studied a color-banded population of approximately 250 purple-crowned fairy-wrens along Annie Creek and the Adcock River at Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (S17°31' E126°6') that has been monitored since 2005. Groups were observed year-round and all offspring banded as nestlings until 2010. From 2011, the population was monitored in 2 visits per year (May/June and November) and all unbanded birds (new offspring and immigrants from outside the core population) were banded (for details see Hidalgo Aranzamendi et al. 2016). From 2016, the population was additionally monitored during the main breeding season (February to April), using the same methods as in 2005–2010.

### Behavioral observations

To study the frequency of social interactions between group members, we conducted behavioral observations where one observer (NT) followed individually color-banded subordinates ("focal

individual,"  $n = 25$  males and 15 females, average age 1.9 years, range: 0.6–5.0) from 23 groups (all consisting of a breeding pair with 1–4 subordinates, and 0–4 fledglings). Each focal individual was followed and observed until it had been in sight for approximately one hour (mean  $\pm$  SE =  $60 \pm 1$  min; total time followed including time out of sight =  $115 \pm 5$  min). One or 2 focal observations were conducted per individual (mean = 1.2); if birds were observed twice, observations took place in different seasons. Focal observations took place during the dry season (May to June 2014 and 2016;  $n = 23$  and  $n = 12$  focal observations, respectively), when almost all birds had completed breeding, and during the wet season of 2016, when most groups were breeding (February to April;  $n = 14$  focal observations); focal observations were not conducted if a nest with nestlings was present. All observations took place during the morning (5:50–11:00 am), when bird activity is highest, during calm, dry weather. The observer was blind to the relatedness of individuals in the group, but not to the sex of adults (which are sexually dichromatic). The individual to be observed was determined before the start of observations, to avoid any bias towards individuals that may be easier to follow. At the time we conducted behavioral observations, many groups had unbanded dependent fledglings (i.e., <3 months old) that were subsequently captured for banding and blood sampling. Genetic relationships of all individuals were confirmed by genotyping (for details see Hidalgo Aranzamendi et al. 2016) and were identical to social relatedness; individuals classified as "related" in our study were first-degree relatives (full sibling, parent-offspring; the 55 dyads considered unrelated included 5 half-siblings from different broods).

### Focal animal continuous sampling (social interactions)

All interactions that took place between the focal individual and each of the other group members (i.e., a dyad,  $n = 144$  dyads excluding fledgling group members) were recorded onto a voice activated sound recorder. This included aggressive interactions (chasing, physical attacks), submissive displays (characterized by bill-gaping and shivering of the wings), and affiliative interactions, which included allopreening and contact-sit (i.e., sitting closely side by side, (almost) touching, often while self-preening; see Figure 1) (Boucherie et al. 2016). Allopreening by definition involves contact-sit. Both these behaviors are considered good indicators of the strength of social bonds in other species (Cords 1997; Silk et al. 2006; Silk et al. 2009; Massen et al. 2010; Boucherie et al. 2016; Kenny et al. 2017). Affiliative and aggressive interactions were recorded during all observations, while submissive displays were recorded in 2016 only. The proportion of time birds were seen (i.e. total time seen/total time followed including out of sight) did not affect whether affiliative interactions (generalized linear mixed model with Territory ID and Bird ID as random effects;  $z = 0.79$ ,  $P = 0.43$ ), aggressive interactions ( $z = 0.05$ ,  $P = 0.96$ ), or submissive displays ( $z = 0.29$ ,  $P = 0.77$ ) were observed during an observation.

### Focal animal instantaneous sampling (time budget)

Throughout each observation, the time budget of the focal subordinate was obtained by recording its behavior every 30 s while it was in sight. Behaviors included: foraging, resting, self-preening, flying, singing, and interacting with group members (aggressive, affiliative, submissive behavior).

### Statistical analyses

All analyses were performed in R, version 3.3.2 (R Core Team 2017). For each dyad (i.e., each combination of focal subordinate



**Figure 1**

Affiliative interactions involve (a) contact-sit, where 2 birds sit in close proximity, and (b) allopreening. Photos by Niki Teunissen/Australian Wildlife Conservancy.

and each of its group members), we determined relatedness (unrelated/first-order relative) and sex (same/opposite) of the 2 individuals, and whether any affiliative interactions, aggressive interactions, and submissive displays were observed between them. Presence/absence of social interactions was used rather than frequencies since all types of social interactions were relatively uncommon (affiliative interactions: mean =  $0.61 \pm 0.12$  per dyad per focal observation; aggressive interactions: mean =  $0.05 \pm 0.03$  per dyad per focal observation; submissive displays: mean =  $0.39 \pm 0.16$  per dyad per focal observation). For each focal subordinate the data consisted of  $x-1$  dyads for groups of size  $x$ ; in all analyses we corrected for this replication across focal individuals by including its identity (Bird ID) nested within Territory ID as a random term in the models. As some groups contained unbanded (and thus not individually recognizable) fledglings at the time of observation, all potential interactions with fledgling group members ( $n = 21$  individuals) were not included in analyses. We assessed seasonal differences by including one factor (“season”) with 3 levels (dry 2014, dry 2016, wet 2016).

We used a composite index of affiliation (relative affiliative vs. aggressive behavior) as an indicator of social bond strength. The relative frequency of affiliative versus aggressive interactions between 2 individuals is generally assumed to be a good measure of the strength of their social bond, since repeated affiliative interactions result in strong social bonds, whereas aggressive interactions negatively affect social bonds (Silk et al. 2006; Lewis et al. 2007; Kutsukake and Clutton-Brock 2008; Silk et al. 2009; Massen et al. 2010). Moreover, due to the rarity of these interactions in our data, combining interactions rather than analyzing them in isolation allowed for more robust statistical testing (see also Silk et al. 2006, 2009 for similar rationale). We computed the affiliation index by combining the occurrence of affiliative and aggressive interactions within dyads, giving each type of interaction equal weighting but opposite effects; a positive value of 1 was assigned if one or more affiliative interactions (allopreening or contact-sit) were observed between 2 individuals, and a negative value of 1 if one or more aggressive interactions were observed, giving a value of  $-1$ ,  $0$ , or  $1$  for each dyad. To test the hypothesis that the strength of social bonds is predicted by the relative balance of nepotism, kin-selected and mating benefits, and reproductive conflict, we included relative sex of both interacting individuals (same, opposite), relatedness of both interacting individuals (unrelated, related), and their interaction. We used a cumulative link mixed model (CLMM) with the ranked ( $1 > 0 > -1$ ) composite index of affiliation per dyad as the dependent

variable using the package “ordinal” (Christensen 2015). The explanatory variables further included sex of the focal subordinate (male, female), status of the interacting individual (subordinate, breeder), group size (since there may be a saturation effect in larger groups) and season (dry 2014, dry 2016, wet 2016). Qualitatively similar results were obtained from separate statistical models for the occurrence of allopreening, contact-sit, and aggressive interactions, respectively (see Supplementary Material I). Although the interacting effect of relative sex and relatedness on affiliation index may differ for males and females, or vary with subordinates’ relatedness to the opposite-sex breeder (since subordinate sex and relatedness to breeders may for example influence the chance of inheriting a breeding position, or the extent of competition; Kingma et al. 2011, 2012), our sample size did not allow for the inclusion of such 3-way interactions in our analyses.

The occurrence of submissive displays during observations was only recorded for the wet and dry season of 2016 ( $n = 76$  dyads) and analyzed separately. Since no submissive displays were directed at subordinate or opposite-sex group members (i.e., complete separation of the data; Figure 3), violating the assumption of homogeneity of variance, we fitted a generalized linear mixed model (GLMM) using Markov chain Monte Carlo (MCMC) techniques from the MCMCglmm package (Hadfield 2010, 2014), to analyze the effect of season (dry and wet 2016 only), status, sex and relatedness on the occurrence of submissive displays. This model included the presence/absence of submissive displays as a categorical response variable with the logit link. Relative sex (same/opposite) and relatedness (related/unrelated), as well as the interaction between them, and the main effects of sex of the focal bird, status of the second bird and season were included as fixed variables. Following the recommendations of Hadfield (2014), the residual variance was fixed at 1, and a Gelman prior with a scale of  $\sigma^2 + \pi^2/3$  was used for the fixed effects, to deal with the issue of complete separation (Gelman et al. 2008). For the random factors, a parameter-expanded prior with a Cauchy distribution ( $V = 1$ ,  $\nu = 1$ ,  $\alpha \cdot \mu = 0$ , and  $\alpha \cdot V = 25^2$ ) was used, as this prior puts less density on values close to zero. The chains were run for 11,000,000 iterations, with a thinning interval of 10,000, and a burn-in interval of 1,000,000, resulting in a sample size of 1000. Visual inspection of the time series and posterior density plots of the parameters confirmed convergence of the model, and the autocorrelation plots of the fixed and random effects showed no sign of autocorrelation. We present posterior mean, 95% credible interval (CI) and  $P$ -values. A similar model was used to test for a correlation between submissive displays and

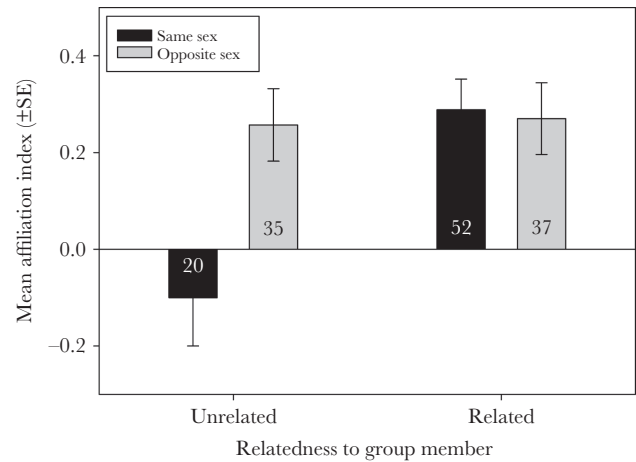
aggressive interactions within dyads, with the presence/absence of submissive displays as response variable and the presence/absence of aggressive interactions as fixed variable. All other model parameters were the same.

We investigated whether there was a trade-off between birds' time allocation to foraging and interacting with group members by testing if engaging in affiliative or aggressive interactions or submissive displays was related to foraging time. In addition, we tested whether this trade-off might vary between the seasons because food availability is much higher during the wet season (Hidalgo Aranzamendi 2017) and this may reduce time budget constraints. We ran generalized linear mixed models with the proportion of time spent foraging as binomial response variable (using the *c*-bind function). The presence/absence of affiliative interactions, the start time of the observation (to control for diurnal variation in time allocation), season (dry 2014, dry 2016, wet 2016), and the 2-way interaction between season and the other 2 variables, were included as fixed effects. We constructed identical models with the presence/absence of aggressive interactions and the presence/absence of submissive displays as independent variables to test for their effect on time allocated to foraging.

## RESULTS

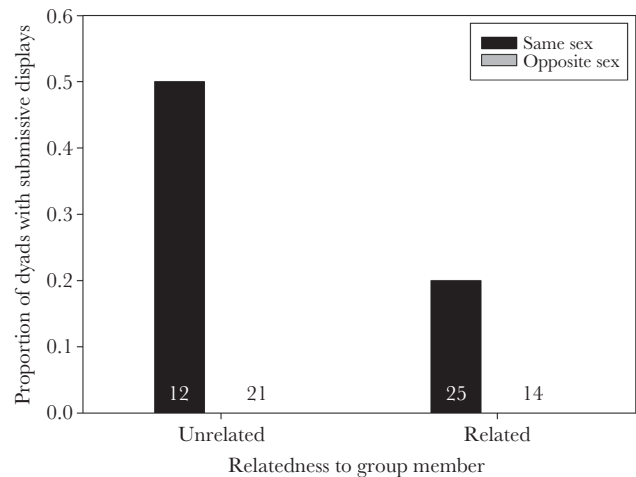
The affiliation index did not differ depending on whether focal subordinates were interacting with subordinate or breeder (dominant) group members (no effect of status; CLMM:  $\beta \pm SE = 0.20 \pm 0.48$ ,  $z = 0.42$ ,  $P = 0.68$ ), nor did it differ with group size ( $\beta \pm SE = -0.19 \pm 0.28$ ,  $z = -0.67$ ,  $P = 0.50$ ), or between male and female subordinates ( $\beta \pm SE = 0.54 \pm 0.51$ ,  $z = 1.04$ ,  $P = 0.30$ ). The effect of relative sex (same/opposite) on the affiliation index depended on relatedness (unrelated/related) of the dyad (interaction term:  $\beta \pm SE = 3.11 \pm 1.33$ ,  $z = 2.35$ ,  $P = 0.02$ ; Figure 2). Subordinates interacting with related group members had a positive mean affiliation index regardless of the sex of the group member (mean affiliation index = 0.29 for same-sex dyads; 0.27 for opposite-sex dyads; Figure 2). In contrast, when subordinates were unrelated to a group member, interactions were more affiliative in opposite-sex dyads (mean affiliation index = 0.26), and more aggressive in dyads of the same sex (mean affiliation index = -0.10; Figure 2). The frequency of affiliative relative to aggressive interactions differed between seasons, with a higher mean affiliation index during the resource-rich wet season (2016) than the dry season of 2014 ( $\beta \pm SE = 1.62 \pm 0.53$ ,  $z = 3.07$ ,  $P < 0.01$ ). Mean affiliation index did not differ significantly between the dry season of 2014 (mean  $\pm SE = 0.68 \pm 0.46$ ) and 2016 (mean  $\pm SE = 1.75 \pm 0.56$ ), nor between the dry season of 2016 and the wet season of 2016 (mean  $\pm SE = 2.30 \pm 0.55$ ).

Subordinates always directed their submissive displays at breeders (never to other subordinates), with submissive displays recorded for 21% of subordinate-breeder dyads (MCMCglmm, effect of status: posterior mean = -5.02, 95% CI = -9.51 to -0.71,  $P < 0.01$ ,  $N = 76$  dyads). Furthermore, submissive displays were directed only at same-sex breeders (effect of relative sex: posterior mean = 6.80, 95% CI = 2.83–11.78,  $P < 0.01$ ; Figure 3). Though submissive displays were recorded more often for unrelated (50% of 12 dyads) compared to related same-sex group members (19% of 25 dyads; Figure 3), we did not detect a significant interaction between relative sex and relatedness (posterior mean = -0.12, 95% CI = -5.74–5.09,  $P = 0.96$ ) or a main effect of relatedness (posterior mean = -1.85, 95% CI = -7.07–2.93,  $P = 0.49$ ). The



**Figure 2**

Variation in dyadic affiliation indices according to relative sex and relatedness of focal subordinates to other group members. Numbers represent total number of dyads in each category.



**Figure 3**

Proportion of dyads for which submissive displays by the focal subordinate were observed during a focal observation according to relative sex and relatedness to group members. Absent bars for opposite-sex dyads reflect the absence of any submissive displays for these. Numbers represent total number of dyads in each category.

occurrence of submissive displays did not differ between male and female subordinates (posterior mean = 1.77, 95% CI = -1.47–5.34,  $P = 0.25$ ), nor with group size (posterior mean = -1.19, 95% CI = -3.30–1.06,  $P = 0.28$ ), or between seasons (posterior mean = 0.63, 95% CI = -1.72–3.09,  $P = 0.62$ ). The occurrence of submissive displays was positively correlated to aggression in dyads (posterior mean = 12.35, 95% CI = 2.43–24.57,  $P < 0.01$ ); for every dyad in which aggression occurred, submissive behavior was also observed—focal subordinates were always submissive while the other member of the dyad (always a breeder) was aggressive—whereas for dyads where no aggression occurred, submissive behavior by the focal bird was observed in 11% of dyads. Most (82%) of submissive displays involved subordinates submitting spontaneously to an approaching breeder, with the remaining 18% (5/28) recorded in reaction to breeder aggression (i.e., <1 min post-aggression). Aggression followed spontaneous submission in only

9% (2/23) of cases, whereas 71% (5 of 7) of aggressive interactions were directed at nonsubmitting individuals. Within dyads, if subordinates submitted to the breeder immediately (<1 min) after aggression, aggression reoccurred in the same focal observation in only 1 of 4 cases, whereas aggression reoccurred in 2 of 3 cases when the subordinate did not submit to the dominant postaggression.

In the dry seasons birds spent a far greater proportion of time foraging overall ( $89.8 \pm 1.1\%$ ) compared to the wet season ( $71.3 \pm 2.7\%$ ) (Tukey's post hoc test:  $\beta \pm SE = 1.36 \pm 0.14$ ,  $z = -9.59$ ,  $P < 0.01$  and  $\beta \pm SE = 1.17 \pm 0.12$ ,  $z = -9.91$ ,  $P < 0.01$  for dry 2014 and dry 2016, respectively, foraging time between dry 2014 and dry 2016 did not differ:  $\beta \pm SE = 0.19 \pm 0.16$ ,  $z = -1.23$ ,  $P = 0.43$ ). Engaging in affiliative interactions was associated with less time spent foraging, depending on the season (GLMM, interaction term:  $\chi^2 = 12.34$ ,  $df = 2$ ,  $P < 0.01$ ): during both dry seasons, individuals spent less time foraging if they engaged in at least one affiliative interaction during an observation, while during the wet season, individuals spent the same (relatively lower) amount of time foraging regardless of whether they engaged in affiliative interactions (Figure 4a). A similar effect on foraging time was found for the interaction between season and submissive displays ( $\chi^2 = 7.90$ ,  $df = 1$ ,  $P < 0.01$ ; Figure 4b), but the occurrence of aggressive interactions was unrelated to time spent foraging ( $\chi^2 = 0.36$ ,  $df = 1$ ,  $P = 0.55$ ), regardless of season (interaction term:  $\chi^2 = 3.08$ ,  $df = 2$ ,  $P = 0.21$ ). For full details on time budget analyses, see Supplementary Material II.

## DISCUSSION

We predicted that fine-scale patterns of affiliative and aggressive interactions between group members would reflect direct (current or future mating opportunities, benefits of parental nepotism) and indirect (kin-selected) benefits and reproductive conflict associated with being part of a social group (Table 1). In support of this prediction, we report a positive affiliation index between subordinate purple-crowned fairy-wrens and their related and opposite-sex unrelated group members, but a negative affiliation index between unrelated same-sex group members, indicating more aggression

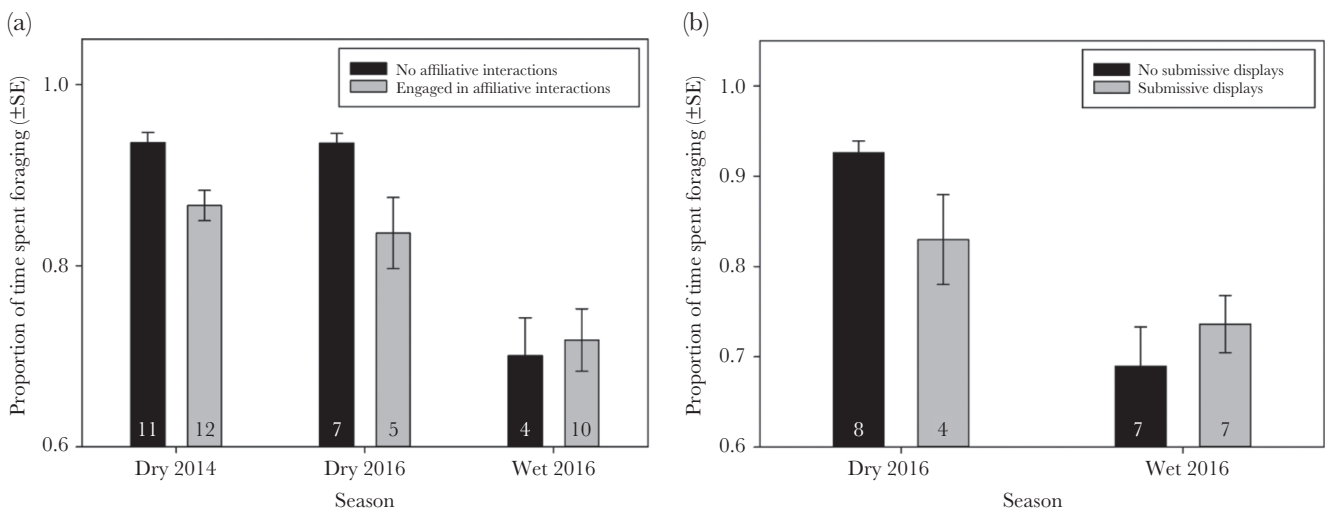
and less affiliation between the latter. Furthermore, subordinates directed submissive displays at same-sex dominant breeders only, in line with predictions that this behavior serves to reduce reproductive conflict. Engaging in submissive or affiliative interactions was associated with decreases in time spent foraging during the dry season (when food availability is low) but not the wet season (when less time is spent foraging). Below, we discuss the implications of these findings.

### Social bonds and benefits

Our findings support the prediction that subordinates form stronger social bonds with group members that may provide benefits, be they kin-selected or potential mating opportunities. Strong social bonds with kin can result in kin-selected fitness benefits through improved survival or reproduction of kin, as well as benefits from nepotism (Ekman et al. 1994, 2000; Kokko and Ekman 2002; Silk et al. 2009; Charpentier et al. 2012). Strong social bonds with potential mates can improve the likelihood of a future breeding partner being alive and/or in good condition once an opportunity arises to take up a breeding position or to establish together as a breeding pair (see e.g., Kingma et al. 2014), or can facilitate access to the breeding opportunity in case of competition with same-sex individuals from within and outside the group. Our results also affirm the importance of kin-based benefits in cooperative breeders—social bonds with relatives were equally strong between opposite and same-sex group members (Figure 2), suggesting that kin-affiliation and kin-selected benefits are not weakened by potential for reproductive conflict. Unrelated same-sex group members on the other hand offer no potential for kin-selected or mating benefits and, in line with our predictions (Table 1), we found a lack of social bonding between these; in fact, relationships were more aggressive (a mean affiliation index of <0; Figure 1), reflecting reproductive competition between these individuals.

### Submissive displays: avoiding aggression from dominants?

In agreement with their different nature, submissive behaviors seem to be driven by different motivations than affiliative-aggressive



**Figure 4**

The mean proportion of time focal subordinates spent foraging in a given season (a) if they engaged in affiliative interactions during the focal observation compared to when they did not, and (b) if they performed submissive displays during the focal observation compared to when they did not. Note that submissive displays were not scored in 2014. Numbers represent total number of subordinates observed in each category.

behaviors. Submissive displays were only directed at same-sex breeders, suggesting a role in appeasement of higher-status individuals that are in reproductive conflict (Table 1). When breeders disappear, they are often replaced by a (related or unrelated) same-sex subordinate if there is one available (Kingma et al. 2011). This, in combination with immediate potential competition over fertilizations (males) and access to the nest (females), suggests a constant reproductive conflict between a breeder and same-sex subordinate. Subordinate group members on the other hand become competitors with each other only when a breeding vacancy appears, and competitive success in acquiring male vacancies is determined mainly by age or extent of breeding plumage (Kingma et al. 2011; Fan et al. 2018). This difference may explain why submissive behavior was never directed at other subordinates. In contrast to our predictions (Table 1), relatedness did not (significantly) affect submissive behavior, although the pattern suggests related subordinates might engage less in submissive behaviors (19% of related vs. 50% of unrelated dyads; Figure 3). Sample size may preclude us from concluding this firmly, however since subordinates can also replace their same-sex parent, submissive behavior to reduce reproductive conflict also applies for these same-sex relatives.

Submission may be a strategy to avoid or minimize aggression from dominant breeders in our study species. Breeders may use aggression strategically to suppress potential reproductive competitors (Kutsukake and Clutton-Brock 2006a; Nelson-Flower et al. 2013). Such targeted aggression can suppress reproductive hormone levels in the recipient, resulting in low or no parentage by subordinates (Young et al. 2006; Brouwer et al. 2009), or even eviction (Kutsukake and Clutton-Brock 2006a). Potential victims of aggression may adopt various strategies to avoid aggression from these group members. For example in meerkats, *Suricata suricatta*, female subordinates will unidirectionally groom the dominant female to avoid aggression (Kutsukake and Clutton-Brock 2008). Since allopreening was generally reciprocal in our study, *M. coronatus* does not seem to adopt a similar strategy. Instead, submissive displays likely function to reduce aggression. Submission was more likely in dyads where aggression was observed; all aggression recorded in our study, although it was quite rare, was directed from a same-sex breeder to a subordinate. Thus, submissive displays are directed only at group members that are reproductive competitors, and mainly at those most likely to be aggressive, as has been found in pukekos, *Porphyrio melanotus*; to our knowledge, the only other study on active submissive behavior in an avian cooperative breeder (Dey and Quinn 2014). The observations that subordinates generally submitted spontaneously to an approaching breeder, and that breeders rarely attacked a submitting subordinate, support that submission may serve to reduce the probability of aggression. This is in contrast to a previous study on meerkats, a species with high rates of aggression, where submission during agonistic situations was associated with an increased probability of reoccurrence of aggression (Kutsukake et al. 2008). This difference may reflect a different function of submission during an aggressive encounter: only submission in peaceful contexts, as seems to be the norm in our study, may function to decrease the probability of aggression and result in more positive relationships (Flack and De Waal 2007).

Although submissive displays come at a cost when resources are scarce (the dry season), high rates of aggression could incur much higher costs, including potential eviction (Kutsukake and Clutton-Brock 2006a; Kutsukake and Clutton-Brock 2008) which may reduce survival or condition (Ridley et al. 2008; Kingma et al. 2016, 2017). By signaling that they are not a threat, subordinates

may form relationships of a more positive nature by reducing aggression from breeders and continue to enjoy the benefits of living in a group. Ultimately, submissive displays may therefore allow social groups to remain stable despite potential conflict.

### Implications: social group composition and benefits of group living

Our results indicate that social group composition should predict the frequency of affiliative and aggressive interactions of group members, and thereby generate individual-specific benefits of group living. Affiliative interactions and social bonds themselves are generally beneficial to the individuals involved (Detillion et al. 2004; Radford and Du Plessis 2006; Lewis et al. 2007; Silk et al. 2009; Sapolsky 2011; Charpentier et al. 2012; Fraser and Bugnyar 2012; Ueno et al. 2015; Villa et al. 2016), whereas aggressive interactions impose costs on individuals instead (Rovero et al. 2000; Lewis et al. 2007; Petit 2010). As a result, social group composition may determine the benefits that subordinates obtain from being part of a social group, and this may ultimately also influence subordinate dispersal. Subordinate purple-crowned fairy-wrens generally do not share groups with unrelated same-sex individuals as often as with unrelated opposite-sex or related individuals ( $N = 20$  vs.  $N = 35\text{--}52$  dyads for subordinates observed in current study, Table 1;  $N = 39$  vs.  $N = 75\text{--}117$  dyads for overall population in 2014–2016), which may be the result of subordinates dispersing more often when they share a group with unrelated same-sex individuals with whom they do not form positive social relationships (Figure 2). In turn, breeders could potentially also strategically use affiliative behavior to entice subordinates to remain in the group (Gill 2012). The higher affiliation index in the breeding season (wet season) compared to one of the 2 nonbreeding seasons suggests that this could be the case for purple-crowned fairy-wrens: affiliative behavior may function to encourage others to stay in the group and help with a breeding attempt. It should be noted though that while mean affiliation index was significantly higher in the wet season (2016) compared to the 2014 dry season, this difference was not significant for the 2016 dry season. Alternatively, birds may increase affiliative behavior during the wet season simply because they have more time available when food is more abundant and they spend less time foraging. It may be beneficial to use this time to invest more in social bonds: affiliating with group members is associated with a reduction in time spent foraging during the dry seasons. Future investigation into whether increases in affiliative behavior, especially during the breeding season, play a role in enticing group members to stay or increase their contributions to offspring care could further our understanding of how these behaviors evolved in the first place.

### CONCLUSION

Our study highlights the important role that social interactions can play in complex social systems, and adds to the limited body of data available for avian systems (Seibert and Crowell-Davis 2001; Radford and Du Plessis 2006; Fraser and Bugnyar 2012; Gill 2012; Dey and Quinn 2014). We show that within-group patterns of affiliative, aggressive and submissive interactions in the purple-crowned fairy-wren coincide with kin-selected and mating benefits of group living as well as reproductive conflict. Moreover, these social interactions appear to affect birds' time allocation to essential maintenance behaviors such as foraging, reflecting a cost of interacting with group members in terms of



time expenditure. As these interactions may aid in subordinates staying and in the resolution of reproductive conflict, they may be crucial for social groups to remain stable. We encourage further studies on potential consequences of behavioral interactions for the occurrence of escalating conflict and subordinate dispersal. For instance, beneficial social bonds with group members may provide one incentive for offspring to delay dispersal and remain on their current territory. Thereby, our results may provide insight into not just social living in general, but also the proximate factors underlying the evolution of group living (e.g., Griesser et al. 2006; Covas and Griesser 2007; Komdeur and Ekman 2010; Kingma et al. 2016).

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Teunissen et al. (2018).

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