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A Bayesian Approach to Social Structure Uncovers Cryptic Regulation of Group Dynamics in *Drosophila melanogaster*

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ABSTRACT: Understanding the mechanisms that give rise to social structure is central to predicting the evolutionary and ecological outcomes of social interactions. Modeling this process is challenging, because all individuals simultaneously behave in ways that shape their social environments—a process called social niche construction (SNC). In earlier work, we demonstrated that aggression acts as an SNC trait in fruit flies (*Drosophila melanogaster*), but the mechanisms of that process remained cryptic. Here, we analyze how individual social group preferences generate overall social structure. We use a combination of agent-based simulation and approximate Bayesian computation to fit models to empirical data. We confirm that genetic variation in aggressive behavior influences social group structure. Furthermore, we find that female decamping due to male behavior may play an underappreciated role in structuring social groups. Male-male aggression may sometimes destabilize groups, but it may also be an SNC behavior for shaping desirable groups for females. Density intensifies female social preferences; thus, the role of female behavior in shaping group structure may become more important at high densities. Our ability to model the ontogeny of group structure demonstrates the utility of the Bayesian model-based approach in social behavioral studies.

Keywords: *Drosophila melanogaster*, approximate Bayesian computation (ABC), social niche construction, courtship, aggression.

Introduction

The process by which individuals shape their social environment is called social niche construction (SNC; Flack et al. 2006; Kohn et al. 2011; Saltz and Foley 2011). In free-living populations, social groups emerge as a consequence of many individuals simultaneously engaging in SNC. These individuals will often vary in important ways, includ-

ing personality and sex (e.g., Griffiths and Magurran 1998; Eldakar et al. 2009; Aplin et al. 2014). This variation may in turn translate into differences in population-wide group structure, such as group size and sex ratio (Sumpter 2010; Jovani and Mavor 2011). Understanding these aspects of group composition is important, because social structure affects opportunities for competition, cooperation, or mating. However, modeling SNC is challenging, because an individual's expressed social phenotype may depend on interactions between sex, genotype, and the available social environment (Saltz and Foley 2011). In these kinds of diverse groups, we need to understand what the differences are between male and female behavior, how these differences shape group structure, and how group structure might feed back into subsequent behavior.

The fruit fly, *Drosophila melanogaster*, is a classic model organism for studying social behavior, sex differences, courtship, and aggression. *Drosophila melanogaster* interacts in groups on food for mating and egg laying, but the behavioral mechanisms that structure these groups are only partially understood. Aggressive behavior reduces aggregation among males (Saltz and Foley 2011) and might be expected to reduce local (within patch) competition for mates for territorially successful males. Earlier work has shown that, across a wide range of conditions, aggressive males gain a mating advantage by excluding other males from the patches of food that females use for egg laying (Hoffmann and Cacyianni 1989, 1990). However, although these studies focused on the direct outcomes of male-male interactions, they did not measure the way in which female social preferences interacted with male behavior. We have shown that the relationship between male aggressive success and mating success varies across social contexts due to female preferences. Females do not always prefer to mate with territorial males and may even mate more often when males are less aggressive (Cabral et al.

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2008; Saltz and Foley 2011; Saltz 2013). This complexity suggests that we need to understand the social determinants of female behavior, including group choice. Female social preferences for males are likely to be complex because of several conflicting selective pressures. To assess the quality of potential mates, or to mate at all, females need to be in groups with at least some males. However, females only mate every few days and may often have reasons to actively avoid males. Exposure to males reduces female health (Pitnick and Garcia-Gonzalez 2002), and females flee unwanted courtship (Spieth 1974). Female-female interactions may also be important in shaping group composition, because they are thought to aggregate to lay eggs (Sarin and Dukas 2009). How to model the outcome of varying social interests and their effects on group structure is an important general problem in animal behavior.

Previously, we demonstrated that genetic variation in male-male aggressive behavior acts as a mechanism of SNC in fruit flies (Saltz and Foley 2011). In aggressive encounters in *D. melanogaster*, males chase other males away from food patches. To evaluate whether genetic variation in male aggression can shape group structure, we formed mini-populations, varying density and genotype. Males and females could interact freely and form groups on food patches in each population. We found that females tended to form aggregations with other females, but males were more evenly distributed among patches than was expected by chance. Overall, flies aggregated more than expected by chance, and male and female presence on patches was highly correlated; there were few groups that had many males in them, but those groups also tended to have large numbers of females in them. Populations of different genotypes had different social structure. Those with the most aggressive genotypes had fewer males on patches and lower variance in male presence among patches.

Although male and female presence on patches was highly correlated, we were unable to assess whether the group choices of males or females were driving that correlation. Additionally, our approach was unable to test for changes in behavior across densities. Because each individual's behavior can be determined by complex feedback and stochastic dynamics (Sumpter 2010), linear approximations are often inadequate for higher-order group processes (Eriksson et al. 2010). Simulation, however, provides a powerful mechanistic approach to describe complex group formation (Jovani and Mavor 2011). In particular, agent-based simulation (ABS) is a particularly appropriate tool with which to study SNC (Bryson et al. 2007), because it operates at the level of individual behaviors and choices. Quantitative approaches have been successful in model fitting in ABS (Amé et al. 2004; Eriksson et al. 2010; Mann 2011), particularly in describing patterns of collective movement in schooling or flocking animals (Ward et al. 2008;

Sumpter et al. 2012; Mann et al. 2014). Although *D. melanogaster* is not known to engage in collective movement, the methodology seems well suited for describing outcomes of individual interactions.

In situations where the potential state space is small, the model is reasonably simple, or there are no missing data, exact methods of model fitting are appropriate. For example, Aplin et al. (2014) applied a maximum-likelihood approach to fit stochastic models of empirical group behavior, whereas Mann et al. (2014) used Bayesian model selection. Our data, however, comprise multiple sampled states and are sampled at discrete time points rather than being observed continuously. Furthermore, because we need to model male and female social preferences independently, our state space is quite large. Because exact methods are not tractable in our context, we use approximate Bayesian computation (ABC) with Monte Carlo Markov chain (MCMC) sampling (Marjoram et al. 2003; Beaumont et al. 2009). ABC is an approach that allows us to estimate model parameters in a principled manner, even in contexts that are analytically intractable. In essence, we replace calculation of the likelihood with simulation and use a Euclidean distance metric to assess model fit. In this way, it is a formalized version of the maximum likelihood approach sometimes used in fitting complex behavioral models (e.g., Ward et al. 2008). Although a number of sampling schemes are possible in ABC, MCMC is a well-worked-out approach that allows us to efficiently sample high-dimensional parameter space (e.g., Mann et al. 2011, 2013).

Material and Methods

The six *D. melanogaster* genotypes used by Saltz and Foley (2011) spanned a range of aggression. Of these, four (W23, W58, W89, and W145) were nearly isogenic lines collected in Winters, California, in 1998. The other two were high-aggression selected (A) and neutral control (N) genotypes, kindly supplied by R. Greenspan. These were created from the common laboratory wild-type stock Canton-S, as described by Dierick and Greenspan (2006).

Simulation

Simulations were designed after the assay of Saltz and Foley (2011) and mimicked the experimental conditions of these assays. We simulated the results of experiments using our six different genotypes at five different densities. Each experimental density $\times$ genotype combination is considered a treatment. Each simulation comprised four food patches, among which flies were able to freely assort (as well as an off-patch state). Each simulated trial contained an equal number of males and females. The density (total number) of flies in the arena ranged from 12 to 20 flies. We

did not attempt to model the lowest three densities of Saltz and Foley (2011), because the sampling variance for these replicates was high. We simulated group choice using a simple joining-and-leaving model (Amé et al. 2004). We modeled group behavior for each fly as a function of a joining rate and a baseline leaving rate as well as social preferences (fig. 1). Social preferences were a fly's affinity for males and for females. Parameters were sex specific, so for each simulation there were a total of eight parameters, four male and four female, comprising the parameter set Θ (fig. 1B). Although it is possible to construct simpler models with fewer parameters, we found highly significant sex differences in these estimates (appendix, available online), which suggests that male and female social preferences should be modeled separately. Events were modeled as a continuous-time Markovian process, with rates determined by rate equations (Otto and Day 2007).

Flies that were off patch could join a group. Group joining J_i was taken to be a simple rate $\exp(j_i)$ for a focal individual i of sex s . Group joining was random with respect to patch (fig. 1A), because (at least over short distances) fruit flies do not appear to use social cues before landing on patches but instead respond to social cues within groups (Saltz 2011). We fixed the male joining parameter j_m at 0 throughout all replicate simulations, rather than

attempting a post hoc scaling of rate parameters. Priors for the female joining parameter j_f were flat between -3.3 and 3.3 , which represents a possible difference of joining rates of more than 700-fold. Flies that were off patch were not considered to belong to any group.

Flies that were on patch left at a rate L_i proportional to their sex-specific leaving rate, l_s , modified by their group context and social parameters as described in equation (1) (fig. 1B). The particular form of our leaving rate equation was a simplified version of the leaving rate equation of Amé et al. (2004), which is a very general rate equation that has been shown to describe group choice very well (e.g., in cockroaches). To reduce the number of parameters that we needed to fit, we did not include their term k , effectively setting the intercept at the sex-specific baseline leaving rate l_s . This means that every additional fly (of a given sex) added to a patch has the same proportional effect as the one before on the leaving rate of a focal fly.

The leaving rate L_i for an on-patch focal individual i of sex s is thus

$$L_i = \exp(l_s) \Pi n_r^{-a_{sr}} \tag{1}$$

given the number of nonfocal individuals n_r of sex r and the sex-specific affinity a_{sr} of the focal individual for them.

Figure 1: Schematic of the agent-based simulation. Females are denoted as gray circles, and males are denoted as black circles. A, Food patches constitute social groups, and individuals may choose to join a patch at random or to leave a patch and be off patch at characteristic rates governed by the model parameters that we are estimating. Female and male joining rate (J_i) for sex i are each a function of a single parameter, j_i and j_m . Leaving rate (L_i) is a function of the sex-specific leaving rate, l_s , the number of nonself males and females in a group, and the sex-specific social parameters describing female attraction to males (a_{fm}) and females (a_{ff}) and male attraction to males (a_{mm}) and females (a_{mf} ; eq. [1]) B, Table of model parameters. C, Table of group-level summary statistics S , calculated from the experiments of Saltz and Foley (2011). These statistics were used to estimate the parameters Θ .

For the affinity parameters, this results in easily interpretable values that are symmetric around 0. A preference value of 0 represents a lack of preference for members of a given sex, a negative value represents a negative affinity (the leaving rate increases), and a positive value represents a positive affinity (the leaving rate decreases). The prior for l_s was identical to j_s , whereas the prior for a_{sr} was flat and ranged between -10 and 10 (appendix). The simulation design was chosen to mimic the experimental set-up of Saltz and Foley (2011; see appendix for details). Summary statistics (fig. 1C and appendix) were chosen to comprehensively describe male and female distributions among patches, male and female covariance among patches, and sampling variance among measurements. We measured the average number of males (mAv) and females (fAv) on patches, the variance of male (mVar) and female (fVar) distribution among patches, and their covariance on patches (mfCovar). We also considered several metrics that were not included in Saltz and Foley (2011), including the mean individual-level group composition statistics: the number of males or females per male (mPerM and fPerM, respectively) and per female (mPerF and fPerF, respectively), because these are better descriptors of individual experience (Jovani and Mavor 2011). We also included the standard deviations of our mAv and fAv metrics (mAvSD and fAvSD, respectively), because these provide estimates of movement between measurements. This results in a total of 11 summary statistics.

ABC

In a Bayesian framework, we describe our certainty about our parameter values, Θ , conditional on the observed data, $\mathcal{D}$, by the posterior distribution, $f(\Theta|\mathcal{D})$. We write $f(\Theta|\mathcal{D}) = f(\mathcal{D}|\Theta)\pi(\Theta)/f(\mathcal{D})$, where $\pi(\Theta)$ is a prior distribution that reflects our existing beliefs regarding the parameters, and $f(\mathcal{D})$ is a normalizing constant. This normalizing constant can be calculated by observing that $f(\Theta|\mathcal{D})$ is a probability distribution and must therefore integrate to 1. The likelihood term $f(\mathcal{D}|\Theta)$, however, is not calculable in this context, because $\mathcal{D}$ is composed of broad summary statistics and does not include the stochastic individual movements described by Θ . We can instead replace the calculation step by a simulation step, generating a pseudolikelihood between the statistics from the data and statistics from the simulation.

We used an ABC MCMC approach to estimate the parameter posterior distributions (Marjoram et al. 2003; Sisson et al. 2007, 2009; Beaumont et al. 2009; for full details, see appendix). The use of MCMC has an advantage in high-dimensional space of searching efficiently, rather than estimating the entire set of possible solutions (as in Perez-Escudero and de Polavieja 2011). We did this using

the set of summary statistics given earlier. As is common in ABC analyses, we use the Euclidean distance metric and define a tolerance, ϵ , that determines the level of agreement required between simulated and observed statistic values during the analysis. Choice of ϵ represents a trade-off between computational efficiency and accuracy of results. The analysis returned a joint-posterior distribution of these parameter values for each treatment. The underlying model did not include explicit parameters governing genetic differences or differences due to density. We instead expected that correlations between preference parameters and density or aggression would reveal the bases of SNC at the level of individual preferences.

For speed, we opted to implement our simulation and ABC algorithm in a custom C++ program. For full details on implementation, stationarity diagnostics, and model validation, see the appendix.

Multimodality

In a majority of treatments, we found that two distinct, mutually exclusive models fit the data, reflected in multivariate bimodal distributions for several parameters (fig. 2A). All but two treatments showed evidence of multimodality in at least one parameter (peaksIDPmisc in R; see appendix). The two parameters that showed the strongest evidence of multimodality were the affinity (or social preference) of males for females (a_{mf}) and the affinity of females for males (a_{fm}). In one of the modes, males exhibited a strong social affinity toward females; in the other, females exhibited a strong social affinity toward males. When we fit these two models separately (model mfHigh: $a_{mf} > a_{fm}$; model mfLow: $a_{mf} < a_{fm}$), evidence of multimodality disappeared in all parameters for all treatments (fig. 2B). Thus, we have a problem of identifiability.

In each treatment, we calculated the Bayes factor representing the relative likelihood of the mfHigh model by splitting the posterior distribution into mfHigh and mfLow samples and dividing the number of samples representing the mfHigh model by those representing the mfLow. A Bayes factor of 1 means the models are equally likely. The Bayes factor for mfHigh ranged from 0.66 to 17.80 across all treatments. The Bayes factor was lower than 1 in only two treatments (W23 $\times$ d14, 0.66; W58 $\times$ d12, 0.90). Given the general level of support for mfHigh, we determined whether we were justified in disregarding the mfLow model. We calculated the joint probability of mfHigh by multiplying the probability of the mfHigh model across all treatments and the probability of the mfLow model across all treatments, then recalculated the overall Bayes factor. The Bayes factor for the joint probability of mfHigh is 10^{17} ; therefore, there is no reason to further consider mfLow.

Figure 2: Bivariate heat map pooling the posterior distributions of parameter estimates of all 30 genotype $\times$ density treatments. There is bimodality within affinity of females for males (a_{fm}), affinity of males for females (a_{mf}), and female leaving rate (l_f). Bimodal distributions like this may represent a lack of identifiability (see appendix). Here, for the combination of a_{mf} and a_{fm} , the two peaks fall into two distinct categories: one in which a_{mf} is higher than a_{fm} (mfHigh) and one in which the opposite is true (mfLow). Because the joint probability of mfHigh is effectively 1, we conduct subsequent analyses only on mfHigh. In the left panel, we show the full data set. In the right panel, the model mfHigh is above the diagonal and mfLow is below.

Corrections for Multiple Testing

When testing for associations between variation in Θ and the predictors aggression, genotype, and density (see “Results”), we performed a number of tests that required correction for multiple testing. For the Wilcoxon signed-rank test, we were primarily interested in establishing that our method was sensitive enough to find significant differences in our parameters for the most conservative comparisons between posteriors. Because we were less interested in accurate, global P values, we opted for the simplest method of calculating the Bonferroni cutoff; that is, we calculated the Bonferroni cutoff on the basis of the total number of tests performed without accounting for the dimensionality of the data. For the regression analysis, because the model parameters had evident covariance structure, we first calculated the effective number of independent dimensions (Cheverud 2001). We performed principal components analysis on the concatenated data set comprising all posteriors for all treatments in the mfHigh model. The first five principal components explained 96.7% of the total variance in the parameters. Because we tested three predictors, this indicates approximately 15 independent tests, and we therefore set the global Bonferroni correction for the regression of Θ on predictors at 0.003.

Results

The ABC output comprised 30 replicates of Θ , with posterior distributions for our seven movement and social preference parameters, for each of our density $\times$ genotype combinations. ABC MCMC output data and R analysis code are archived in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.49r20> (Foley et al. 2015). Source code and detailed readmes are also archived in a git repository, <https://bitbucket.org/brfoley76/flyabc>.

Variation among Posteriors

We first established that the posteriors of Θ varied among genotypes and densities (treatments) and that we had the power to detect these differences, given our sampling rate. We thus performed a series of Wilcoxon signed-rank tests for pairs of posteriors. We compared the distributions of all posteriors for a given parameter that were either within genotype but different by one unit of density or within density between genotypes that were closest pairs in aggression levels. These comparisons were those we expected to be most similar. Even these conservative comparisons showed that posteriors varied greatly among treatments. Among the 24 density pairs for all seven parameters (168 comparisons), only 53 comparisons did not show significant differences after Bonferroni correction. Among the

25 aggression pairs for all seven parameters (175 comparisons), only 54 comparisons were not significantly different after Bonferroni correction. Two parameters (female leaving rate, l_f , and male affinity for females, a_{mf}) accounted for over half of the nonsignificant results—28 and 30 comparisons for density and aggression, respectively. This suggests that five of our seven parameters might be particularly important in shaping variation in group outcomes.

Genotype and Aggression Effects

Given significant differences in parameter estimates among treatments, we explored whether this variation was a result of genotype and density. Because we also had genotypic values for aggression (Saltz and Foley 2011), we used aggression as an additional predictor. To detect the directional effects of our predictors across all treatments, we used a summary (the marginal mean of each posterior) for each treatment and parameter combination. Subsequent calculations were performed using these summaries. We further investigated whether the differences in parameter estimates could be used to explain observed patterns of group structure.

Male and female group joining rates j_m and j_f , as well as male-male affinity, a_{mm} , were all correlated with both genotype and aggression (fig. 3A, 3B). The strongest correlation for both aggression and genotype was with a_{mm} . Aggression is male-directed behavior toward other males in *Drosophila* (see Chen et al. 2002; Nilsen et al. 2004; Dieckrick and Greenspan 2006; Cabral et al. 2008). We therefore expected that aggression would be most correlated with a_{mm} in our analysis. It serves as a validation of the model that this is the case (estimate [est] = -0.37 , $F_{1,28} = 14.95$, $P < .001$, adjusted R^2 [adjrsq] = 0.32) and was significant at the global Bonferroni threshold (see “Material and Methods”). Because our lines were chosen for their extreme genetic values in male-male aggression, it is likewise encouraging that we found evidence for genetic variation in a_{mm} among the lines in our treatments ($F_{5,24} = 4.52$, $P = .005$, adjrsq = 0.38). Although this did not quite meet the global Bonferroni threshold of $P < .0033$, the consistency of the effect among predictors suggests the association between a_{mm} and genotype is real.

Having established that a_{mm} is significantly related to aggression and likely varies with genotype, we attempted to understand what elements of group structure are shaped by male-male interactions. We tested for an effect of parameter estimates on group-level outcomes among our treatments using linear models, with density as a covariate (fig. 3C). We found that males with low values of a_{mm} had fewer other males in their groups (lower mPerM; est = 0.18, $t = 3.72$, $P < .001$, $df = 27$). Likewise, low values of a_{mm} correlated with overdispersion, or decreased variance in the

Figure 3: Plots for parameters showing significant correlations with predictors. Subfigure axes are denoted by the subheadings as $Y \sim X$. In linear models with genotype as a factor, significant effects were found for male joining rate (j_m), female joining rate (j_f), and male-male affinity (a_{mm} ; A). In linear models with genotypic aggression values as a quantitative trait, effects were found for j_m , j_f , and a_{mm} (B). In linear models with treatment density (number of individuals), effects were found for female-male affinity (a_{fm}) and female-female affinity (a_{ff} ; C).

numbers of males among patches (lower mVar; est = 0.16, $t = 3.56$, $P = .001$, $df = 27$). This is consistent with one definition of aggression as a male-male displacement strategy in *D. melanogaster* (Wang and Anderson 2010). One might assume that aggression is a competitive strategy that males engage in to gain access to females (Hoffmann and Cacoyianni 1989), but in fact both increased aggression (est = -0.08 , $t = -2.73$, $P = .011$, $df = 27$) and the corresponding low a_{mm} (est = 0.14, $t = 3.12$, $P = .004$, $df = 27$) had a slightly negative relationship with our empirical measure of the number of females per on-patch male (fPerM).

In addition to a_{mm} , sex-specific joining rates for males and females, j_m and j_f , varied significantly among the genotypes (j_m : $F_{5,24} = 3.36$, $P = .019$, adjrsq = 0.29; j_f : $F_{5,24} = 3.44$, $P = .017$, adjrsq = 0.30) and with aggression (j_m : est = 0.49, $F_{1,28} = 5.72$, $P = .024$, adjrsq = 0.14; j_f : est = 0.39, $F_{1,28} = 5.63$, $P = .025$, adjrsq = 0.14). The higher the overall aggression levels were, the higher the group joining rates were. The consistency of the effects of multiple predictors on these parameters supports their significance, although individually they do not meet the Bonferroni cutoff. The relationship between j_m or j_f and group structure was complex and differed between their corresponding sexes. Higher values of j_m and j_f should result in a higher average number of males (mAv) and females

(fAv), respectively, on patches, because increased joining rates were not offset by correlated higher leaving rates. We found support for this prediction for males (est = 0.05, $t = 4.29$, $P < .001$) but not females (est = 0.03, $t = 1.84$, $P = .07$). Higher values of j_f did correspond with one aspect of group structure: reduced male-female correlation on patches (mfCor; est = -0.3 , $t = -3.73$, $P < .001$, adjrsq = 0.51), suggesting one way in which females might shape their group context.

Male Disruption of Preferred Female Groups

Analysis in an agent-based simulation framework allows us to evaluate the plausibility of proposed hypotheses relating parameter values to group structure. We can vary one or more parameters in a series of test simulations and examine the effects without needing to explicitly redefine all the interacting dynamics (appendix). Here, we manipulate the three aggression-related parameters, holding the other parameters constant. This enables us to determine whether these parameters by themselves can explain the patterns we see and whether there is a plausible mechanism underlying the effect. In this case, we investigate changes in movement rates to evaluate social dynamics. Because aggression is a behavioral interaction where

males displace other males, we might expect overall male movement rates to be higher in aggressive environments.

We simulated high-aggression and low-aggression treatments using typical values of parameters from our set of posterior distributions. All conditions in these simulations were identical, but we mimicked high-aggression versus low-aggression values of j_f , j_m , and a_{mm} . Our simulations include an internal clock against which fly movement rate is calculated. We recorded the length of time between fly moves as well as the relative number of male and female fly moves. In the set of parameters mimicking the high-aggression conditions, overall fly movement rate was significantly greater, compared with the low-aggression scenario (est = -21.38, $t = -18.45$, $P < .001$, $df = 58$). Moreover, the proportion of times males moved in the high-aggression treatment was higher (est = 0.02, $t = 5.72$, $P < .001$, $df = 58$). These results are consistent with the idea that aggressive males are driving each other off patches more frequently than nonaggressive males are driving each other off patches.

It is not immediately obvious why female moving rates should covary with male aggression. However, given that males seem to move more often in high-aggression treatments, we hypothesized that male-female encounter rates are higher in these treatments. Female reaction to males is mediated by the term a_{fm} , and a_{fm} is consistently negative (fig. 2B, above diagonal), indicating that females will respond to increased numbers of males on patches by leaving.

To test the role of displaced males in disrupting female group structure, we set the preference of males for females, a_{mf} , to 1 (nearly neutral) in the high-aggression simulation. This will reduce the confounding effects of overall mobility with male social preferences for female groups. The average number of females on patches increased dramatically with lowered a_{mf} (est = 0.86, $t = 33.07$, $P < .001$, $df = 58$), and the ratio of female movement to male movement decreased (est = -0.29, $t = -52.22$, $P < .001$, $df = 58$).

Together, these results suggest a plausible mechanism for the relationship between aggression and female group preferences. Males with greater mobility preferentially aggregate with females, disrupting female groups in turn. In this scenario, the negative correlation between j_f and $mfCor$ and the lack of correlation between j_f and fAv indicate that females are reacting to nonpreferred groups by modifying their group choice parameters (fig. 4A). If so, the correlation between genotype and j_f is an example of an indirect genetic effect (Moore et al. 1997).

Density Effects

We found significant density effects (after global Bonferroni correction) in the two female social preference parameters. Female preference for males, a_{fm} (est = -0.59,

Figure 4: Graphical representation of our proposed mechanisms comprehensively explaining group-level outcomes from variation in individual-level parameters. Females are denoted as gray circles, and males are denoted as black circles. **A**, Our proposed mechanism for how variation in aggression indirectly affects female group joining parameters. When aggression is high (i.e., when male-to-male affinity [a_{mm}] is low), males move between groups more often. They are thus more likely to encounter groups of females. Because female-to-male affinity (a_{fm}) is consistently negative, when males join these groups, the groups are destabilized, and females leave and must find a new patch. **B**, We found that density affects both a_{fm} and female-to-female affinity (a_{ff}) in opposing ways. We propose that the effects of this change cancel out at the group level via a negative feedback loop involving male preferences for females. Arrows indicate a positive effect, and whisker indicates an inhibitory effect.

$F_{1,28} = 10.733$, $P = .003$, $\text{adjrsq} = 0.25$), was more negative at higher density; female preference for females, a_{ff} (est = 0.59, $F_{1,28} = 13.57$, $P = .001$, $\text{adjrsq} = 0.30$), was increasingly positive at higher densities (fig. 3C). In Saltz and Foley (2011), using conventional analyses, these differences in female behavior across densities were cryptic.

We expected to see more females in groups with other females in those treatments where we estimated high a_{ff} , as described by our summary statistics $fPerF$ and $fVar$. Instead, we found that $fVar$ did not correlate with a_{ff} . Moreover, the correlation between a_{ff} and $fPerF$ was in the opposite direction to our expectation (est = -0.098, $t = -2.40$, $P = .024$, $df = 27$). Likewise, we expected females would be less often on patches with males in treatments where we estimated low values of a_{fm} . This would

be reflected in a lower value of our male-female correlation statistic (mfCor) and sex ratio statistics of males per female (mPerF) and females per male (fPerM). However, among the treatments, only mfCor varied with a_{fm} in the predicted direction ($est = 0.035$, $t = 2.35$, $P = .026$, $df = 27$), and we did not detect any correlation between a_{fm} and fPerM or mPerF. Because the differences in a_{fm} and a_{ff} across densities were equal in magnitude and in the opposite direction, we hypothesized that they might, in effect, cancel each other out via a mechanism similar to that described above (see “Male Disruption of Preferred Female Groups”). An increased value of a_{ff} will lead to groups with more females. However, because a_{mf} is uniformly large and positive, groups with more females will come to attract more males. Since a_{fm} is highly negative, this will make the group less attractive to females (fig. 4B).

Additional simulations confirmed that our proposed mechanism could plausibly account for the group structure we observed. We ran simulations with a_{ff} and a_{fm} corresponding to either high-density or low-density values, holding all other parameter values constant. We first tested the effects of changing a_{ff} and a_{fm} together and independently. We found that, when we changed them independently, the values of fVar or fPerF changed significantly (appendix). However, when we changed the values of a_{fm} and a_{ff} simultaneously, the values of these summary statistics did not change. We then evaluated whether male preferences for females might play a role in regulating this process. We set the male preference for females, a_{mf} , to 1 (nearly neutral). When we then tested high-density and low-density values of a_{ff} and a_{fm} , there was a large difference in group structure. In particular, fVar increased, as did fPerF; that is, a very few groups became increasingly female biased. This result indicates that opposing social preferences between the sexes may regulate group structure through a process of negative feedback and that increasingly extreme female preferences may help to buffer this process with increasing density.

Discussion

Understanding the behavioral mechanisms that give rise to group structure (i.e., SNC) is central to predicting the evolutionary and ecological outcomes of social interactions. These interactions are best modeled at the level of individual choices; therefore, we used ABS with ABC model-fitting techniques. Using this approach in *D. melanogaster*, we found that effects of density and aggression on group structure that were ambiguous when we examined group-level summary statistics were more transparent when we modeled them at the individual level. We have shown that there is an effect of female group choice

on overall social structure. This has important implications for understanding male aggressive behavior. Although some studies have shown that males who directly exclude other males from food may directly increase their mating success (Hoffmann and Cacoyianni 1989), there are a number of exceptions to this pattern (Cabral et al. 2008; Saltz and Foley 2011). Our current results highlight the importance of the indirect effects of male behavior on female group choice. In particular, we found that heightened aggression might degrade the desirability of social environments for females, which may help explain why there are multiple successful social strategies for male *D. melanogaster*.

Our results give novel insight into the way that differences between the sexes define social structure in *D. melanogaster* and point to a dynamic process of SNC that actively involves both sexes. The consistent negative affinity of females for males was not a priori predictable. Although males can damage females with intense courtship or mating (Pitnick and Garcia-Gonzalez 2002), it is not obvious that males should behave in ways that drive females away from patches. In fact, we found an extremely strong positive affinity of males for females, consistent with the effort males spend in courtship behavior (Greenspan and Ferveur 2000). In addition to between-sex interactions, within-sex interactions were also important in shaping group structure. We found that females tended to have positive affiliative tendencies, consistent with descriptions of egg-laying aggregation (Sarin and Dukas 2009). For males, the strongly negative male-male affinity that we found was consistent with the role of male-male aggression as an SNC behavior previously reported in Saltz and Foley (2011).

We found that complex male-female behavioral interactions that depended on density generated the social structures we observed in Saltz and Foley (2011). In our earlier work, we were unable to demonstrate a role of female behavior or response to the social environment in SNC. Here, changes in female parameters with changes in male aggression and density show that female social group choice plays an active role in shaping group structure. The effects of female group choice were not directional, however, and were more easily interpreted as buffering the effects of directional male preferences. Strong male preferences for being in groups with females apparently led to disruption of females' preferred groups at both high aggression and high density. Joining rates in both sexes were perturbed under high aggression. Our model suggests that displaced males preferentially aggregate in groups with more females, in turn influencing the females to leave. The fact that females seem to be increasing their joining rates without changing their overall time spent on patches is consistent with results showing that individuals have a baseline preference for the proportion of time they spend on patches (Saltz

2011). At high densities, female social preferences were increasingly strong. Our predictions, based on changes of a_{ff} and a_{fm} with density, were that, at high densities, larger, more female-biased groups should form. Models suggest that male affinity for females disrupts these groups. Together, these results are consistent with published observations (Hoffmann and Cacoyianni 1990) showing that mobile, nonterritorial males may even chase females between patches.

The effects of the opposing male-female group dynamic point to an underappreciated role of decamping (or female negative group choice) as an SNC trait and as an important component of courtship (Spieth 1974). Mating can occur only in groups with both males and females in them. Therefore, preventing female decamping has an important role in male mating success. For males, aggression directly removes competitors from a group by displacing other males. It may also have an important indirect role in increasing the number of females in a group, via females' preferences for fewer males. Open-ended selection for increased aggression does not seem to occur, however. According to indirect genetic effect theory, the net SNC effect of aggression is expected to depend on the behavior of all other males in the population (Moore et al. 1997). It is telling that increased aggression has the unexpected effect of disrupting preferred groups for both sexes. We found in Saltz and Foley (2011) that the least aggressive genotypes had large groups with more males and high mating success. There may, then, be emergent social niches for stable, relatively large groups that contain less aggressive males.

The study of complex systems, including social systems, is of growing importance. Our article demonstrates the power of a model-based analysis in such contexts. Power is gained because behavior is modeled in detail, at the individual level. However, where individual-level modeling is not accompanied by individual-level data, an explicit solution is generally impossible. Simulation and Bayesian methods have proven their worth in the field of behavior, particularly where there is complete information (e.g., Mann 2011; Perez-Escudero and de Polavieja 2011; Arganda et al. 2012; Aplin et al. 2014; Mann et al. 2014). However, the form of our data—multiple sampled states describing spatial distributions across time—is common in animal behavior research. For instance, field observations may be restricted to spot-sampling distributions of individuals or patterns of group membership (e.g., Wittemyer et al. 2005; Jovani et al. 2008; Oh and Badyaev 2010), and tools to analyze this kind of data will be valuable. Here, we invoked ABC methodology, an approach that has gained traction in recent years in a variety of fields. The ABC method may be complementary to other emerging methods of model building and fitting (Pratt et al. 2005; Franz and Nunn 2009). For example, we used simple dy-

namic models from the animal behavior to characterize variation resulting from genotype, density, and a candidate behavior (aggression) in many replicate data sets. Once the basic dynamics of a system have been described, one could use ABC with these models to estimate the underlying parameter values that lead to patterns of group behavior, such as schooling or hierarchy development (Hemelrijk 1999); such methods are also applicable in human social sciences (Smith and Conrey 2007) and in studying other complex social groups, such as in flies.

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Literature Cited

- Amé, J., C. Rivault, and J. Deneubourg. 2004. Cockroach aggregation based on strain odour recognition. *Animal Behaviour* 68:793–801. doi:10.1016/j.anbehav.2004.01.009.
- Aplin, L. M., D. R. Farine, R. P. Mann, and B. C. Sheldon. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences* 281:20141016.
- Arganda, S., A. Pérez-Escudero, and G. G. de Polavieja. 2012. A common rule for decision making in animal collectives across species. *Proceedings of the National Academy of Sciences of the USA* 109:20508–20513. doi:10.1073/pnas.1210664109.
- Beaumont, M., J. Cornuet, J. Marin, and C. Robert. 2009. Adaptive approximate Bayesian computation. *Biometrika* 96:983–990.
- Bryson, J., Y. Ando, and H. Lehmann. 2007. Agent-based modelling as scientific method: a case study analysing primate social behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:1685–1698.
- Cabral, L., B. Foley, and S. V. Nuzhdin. 2008. Does sex trade with violence among genotypes in *Drosophila melanogaster*? *PLoS ONE* 3:e1986.
- Chen, S., A. Lee, N. Bowens, R. Huber, and E. Kravitz. 2002. Fighting fruit flies: a model system for the study of aggression. *Proceedings of the National Academy of Sciences of the USA* 99:5664–5668.
- Cheverud, J. M. 2001. A simple correction for multiple comparisons in interval mapping genome scans. *Heredity* 87:52–58.
- Dierick, H., and R. Greenspan. 2006. Molecular analysis of flies selected for aggressive behavior. *Nature Genetics* 38:1023–1031. doi:10.1038/ng1864.
- Eldakar, O., M. Dlugos, J. Pepper, and D. Wilson. 2009. Population structure mediates sexual conflict in water striders. *Science* 326:816. doi:10.1126/science.1180183.

- Eriksson, A., M. N. Jacobi, J. Nystrom, and K. Tunstrom. 2010. Determining interaction rules in animal swarms. *Behavioral Ecology* 21:1106–1111. doi:10.1093/beheco/arq118.
- Flack, J., M. Girvan, F. de Waal, and D. Krakauer. 2006. Policing stabilizes construction of social niches in primates. *Nature* 439:426–429. doi:10.1038/nature04326.
- Foley, B., J. B. Saltz, S. V. Nuzhdin, and P. Marjoram. 2015. Data from: A Bayesian approach to social structure uncovers cryptic regulation of group dynamics in *Drosophila melanogaster*. American Naturalist, Dryad Digital Repository, doi:10.5061/dryad.49r20.
- Franz, M., and C. Nunn. 2009. Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences* 276:1829–1836. doi:10.1098/rspb.2008.1824.
- Greenspan, R., and J. Ferveur. 2000. Courtship in *Drosophila*. *Annual Review of Genetics* 34:205.
- Griffiths, S., and A. Magurran. 1998. Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour* 56:689–693. doi:10.1006/anbe.1998.0767.
- Hemelrijk, C. 1999. An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B: Biological Sciences* 266:361–369. doi:10.1098/rspb.1999.0646.
- Hoffmann, A., and Z. Cacyianni. 1989. Selection for territoriality in *Drosophila melanogaster*: correlated responses in mating success and other fitness components. *Animal Behaviour* 38:23–34.
- . 1990. Territoriality in *Drosophila melanogaster* as a conditional strategy. *Animal Behaviour* 40:526–537.
- Jovani, R., and R. Mavor. 2011. Group size versus individual group size frequency distributions: a nontrivial distinction. *Animal Behaviour* 82:1027–1036. doi:10.1016/j.anbehav.2011.07.037.
- Jovani, R., D. Serrano, E. Ursua, and J. L. Tella. 2008. Truncated power laws reveal a link between low-level behavioral processes and grouping patterns in a colonial bird. *PLoS ONE* 3:e1992. doi:10.1371/journal.pone.0001992.
- Kohn, G., A. King, L. Scherschel, and M. West. 2011. Social niches and sex assortment: uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour* 82:1015–1022. doi:10.1016/j.anbehav.2011.07.035.
- Mann, R. P. 2011. Bayesian inference for identifying interaction rules in moving animal groups. *PLoS ONE* 6:e22827. doi:10.1371/journal.pone.0022827.
- Mann, R. P., R. Freeman, M. Osborne, R. Garnett, C. Armstrong, J. Meade, D. Biro, T. Guilford, and S. Roberts. 2011. Objectively identifying landmark use and predicting flight trajectories of the homing pigeon using Gaussian processes. *Journal of the Royal Society Interface* 8:210–219. doi:10.1098/rsif.2010.0301.
- Mann, R. P., J. E. Herbert-Read, Q. Ma, L. A. Jordan, D. J. T. Sumpter, and A. J. W. Ward. 2014. A model comparison reveals dynamic social information drives the movements of humbug damselfish (*Dascyllus aruanus*). *Journal of the Royal Society Interface* 11:20130794. doi:10.1098/rsif.2013.0794.
- Mann, R. P., A. Perna, D. Strombom, R. Garnett, J. E. Herbert-Read, D. J. T. Sumpter, and A. J. W. Ward. 2013. Multi-scale inference of interaction rules in animal groups using Bayesian model selection. *PLoS Computational Biology* 9:e1002961. doi:10.1371/journal.pcbi.1002961.
- Marjoram, P., J. Molitor, V. Plagnol, and S. Tavaré. 2003. Markov chain Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the USA* 100:15324–15328.
- Moore, A., E. D. Brodie, III, and J. Wolf. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* 51:1352–1362.
- Nilsen, S., Y.-B. Chan, R. Huber, and E. Kravitz. 2004. Gender-selective patterns of aggressive behavior in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the USA* 101:12342–12347.
- Oh, K. P., and A. V. Badyaev. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *American Naturalist* 176:E80–E89.
- Otto, S., and T. Day. 2007. A biologist's guide to mathematical modeling in ecology and evolution. Princeton University Press, Princeton, NJ.
- Perez-Escudero, A., and G. G. de Polavieja. 2011. Collective animal behavior from Bayesian estimation and probability matching. *PLoS Computational Biology* 7:e1002282. doi:10.1371/journal.pcbi.1002282.
- Pitnick, S., and F. Garcia-Gonzalez. 2002. Harm to females increases with male body size in *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences* 269:1821–1828. doi:10.1098/rspb.2002.2090.
- Pratt, S., D. Sumpter, E. Mallon, and N. Franks. 2005. An agent-based model of collective nest choice by the ant *Temnothorax al-bipennis*. *Animal Behaviour* 70:1023–1036. doi:10.1016/j.anbehav.2005.01.022.
- Saltz, J. B. 2011. Natural genetic variation in social environment choice: context-dependent gene-environment correlation in *Drosophila melanogaster*. *Evolution* 65:2325–2334. doi:10.1111/j.1558-5646.2011.01295.x.
- . 2013. Genetic composition of social groups influences male aggressive behaviour and fitness in natural genotypes of *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences* 280:20131926.
- Saltz, J. B., and B. Foley. 2011. Natural genetic variation in social niche construction: social effects of aggression drive disruptive sexual selection in *Drosophila melanogaster*. *American Naturalist* 177:645–654.
- Sarin, S., and R. Dukas. 2009. Social learning about egg-laying substrates in fruit flies. *Proceedings of the Royal Society B: Biological Sciences* 276:4323–4328. doi:10.1098/rspb.2009.1294.
- Sisson, S., Y. Fan, and M. Tanaka. 2007. Sequential Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the USA* 104:1760–1765.
- . 2009. Correction for Sisson et al. sequential Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the USA* 106:16889.
- Smith, E., and F. Conrey. 2007. Agent-based modeling: a new approach for theory building in social psychology. *Personality and Social Psychology Review* 11:87–104. doi:10.1177/1088868306294789.
- Spieth, H. 1974. Courtship behavior in *Drosophila*. *Annual Review of Entomology* 19:385–405. doi:10.1146/annurev.en.19.010174.002125.
- Sumpter, D. J. T. 2010. Collective animal behavior. Princeton University Press, Princeton, NJ.
- Sumpter, D. J. T., R. P. Mann, and A. Perna. 2012. The modelling cycle for collective animal behaviour. *Interface Focus* 2:764–773. doi:10.1098/rsfs.2012.0031.
- Wang, L., and D. Anderson. 2010. Identification of an aggression-promoting pheromone and its receptor neurons in *Drosophila*. *Nature* 463:227–U114. doi:10.1038/nature08678.

Ward, A. J. W., D. J. T. Sumpter, L. D. Couzin, P. J. B. Hart, and J. Krause. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences of the USA* 105:6948–6953. doi:10.1073/pnas.0710344105.

Wittemyer, G., I. Douglas-Hamilton, and W. Getz. 2005. The socioecology of elephants: analysis of the processes creating multitiered

social structures. *Animal Behaviour* 69:1357–1371. doi:10.1016/j.anbehav.2004.08.018.

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“The species of *Camarasaurus* and *Amphicælias*, which attained to the most gigantic proportions, are remarkable for the light construction of the vertebræ anterior to the tail. [...] The elevation of the middle line of the back must have been extraordinary in the *Amphicælias altus* [pictured], and the huge knob at the summit of the neural spine indicates the strength of the longitudinal ligament which connected the vertebræ with each other and with the head.” From “On the Saurians Recently Discovered in the Dakota Beds of Colorado” by E. D. Cope (*The American Naturalist*, 1878, 12:71–85).