

2 **Testosterone-mediated behavior shapes the emergent properties of social**  
3 **networks**

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## 16 **Abstract**

1. Social networks can vary in their organization and dynamics, with implications for  
18 ecological and evolutionary processes. Understanding the mechanisms that drive social  
network dynamics requires integrating individual-level biology with comparisons across  
20 multiple social networks.
2. Testosterone is a key mediator of vertebrate social behavior and can influence how  
22 individuals interact with social partners. Although the effects of testosterone on  
individual behavior are well established, no study has examined whether hormone-  
24 mediated behavior can scale up to shape the emergent properties of social networks.
3. We investigated the relationship between testosterone and social network dynamics in the  
26 wire-tailed manakin, a lekking bird species in which male-male social interactions form  
complex social networks. We used an automated proximity system to longitudinally  
28 monitor several leks and we quantified the social network structure at each lek. Our  
analysis examines three emergent properties of the networks: social specialization (the  
30 extent to which a network is partitioned into exclusive partnerships), network stability  
(the overall persistence of partnerships through time), and behavioral assortment (the  
32 tendency for like to associate with like). All three properties are expected to promote the  
evolution of cooperation. As the predictor, we analyzed the collective testosterone of  
34 males within each social network.
4. Social networks that were composed of high-testosterone dominant males were less  
36 specialized, less stable, and had more negative behavioral assortment, after accounting  
for other factors. These results support our main hypothesis that individual-level hormone  
38 physiology can predict group-level network dynamics. We also observed that larger leks

with more interacting individuals had more positive behavioral assortment, suggesting  
40 that small groups may constrain the processes of homophily and behavior-matching.

5. Overall, these results provide evidence that hormone-mediated behavior can shape the  
42 broader architecture of social groups. Groups with high average testosterone exhibit  
social network properties that are predicted to impede the evolution of cooperation.

44

**Keywords:** androgens, behavioral endocrinology, collective behavior, cooperation, dynamic  
46 networks, social networks, testosterone

## Introduction

48 Behavioral interactions are the foundation of social network structures that can vary through  
time, among populations, and across species. Network structures play an important role in many  
50 ecological and evolutionary processes, including the spread of diseases (Sah *et al.* 2018;  
Stroeymeyt *et al.* 2018), the transmission of information and resources (Aplin *et al.* 2012;  
52 Maldonado-Chaparro *et al.* 2018), and selection on individual behavior (Ohtsuki *et al.* 2006). A  
major challenge is understanding how individual-level factors, such as physiological and  
54 behavioral mechanisms, scale up to drive the emergent structural properties of social groups  
(Krause & Ruxton 2002). Linking these two levels of analysis is difficult because it requires  
56 integrating individual-level data with repeated measures of entire social groups (Sah *et al.* 2017).

Here, we use a comparison of multiple social networks through time to investigate how  
58 hormone-mediated behavior shapes the higher-order structure of social networks. Testosterone is  
a steroid hormone that is well known for its influence on social behavior and its sensitivity to  
60 changes in the social environment (Wingfield *et al.* 1990; Adkins-Regan 2005; Goymann 2009).  
Testosterone often promotes physical aggression and other behaviors associated with social  
62 dominance (Oyegbile & Marler 2005; Fuxjager *et al.* 2010). Testosterone can also promote  
status-seeking behaviors in a non-aggressive context, including cooperative and gregarious  
64 behavior (Eisenegger *et al.* 2011; Boksem *et al.* 2013; Ryder *et al.* 2020). Overall, these  
hormone-signaling pathways are essential for the development and modulation of complex  
66 behavioral phenotypes (Cohen *et al.* 2012).

To investigate how testosterone is associated with social network dynamics, we studied  
68 the wire-tailed manakin (*Pipra filicauda*), a bird species in which the males engage in  
coordinated displays with each other at sites known as leks. In *P. filicauda*, males exhibit two

70 social status classes: the dominant males who hold territories on the leks, and subordinate,  
“floater” males who must acquire a territory on a lek before they can mate (Heindl 2002; Ryder  
72 *et al.* 2011a). Male social partnerships in wire-tailed manakins can be remarkably stable and  
typically occur between two unrelated males, most commonly, but not exclusively, between a  
74 territory-owner and a floater (Ryder *et al.* 2011a; Dakin & Ryder 2020). Two features of the  
manakin leks make them especially well-suited to studying the relationship between hormones  
76 and group-level social structure. First, testosterone is known to affect the social behavior of  
individual male wire-tailed manakins (Ryder *et al.* 2020). Second, these partnerships among  
78 males form the basis of complex and dynamic social networks that are replicated across leks,  
facilitating a comparative approach (Dakin & Ryder 2018, 2020). Given this background, we  
80 sought to test whether testosterone and its effects on male behavioral phenotype could drive the  
emergent properties of the social network.

82 The broader function of male-male social behavior and coordinated displays in the  
manakin family has been the subject of considerable study (e.g., Prum 1994; DuVal 2007;  
84 McDonald 2007; Ryder *et al.* 2008, 2009; Díaz-Muñoz *et al.* 2014). One possible function is that  
dyadic displays may be competitive and/or they may serve to maintain an individual’s position in  
86 a dominance hierarchy (Prum 1994; Heindl 2002). Social interactions may also represent  
cooperative coalitions that provide benefits to both parties (Ryder *et al.* 2008, 2009). The  
88 potential competitive and cooperative functions of male-male social behavior are not mutually  
exclusive, and function may be context- and/or status-specific (Ryder *et al.* 2008). Coordinated  
90 displays may also be a vestige of ancestral cooperative behavior (i.e., the behavior may have  
been directly beneficial to both parties in the past, and it persists today, even if it no longer has  
92 adaptive benefits; Prum 1994). Given this background and recent evidence that testosterone

modulates male social behavior in wire-tailed manakins (Ryder *et al.* 2020), we focused this  
94 study on three emergent properties of the social networks formed by male-male interactions that  
can influence the evolution and maintenance of cooperation (Fig. 1).

96 The first property we examined, social specialization, seeks to capture the exclusivity of  
the relationships between partners in a social network. In the context of manakin behavior,  
98 highly specialized networks are well-partitioned among specific territory-owner and floater  
relationships, as illustrated in Fig. 1A. In humans, social specialization has been found to  
100 maximize the ability of a team to successfully perform a challenging task (Jehn & Shah 1997). In  
manakins, we expect specialization to improve the familiarity of social partners and the  
102 behavioral coordination of their displays. Greater specialization is also expected to minimize  
conflict over mating and territorial ascension opportunities (Schjelderup-Ebbe 1922; McDonald  
104 1993).

The second property, network stability (Fig. 1B), quantifies the average persistence of  
106 social partnerships through time (Poisot *et al.* 2012; Dakin & Ryder 2020). Coordinated displays  
in manakins require the synchronization of complex behaviors, and previous empirical work  
108 indicates that longer partnership tenure has a positive effect on display coordination (Trainer &  
McDonald 1995; Trainer *et al.* 2002). Greater temporal stability of partnerships also increases  
110 the opportunity for familiarity and reciprocity within a social network (Trivers 1971; Roberts &  
Sherratt 1998; Croft *et al.* 2006).

112 The third property, behavioral assortment (Fig. 1C), captures the extent to which males  
interact with partners who express similar behaviors (i.e., is like associated with like? Croft *et al.*  
114 2006; Farine 2014). At the proximate level, positive assortment may represent the outcome of  
generalized reciprocity and/or partner choice (Fowler & Christakis 2010; Dakin & Ryder 2018).

116 At the ultimate level, positive assortment has also been shown to promote the evolution of  
cooperation (Ohtsuki *et al.* 2006). To quantify the overall behavioral assortment of the manakin  
118 networks, we focused on two correlated metrics of social behavior within the network: “strength”  
(a male’s frequency of daily social interactions) and “degree” (his daily number of social  
120 partnerships; Dakin & Ryder 2018). We used a composite measure of assortment that averaged  
the assortativity indices of these two phenotypes.

122 As a potential predictor of specialization, stability, and assortment, we quantified the  
collective testosterone of the manakin leks (Fig. 2; Akinola *et al.* 2016). Because hormone-  
124 behavior relationships are status-specific in manakins and many other species (Eisenegger *et al.*  
2011; Boksem *et al.* 2013; Ryder *et al.* 2020), we analyzed collective testosterone for each of the  
126 two status classes separately. High individual testosterone levels are associated with reduced  
sociality in dominant males, but increased sociality in subordinate males (Ryder *et al.* 2020). We  
128 therefore predicted that the average (or collective) testosterone of territorial males in a group  
would be negatively associated with its specialization, stability, and assortment. In contrast, we  
130 predicted that the collective testosterone of floater males in a group would be positively  
associated with these three emergent properties of the social network.

132

## Materials and Methods

### 134 *Study Population*

We studied wire-tailed manakins (*Pipra filicauda*) at the Tiputini Biodiversity Station in  
136 Orellana Province, Ecuador (0° 38’ S, 76° 08’ W). This population of *P. filicauda* has been  
studied and individuals color-banded annually since 2002 (e.g., Ryder *et al.* 2008, 2009). The  
138 present study was conducted on 11 leks during peak breeding activity (December-March) across

three field seasons: 2015-16, 2016-17 and 2017-18. All research was approved by the  
140 Smithsonian ACUC (protocols #12-23, 14-25, and 17-11) and the Ecuadorean Ministry of the  
Environment (MAE-DNB-CM-2015-0008).

142

### *Testosterone Assessment*

144 Male manakins were captured using mist-nets on the leks as described in (Ryder *et al.* 2020). We  
deployed up to 16 mist-nets simultaneously at a given lek, with the intention of capturing every  
146 male on the lek. We rotated the nets between leks with the goal of capturing each male up to  
three times per field season. Each mist-net was checked on a 30-minute schedule with variation  
148 resulting from capture rate (i.e., multiple birds being caught on the same net run; Vernasco *et al.*  
2019; Ryder *et al.* 2020). The amount of time a male spends in the net has a subtle, but  
150 significant, negative effect on his circulating testosterone (Vernasco *et al.* 2019). Therefore, we  
used video monitoring to determine the duration of time that each bird was in the mist-net prior  
152 to blood sampling, so that it could be accounted for in further analyses (mean = 17.5 minutes, SD  
= 10.3 minutes, range = 1–72 minutes). Following removal of a male from the mist-net, a small  
154 blood sample (< 125uL) was taken from the brachial vein and stored on ice prior to being  
centrifuged at 10,000 rpm for 5 min, as described in previous studies (Ryder *et al.* 2011b;  
156 Vernasco *et al.* 2019; Ryder *et al.* 2020). Plasma volume was measured to the nearest 0.25 ul and  
stored in 0.75 ml of 100% ethanol (Goymann *et al.* 2007). Testosterone was double extracted  
158 from the plasma using dichloromethane. Following extraction, a direct radioimmunoassay was  
used to measure the total plasma androgen concentration (ng/ml) adjusted by the extraction  
160 efficiency and plasma volume of each sample (Eikenaar *et al.* 2011; Ryder *et al.* 2011b).  
Hormone assays were conducted annually, and the detection limits were 0.12, 0.08, and 0.09



162 ng/ml for 2015-16, 2016-17 and 2017-18, respectively; any sample that fell below the assay-  
specific limit of detection was assigned that limit as its testosterone concentration as a most  
164 conservative estimate. The extraction efficiency for all samples was between 62-73%, and the  
intra-assay coefficients of variation were 6.6%, 11.6%, and 9.2% for 2015-16, 2016-17 and  
166 2017-18, respectively; the inter-assay coefficient of variation was 19.5%.

### 168 ***Behavioral Recording***

We used an automated data-logging system to monitor male-male interactions on the display  
170 territories of the leks (Ryder *et al.* 2012; Dakin & Ryder 2018; Ryder *et al.* 2020). The territories  
on these leks are specifically used for male-male coordinated social displays (as described in  
172 Schwartz & Snow 1978). At the beginning of each field season, male manakins were outfitted  
with coded nano-tags (NTQB-2, Lotek Wireless; 0.35 g). The tags transmitted a unique VHF  
174 signal ping once per 20 s for three months. In total, 296 tag deployments were performed on 180  
individuals (mean 1.7 field seasons per male  $\pm$  SD 0.7), 178 of whom also had hormone data  
176 (mean number of hormone samples per male = 3  $\pm$  SD 1.5). Approximately 10 days ( $\pm$  SD 7)  
after tagging and sampling was completed at a given lek, a proximity data-logger (SRX-DL800,  
178 Lotek Wireless) was deployed within each display territory at the lek to record tagged males  
within a detection radius of 30 m (a distance that corresponds to the typical diameter of a  
180 manakin display territory; Heindl 2002; Dakin & Ryder 2018).

Proximity recording sessions ran from 06:00 to 16:00 for ~6 consecutive days ( $\pm$  SD 1  
182 day) and were performed ~3 times per field season at a given lek. Occasionally, the length of a  
recording session was extended due to extenuating circumstances such as inclement weather.  
184 The recording sessions were scheduled to be distributed evenly throughout each field season at

each lek, to minimize any confounding seasonal effects. Each recording session represents an  
186 observation of the social network at a given lek. In total, we conducted 86 recording sessions  
(29,760 data-logger hours) representing repeated measures of the social activity at 11 leks during  
188 three field seasons (see Fig. S1 in the supplement for additional details on the sampling regime).

Prior to data-logger deployment, each territory was also observed on non-recording days  
190 to identify the territory-holder based on his color-bands, following previous studies (Ryder *et al.*  
2008, 2009). These status assignments were subsequently verified in the proximity data.

192

### ***Data Processing and Statistical Analysis***

194 All computational and statistical analyses were performed in R (R Core Team 2018). Network  
illustrations were made using the igraph package (Csardi *et al.* 2018).

196

### ***Social Interactions***

198 Social networks were constructed by first defining interactions between two males that occurred  
on the display territories. To do this, a computational algorithm was used to identify joint  
200 detections, wherein two males were located at the same display territory within a pre-defined  
spatial and temporal threshold (Ryder *et al.* 2008, 2012; Dakin & Ryder 2018). For the temporal  
202 threshold, the two males had to occur < 45 s apart. This temporal threshold was chosen to allow  
for the fact that each tag pinged with a 20 second pulse rate, such that overlapping individuals  
204 could have up to a 40 s gap between their respective pings. For the spatial threshold, the two  
males had to have a difference in received signal strength values ( $\Delta$  RSSI) < 10. This threshold  
206 corresponded to a typical distance between 0 to 5 m apart in a ground-truthing experiment  
(Dakin & Ryder 2018). Hence, according to our definition, a social interaction is initiated only

208 after males come within this approximate spatial threshold. We chose this spatial threshold  
because it is close enough to permit visual and acoustic contact during typical social behaviors  
210 (such as those described in Schwartz & Snow 1978). After completing our study, we also  
performed a sensitivity analysis to verify that our main results were robust to alternative spatial  
212 threshold definitions (see supplement for details).

Any repeated co-occurrence of the two males within 5 minutes was considered to be part  
214 of the same social interaction, but after a gap of  $\geq 5$  minutes, it was considered to be a new  
interaction between those two males. The average duration of social interactions defined by this  
216 method was 5.1 min  $\pm$  SD 13.3, 8.8 min  $\pm$  SD 20.1, and 7.0 min  $\pm$  SD 20.5 in the three respective  
field seasons, further indicating that these were sustained social interactions, rather than random  
218 encounters.

In total, we identified 36,885 social interactions over the three field seasons of study.  
220 These interactions were used to define a weighted social network for each lek recording session.  
The nodes in the network were the individual males, and the edges were weighted by the number  
222 of social interactions between each pair of males. An earlier validation study compared social  
interactions that were detected by the proximity system with those that were directly observed  
224 for 11 males (Ryder *et al.* 2012), and confirmed that all of the interactions detected by the  
proximity system were also directly observed.

226

### ***Null Model Validation of the Social Networks***

228 Two broad classes of methods have been described for building social networks: (i) networks  
that are built based purely on the proximity of animals unrelated to their behavioral context  
230 (“gambit of the group”), and (ii) networks that are built based on specific behavioral criteria that

are directly observed (Franks *et al.* 2010; Croft *et al.* 2011; Farine 2015). Although the  
232 interactions in our study were not directly observed, they were recorded at specialized display  
perches that have a known function in male-male social interactions (Schwartz & Snow 1978;  
234 Ryder *et al.* 2011a). Hence, they do not qualify as the gambit of the group. To further  
demonstrate this point, we performed a pre-network permutation of the raw data to determine  
236 whether the observed network edges occurred more often than expected by chance (Farine 2017).  
This analysis was highly conservative in that it preserved key features of the data including male  
238 visit rates to specific territories within each recording session and lek; it is described in detail in  
the supplement and Fig. S2. The results demonstrated that 95% of the observed network edges  
240 had a greater edge weight than expected under stringent permutation conditions. Moreover, these  
preferred edges had edge weights that were 10-fold to 50-fold greater than expected by chance  
242 under these stringent conditions (Fig. S2). This provides an additional validation to our approach,  
because it indicates that the observed network edges were nearly always preferred, even relative  
244 to other possible interactions within the same lek. These results are also consistent with a  
previous validation study indicating that these methods capture male-male coalition partnerships  
246 that are directly observed (Ryder *et al.* 2012).

Although pre-network data permutations are sometimes used to derive adjusted  
248 association indices, or to prune networks prior to further analysis, we did not take this approach  
for several reasons. First, the statistical rarity of a relationship in our system does not *a priori*  
250 define the importance of any one social interaction, especially given that all of the interactions  
occurred on display territories with specialized function. A single interaction between two rarely  
252 interacting males may have been highly consequential (e.g., if one of those males had a highly  
influential hormone-behavioral phenotype). Conversely, a single interaction between two

254 frequently interacting males may have been relatively unimportant. It would be unwarranted to  
assume that partnership rarity indicates the importance of any single interaction in this context.  
256 Second, and perhaps more importantly, the goal of this study was a comparison across multiple  
networks. Some networks are genuinely less preferential, and more random, than others. If we  
258 modified the network edges based on permutation-based indices, it would disproportionately  
prune the truly random networks, introducing a source of bias that would be contrary to our main  
260 goal. Hence, all further analyses are based on networks where the edge weights are given by the  
observed number of interactions, as this method is most appropriate for our study system and  
262 aims. Below, we also describe a separate node-label permutation that provided an additional  
check on our final statistical analyses.

264

### ***Social Specialization***

266 To quantify social specialization, we sought a metric that would capture the extent to which a  
network was partitioned into exclusive social relationships (as opposed to a network made up of  
268 non-specific or non-exclusive partnerships). To do this, we used a network metric of  
specialization that is commonly used in community ecology called  $H_2'$  (Blüthgen *et al.* 2006).  
270 An advantage of  $H_2'$  is that it is standardized against a theoretical maximum, based on the  
overall activity levels of different nodes and Shannon entropy (Blüthgen *et al.* 2006); this makes  
272 it possible to compare the extent of specialization across different bipartite networks in a  
standardized way. To apply this metric to our manakin data, we converted each lek's social  
274 network into its bipartite adjacency matrix (Fig. 1A), with floaters along one axis, and territory-  
holders on the other, and then calculated social specialization as  $H_2'$  using the bipartite package  
276 (Dormann *et al.* 2019). Higher values of specialization indicate that the network is well-

partitioned (i.e., made up of exclusive relationships), as illustrated in Fig. 1A. We chose to focus  
278 on floater-territorial specialization because these two social classes are well-defined and floater-  
territorial partnerships tend to be the most common in this species (Fig. S3; see also Ryder *et al.*  
280 2011a).

Our measure social specialization at the network level,  $H_2'$ , can also be related to the  
282 exclusivity of social partnerships at the individual level, as used in (Sih *et al.* 2009; Edenbrow *et*  
*al.* 2011; Dakin & Ryder 2018). All else being equal, a highly specialized network is expected to  
284 be made up of individuals who are relatively more exclusive and/or more important towards their  
partners, *sensu* (Sih *et al.* 2009; Dakin & Ryder 2018). Because  $H_2'$  has the properties described  
286 in the previous paragraph, it is more appropriate as the network-level metric of social  
specialization. Note that it is possible, and perhaps even common, for the edge weights in a  
288 highly specialized network to be relatively invariant if the network is not fully connected, as  
shown in the example manakin networks in Fig. 1A. Hence, specialization based on  $H_2'$  is not in  
290 principle related to the network-average coefficient of variation of each individual's edge  
weights (Maldonado-Chaparro *et al.* 2018).

292

### ***Network Stability***

294 We define network stability as the average persistence of network edges through time (Dakin &  
Ryder 2020). To quantify the stability of manakin networks, we compared each lek's social  
296 network from a given recording session to its subsequent recording session within the same field  
season (Fig. 1B). Network stability was then calculated as the number of male-male partnerships  
298 (binary network edges) shared by both time points divided by the number of partnerships at  
either time point (Dakin & Ryder 2020). Higher values of stability indicate greater persistence of

300 social relationships within the network, independent of any changes in the representation of  
particular males (nodes) (Poisot *et al.* 2012). To focus this measure on the persistence of strong  
302 relationships, we computed network stability of partnerships that occurred at least six times  
following (Dakin & Ryder 2020). The threshold of six was chosen because it corresponds to an  
304 average rate of one social interaction per day in our data. We conducted an additional sensitivity  
analysis to verify that alternative thresholds for the stability calculation (greater or less than six)  
306 did not change our main results (see supplement for details). Previous work using this metric of  
stability has shown that the wire-tailed manakin social networks are far more stable than  
308 expected by chance (Dakin & Ryder 2020).

### 310 ***Behavioral Assortment***

Assortment refers to the extent to which individuals associate with similar partners (Fig. 1C); it  
312 can be due to partner choice (homophily), shared environments, or the social transmission of  
behavior (Dakin & Ryder 2018). Assortment was quantified using Newman's assortativity index,  
314 which is a correlation coefficient for the statistical association among linked nodes within a  
network. It ranges from  $-1$  (a negative association), through  $0$  (no association), and up to  $+1$  (a  
316 positive association). To quantify the assortment of social behaviors, we first determined the  
daily frequency of two behaviors for each male: his number of social interactions per day  
318 (strength), and his number of unique social partnerships per day (degree). Strength and degree  
are both repeatable measures of a male's social behavior in our study population (Dakin & Ryder  
320 2018). We used the average log-transformed values of each male's strength and degree within  
the recording session, and then calculated the assortativity coefficient for the entire social  
322 network using the algorithm for weighted networks in the assortnet package (Farine 2016).

Because assortativity values for strength and degree were highly correlated (Pearson's  $r = 0.78$ ,  $p < 0.0001$ ,  $n = 86$  networks), we took the average of these two values as the measure of overall behavioral assortment within the social network. Note that we used log-transformed values of strength and degree because these two variables are strongly positively skewed (Dakin & Ryder 2018; Ryder *et al.* 2020), and assortativity is based on a Pearson's correlation. Finally, we also computed the assortativity of the two discrete status classes (floater and territory-holder), to ensure that our analysis of behavioral assortment was not solely driven by status-assortment.

330

### ***Collective Testosterone***

To understand how hormones might predict network properties, we derived a measure of collective testosterone of each social network. This was based on the hormonal trait that was the best predictor of social behavior in our previous study, referred to as "mean testosterone" (Ryder *et al.* 2020). A male's mean testosterone is his average residual circulating testosterone. It is calculated using a linear regression of log-transformed testosterone to statistically account for the effects of field season, Julian date, time of day when captured, and duration of restraint, all of which may influence point estimates of a male's baseline hormone level (Vernasco *et al.* 2019). Hence, mean testosterone represents a standardized measure of a male's circulating testosterone, independent of his capture conditions (Fig. 2A). Next, to determine collective testosterone, we took the average mean testosterone for each social network, weighted by the interaction frequency (strength) of the males within the network (Fig. 2B). Collective testosterone is thus a group-level characteristic that is weighted towards the males that made the greatest contribution to group social structure. In other words, networks with low collective testosterone are made up of mostly low-testosterone individuals, whereas networks with high collective testosterone are



346 made up of mostly high-testosterone individuals. We calculated collective testosterone separately  
for each status class, because the effects of hormones on social behavior are status-dependent  
348 (Eisenegger *et al.* 2011; Boksem *et al.* 2013; Ryder *et al.* 2020).

### 350 *Statistical Analysis*

To evaluate the hypothesis that collective testosterone predicts network properties, we analyzed  
352 mixed-effects models of the social network properties in the lme4 package (Bates *et al.* 2018).  
The three response variables were social specialization, network stability, and behavioral  
354 assortment (Fig. 1). We used Akaike's Information Criterion (AIC) to compare four candidate  
models for each response variable, as follows: (1) collective testosterone of territory-holders +  
356 collective testosterone of floaters; (2) collective testosterone of territory-holders; (3) collective  
testosterone of floaters, and (4) no testosterone predictors. All of the models included additional  
358 fixed effects to account for field season (a categorical variable with three levels), the average  
Julian date of the recording session, the average number of recorded hours per territory, and the  
360 size of the social network (number of individuals), as well as a random effect of lek to account  
for repeated measures.

362 Model comparison was performed on models fit with maximum likelihood, and the best-  
fit models were re-fit using restricted estimation of maximum likelihood (REML) to derive  
364 parameter estimates (Zuur *et al.* 2009). We used the lmerTest package to compute p-values for  
parameter estimates in the mixed-effects models based on Satterthwaite's method (Kuznetsova *et*  
366 *al.* 2018). We also report Nakagawa and Schielzeth's  $R^2_{\text{LMM}}$  values as an estimate of effect size  
(Nakagawa & Schielzeth 2013). We verified that all models met the assumptions of linear  
368 regression analyses. First, we checked that the Pearson residuals met the assumption of

normality. We visually inspected the partial residual plots for each fixed and random effect, to  
370 confirm that there were no outliers or departures from the assumption of homoscedasticity. To  
check for multicollinearity, we used the performance package (Lüdecke *et al.* 2019) to calculate  
372 variance inflation factors (VIFs), and we verified that all VIFs were between 1 – 1.8.

### 374 *Sample Sizes and Exclusions*

In two field seasons (2016-17 and 2017-18), we performed an experiment as part of a separate  
376 study to test the influence of transiently-elevated testosterone on individuals (n = 5 individuals in  
2016-17 and n = 4 in 2017-18; Ryder *et al.* 2020). The results of that experiment demonstrated  
378 that elevated testosterone caused a temporary decrease in the frequency and the number of social  
partnerships in the altered males (Ryder *et al.* 2020). It is important to note that this experiment  
380 was not designed to test emergent properties at the network level, because it was conducted on a  
limited scale with only one or two individuals temporarily altered within each lek. We therefore  
382 excluded the 6 post-manipulation networks from the main analysis in this study. We verified that  
when we included these manipulated leks, all of our main conclusions were unchanged.

384 After excluding the 6 post-manipulation observations, 80 of the original 86 recording  
sessions remained. Table 1 summarizes the sample sizes for the network-level analyses. In 10  
386 cases, specialization could not be calculated because the bipartite network did not have sufficient  
data to determine  $H_2'$ . Stability could not be calculated in 26 cases, when either the recording  
388 session occurred at the end of a field season, or when there were insufficient partnerships that  
met the criteria for the stability calculation.

390

### *Node-label Permutation Analysis*

392 To evaluate the possibility that our results could be influenced by other properties of the leks that  
were independent of hormonal traits, we also performed a statistical permutation of the post-  
394 network data (Farine 2017). The purpose of this analysis was to verify that the results were  
driven by (and sensitive to) the relative contribution and social position of different males. To do  
396 this, we performed a statistical permutation that randomized the node labels (male IDs) within  
each of the social networks, retaining network topology, and leaving each male's testosterone  
398 traits unchanged. Hence, this analysis preserved which males were present in which recording  
session, but it randomized the relative position and contribution of each male. After generating  
400 1,000 of these node-label permutation datasets, we recalculated specialization, stability, and  
assortment, and then refit the top models from our mixed-model analysis. We then compared the  
402 slope estimates from the observed data to those derived from 1,000 node-label permutations. As  
a one-sided p-value, we calculated the proportion of slope estimates from the node-label  
404 permutations that were more negative than the corresponding estimate from the observed data.

## 406 **Results**

The lek social networks had 14 males on average, but there was considerable variation among  
408 leks ranging from 3 to 43 individuals (Fig. S1). Additional descriptive statistics are provided in  
Table 1. Although network size has a lognormal distribution (Fig. S1), all other emergent  
410 properties of the social structure were approximately normally distributed (Fig. S4).

412

414

416 **Table 1. Descriptive statistics for manakin social networks.** Means and standard deviations  
(SD) are provided for each field season. The bottom row provides the sample sizes for the  
418 number of social networks analyzed ( $n_{\text{obs}}$ ) at each lek ( $N_{\text{lek}}$ ). Additional data is provided in the  
supplement in Fig. S1 and Fig. S4.

Field season	Network size (# birds)	Social specialization	Network stability	Behavioral assortment	Collective T (terr.)	Collective T (floa.)
15-16	14.5 (8.9)	0.50 (0.22)	0.43 (0.25)	0.01 (0.36)	0.44 (0.42)	-0.31 (0.56)
16-17	17.8 (10.5)	0.30 (0.24)	0.47 (0.20)	0.06 (0.30)	0.49 (0.24)	-0.22 (0.37)
17-18	10.3 (4.5)	0.42 (0.30)	0.42 (0.27)	0.02 (0.37)	0.43 (0.40)	-0.70 (0.46)
Sample size	$n_{\text{obs}} = 80$ $N_{\text{lek}} = 11$	$n_{\text{obs}} = 70$ $N_{\text{lek}} = 11$	$n_{\text{obs}} = 54$ $N_{\text{lek}} = 11$	$n_{\text{obs}} = 80$ $N_{\text{lek}} = 11$	$n_{\text{obs}} = 80$ $N_{\text{lek}} = 11$	$n_{\text{obs}} = 80$ $N_{\text{lek}} = 11$

420 We found that the collective testosterone of territorial males could predict all three emergent  
properties of the social networks (specialization, stability, and assortment). The leks with greater  
422 representation of high-testosterone territorial males were less specialized, less stable, and more  
negatively assorted (Fig. 3; all  $p \leq 0.03$  in mixed-effects models). The slope coefficients for these  
424 three relationships were also all greater than expected under a node-label permutation (inset  
panels, Fig. 3; all  $p < 0.02$ ). Model selection results for the observed data indicated considerable  
426 uncertainty in the best-fit model for each of the three network properties analyzed (Table S1).  
However, the collective testosterone of territory-holders was a significant predictor in all of the  
428 best-supported models (Table S2). In contrast, the collective testosterone of floater males was  
not a significant predictor of network properties in any of the best-fit models (Table S2).

430 We did not detect any significant effects of Julian date on network properties within our  
study period, but we did observe some significant year-to-year differences (e.g., social  
432 specialization and behavioral assortment in Table S2). Assortment was the only property that  
was significantly related to network size and recording effort (Table S2). All else being equal,  
434 behavioral assortment was more positive in larger networks, and it was more negative in  
networks that had longer recording sessions.

436  $R^2_{\text{LMM}(m)}$  provides an estimate of the proportion of variance explained by the fixed effects  
in a model (Table S1). The  $R^2_{\text{LMM}(m)}$  for assortment in the best-fit model was 0.52. This indicates  
438 that about 52% the variation in behavioral assortment could be explained by the combined  
associations with collective testosterone, network size, sampling effort, and annual variation  
440 (Table S2). The  $R^2_{\text{LMM}(m)}$  for stability was 0.12, indicating that collective testosterone and the  
other predictors (network size, sampling effort, year) could explain about 12% the variation in  
442 that metric (Table S2). Finally, for specialization, the  $R^2_{\text{LMM}(m)}$  indicated that the combined  
effects of testosterone and these other sources of variation together explained about 20% of the  
444 variation (Table S2).

## 446 **Discussion**

The collective testosterone of the dominant, territory-holding males within a lek was associated  
448 with multiple emergent properties of the social network (Fig. 3). Variation in collective  
testosterone is a function of both the number of high-testosterone males and their frequency of  
450 social interactions. Our results indicate that the hormone-mediated behavior of these individuals  
may affect all three social network properties of specialization, stability and assortment. This  
452 indicates that the effects of testosterone on dominant males may mediate an extended phenotype  
with the power to shape social structure (Dawkins 1982). In contrast, the collective testosterone  
454 of floater males was not significantly associated with any of the emergent network properties  
(Table S2).

456 How can the relationship between hormone levels and network properties be explained in  
terms of individual mechanisms? Given that testosterone has antagonistic effects on the sociality  
458 of territorial males (Ryder *et al.* 2020; Vernasco *et al.* 2020), we hypothesize that the behavior of

high-testosterone individuals can cause several features of the social organization to break down.

460 Our previous results showed that high-testosterone dominant individuals have a reduced ability  
to attract and maintain social partners (Ryder *et al.* 2020). We propose that this weakening of  
462 social relationships may cause floater males to prospect elsewhere for new partners, negatively  
affecting both the stability and specialization of the lek network as a whole. Likewise, high-  
464 testosterone dominant males may inhibit the processes of social contagion, reciprocity, and/or  
behavioral matching that can cause positive behavioral assortment (Dakin & Ryder 2018).

466 Recent studies have found that in other social animals, sparse and specialized social networks  
can be associated with fitness benefits (Stroeymeyt *et al.* 2018); hence, a breakdown to this  
468 organization may incur costs (Maldonado-Chaparro *et al.* 2018). Testing our proposed  
mechanism for the link between hormone-mediated behavior and network dynamics will require  
470 direct observation of the individual social behaviors that occur within dyads, and how these  
behaviors change through time. Because our current data cannot assess the fine-scale valence of  
472 social interactions, further studies are needed that combine direct observation with high-  
throughput data on social network dynamics.

474 We included several additional parameters in our analyses to account for social network  
size and sampling effort. Although it was not one of our main hypotheses, we noted that network  
476 size was positively associated with behavioral assortment (Table S2). In other words, males were  
more likely to associate with behaviorally similar partners in larger leks, whereas they were more  
478 likely to associate with dissimilar partners in smaller leks. Effects of group size on assortment  
have been noted in a few other studies, although the form of this relationship varies (Griffiths &  
480 Magurran 1997; Ilmarinen *et al.* 2017; McDonald *et al.* 2017). In manakins and other lekking  
systems, larger leks are known to have heightened display activity and higher female visitation

482 rates (Lank & Smith 1992; Durães *et al.* 2009). This raises the possibility that social facilitation  
and heightened activity may be associated with increased homophily and/or behavioral matching  
484 (either through partner choice, contagion, or reciprocity). Another plausible explanation is that  
smaller social groups may constrain these behavioral processes, by making it more difficult to  
486 find or match a suitable partner. This hypothesis could be explored in experiments on captive  
systems and simulation models.

488 Behavioral assortment was also more positive in networks that were recorded for less  
time in our study (in other words, leks where males associated with behaviorally similar partners  
490 tended to be recorded for fewer days). Recording time was designed to be approximately even  
among leks (Fig. S1), with the most common reason for an extended recording duration being  
492 inclement weather that extended the recording session. Therefore, we speculate that inclement  
weather may have reduced the amount of behavioral matching (assortment) while also affecting  
494 recording time. Although we did not collect data on weather at each lek as this was not our main  
goal, the question of how inclement weather affects group-level social dynamics is an interesting  
496 one that merits further study.

Conducting experimental tests of causation at the level of whole social networks remains  
498 a major challenge in ecology (Pinter-Wollman *et al.* 2014; James *et al.* 2009). Although our  
node-label permutation analysis provides evidence that our results are not merely due to  
500 structural differences among networks, we cannot rule out the possibility that high-testosterone  
individuals chose to participate in certain networks due to other factors that may also influence  
502 the emergent properties of the network (e.g., environmental quality and/or female activity). It is  
important to note that in this system, as in many other wild animals, controlled experimental  
504 manipulations of the broader social network structure are not yet possible (Zyphur *et al.* 2009;

Akinola *et al.* 2016). Nevertheless, our data here indicate that the increased prevalence of  
506 dominant, high-testosterone individuals can predict changes social dynamics and subsequent  
higher-order network structure. These findings establish that hormone-behavior relationships are  
508 not limited to one individual, but instead hormones have population-level consequences  
(McClintock 1981; Robinson 1992).

510         Increasing evidence demonstrates that the structure and stability of social networks is  
often associated with benefits—and costs—during foraging, breeding, and disease outbreaks (Silk  
512 *et al.* 2010; Maldonado-Chaparro *et al.* 2018; Riehl & Strong 2018; Stroeymeyt *et al.* 2018).  
Given the widespread influence of steroid hormones on social interactions across vertebrates  
514 (Adkins-Regan 2005), we expect that collective testosterone will be broadly associated with  
social network properties in other systems. The direction of these effects may depend on the  
516 context of the behavioral interactions that form the social network, and whether these  
interactions are primarily cooperative or competitive in nature. Taken together with previous  
518 studies, we propose that testosterone-mediated behavior can alter social network dynamics in  
ways that often impede the evolution of stable social relationships and cooperation.



## 520 **Figure Legends**

### 522 **Figure 1. Example social networks illustrating social specialization, network stability, and**

**behavioral assortment.** (A) Social specialization is measured using the bipartite form of the

524 social network. In the example on the left, the associations between floater males and territory-holders are poorly partitioned, creating a network with a relatively low specialization. On the

526 right, there is greater partitioning, such that each floater male maintains a smaller number of associations with specific territory-holding males. (B) Network stability is measured by

528 evaluating the persistence of partnerships from one recording session ( $t_1$ ) to the next ( $t_2$ ). The example at the top of (B) has a lower stability than the example on the bottom. (C) Behavioral

530 assortment measures the tendency of like to associate with like. In (C), nodes are shaded to indicate a continuous gradient of daily behavior (in this case, each male's average daily strength

532 is shown). In the example network on the left, the males tend to associate with behaviorally

dissimilar partners, yielding a negative behavioral assortment. In the example on the right, the

534 males tend to associate with behaviorally similar partners, yielding a positive assortment. See Table 1 for additional data.

536

**Figure 2. Collective testosterone of manakin social networks.** (A) Circulating testosterone

538 varies among individual males. This graph shows repeated measures from 210 individual male manakins, sorted along the x-axis by mean testosterone, a standardized measure of a male's

540 average circulating testosterone level (Ryder *et al.* 2020). Opacity is used to denote the two male status classes (with subordinate floaters colored semi-transparent, and dominant territory-holders

542 colored opaque). Color ramping is used to denote each individual's hormone phenotype. (B-D)

544 These data were used to define collective testosterone in the present study. Node colors indicate  
an individual's mean testosterone following the scale in (A). The collective testosterone of each  
social network is calculated as the average of the individual hormone phenotypes, weighted by  
546 strength, and is shown below each example. Collective testosterone was determined for each  
status class separately. See Table 1 for additional data.

548

**Figure 3. Collective testosterone predicts the structure of the social network.** The networks  
550 with higher-testosterone dominant males were less specialized, less stable over time, and had  
more negative behavioral assortment. Each plot shows the partial residuals from a statistical  
552 analysis that also accounts for field season, the average Julian date of the recording session, the  
number of recording hours, network size, and lek identity. Because floater and territorial males  
554 can differ in behavior, the analysis of behavioral assortment also accounted for status assortment  
within each network. Different symbols are used to indicate repeated measures of 11 different  
556 leks, colored according to the collective testosterone scale in Fig. 2. Inset panels show the results  
of node-label permutation tests. In each case, the slope in the best-fit model (solid vertical line) is  
558 significantly more negative than expected based on the distribution of permuted estimates (grey  
distribution, dotted line is at 0). See Tables S1-S2 for additional data.

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566 **Author Contributions**

RD, ITM, BMH, and TBR designed the study. ITM, BMH, BJV, and TBR collected the data.  
568 RD, ITM, and TBR analyzed the data. RD and TBR wrote the manuscript. All authors edited the  
manuscript.

570

**Declaration of Interests**

572 The authors declare no competing interests.

574 **Data Availability**

All data and R scripts necessary to reproduce this study are available for download at:

576 <https://figshare.com/s/13a311662fee686fa4f3>

578 **Supporting Information**

Supplemental text, Figures S1-S5, and Table S1-S3 in the attached PDF

580

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Figure 1

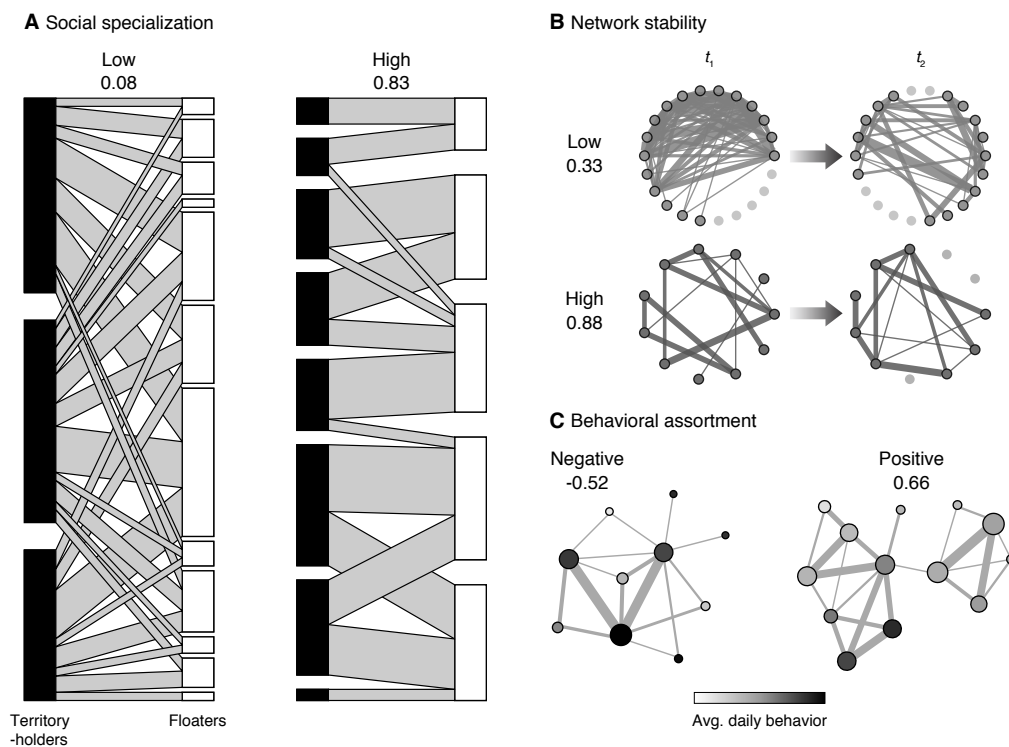


Figure 2

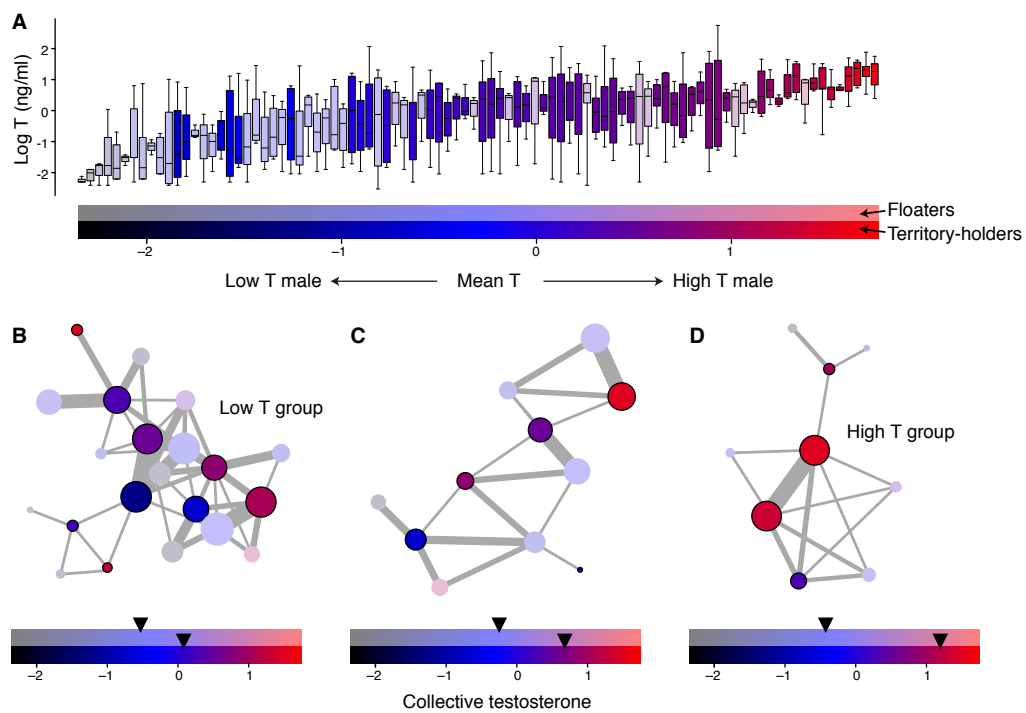


Figure 3

