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Testosterone-mediated behavior shapes the emergent properties of social networks

Roslyn Dakin[1,2], Ignacio T. Moore[3], Brent M. Horton[4], Ben J. Vernasco[3], T. Brandt Ryder[1,5]

[1]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20013, USA
[2]Current address: Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada
[3]Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia 24061, USA
[4]Department of Biology, Millersville University, Millersville, Pennsylvania 17551, USA
[5]Current address: Bird Conservancy of the Rockies, Fort Collins, Colorado, 80525, USA

Correspondence: rydert@si.edu

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Abstract

1. Testosterone is a key regulator of vertebrate social behavior. As such, testosterone can mediate and respond to social interaction dynamics.
2. Although experiments have demonstrated that testosterone signaling pathways can influence aggression and cooperation, no study has examined the links between hormone levels, behavioral phenotypes, and emergent properties of the social network. In other words, how do mechanisms underlying an individual's social behavior scale-up to influence the emergent properties of the social network?
3. Here, we address this question by studying wire-tailed manakins, a species of bird in which males cooperate to court females at sites known as leks. Our previous experiments established that testosterone can influence the social behavior of individual male manakins. In the present study, we use an automated proximity system to monitor multiple manakin leks and measure the social network at each lek repeatedly through time. We also quantified the testosterone phenotype of all individuals in the lek.
4. Our analysis examines how the collective hormone phenotype of individuals within the lek affects three emergent properties of the social network: social specialization (the exclusivity of social relationships), network stability (the persistence of partnerships through time), and behavioral assortment (like associating with like). These three properties are expected to enhance the benefits of cooperation. We found that the manakin social networks with high-testosterone, dominant individuals were less specialized, less stable, and had more negative behavioral assortment.

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5. These results provide evidence that hormones can act as an extended phenotype that shapes the broader social architecture of animal groups. High-testosterone groups exhibit collective behaviors that are predicted to impede the evolution of cooperation.

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

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Introduction

Testosterone signalling pathways can both mediate and respond to dynamic social environments in a diversity of vertebrates (Wingfield *et al.* 1990; Oyegbile & Marler 2005; Adkins-Regan 2005; Goymann 2009; Fuxjager *et al.* 2010; Eisenegger *et al.* 2011). For example, hormone-signaling pathways at the level of the individual are essential for the development and expression of complex behavioral phenotypes (Cohen *et al.* 2012), which are hypothesized to shape social interaction dynamics and higher order social network structure. Testing this hypothesis is challenging, because it requires linking fine-scale measures of behavior and physiology with broad-scale measurements that characterize the collective behavior of the group (Krause & Ruxton 2002).

Here, we leverage a large and comprehensive dataset on the circulating hormone levels, behavioral phenotypes, and social networks of a cooperative bird, the wire-tailed manakin (*Pipra filicauda*), to test the hypothesis that testosterone-mediated behavior drives emergent social structure. Male wire-tailed manakins form cooperative display coalitions on sites known as leks to attract females (Heindl 2002). These coalition partnerships are essential for male fitness (Ryder *et al*. 2008, 2009) and form the basis of complex and dynamic social networks (Ryder *et al*. 2008, 2011a; Dakin & Ryder 2018). The social networks of wire-tailed manakins can also exhibit temporal variation in structure (Dakin & Ryder preprint in review). This is important because the emergent properties of the social network are theoretically predicted to influence the costs and benefits of cooperation, and hence shape selection on individual behavior. For example, cooperation in social networks is favored when individuals interact with a limited set of familiar partners, when these relationships are temporally stable, and when helping is

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reciprocated by immediate neighbors in the group (Trivers 1971; Roberts & Sherratt 1998; Ohtsuki *et al.* 2006).

Can hormone-phenotypes at the individual level scale-up to influence these processes? We have previously shown that male manakins differ in their circulating testosterone levels, with some individuals have consistently higher testosterone than others (Fig. 1A). Moreover, variation in testosterone level can also explain repeatable, among-individual differences in the frequency and number of social partnerships (Ryder *et al.* in press). As observed in other vertebrates (Eisenegger *et al.* 2011; Boksem *et al.* 2013), these hormone-behavior relationships are status-specific in wire-tailed manakins. Among dominant, territory-holding males, high testosterone levels are associated with reduced cooperative behavior (Ryder *et al.* in press). However, in the subordinate, "floater" males, high testosterone is associated with increased cooperative behavior and subsequent territory acquisition (Ryder *et al.* in press), both of which are essential for reproductive fitness (Ryder *et al.* 2008, 2011b).

In this study, we used an automated proximity data-logging system to record over 36,000 unique male-male social interactions. These data allowed us to analyze repeated measures of the weighted social networks at 11 different leks where manakin coalitions occur. A recent study showed that the collective hormonal profile of human social groups can predict group success at social tasks (Akinola *et al.* 2016). Hence, we similarly defined "collective testosterone" for manakin groups as the weighted average testosterone phenotype of the individuals comprising each lek social network, whereby each male's contribution was weighted by his social activity (i.e., frequency of cooperative interactions or "strength"). Because hormone-behavior relationships are status-specific (Ryder *et al.* in press), collective testosterone was calculated for each of the two status classes separately. As illustrated in Fig. 1B, this measure ranks social

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networks on a scale ranging from those made up of mostly low-testosterone individuals, to those made up of mostly high-testosterone individuals.

We evaluated whether collective testosterone was associated with three emergent properties of social networks. The first property, social specialization, is a measure of the exclusivity of the relationships between coalition partners. To quantify specialization at the network level, we used the H_2' metric from community ecology, which provides a standardized ranking of bipartite networks on a scale from highly generalized to highly specialized (Blüthgen *et al.* 2006). In the context of manakin behavior, highly specialized networks exhibit a high frequency of exclusive partnerships between males of different status classes, as illustrated in Fig. S1. In other species, social specialization has been found to maximize the quality and coordination of different types of behaviors (Jehn & Shah 1997; Laskowski *et al.* 2016); in manakins, we expect specialization to improve the signal quality of male-male courtship displays. Greater specialization is also expected to minimize conflict over mating and territorial ascension opportunities (Schjelderup-Ebbe 1922; McDonald 1993).

The second property, network stability, quantifies the average persistence of social partnerships through time (Dakin & Ryder preprint in review; Poisot *et al.* 2012). Coalition partnerships require the coordination of complex behaviors, and previous empirical work 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 the opportunity for sustained reciprocity within the network (Trivers 1971; Roberts & Sherratt 1998; Croft *et al.* 2006). The third property, behavioral assortment, captures the extent to which males interact with partners who express similar behaviors (i.e., is like associated with like? (Croft *et al.* 2006; Farine 2014)). At the proximate level, positive assortment may represent the

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outcome of generalized reciprocity (Fowler & Christakis 2010; Dakin & Ryder 2018). 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 networks, we used a composite measure that averaged the assortativity of "strength" (a male's frequency of cooperative interactions) with that of "degree" (his number of cooperative partnerships) (Dakin & Ryder 2018). Examples of networks illustrating behavioral assortment are also shown in Fig. S1.

Materials and Methods

Study Population

We studied wire-tailed manakins (*Pipra filicauda*) at the Tiputini Biodiversity Station in Orellana Province, Ecuador (0º 38' S, 76º 08' W). This population of *P. filicauda* has been studied and individuals color-banded annually since 2002 (Ryder *et al.* 2008, 2009). Wire-tailed manakins are a long-lived species in which the males form cooperative display coalitions to court females on sites known as leks (Heindl 2002). There are two male status classes in *P. filicauda*: subordinate non-territorial floater males, and dominant territorial males. Previous research has established that territory ownership is a prerequisite for mating, and that both floaters and territory-holders benefit from cooperative partnerships (Ryder *et al.* 2008, 2009). Specifically, floaters with more social partners are more likely to inherit a territory, and territory-holders with more partners achieve greater reproductive success (Ryder *et al.* 2008, 2009). The present study was conducted on 11 leks where the males perform their cooperative courtship displays during peak breeding activity (December-March) across three field seasons: 2015-16, 2016-17 and 2017-18 (Ryder *et al.* in press). All research was approved by the Smithsonian ACUC (protocols

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#12-23, 14-25, and 17-11) and the Ecuadorean Ministry of the Environment (MAE-DNB-CM-2015-0008).

Testosterone Assay

Male manakins were caught at leks using mist-nets up to three times per field season. Following capture and removal from the mist net, a small 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 (Ryder *et al*. 2011b; Vernasco *et al*. 2019; Ryder *et al*. in press). Plasma volume was measured to the nearest 0.25 ul and stored in 0.75 ml of 100% ethanol (Goymann *et al.* 2007). Plasma testosterone was double extracted using dichloromethane. Following extraction, direct radioimmunoassay was used to measure the total plasma androgen concentration (ng/ml) adjusted by the extraction 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 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 conservative estimate. As reported in our previous study (Ryder *et al.* in press), 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 2017-18, respectively; the inter-assay coefficient of variation was 19.5%.

Behavioral Assay

To quantify social behaviors, we used an automated proximity data-logging system to monitor the activity on the territories of 11 leks (Ryder *et al*. 2012; Dakin & Ryder 2018; Ryder *et al.* in

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press). At the beginning of each field season, males were outfitted with a coded nano-tag (NTQB-2, Lotek Wireless; 0.35 g). The tags transmitted a unique VHF signal ping once per 20 s for three months. In total, 296 tag deployments were performed on 180 individual males, 178 of whom also had hormone data (mean 3 hormone samples per male ± SD 1.5). Approximately 10 days (± SD 7) after tagging and sampling was completed at a given lek, a proximity data-logger (SRX-DL800, Lotek Wireless) was deployed within each territory to record tagged males within a detection radius of 30 m (a distance that corresponds to the average diameter of a manakin display territory (Heindl 2002; Dakin & Ryder 2018)). Proximity recording sessions ran from 06:00 to 16:00 for ~6 consecutive days (± SD 1 day) and were performed ~3 times per season at each lek. Prior to data-logger deployment, each territory was also observed on non-recording days to identify the territory-holder based on his color-bands, following the protocol in previous studies (Ryder *et al*. 2008, 2009). These status assignments were subsequently verified in the proximity data. In total, we conducted 86 recording sessions (29,760 data-logger hours) representing repeated measures of the social activity at 11 different leks.

To quantify social interactions in the proximity data, the tag detections were filtered using an spatiotemporal algorithm to identify unique joint detections, when two males were located within a display territory (Ryder *et al.* 2008, 2012; Dakin & Ryder 2018). A detailed description of the algorithm is provided in (Dakin & Ryder 2018). A ground-truthing experiment in that study also confirmed that these joint detections represent occasions when two males were < 5 m apart (Dakin & Ryder 2018), corresponding to the range required for a typical male-male social display (Heindl 2002). An additional validation study also confirmed that the social interactions defined by this method corresponded to display coalitions that were directly

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observed (Ryder *et al.* 2012). In total, we identified 36,885 unique social interactions over the three field seasons in this study.

Quantification and Statistical Analysis

All quantitative analyses were performed in R (R Core Team 2018).

Network Analysis

We used the igraph package (Csardi & coathors 2018) to construct a weighted social network for each lek recording session. The individual males who interacted on the lek were defined as the nodes, and the links (or edges) between them were weighted by the social interaction frequencies. We quantified three emergent network properties for each lek recording session: social specialization, network stability, and behavioral assortment, as described below.

For specialization, we sought a measure that would capture the extent to which a network was partitioned into exclusive social relationships (as opposed to a network made up of non-specific or non-exclusive partnerships). To do this, we used a network metric of specialization that is commonly used in community ecology to analyze ecological networks, called H_2' (Blüthgen *et al.* 2006). 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 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 social network into its bipartite adjacency matrix, with floaters along one axis, and territory-holders on the other, and then calculated social specialization as H_2' using the bipartite package (Dormann *et al.* 2019). Higher values of this metric indicate that the network is made up

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of more exclusive relationships, as illustrated in Fig. S1. We chose to focus on floater-territorial specialization because these are by far the most common partnerships in this social system with reproductive benefits to both parties (Ryder *et al*. 2011a).

To quantify the stability of social relationships, we compared each lek social network derived from one recording session to that derived from the subsequent recording session within the same field season (if available). Network stability was then calculated as the number of male-male partnerships (network edges) shared by both time points divided by the number of partnerships at either time point (i.e., the intersection divided by the union (Dakin & Ryder preprint in review)). Higher values of stability indicate greater persistence of social relationships within the network, independent of any changes in the representation of particular males (nodes) (Poisot *et al*. 2012). To reduce the influence of partnerships that occurred only rarely (Farine *et al*. 2017), prior to the stability calculation we filtered the data to include only significant edges that occurred more often than expected in 1,000 random permutations of the interaction data, and at least six times during a recording session (i.e., on average, once per day). Our previous work has established that network stability is robust to alternative thresholds for occurrence and that the wire-tailed manakin networks are more stable than expected by chance (Dakin & Ryder preprint in review).

Assortment refers to the extent to which individuals associate with similar partners; it 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, 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 positive association). To quantify the assortment of cooperative behaviors, we first determined

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the daily frequency of two behaviors for each male: his number of social interactions (strength), and his number of unique social partnerships (degree) per day (Dakin & Ryder 2018). Strength and degree are both repeatable measures of a male's cooperative behavior in our study population (Dakin & Ryder 2018). Next, we computed the average log-transformed strength and degree within the recording session for each individual, and then calculated a weighted assortativity coefficient for the entire social network using the assortnet package (Farine 2016). Because assortativity values for strength and degree were highly correlated (Pearson's $r = 0.78$, $p < 0.0001$, $n = 86$), we took the average of these two values as the measure of overall behavioral assortment within the social network. Finally, we also computed the assortativity of the two discrete status classes, to ensure that our analysis of behavioral assortment was not solely driven by status-specific patterns of assortment.

Statistical Models

Following our previous study (Ryder *et al.* in press), we characterized each male's average circulating testosterone after statistically accounting for capture conditions ("mean T" in (Ryder *et al.* in press)), including the time of day and duration of time the bird was in the mist-net (Vernasco *et al.* 2019). This measure of among-individual testosterone variation was a significant predictor of cooperative behavior in our study system, albeit with different relationships within each status class (Ryder *et al.* in press). To quantify collective testosterone, we took the average "mean T" within the social network, weighted by each male's interaction frequency (strength) as a measure of his contribution to the network. We calculated collective testosterone separately for each status class because the effects of hormones on social behavior

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are status-dependent in this and other species (Eisenegger *et al.* 2011; Boksem *et al.* 2013; Ryder *et al.* in press).

To evaluate whether collective testosterone could explain emergent social network properties, we fit mixed-effects models using the packages lme4 and lmerTest (Bates *et al.* 2018; Kuznetsova *et al.* 2018). Each model was fit with a random effect of lek to account for repeated measures (n = 86 measures of 11 leks, except for stability which had n = 60 because stability requires a subsequent recording session). We used Akaike's Information Criterion to compare goodness-of-fit for four candidate models, as follows: (1) collective testosterone of territory-holders + collective testosterone of floaters; (2) collective testosterone of territory-holders; (3) collective testosterone of floaters, and (4) no testosterone predictors. All of the candidate models also included additional fixed effects to account for field season (a categorical variable with three levels), the average Julian date of the recording session, the number of recorded hours per territory, and the size of the social network (number of individuals). Continuous predictors were standardized (mean = 1, SD = 1) prior to being entered into the analysis so that the slope estimates would be comparable with other models. Model selection was performed on models fit with maximum likelihood, and then the best-fit models were refit using restricted estimation of maximum likelihood (REML) to determine p-values (Zuur *et al.* 2009). We used the lmerTest package to compute p-values for generalized mixed-effects models based on Satterthwaite's method (Kuznetsova *et al.* 2018).

In two field seasons (2016-17 and 2017-18), nine of the territory-holders were part of an experiment testing the influence of transiently-elevated testosterone on individual behavior (n = 5 individuals in 2016-17 and n = 4 in 2017-18 (Ryder *et al.* in press)). The results of that experiment demonstrated that elevated testosterone caused a temporary decrease in the frequency

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and the number of cooperative partnerships in the altered males, relative to control males (Ryder *et al.* in press). However, it is important to note that this experiment was not designed to test effects at the collective level, because it was conducted on a limited scale whereby only one or two individuals were temporarily altered in only four leks. Therefore, our main analysis here excluded data from recording sessions at manipulated leks. However, we verified that when we repeated our analyses including these manipulated leks, the main conclusions were unchanged. Furthermore, we did not detect any statistically significant effect of the individual hormone manipulation on the three network-level properties (i.e., specialization, stability, and assortment; all $p > 0.16$). Finally and most importantly, controlling for the manipulation also did not affect any of our conclusions about collective testosterone shown in Fig. 2

Randomization Test

We performed a randomization test using a null model (Farine *et al*. 2017) to assess the effect of randomizing each social network, leaving the testosterone data unchanged. To generate the null data, we randomly permuted the node labels (ID labels) within each of the 86 social networks, retaining all other features of the social network. After generating each null dataset, we recalculated the network-level properties (specialization, stability, and assortment), and then refit the top models from our original analysis. We then compared the slope estimates from the observed data to the values obtained from 1,000 of these null permutations.

Perturbation Analysis

We performed a social perturbation analysis to determine the sensitivity of our results to the composition of the social network (Pinter-Wollman *et al.* 2014). This simulation exercise

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proceeded by selectively removing males from the social networks in the observed data, to test how much perturbation was necessary to disrupt our main results. We set the number of individuals removed as a constant proportion of the total number of individuals in the network so that the effect size would be standardized across heterogeneous networks. To do this, we performed six iterations removing an increasing number of either floater or territory-holding males with each iteration (node removal iterations = 10%, 20%, 30%, 40%, 50%, and 60% of the individuals in the relevant status class). The number of individuals removed from each network was rounded, such that it was at least one, but not all of the individuals from that status class. To evaluate the effect of gradually increasing the amount of social perturbation, the simulation proceeded by removing less social (i.e., low-strength) individuals first. After severing all social ties of the removed individuals, we recalculated the network properties, and refit the top models from our original analysis (Table S1). Then, we compared the beta coefficients for collective testosterone (standardized slope estimates) to those derived from the original data. A result was considered robust to perturbation if two criteria were met: the slope in the removal analysis was significantly different from 0, and it was within the 95% confidence interval of the slope from the original data.

Results

We found that the collective testosterone of territorial males could predict all three properties of the social networks. Specifically, the leks with a greater number of high-testosterone territorial males were less specialized, less stable, and more negatively assorted (Fig. 2; all $p < 0.03$). The coefficients of these relationships were also greater than expected under a null permutation of the data within each social network (inset panels, Fig. 2; all $p < 0.015$).

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We found that removing as few as 10% of the males in either social class (dominant territory-holders or subordinate floaters) eliminated the relationship between stability and collective testosterone. This indicates that stability is highly sensitive to the presence of both status classes of males within the network. In contrast, behavioral assortment was more robust to the removal of individuals: we had to drop 40% of the territory-holders, or 60% of the floaters, to disrupt its association with testosterone. Finally, the sensitivity of social specialization was also status-dependent: we found that removing only a few floaters (10%) decoupled the relationship between specialization and testosterone, whereas 40% of the territorial individuals had to be removed to eliminate this result.

Discussion

We found that the collective testosterone of dominant, territory-holding males predicted multiple features of the social network structure. In contrast, the collective testosterone of the floater males did not predict social network properties. Therefore, although testosterone may determine the behavior of both floater and dominant males (Ryder *et al.* in press), its effects on dominant males may represent an extended phenotype that ultimately determines social structure (Dawkins 1982).

How can the relationship between hormone levels and network properties be explained in terms of individual behaviors? Given that testosterone has antagonistic effects on the cooperative behavior of territorial males (Ryder *et al.* in press), we hypothesize that the behavior of high-testosterone individuals causes multiple properties of stable cooperative networks to rapidly break down. Based on our results in previous studies (Dakin & Ryder preprint in review; Ryder *et al.* in press), the high-testosterone dominant individuals have a reduced ability to attract and

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maintain stable coalition partners (Ryder *et al.* in press). This weakening of coalition bonds may cause floater males to prospect elsewhere for new partnerships, negatively impacting both the overall specialization and stability of the social network (Dakin & Ryder preprint in review). Likewise, we propose that behavioral assortment becomes more negative in social networks with many high-testosterone individuals, because these individuals may inhibit the processes of social contagion, reciprocity, and/or behavioral coordination that contribute to positive assortment (Dakin & Ryder 2018).

Our perturbation analysis suggests that the behavior of the floater males (i.e., initiating partnerships) may play a key role in determining social specialization within the network. Although this analysis is not a substitute for experimental tests *in vivo* (Zyphur *et al.* 2009; Akinola *et al.* 2016), it can provide a good indication of the importance of particular individuals to emergent properties of the network. Conducting experimental tests of causation at the level of whole social networks remains a major challenge (Pinter-Wollman *et al.* 2014; James *et al.* 2009). With the present data, we cannot rule out the possibility that high-testosterone individuals chose to participate in certain networks due to other factors that may also influence emergent network properties (e.g., environmental quality and/or female activity). Nevertheless, our data show that the increased prevalence of dominant individuals with high-testosterone is associated with behavioral dynamics and changes to higher-order social structure that can ultimately destabilize cooperation. These findings establish that hormone-behavior relationships are not limited to one individual, but instead they may act as extended phenotypes that have population-level consequences (McClintock 1981; Dawkins 1982; Robinson 1992). Specifically, we suggest that testosterone is a physiological driver of social network dynamics that may impede the evolution of cooperation.

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Figure Legends

Figure 1. Testosterone varies at the level of the social network. (A) Circulating testosterone varies within- and among-individuals. This graph shows repeated measures from 210 individual male manakins, sorted along the x-axis by their average testosterone level (standardized "mean T"; modified from Ryder et al. (Ryder *et al.* in press)). Opacity is used to denote the two male status classes (with subordinate floaters colored semi-transparent, and dominant territory-holders colored opaque) and color ramping is used to denote each individual's hormone phenotype. (B-D) Three examples of the social network structure and hormone phenotypes at manakin display leks. Each node (circle) represents an individual male who engaged in social interactions at the lek. Node size is scaled to his interaction frequency ("strength"); this parameter is also used to weight each male's contribution to collective testosterone. Edge thicknesses are also scaled to the log-transformed interaction frequencies for each observed coalition. Node colors indicate an individual's hormone phenotype following the scale in (A). The collective testosterone of the social network is calculated as the average of the individual hormone phenotypes within the social network, weighted by strength as a measure of each male's contribution. Because hormone-mediated cooperation is status-specific (Ryder *et al.* in press; Eisenegger *et al.* 2011), collective testosterone was determined for each status class separately (indicated by the semi-transparent and opaque color scales for floaters and territory-holders, respectively). See Figure S1 for additional data.

Figure 2. Collective testosterone predicts the emergent properties of cooperative social networks. Lek social networks with greater representation of high-testosterone territorial

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individuals were less specialized (i.e., partnerships were less exclusive), less stable over time, and had more negative behavioral assortment (i.e., individuals tended to associate with more dissimilar partners). Each plot shows the partial residuals from a statistical analysis that also accounts for field season, the average Julian date of the recording session, the number of recorded hours per territory, and network size (fixed effects), as well as a random effect of lek identity. Because the two status classes differ in behavior (Dakin & Ryder 2018), the analysis of behavioral assortment also accounted for assortment of the status classes within each network as an additional covariate. Different symbols are used to indicate repeated measures of 11 different leks networks, colored according the collective testosterone gradient in Figure 1B. Inset panels show the results of a null randomization test. In each case, the slope in the best-fit model (solid vertical line) was significantly more negative than expected in the null permutations of the social networks (grey distribution; dotted vertical line indicates 0; all p-values < 0.015). See Tables S1 and S2 for additional data.

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Author Contributions

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

Declaration of Interests

The authors declare no competing interests.

Data Availability

All data and R scripts necessary to reproduce this study are available for download at: https://figshare.com/s/13a311662fee686fa4f3

Supporting Information

Figure S1 and Table S1-S2 in the attached PDF

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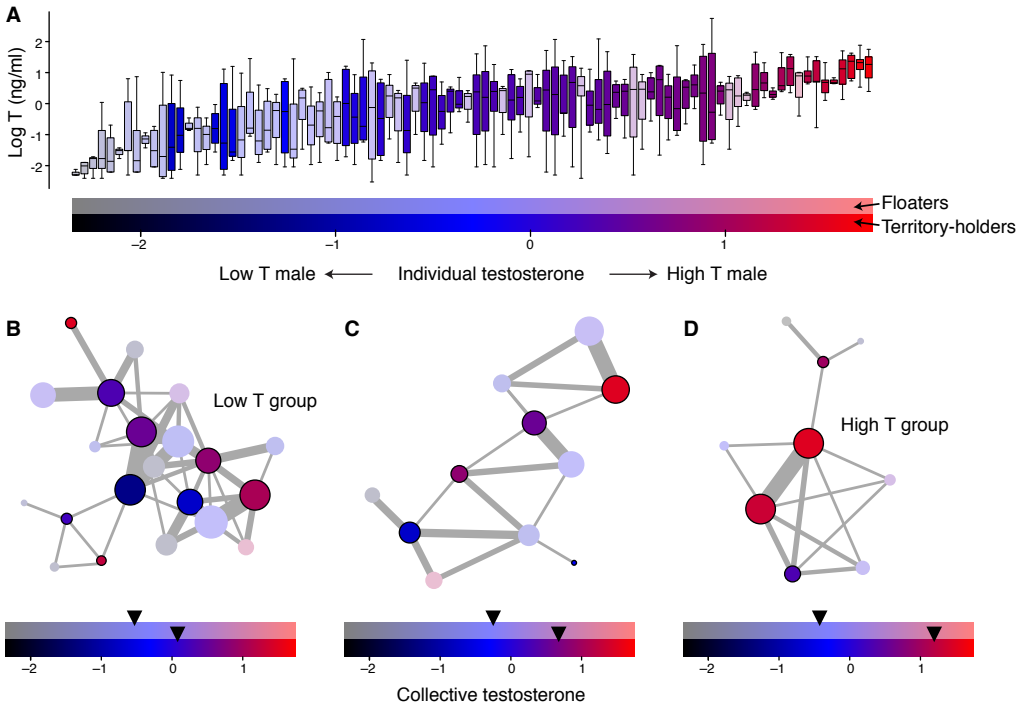
Figure 1



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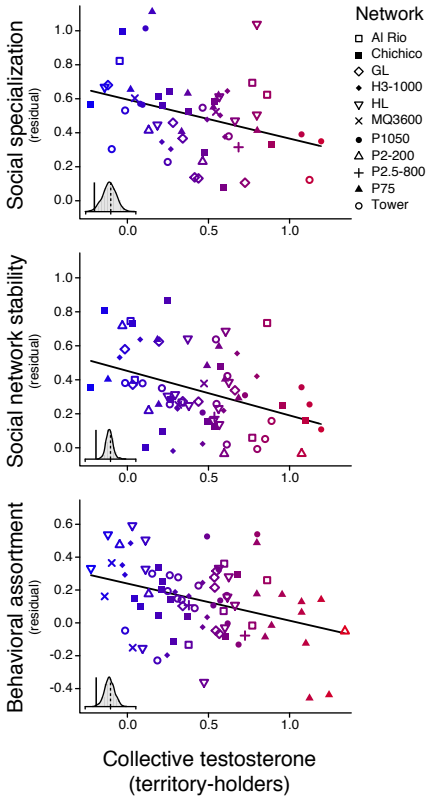
Figure 2