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Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game



Pranjali H. Mehta^{a,*}, Nicole M. Lawless DesJardins^{a,1}, Mark van Vugt^{b,c}, Robert A. Josephs^d

^a Department of Psychology, University of Oregon, United States

^b Social and Organizational Psychology Group & Institute for Brain and Behavior, Vrije Universiteit (VU), Amsterdam, The Netherlands

^c Department of Politics, University of Oxford, United Kingdom

^d Department of Psychology, University of Texas at Austin, United States

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ABSTRACT

A contribution to a special issue on Hormones and Human Competition.

Testosterone is theorized to influence status-seeking behaviors such as social dominance and competitive behavior, but supporting evidence is mixed. The present study tested the roles of testosterone and cortisol in the hawk-dove game, a dyadic economic decision-making paradigm in which earnings depend on one's own and the other player's choices. If one person selects the hawk strategy and the other person selects the dove strategy, the player who selected hawk attains a greater financial pay-off (status differentiation). The worst financial outcome occurs when both players choose the hawk strategy (status confrontation). Ninety-eight undergraduate students (42 men) provided saliva samples and played ten rounds of the hawk-dove game with another same-sex participant. In support of the hypothesis that testosterone is related to status concern, individuals higher in basal testosterone made more hawk decisions — decisions that harmed the other player. Acute decreases in cortisol were also associated with more hawk decisions. There was some empirical support for the dual-hormone hypothesis as well: basal testosterone was positively related to satisfaction in the game among low basal-cortisol individuals but not among high basal-cortisol individuals. There were no significant sex differences in these hormonal effects. The present findings align with theories of hormones and status-seeking behavior at the individual level, but they also open up new avenues for research on hormone profiles at the collective level. Our results suggest that the presence of two or more high-testosterone members increases the likelihood of status confrontations over a limited resource that can undermine collective outcomes.

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Status hierarchies are universal across human cultures and in many other social animals. Higher status provides benefits that promote survival and reproduction, such as preferential access to food and mates, making status attainment an attractive prospect (Ellis, 1994). Indeed, scholars have noted that the desire for status is a fundamental social motive (Anderson et al., 2015). One key behavioral mechanism for attaining higher rank in many species is through displays of dominance toward another conspecific — such as challenges and attacks — in socially competitive situations (Cheng et al., 2013). If the other conspecific engages in deference behavior and bows out of the conflict, then the dominance-displayer is granted the higher status position and in turn greater access to resources. But dominance can be risky because the other conspecific may also display dominance. In a scenario in which both competitors behave dominantly and neither is willing to defer to

the other, fierce competition may ensue, leading to substantial losses for both competitors (e.g., injury, loss of resources to a third conspecific who is not engaging in a costly dominance battle). Thus, dominance has advantages because it leads to higher status if one's competitor backs down, but dominance also has a potential downside by fueling costly confrontations. It follows that deference is another viable strategy because it allows individuals to avoid costly conflicts over status. Inspired by evolutionary game theory, we examine hormones and decision-making in the hawk-dove game, a dyadic economic paradigm that is theorized to model dominance-deference strategies and the emergence of social hierarchy (Maynard-Smith, 1982). We test the hypothesis that individuals with higher testosterone concentrations are more likely to choose a dominance strategy (hawk) over a deference strategy (dove) in repeated interactions with another real player.

Prevailing theories propose that testosterone should influence behaviors implicated in the pursuit of status—such as aggressive, competitive, and dominant behaviors—especially during periods of social competition or challenge (Wingfield et al., 1990; Mazur and Booth, 1998; Archer, 2006). Evidence in support of this *challenge hypothesis*

* Corresponding author at: Department of Psychology, University of Oregon, Eugene, OR 97403, United States.

E-mail address: mehta@uoregon.edu (P.H. Mehta).

¹ These authors contributed equally to the paper.

has emerged across a variety of non-human animal species (e.g., birds, Wingfield et al., 1990; mice, Trainor et al., 2004; fish, Oliveira et al., 2009). Research in humans also demonstrates connections between testosterone and status-seeking behavior (for reviews, see Mazur and Booth, 1998; Archer, 2006; Eisenegger et al., 2011; Hamilton et al., 2015). Both endogenous testosterone and exogenously elevated testosterone are positively related to markers of dominance motivation (van Honk et al., 2001; Schultheiss et al., 2005; Josephs et al., 2006; Hermans et al., 2008; Bos et al., 2012; Terburg et al., 2012; Terburg and van Honk, 2013; Goetz et al., 2014; Enter et al., 2014; Radke et al., 2015; Mehta et al., 2008; Zilioli and Watson, 2013; van der Meij et al., 2016), aggressive behavior (Carré et al., 2009; Carré and Olmstead, 2015), competitive behavior (Mehta and Josephs, 2006; Carré and McCormick, 2008; Mehta et al., 2008, 2009; Slatcher et al., 2011; Mehta et al., 2015b, 2015c; Reimers and Diekhof, 2015; Hahn et al., 2016; Eisenegger et al., 2016), and reduced prosocial behaviors including trust, perspective-taking, cooperation, and empathy (Hermans et al., 2006; Mehta et al., 2009; Bos et al., 2010; van Honk et al., 2011; Boksem et al., 2013; Wright et al., 2012; Ronay and Carney, 2013; Edelstein et al., 2014).

Whereas high-testosterone individuals strive for high status and find low-status positions aversive, low-testosterone individuals are uncomfortable in high-status positions and seem to prefer lower status as well as cooperative social contexts (Josephs et al., 2006; Newman et al., 2005; Mehta et al., 2008, 2009; Zyphur et al., 2009; Wright et al., 2012). These findings suggest that low-testosterone individuals may be especially sensitive to the costs of dominance and status pursuit, such as an increased likelihood of costly conflicts. As a result, low-testosterone individuals may enact deference behaviors as a strategy to avoid costly status battles (Mehta and Josephs, 2006; Wingfield et al., 1990; Josephs et al., 2006).

Despite evidence linking testosterone to social behavior and status motivation, many discrepant results have also emerged. For example, research results from studies of testosterone and human economic social interactions such as bargaining games have been highly inconsistent (Burnham, 2007; Eisenegger et al., 2009; Zak et al., 2009; Zethraeus et al., 2009; Mehta and Beer, 2010; Diekhof et al., 2014; Mehta et al., 2015a; Kopsida et al., 2016). The inconsistencies may arise because these prior studies on economic social decisions have failed to tap into the motivational processes critical for revealing testosterone's behavioral effects. New studies of testosterone and decision-making are needed that more closely model status competitions and the emergence of social hierarchies. Further, prior studies have generally examined anonymous one-shot social interactions with fictitious players. Real-world competitions typically occur over longer periods of time in repeated social interactions with an actual person. Experimental designs that examine status-based interactions using a series of repeated interactions with the same person may reveal clearer associations between testosterone and social decision-making.

The hawk-dove game is a dyadic decision-making paradigm that is theorized to model status interactions and hierarchy emergence (Maynard-Smith, 1982; Matsumura and Kobayashi, 1998; Neugebauer et al., 2008; van Vugt and Tybur, 2015). Each individual can adopt a dominance (hawk) or deference (dove) strategy, and each player's strategy has implications for the distribution of resources between the two players. This game is also known as the chicken game. The name chicken comes from a game in which two car drivers drive toward each other. One must swerve or both will crash. If one driver swerves and the other does not, the one who swerves is called the chicken (coward).

Fig. 1 shows the pay-offs associated with dominance (hawk) and deference (dove) strategies. If both players choose the dove strategy, then both players receive a moderate pay-off (upper left quadrant of Fig. 1). This outcome indicates that the two individuals chose to avoid a status confrontation and cooperate instead. If both players choose the hawk strategy, then this situation results in the worst possible

		Player 2	
		Dove	Hawk
Player 1	Dove	2, 2	1, 4
	Hawk	4, 1	0, 0

Fig. 1. Pay-off matrix for hawk-dove game. Pay-offs depend on each player's decision. In each box, pay-off for player 1 is listed first followed by pay-off for player 2.

outcome (lower right quadrant of Fig. 1). This indicates a status confrontation that leads to losses for both parties. If one player selects the hawk strategy and the other the dove strategy, the player who chose the hawk strategy earns a much higher pay-off than the other player (upper right and lower left quadrants of Fig. 1). Ending up in either the upper right or lower left quadrants of Fig. 1 (a hawk-dove combination) signifies the best collective outcome (if one adds up the pay-offs of players 1 and 2) and indicates that the individual who chose the hawk strategy attains higher status than the other player (status differentiation, as indicated by unequal pay-offs). The hawk-dove combination is also the most beneficial outcome for each individual. That is, if player 1 expects that player 2 will adopt the hawk strategy, then player 1 achieves a higher pay-off by adopting the dove strategy (upper right quadrant of Fig. 1). But if player 1 expects that player 2 will adopt the dove strategy, then player 1 achieves a higher pay-off by adopting the hawk strategy (lower left quadrant of Fig. 1). The hawk-dove combination represents what is referred to as the game equilibrium and is akin to the formation of a social hierarchy because resources are distributed unequally (van Lange et al., 2013; van Vugt and Tybur, 2015).²

Through the lens of this game, an evolutionary analysis suggests that natural selection would have favored a mixed population of hawks and doves in many social species (Maynard-Smith, 1982). With too many doves in a population, hawks gain status and acquire more resources. And with too high a hawk population, costly competitions among hawks are rampant; doves thrive in such an environment by cooperating with other doves and avoiding competition with hawks. Supporting the advantages of a mixed hawk-dove population, empirical of hawk and dove tactics in many species. For example, male dung beetles (*Onthophagus taurus*) are dimorphic in their body types (Hunt and Simmons, 2001). "Major" males are larger, grow head horns, and have excellent fighting ability as a result. "Minor" males are smaller, remain hornless, and have poorer fighting ability. Major males fight for access to females, but minor males defer status to major males and mate with females by sneaking copulations. Evidence for different social tactics (e.g., hawk versus dove) is found in many other species as well, including earwigs, spiders, salmon, birds, and orangutans (Forslund, 2003; Fromhage and Schneider, 2005; Thomaz et al., 1997; Kokko et al., 2014; Harrison and Chivers, 2007).

The hawk-dove game also has relevance for understanding status interactions in humans and how these interactions impact individual and collective outcomes. According to the structure of the hawk-dove game, both players have incentives to establish a dominant-subordinate relationship (hawk-dove combination). Research in humans provides evidence in line with this core principle of the game. Humans are indeed

² If interactions settle into an equilibrium state and if each player assumes that the other player's strategy is set in stone, the interaction is likely to remain at this equilibrium state because neither player obtains a better outcome by switching to a different strategy. In game theory terminology, this is known as the Nash equilibrium.

motivated to enter into hierarchical relationships themselves (Tiedens et al., 2007), and they show a preference for hierarchical relationships in others (Zitek and Tiedens, 2012). The structure of the hawk-dove game also indicates that the hawk-dove combination leads to better collective outcomes (higher pay-offs if you add both players' earnings together) than the hawk-hawk combination or the dove-dove combination. Recent evidence of status processes in human dyads and groups is also consistent with these principles of the hawk-dove game (e.g., Greer et al., 2011; Bendersky and Hays, 2012; Ronay et al., 2012; Swaab et al., 2014; Kilduff et al., 2016). For example, groups randomly assigned to have one dominant and one subordinate individual (hawk-dove combination) performed better on an interdependent task than groups randomly assigned to have all-dominant individuals (hawk-hawk); groups randomly assigned to have all-subordinate individuals (dove-dove) showed intermediate performance (Ronay et al., 2012). Further, status conflict explained why groups with all-dominant individuals performed especially poorly, and status differentiation explained by groups with a mix of dominants and subordinates performed especially well. Other research shows similar benefits of status differentiation in dyadic interactions, such as better joint outcomes in negotiations (Tiedens et al., 2007; Wiltermuth et al., 2015). Collectively, this body of research provides evidence for the relevance of the hawk-dove game for understanding status processes in human dyads and groups. The hawk-dove game and this body of research are consistent with functional theories of hierarchy (cf. Ronay et al., 2012). These theories propose that a clear status hierarchy has adaptive value for the group as a whole by allowing coordination among group members, reducing status conflicts, and improving group productivity. In contrast, an absence of a clear hierarchy decreases coordination, increases status conflicts, and impairs collective performance.

Despite the theoretical assertion that testosterone should be related to dominance and concern for status, testosterone's effect on decision-making in the hawk-dove game remains untested. This is particularly surprising because the hawk-dove game is a social economic game that is theorized to model status interactions and hierarchy emergence directly (van Vugt and Tybur, 2015). The present study was designed to fill this empirical gap. Participants of the same sex reported to the lab two at a time, provided saliva samples to measure endogenous hormone concentrations, and then played ten rounds of the hawk-dove game for real monetary consequences. Feedback on the other player's decision-making was provided after each round of play. We hypothesized that basal testosterone would be positively related to the number of hawk decisions across the ten rounds of the game. This prediction is informed by theories suggesting that high-testosterone individuals should be motivated to attain higher status and avoid low status by engaging in dominant behaviors, whereas low-testosterone individuals should be less motivated to attain high status and may actually prefer low-status positions and thus engage in deference behaviors (Mazur and Booth, 1998; Josephs et al., 2006; Mehta et al., 2009).

Our primary hypotheses focused on baseline testosterone as a predictor of future behavior in the hawk-dove game, but we also collected additional saliva samples to measure changes in testosterone concentrations. Testosterone levels can fluctuate during and after competitive social interactions, and these fluctuations are sometimes related to competitive, aggressive, and socially dominant behaviors (Wingfield et al., 1990; Mazur and Booth, 1998; Mehta and Josephs, 2006; Carré and Olmstead, 2015; Hamilton et al., 2015). Thus, we conducted analyses to examine testosterone changes during and after the game and whether these changes were associated with hawk-dove decisions.

Saliva samples in the study were also analyzed for cortisol because this hormone has been also been studied in relation to status-relevant behaviors such as dominance and aggression. The findings in various studies, however, are inconsistent. Some studies show that low baseline cortisol or short-term decreases in cortisol are related to greater aggression and anti-social punishment (Alink et al., 2008; Platje et al., 2013; Pfattheicher and Keller, 2014) as well as reduced social affiliation

(Berger et al., 2016), whereas other studies show that high cortisol is related greater aggressive behavior (increased cortisol reactivity, Geniole et al., 2011; exogenous cortisol administration: Böhnke et al., 2010). Another line of research on the dual-hormone hypothesis demonstrates that cortisol interacts with testosterone to predict status-relevant behaviors (Mehta and Prasad, 2015). The most common dual-hormone pattern is that testosterone is positively related to status-relevant behaviors such as dominance, but only among individuals with low cortisol levels. Yet a few studies have shown a different dual-hormone pattern: testosterone is positively related to aggressive behavior following social provocation, cheating behavior, and psychopathic traits especially among individuals with high cortisol concentrations (Geniole et al., 2011; Denson et al., 2013; Welker et al., 2014; Lee et al., 2015; see also Geniole et al., 2013, Mazur and Booth, 2014 for non-significant dual-hormone interactions). Given these mixed findings on cortisol's role in social behavior, we explored whether cortisol, either alone or in interaction with testosterone, was related to hawk-dove decisions.

Our main goal in this study was to test associations between endocrine systems and hawk-dove decisions, but we also examined psychological correlates of hormone concentrations in order to advance theory on the mechanisms for hormonal influences on behavior. Some theories propose that reward motivation may be a key mechanism for testosterone's behavioral effects (Welker et al., 2015; see also Bos et al., 2012 and Eisenegger et al., 2011). This theorizing is informed by evidence that testosterone enhances activity in dopaminergic neural reward regions such as the ventral striatum (Packard et al., 1997; Hermans et al., 2010; Op de Macks et al., 2011). Testosterone is also positively related to psychological factors linked to reward, such as task enjoyment and positive affect (Amanatkar et al., 2014; Mehta et al., 2015b, 2015c). Null effects of testosterone on psychological factors implicated in reward have also been reported (e.g., non-significant effects of testosterone on mood: Aarts and van Honk, 2009; Bos et al., 2010; Terburg et al., 2012), but these studies did not investigate interactions with cortisol. Research on the dual-hormone hypothesis suggests testosterone's positive effect on reward-related psychological states may be strongest among individuals low in cortisol (Welker et al., 2015). For example, a study of face-to-face competitive bargaining revealed that a profile of elevated testosterone combined with reduced cortisol was related to high relationship satisfaction (Mehta et al., 2015a). Building on this preliminary evidence, we tested the extent to which testosterone and cortisol were related to self-reported satisfaction³ and positive affect in the hawk-dove game.

1. Methods

1.1. Participants

Ninety-eight undergraduate students (42 men) at the University of Texas at Austin were recruited as part of a larger study on economic decision-making, hormones, and personality. Participants were eligible to participate if they were a University of Texas at Austin undergraduate student; graduate students, staff, faculty at the university, and individuals not affiliated with the university were not eligible to participate. Participants were paid according to their earnings during the hawk-dove game. Participants were aware that they would be making financial decisions as part of the study and that payment was contingent on their choices, but the details of the game were not explained to them ahead of time. All procedures were approved by the University of Texas at Austin Institutional Review Board.

³ We use the general term satisfaction because this self-report measure included questions that assessed task enjoyment, satisfaction with earnings, desire to play the economic game again, satisfaction with how one played the game, and liking of one's partner based on how the partner played the game. See methods section for more details.

1.2. Procedure

Participants completed online questionnaires and exercises prior to reporting to the lab.⁴ Participants then reported to the lab in same-sex pairs between 11:00 AM and 5:30 PM to minimize the effects of circadian fluctuations in testosterone and cortisol levels (Schultheiss and Stanton, 2009). We studied same-sex pairs to reduce the influence of mating motives that are expected to play a role in opposite-sex social interactions among heterosexual participants (Slatcher et al., 2011). Most pairs of participants were either acquaintances or strangers. One pair of participants reported being friends, but excluding them from the dataset does not alter the primary results. This pair was retained in all analyses to maximize statistical power.

Participants reported to a waiting room for several psychological studies. Because the experimenter was instructed to greet participants upon arrival, participants had minimal opportunity for interaction before the study began. Upon arrival, the experimenter led each participant to a separate room, obtained informed consent, and collected a saliva sample. The sample was immediately brought to a nearby freezer for storage. This sample was collected to measure baseline testosterone and cortisol concentrations prior to the hawk-dove game. Participants then completed a questionnaire that assessed their momentary self-reported affect with instructions to indicate “to what extent you feel this way *right now*” (Time 1 Positive and Negative Affect Schedule, PANAS, Watson et al., 1988). All subsequent affect measures used these same instructions.

After completing the baseline saliva sample and questionnaire, participants were told that they would be playing an economic decision-making task for real monetary consequences with the other participant. There was no opportunity for communication between participants during the game because participants were in separate rooms. The rules of the hawk-dove game were explained to participants with written and verbal instructions including a pay-off matrix. The pay-off matrix and written instructions provided to participants are included in the Supplementary material (Fig. S1 and Appendix). The choices in the game were labeled A and B. The name of the game was not mentioned to participants, and the experimenter referred to the choices only as “choice A” and “choice B” throughout the experiment. After placing the pay-off matrix and the written instructions in front of participants (see Supplementary material), the experimenter used the following script to explain the game:

“In this game, you can choose either A or B. And the other participant can choose either A or B, but how much money each of you earns depends on the choices both of you make. The grid shows how much you would make in white, and how much the other participant would make in a shaded gray. Now let’s go through all of the possible scenarios. The first scenario is if you choose A and the other participant also chooses A. If that happens, then you both will earn \$2. [Point to the appropriate box in the grid for the (A, A) scenario.] If you both choose B, then you both make nothing. [Again, point to the appropriate box in the grid for the (B, B) scenario.] However, if one of you chooses A and the other person chooses B, then whoever chooses B makes more money, and whoever chooses A makes less money. That is, whoever chooses B makes \$4.00, and whoever chooses A makes \$1.00. So for instance, say you decide to choose B and the other participant decides to choose A in a given round. Then that would mean this scenario [Point to the scenario in the lower left hand corner of the grid.] Remember, your pay-off is in white and the other participant’s pay-off is shaded gray. So that means you would earn \$4.00 and the other participant would earn \$1.00. But let’s say you choose A, but the other participant chooses B. Then that would mean this scenario [Point to scenario in the upper right hand corner

of the grid.] Then that would mean you would make \$1.00 and the other person would make \$4.00. So essentially, the game works such that choosing B might give you more money [Point the lower left hand corner box], but it’s risky because you could also make nothing if the other participant chooses B as well [Point to the B, B box again.] “This other sheet [Point to the written instructions sheet] says the same thing as the grid, but it’s in words. Some people understand the game better in words. There is no right or wrong way to play the game. Play this game however you would like.”

After written and verbal instructions were provided, participants completed a short quiz to make sure they understood the rules of the game prior to continuing with the experiment. If there were any incorrect responses, the experimenter clarified the game rules prior to game play. This quiz is also included in the Supplementary material. Then participants played five rounds of the hawk-dove game. Participants were handed a tracking sheet to track their own choices, their partner’s choices, and the financial outcomes in each of the five rounds of the game. The rationale for having participants record this information was to reduce potential confounds associated with variability in memory for past choices and financial outcomes. The participant tracking sheet included only five rounds, and participants were unaware that the experiment would later include another five rounds. Each participant sat in a separate room while they played the game. In each round of play, participants made a decision and placed their choice card (a card with the letter “A” on it or a card with the letter “B” on it) in an envelope and handed their envelope to the experimenter. The experimenter collected each participant’s decision and determined how much money each participant earned. The experimenter recorded participant choices at this time. After recording the decisions that each participant made, the experimenter then placed a piece of paper in each participant’s envelope indicating how much he or she earned and handed the envelope back to each participant. This process was repeated for five rounds of play.

After five rounds of play participants filled out a short questionnaire, which consisted of self-reported momentary affect (Time 2 PANAS, Watson et al., 1988) as well as five questions to assess satisfaction with multiple aspects of the economic game. Specifically, participants were asked to indicate the extent to which they agreed with the following statements on a 7-point scale (1 = Disagree strongly; 7 = Agree strongly): ‘I enjoyed the game’; ‘I am satisfied with how much money I earned in the game’; ‘I want to play the game again’; ‘I am satisfied with how I played the game’; ‘Based on how the other participant played the game, I think I would like him/her’. Participants then provided a second saliva sample in the same manner as the first sample.

Then participants were handed another tracking sheet and played five more rounds of the game with the same participant using the same procedures, followed by another brief questionnaire that assessed self-reported momentary affect (Time 3 PANAS, Watson et al., 1988) and satisfaction with the game using the same five items. Participants then provided a third saliva sample in the same manner as the first two samples. At the end of the study, participants were debriefed and paid in cash based on what they earned during ten rounds of the game ($M = \$16.51$, $SD = \$5.05$).

Overall, participants played ten rounds of the game-hawk dove game in two blocks of five rounds. We chose to study ten rounds of play instead of fewer rounds to better estimate participants’ general tendencies to choose the hawk versus dove strategy over multiple rounds of play. Further, as mentioned in the introduction, prior studies of steroid hormones in economic games have generally investigated anonymous one-shot (i.e., one round of play) economic social interactions with fictitious players. Real-world status-relevant social interactions, however, typically occur over longer periods of time in repeated interactions with an actual person. Thus, our experimental design extends prior research by investigating naturally occurring behavior in repeated economic social interactions.

⁴ Details about online questionnaires and exercises can be found in Mehta (2007).

1.3. Measures

1.3.1. Hawk-dove decisions

The total number of hawk decisions for each participant across the ten rounds of play served as our primary dependent variable. For example, a score of 8 would indicate that the player made 8 hawk decisions and 2 dove decisions.

1.3.2. Task satisfaction

Scores on the five task-related satisfaction questions showed good internal reliability (Cronbach's alpha = 0.85) and therefore were averaged together to create a composite measure of task satisfaction. Scores on this task satisfaction measure assessed after the first five rounds of play and the next five rounds of play did not significantly differ from each other. Consequently, ratings from the two time points were averaged to create a global measure of satisfaction in the hawk-dove game.

1.3.3. Affect

Positive and negative affect scores were calculated at the three time points (Watson et al., 1988; Time 1 Positive Affect Cronbach's alpha = 0.67; Time 2 Positive Affect Cronbach's alpha = 0.92; Time 3 Positive Affect Cronbach's alpha = 0.93; Time 1 Negative Affect Cronbach's alpha = 0.75; Time 2 Negative Affect Cronbach's alpha = 0.76; Time 3 Negative Affect Cronbach's alpha = 0.77).

1.3.4. Earnings

Money earned across all ten rounds of play is contingent on one's own decisions and one's partner's decisions according to the rules of the game. Our primary analyses focused on hawk-dove decisions because the structure of the game is such that hormones are likely related to earnings indirectly through hawk-dove decisions. In supplemental analyses we report additional statistical models for money earned.

1.4. Hormone analysis

The saliva samples were shipped on dry ice to Yerkes Biomarkers Laboratory (Emory University, Atlanta, GA). The samples were analyzed using radioimmunoassay kits for testosterone and enzymeimmunoassay kits for cortisol (Diagnostic Systems Laboratories, Webster, TX). All samples were assayed in duplicate. Average intra-assay coefficients of variation (CVs) were 8.58% for testosterone and 7.61% for cortisol. Inter-assay CVs averaged across low and high controls have been shown to be 16.24% for testosterone and 3.50% for cortisol using this laboratory.

Because the raw cortisol distribution was positively skewed, basal cortisol was log-transformed and then grand-mean centered. Basal testosterone scores were standardized separately for men and women by converting the raw scores for every participant to z-scores (Kornienko et al., 2016; Mehta and Josephs, 2010; Stanton, 2011; Tackett et al., 2014). High scores on this distribution indicate high testosterone levels relative to other individuals of the same sex. Analyses for hormone changes examined changes from baseline to immediately after the hawk-dove game (time 3 cortisol minus time 1 cortisol, time 3 testosterone minus time 1 testosterone). We report follow-up analyses with measures of hormone changes from baseline to during the hawk-dove game (time 2 hormone level minus time 1 hormone level). Cortisol change scores were grand-mean centered. Similar to the analyses for basal testosterone, testosterone change scores were standardized separately for men and women by converting raw change scores for every participant to z-scores. Consistent with previous papers, our main analysis combined men and women. There are two important advantages to combining men and women in the same analysis. First, statistical power is increased in a combined analysis. Second, patterns of hormone-behavior relationships can be examined for statistically significant sex differences in a combined analysis. In addition to our main analyses that

Table 1

Descriptive statistics for study measures.

	Full sample		Men		Women	
	(n = 98)		(n = 42)		(n = 56)	
	M	SD	SD	M	SD	M
Testosterone time 1 (pg/mL)	63.65	54.20	117.78	39.48	23.04	10.13
Testosterone time 2	62.20	54.38	117.31	38.39	20.86	7.57
Testosterone time 3	61.30	55.33	115.80	42.51	20.43	9.15
Time 2 minus time 1 testosterone change	-1.45	14.04	-0.47	20.23	-2.18	6.40
Time 3 minus time 1 testosterone change	-2.34	17.72	-1.98	25.91	-2.61	7.29
Cortisol time 1 (µg/dL)	0.67	0.29	0.71	0.32	0.65	0.27
Cortisol time 2	0.64	0.28	0.73	0.35	0.57	0.19
Cortisol time 3	0.60	0.26	0.69	0.33	0.52	0.17
Time 2 minus time 1 cortisol change	-0.04	0.21	0.02	0.26	-0.08	0.15
Time 3 minus time 1 cortisol change	-0.08	0.26	-0.02	0.34	-0.12	0.18
Positive affect time 1 ^{a,b}	3.00	1.05	2.99	0.70	3.01	1.25
Positive affect time 2 ^b	3.02	0.88	3.09	0.82	2.96	0.92
Positive affect time 3 ^b	2.96	0.93	3.00	0.93	2.93	0.94
Negative affect time 1 ^{a,b}	1.41	0.40	1.45	0.43	1.38	0.37
Negative affect time 2 ^b	1.43	0.43	1.48	0.42	1.40	0.44
Negative affect time 3 ^b	1.39	0.44	1.41	0.47	1.38	0.43
Satisfaction	5.27	1.06	5.40	1.00	5.18	1.09
Number of hawk decisions	5.24	2.07	5.14	2.60	5.32	1.57
Money earned (\$)	16.56	5.02	15.83	5.94	17.11	4.16

Time 1 = baseline affect was measured after hawk-dove game instructions but prior to game play; time 1 hormone measure was measured prior to hawk-dove game instructions; time 2 = after five rounds of play; time 3: After all ten rounds of play.

^a Two males had missing data for the baseline affect measure.

^b Measured with the PANAS (Watson et al., 1988).

included both men and women, we also conducted follow-up analyses that examined men and women separately.

2. Results

2.1. Descriptive statistics and preliminary analyses

Descriptive statistics and correlations for the main study variables are shown in Tables 1 and 2. Table S1 reports correlations separately for men and women. As shown in Table 1, participants made hawk decisions about 50% of the time (M hawk decisions = 5.24, SD = 2.07), and number of hawk decisions did not vary between males and females ($F(1,96) = 0.18, p = 0.67$). Out of the ten rounds of play, an average of 2.45 rounds of play (SD = 2.27) led to a cooperative outcome (dove-dove combination, upper left quadrant of Fig. 1), an average of 2.92 rounds (SD = 1.95) led to a status confrontation outcome (hawk-hawk combination, lower right quadrant of Fig. 1), and an average of 4.63 rounds (SD = 1.95) led to a status differentiation outcome (hawk-dove or dove-hawk combination, upper right or lower left quadrants of Fig. 1). Table S2 shows the frequency of outcomes for all 49 pairs, and Table S3 reports the frequency of hawk and dove decisions for each of the ten rounds of play.

We tested whether hormone concentrations changed over the course of the hawk-dove game and whether these changes depended on gender. We conducted mixed-model general linear model (GLM) analyses with time of hormone measurement (baseline sample collected prior to the hawk-dove game, during-game sample, or post-game sample) as a within-subjects factor, gender as a between-subjects factor, and time since waking as a covariate.⁵ The GLM analysis for cortisol revealed a main effect of time ($F(1.62, 149.26) = 7.35, p = 0.002$,

⁵ Mauchly's test for sphericity indicated that the sphericity assumption was violated, so Huynh-Feldt corrections were applied in these mixed-models analyses.

Table 2
Correlations between primary study measures.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Time 1 T	–												
2. T change, time 1 to 2	–0.51**	–											
3. T change, time 1 to 3	–0.37**	0.73**	–										
4. Time 1 C	0.20†	–0.14	–0.25*	–									
5. C change, time 1 to 2	–0.11	0.17	0.13	–0.43**	–								
6. C change, time 1 to 3	–0.15	0.16	0.29**	–0.53**	0.82**	–							
7. Time since waking	–0.13	0.05	0.09	–0.34**	–0.07	0.06	–						
8. Hawk decisions (A)	0.23*	–0.10	–0.12	0.10	–0.12	–0.22*	–0.03	–					
9. Hawk decisions (P)	0.08	0.10	–0.03	–0.11	0.09	–0.02	0.08	0.65**	–				
10. Money earned	0.00	–0.11	0.01	0.12	–0.14	–0.10	–0.28**	–0.36**	–0.79**	–			
11. Satisfaction	0.14	–0.05	0.04	0.09	0.09	0.05	–0.11	–0.29**	–0.37**	0.34**	–		
12. Positive affect	0.19†	–0.08	–0.16	0.03	0.07	–0.09	–0.09	0.00	0.01	0.05	0.27**	–	
13. Negative affect	0.00	–0.01	0.02	0.07	–0.03	–0.09	0.04	0.12	0.16	–0.16	–0.30**	0.23*	–

† $p < 0.10$. * $p < 0.05$. ** $p < 0.01$.

Notes: T = testosterone; C = cortisol; A = actor; P = partner. Testosterone was standardized within sex. Cortisol was log-transformed. Time since waking (in hours) is missing for three participants. Hawk Decisions = Number of hawk decisions in the hawk-dove game across the ten rounds of play. Money earned = total earnings in the hawk-dove game across the ten rounds of play. Self-reported satisfaction consisted of participants' responses to the following items rated on a 7-point scale (1 = Disagree strongly; 7 = Agree strongly), averaged across the two measurement time points: 'I enjoyed the game'; 'I am satisfied with how much money I earned in the game'; 'I want to play the game again'; 'I am satisfied with how I played the game'. Based on how the other participant played the game, I think I would like him/her'. Positive and negative affect are averaged across the three time points.

$\eta^2_{\text{partial}} = 0.074$) and a time \times gender interaction ($F(1.62, 149.26) = 4.10, p = 0.026, \eta^2_{\text{partial}} = 0.043$). Separate analyses in each gender revealed a main effect of time in women ($F(1.86, 98.29) = 18.99, p < 0.001, \eta^2_{\text{partial}} = 0.264$) but not in men ($F(1.52, 57.68) = 0.66, p = 0.482, \eta^2_{\text{partial}} = 0.017$). As shown in Table 1, women's cortisol levels decreased consistent with circadian decline, whereas men's cortisol levels remained relatively steady over the course of the game. The GLM analysis for testosterone revealed no significant effects of time or a time \times gender interaction (p 's > 0.25), but exploratory follow-up analyses in each gender again revealed a main effect of time only in women ($F(1.85, 98.07) = 5.00, p = 0.010, \eta^2_{\text{partial}} = 0.086$) but not in men ($F(1.68, 63.69) = 0.22, p = 0.76, \eta^2_{\text{partial}} = 0.006$). Similar GLM analyses for changes in self-reported positive and negative affect revealed non-significant effects (p 's > 0.10). Overall, these analyses indicate that cortisol and testosterone levels decreased over the course of the game in women but not in men.

2.2. Statistical analysis strategy: actor-partner interdependence models

Data in social interaction studies such as this one are not independent: One person's behavior affects the other person's behavior. Indeed, the number of hawk decisions that participants made were positively correlated with the number of hawk decisions made by their partner, $r = 0.65, p < 0.01$, which aligns with some prior research (McClintock and Liebrand, 1988). To account for the non-independence of observations within a given dyad, statisticians have developed the Actor-Partner Interdependence Model (APIM; Kashy and Kenny, 2000; Kenny, 1996; Kenny et al., 2006). APIM allows researchers to simultaneously estimate the association between one's own personal characteristics and one's own behavior (e.g., the association between person A's testosterone and person A's hawk decisions)—called *actor effects*—as well as the association between the partner's personal characteristics and one's own behaviors (e.g., the association between person B's testosterone levels and person A's hawk decisions)—called *partner effects*. We hypothesized that there would be an actor effect of basal testosterone on hawk decisions. That is, we expected that one's own basal testosterone levels would predict one's own hawk decisions when accounting for the interdependent nature of the data in APIM. APIM models were estimated with REML in SPSS Mixed (Version 22). Our primary analyses focused on baseline testosterone as a predictor of future hawk-dove decisions, but we conducted additional APIM analyses for baseline cortisol as well as changes in both testosterone and cortisol. There was one outlier for time three minus time one cortisol change that was more than

five standard deviations above the mean. This cortisol change score was winsorized to three standard deviations above the mean for the APIM analyses. Importantly, the effects for cortisol change remained robust regardless of how the outlier was handled (including the raw score, the winsorized score, or removing it from the dataset). In addition to conducting our primary APIM analyses for hawk-dove decisions, we also conducted secondary APIM analyses for self-reported satisfaction, self-reported affect, and earnings. For a study of testosterone and competitive mating behaviors that used APIM analyses, see Slatcher et al., 2011.

2.3. Decisions in the hawk-dove game

2.3.1. Basal hormone concentrations

In agreement with our main hypothesis, APIM analyses revealed a significant actor effect of basal testosterone on decision-making such that participants with higher levels of testosterone chose hawk decisions more often than participants with lower levels of testosterone (b

Table 3
Basal testosterone predicting number of hawk decisions in the hawk-dove game.

	b	se	df	t	p	95% CI		Rho
						Lower	Upper	
Model 1								0.66
Constant	5.24	0.26	47.00	19.80	0.00	4.71	5.78	
Actor basal testosterone	0.47	0.20	69.67	2.36	0.02	0.07	0.87	
Partner basal testosterone	0.11	0.20	69.67	0.54	0.59	–0.29	0.51	
Model 2								0.67
Constant	5.03	0.42	43.00	12.00	0.00	4.19	5.88	
Actor basal testosterone	0.45	0.20	63.23	2.21	0.03	0.04	0.86	
Partner basal testosterone	0.15	0.20	63.23	0.72	0.48	–0.26	0.56	
Actor time since waking	–0.08	0.09	87.07	–0.89	0.38	–0.27	0.10	
Partner time since waking	0.15	0.09	87.07	1.58	0.12	–0.04	0.33	
Gender	0.36	0.55	43.00	0.66	0.52	–0.75	1.48	

Notes: Testosterone was standardized within sex. Hawk decisions = number of hawk decisions in the hawk-dove game across the ten rounds of play. Time since waking = grand-mean centered hours since waking. Rho = degree of interdependence in the dependent variable within dyads. Gender: 0 = male, 1 = female.

$= 0.47$, $se = 0.20$, $t(69.67) = 2.36$, $p = 0.02$; Table 3 Model 1).⁶ There was no evidence for a partner effect of basal testosterone; that is, a partner's basal testosterone levels did not significantly predict the participant's own choices. The significant actor effect of basal testosterone on decisions in the hawk-dove game remained statistically significant when controlling for gender and time since waking (Table 3, Model 2). Because basal testosterone levels were standardized within sex for this analysis, the slope of 0.47 can be interpreted to indicate that for every one standard deviation increase in basal testosterone levels (relative to other individuals of the same sex), the number of hawk decisions increases by 0.47.

We ran another model in which gender was included as a between-dyads moderator of the effect of testosterone on decision-making. Neither the main effect of gender nor any of the interactions with gender were significant (p 's > 0.25). We also conducted separate analyses in male and female dyads to confirm that the same pattern emerged, but we did not expect statistically significant effects due to the reduced statistical power. These analyses showed similar positive associations between basal testosterone and the number of hawk decisions in males ($b = 0.76$, $se = 0.38$, $t(26.68) = 2.02$, $p = 0.05$) and in females ($b = 0.26$, $se = 0.21$, $t(41.99) = 1.24$, $p = 0.22$). Overall, the results indicate that the effect of basal testosterone on hawk-dove decisions did not statistically differ between male and female dyads.⁷

We conducted APIM analyses to explore whether basal cortisol also predicted the number of hawk decisions. There were no significant actor or partner effects for basal cortisol (p 's > 0.10). An additional APIM analysis that included basal cortisol and its interactions with basal testosterone revealed no significant interactions (p 's > 0.20), but there was still a significant actor effect of basal testosterone on the number of hawk decisions ($b = 0.44$, $se = 0.21$, $t(65.06) = 2.13$, $p = 0.037$).⁸ APIM analyses that tested whether gender moderated any of basal cortisol's effects revealed no significant interactions (p 's > 0.05). Together, these analyses indicate a robust effect of one's own basal testosterone levels on one's own hawk-dove decisions but no significant effects for basal cortisol.

2.3.2. Hormone changes

We conducted an APIM analysis to examine whether testosterone change from before to after the hawk-dove game (time 3 testosterone minus time 1 testosterone) was related to the number of hawk decisions over the ten rounds of play. The analysis revealed no significant actor or partner effects (p 's > 0.10). An additional APIM analysis that included interactions with gender found no significant testosterone change \times gender interactions (p 's > 0.10). Follow-up analyses that explored testosterone change from before to during the hawk-dove

⁶ Degrees of freedom are calculated using the Satterthwaite approximation, which generates degrees of freedom that are between the number of individuals and the number of dyads (Kenny et al., 2006).

⁷ To address a reviewer comment, we also examined the association between raw basal testosterone levels and the number of hawk decisions when controlling for participant sex. This analysis has statistical drawbacks (see Stanton, 2011) but can be considered together with our main analyses. A partial correlation between raw basal testosterone and the number of hawk decisions controlling for gender revealed a robust positive correlation in line with our primary analyses ($r = 0.26$, $p = 0.009$). An APIM analysis with actor raw basal testosterone, partner raw basal testosterone, and gender as predictors of the number of hawk decisions revealed a significant positive effect of actor basal testosterone on the number of hawk decisions ($b = 0.02$, $SE = 0.01$, $t(69.68) = 2.69$, $p = 0.009$) and no significant partner effect ($p = 0.71$) in line with the primary analyses. These results show that the association between basal testosterone and the number of hawk decisions is robust when analyzing raw basal testosterone levels.

⁸ Even though the dual-hormone interaction was not significant, we conducted exploratory simple slopes analyses (Aiken and West, 1991) to inform follow-up studies with greater statistical power. There was a statistically significant positive simple slope between basal testosterone and the number of hawk decisions among individuals high in basal cortisol (+1SD: $b = 0.68$, $se = 0.30$, $t(57.30) = 2.30$, $p = 0.025$) and non-significant positive slope between basal testosterone and the number of hawk decisions among individuals low in basal cortisol (−1 SD: $b = 0.21$, $se = 0.32$, $t(64.06) = 0.63$, $p = 0.50$).

Table 4
Cortisol change (time 3 minus time 1) predicting number of hawk decisions.

	<i>B</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>p</i>	95% CI		<i>Rho</i>
						Lower	Upper	
Model 1								
Constant	5.22	0.26	47.00	19.86	0.00	4.69	5.75	0.67
Actor cortisol change	−2.43	0.91	62.36	−2.67	0.01	−4.25	−0.61	
Partner cortisol change	−0.69	0.91	62.36	−0.76	0.45	−2.51	1.13	
Model 2								
Constant	5.16	0.42	43.00	12.38	0.00	4.32	6.00	0.67
Actor cortisol change	−2.58	0.96	56.40	−2.70	0.01	−4.49	−0.66	
Partner cortisol change	−1.13	0.96	56.40	−1.18	0.24	−3.04	0.79	
Actor time since waking	−0.07	0.09	87.35	−0.75	0.46	−0.25	0.11	
Partner time since waking	0.14	0.09	87.35	1.49	0.14	−0.05	0.32	
Participant sex	0.08	0.56	43.00	0.14	0.89	−1.05	1.21	

Notes: Cortisol change = grand-mean centered time 3 cortisol minus time 1 cortisol. The dependent variable was the number of hawk decisions in the hawk-dove game across the ten rounds of play. Time since waking = grand-mean centered hours since waking. *Rho* = degree of interdependence in the dependent variable within dyads. Participant sex: 0 = Male, 1 = Female.

game (time 2 testosterone minus time 1 testosterone) also revealed no significant effects (p 's > 0.10). These analyses indicate no significant associations between testosterone change and decision making in the hawk-dove game.

Next we conducted an APIM analysis to examine whether cortisol change from before to after the hawk-dove game (time 3 cortisol minus time 1 cortisol) was related to hawk-dove decisions. As shown in Table 4 Model 1, there was a significant actor effect of cortisol change ($b = -2.43$, $se = 0.91$, $t(62.36) = -2.67$, $p = 0.010$). The negative slope indicates that individuals who decreased in cortisol made hawk decisions more often than individuals who increased in cortisol. This significant effect of actor cortisol change on hawk-dove decisions remained statistically significant when controlling for gender and time since waking (see Table 4 Model 2). There were no significant partner effects. APIM analyses that explored the moderating role of gender revealed a robust main effect for actor cortisol change ($b = -3.67$, $se = 1.17$, $t(58.68) = -3.13$, $p = 0.003$), but the actor cortisol change \times gender interaction was not significant ($b = 3.30$, $se = 1.95$, $t(59.37) = 1.70$, $p = 0.10$). These analyses indicate that the negative association between actor cortisol change and the number of hawk decisions did not statistically differ between male and female dyads.⁹

Further APIM analyses with cortisol changes from before to the middle of the game (time 2 cortisol minus time 1 cortisol) did not reveal significant effects (p 's > 0.20). We also ran APIM models to test whether testosterone and cortisol changes (time 3 minus time 1 as well as time 2 minus time 1 scores) interacted to predict decisions in the game. There were no significant interactions between testosterone and cortisol change (p 's > 0.40), but the robust main effect for actor cortisol change (time 3 minus time 1 cortisol) once again emerged in these models (p 's < 0.03). Overall, these results indicate that one's cortisol

⁹ Despite not finding a significant interaction with gender, we conducted exploratory analyses separately within each sex to inform follow-up research. We did not expect statistically significant effects due to the substantial reduction in statistical power. These analyses revealed that the effect of actor cortisol change on the number of hawk decisions was in the same direction in both sexes but was driven by male dyads (men: $b = -3.67$, $se = 1.44$, $t(23.61) = -2.55$, $p = 0.018$; women: $b = -0.37$, $se = 1.24$, $t(37.57) = -0.30$, $p = 0.77$). The non-significant actor cortisol change \times gender interaction indicates that these slopes did not statistically differ. Future research with greater statistical power is needed to identify sex differences in the association between cortisol change and hawk-dove decisions.

change from before to after the game was robustly related to decisions in the hawk-dove game.

2.3.3. Analyses of the first decision

The first decision made by each member of a dyad is not dependent on the other player's decisions. Thus, we conducted binary logistic regression analyses with the first decision only as a binary dependent variable. These analyses revealed non-significant effects for basal hormones or hormone changes on the first decision ($p > 0.20$). The overall pattern of results shows that hormonal associations with decision-making in the hawk-dove game emerged across all ten rounds of play but not in the first round of play alone.¹⁰

2.4. Satisfaction

Next we examined hormonal associations with task satisfaction. Separate analyses for basal testosterone and basal cortisol revealed non-significant effects ($p > 0.10$), but there was a statistically significant actor basal testosterone \times actor basal cortisol interaction on satisfaction ($b = -0.69$, $se = 0.27$, $t(80.45) = -2.51$, $p = 0.014$; Table 5 Model 1).¹¹ This dual-hormone interaction remained statistically significant in a second model that controlled for time since waking and gender ($b = -0.72$, $se = 0.29$, $t(74.327) = -2.52$, $p = 0.014$, Table 5 Model 2). In agreement with the dual-hormone hypothesis (Mehta and Prasad, 2015), simple slopes analyses (Aiken and West, 1991) revealed a positive association between basal testosterone and task satisfaction among low-cortisol individuals ($b = 0.47$, $se = 0.17$, $t(79.79) = 2.80$, $p = 0.006$) but a non-significant negative association between basal testosterone and satisfaction among high-cortisol individuals ($b = -0.12$, $se = 0.15$, $t(71.54) = -0.76$, $p = 0.45$; see Fig. 2).

We conducted an additional analysis in which gender was included as a between-dyads moderator of the effects of testosterone and cortisol on satisfaction. Neither the main effect of gender nor any of the interactions with gender were significant ($p > 0.10$). We also conducted separate analyses in male and female dyads to confirm that the same dual-hormone interaction pattern emerged, but we did not expect statistically significant effects due to the reduced statistical power. These analyses showed similar patterns for the actor basal testosterone \times actor basal cortisol interaction on satisfaction in males ($b = -1.08$, $se = 0.54$, $t(30.364) = -2.02$, $p = 0.052$) and in females ($b = -0.68$, $se = 0.37$, $t(39.319) = -1.86$, $p = 0.071$). Taken together, these results indicate that the dual-hormone interaction effect on satisfaction did not significantly differ between male and female dyads.

Because satisfaction was positively correlated with positive affect and negatively correlated with negative affect (see Table 2), we tested whether the dual-hormone interaction on satisfaction remained when controlling for actor and partner positive and negative affect. This APIM analysis again revealed a significant actor basal testosterone \times actor basal cortisol interaction on satisfaction ($b = -0.55$, $se = 0.25$, $t(80.10) = -2.16$, $p = 0.034$). This pattern indicates that the dual-hormone interaction effect on satisfaction in the hawk-dove game cannot be explained by general positive or negative affect.

APIM models were also run to estimate associations between hormone change measures and satisfaction. We closely followed the

¹⁰ We also conducted exploratory analyses testing whether gender moderated basal testosterone's or cortisol change's association with tendency to choose hawk for the first decision alone. The gender \times basal testosterone interaction was not significant, but the gender \times cortisol change interaction was ($b = 6.16$, $se = 2.40$, $p = 0.01$). Follow-up analyses in each sex indicated that cortisol change was negatively related to the probability of choosing hawk in men ($b = -3.79$, $se = 1.74$, $p = 0.03$, $e^b = 0.023$) but not in women ($b = 2.37$, $se = 1.66$, $p = 0.15$, $e^b = 10.73$).

¹¹ To provide a rough estimate of effect size for the interaction, we also conducted a multiple-regression analysis with basal testosterone, basal cortisol, and their interaction as predictors of satisfaction. The interaction was statistically significant and explained an additional 5.37% of the variance in satisfaction scores, which matches effect sizes reported in previous dual-hormone interaction research (e.g., $\Delta R^2 = 4.8\%$, Study 1 of Mehta and Josephs, 2010).

Table 5
Basal hormone levels predicting satisfaction in the hawk-dove game.

	B	se	df	t	p	95% CI		Rho	
						Lower	Upper		
Model 1									
Constant	5.32	0.13	45.00	41.02	0.00	5.06	5.58	0.43	
Actor basal T	0.17	0.11	81.71	1.62	0.11	-0.04	0.39		
Partner basal T	-0.13	0.11	81.71	-1.19	0.24	-0.34	0.09		
Actor basal C	0.04	0.26	78.89	0.15	0.88	-0.48	0.56		
Partner basal C	0.40	0.26	78.89	1.51	0.14	-0.13	0.92		
Actor basal T \times basal C	-0.69	0.27	80.45	-2.51	0.01	-1.23	-0.14		
Partner basal T \times partner basal C	0.03	0.27	80.45	0.11	0.91	-0.52	0.58		
Model 2									
Constant	5.45	0.20	41.00	26.61	0.00	5.04	5.87		0.43
Actor basal T	0.18	0.11	75.04	1.62	0.11	-0.04	0.40		
Partner basal T	-0.13	0.11	75.04	-1.14	0.26	-0.35	0.09		
Actor basal C	-0.07	0.30	73.07	-0.22	0.82	-0.66	0.52		
Partner basal C	0.30	0.30	73.07	1.02	0.31	-0.29	0.89		
Actor basal T \times basal C	-0.72	0.29	74.33	-2.52	0.01	-1.29	-0.15		
Partner basal T \times partner basal C	0.00	0.29	74.33	0.00	1.00	-0.57	0.57		
Actor time since waking	-0.03	0.06	78.70	-0.44	0.66	-0.14	0.09		
Partner time since waking	-0.04	0.06	78.70	-0.71	0.48	-0.16	0.08		
Gender	-0.19	0.27	41.00	-0.73	0.47	-0.73	0.34		

Notes: T = testosterone; C = cortisol. Basal testosterone was standardized within sex. Time since waking = grand-mean centered hours since waking. Rho = degree of interdependence in the dependent variable within dyads. Gender: 0 = Male, 1 = Female. Self-reported satisfaction consisted of participants' responses to the following items rated on a 7-point scale (1 = Disagree strongly; 7 = Agree strongly), averaged across the two measurement time points: 'I enjoyed the game'; 'I am satisfied with how much money I earned in the game'; 'I want to play the game again'; 'I am satisfied with how I played the game'. Based on how the other participant played the game, I think I would like him/her'. Ratings from the two time points were averaged to create a global measure of satisfaction in the hawk-dove game.

hormone change analyses reported earlier for hawk-dove decisions. These APIM models testing associations between hormone changes and satisfaction revealed no significant hormonal effects ($p > 0.09$).

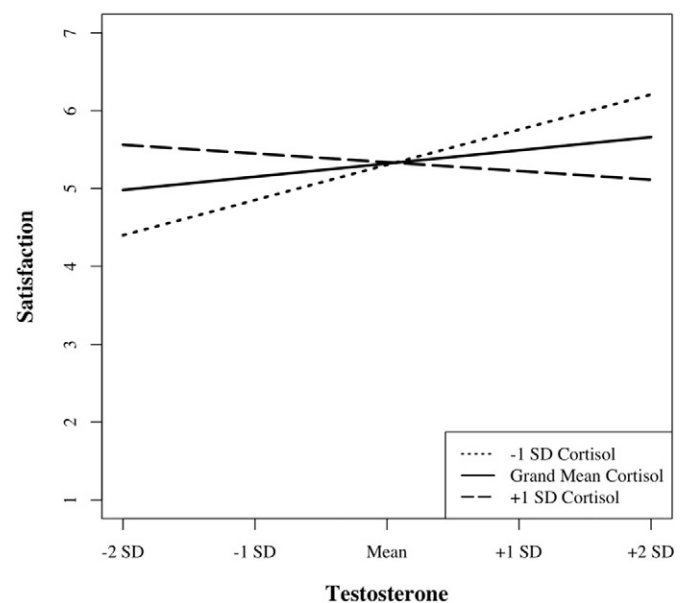


Fig. 2. Interaction between basal testosterone and basal cortisol predicting self-reported satisfaction in the hawk-dove game. SD = standard deviation. Basal testosterone was standardized within sex prior to analysis.

2.5. Supplementary analyses

2.5.1. Affect

Supplemental analyses for self-reported affect revealed a trend toward an association between higher actor basal testosterone and increased positive affect. This pattern is consistent with the positive correlation reported in Table 2 (Tables S4 and S5). There were no other robust hormonal effects for positive or negative affect. Thus, endocrine effects were stronger for satisfaction than for general positive or negative affect.

2.5.2. Changes over time

Supplemental analyses comparing the first five rounds to the last five rounds of play revealed that hormonal associations with hawk-dove decisions and satisfaction did not statistically vary between these time points.

2.5.3. Earnings

Consistent with the structure of the game shown in Fig. 1, supplemental analyses for money earned confirmed that one's own hawk decisions caused economic harm to one's partner. Further, there was a trend for high testosterone individuals' partners to show reduced earnings (Table S6). A comparable effect was seen for cortisol change; that is, the partners of individuals who experienced the largest decreases in cortisol levels also showed somewhat reduced earnings (Table S7). Thus, the overall pattern of results indicates that individuals with higher basal testosterone levels made more hawk decisions, and these decisions in turn caused economic harm to higher testosterone individuals' partners. Similarly, individuals who decreased in cortisol levels from before to after the game made more hawk decisions, and these decisions in turn caused economic harm to their partners.

3. Discussion

The present study is the first to test the roles of testosterone and cortisol in the hawk-dove game, a dyadic decision-making paradigm that is theorized to model status interactions and hierarchy emergence (Maynard-Smith, 1982; Matsumura and Kobayashi, 1998; Neugebauer et al., 2008; van Vugt and Tybur, 2015). In each round each player selects either the dominance (hawk) or deference (dove) strategy, and both players' strategies jointly determine the distribution of resources between the two players. Pairs of same-sex participants played ten rounds of the game with feedback on decisions and the distributions of resources after each round of play. Supporting our main hypothesis, there was a positive association between basal testosterone and the number of hawk decisions – decisions that caused economic harm to the other player. That is, high-testosterone players (high testosterone relative to other individuals of the same sex) were more likely to choose the dominance strategy (hawk), whereas low-testosterone players (low testosterone relative to other individuals of the same sex) were more likely to choose the deference strategy (dove). The same pattern between basal testosterone and behavior emerged in males and females. This novel result connecting testosterone to dominance-deference behavioral strategies in the hawk-dove game supports theories proposing that higher testosterone should encourage status-relevant behaviors such as social dominance and aggression (Mazur and Booth, 1998; Josephs et al., 2006), whereas lower testosterone should be related to socially submissive behaviors (Wingfield et al., 1990; Archer, 2006; Josephs et al., 2006; Mehta et al., 2009).

There are several proximate mechanisms related to status motives that may explain testosterone's effect on hawk-dove decisions. Consistent with theorizing that the hawk-dove game models status competitions and hierarchy emergence (Maynard-Smith, 1982; Matsumura and Kobayashi, 1998; Neugebauer et al., 2008; van Vugt and Tybur, 2015), one explanation is that high-testosterone individuals may have perceived the hawk-dove game as a status competition where the

winner is the player who earns more money (high status) and the loser is the player who earns less money (low status). Players with higher testosterone may have selected the hawk strategy to avoid a position of low status relative to the other player (that is, to prevent a competitive loss). This avoidance of low status is accomplished because selecting hawk leads either to (i) high status if the other player chooses dove (a competitive win, \$4 compared to the other player's \$1); or (ii) equal status if the other player chooses hawk as well (a tie outcome where both players earn \$0). Only the dove strategy runs the risk of a low-status position should the other player choose hawk (\$1 compared to the other player's \$4). This low-status prevention mechanism aligns with evidence suggesting that high-testosterone individuals are more comfortable in high-status positions and find low-status positions (e.g., defeat in competition) stressful and aversive (Josephs et al., 2006; Newman et al., 2005; Mehta et al., 2008). This interpretation is also consistent with growing evidence suggesting that exogenous testosterone administration in both men and women increases sensitivity to status threat cues and motivates dominant behaviors (e.g., van Honk et al., 2001; Hermans et al., 2006; Hermans et al., 2008; Wright et al., 2012; Bos et al., 2010, 2012; Terburg et al., 2012; Boksem et al., 2013; Goetz et al., 2014; Enter et al., 2014; Radke et al., 2015; Mehta et al., 2015c). In contrast, low-testosterone individuals may find high-status positions uncomfortable and may actually prefer lower status as well as social cooperation (e.g., Wingfield et al., 1990; Josephs et al., 2006; Mehta et al., 2009; Wright et al., 2012; Edelman et al., 2014). As a result, low-testosterone individuals tend to avoid status conflicts and adopt deference behaviors instead.

A related psychological explanation is that basal testosterone may be related to hawk-dove decisions via expectations about the other player's dominance versus deference behaviors. As explained in the introduction, the hawk-dove combination is the most beneficial outcome for each individual. If player 1 expects that player 2 will choose dove, then player 1 achieves a higher pay-off by choosing hawk (lower left quadrant of Fig. 1). If player 1 expects that player 2 will choose hawk, then player 1 achieves a higher pay-off by choosing dove (upper right quadrant of Fig. 1). High-testosterone players may choose the dominance behavioral strategy more often (hawk) because they may expect their partners to choose the deference strategy (dove), but low-testosterone players may choose the deference behavioral strategy ("dove") because they may expect their partners to choose the dominance strategy (hawk). This explanation aligns with a key principal of the hawk-dove game – that it models social hierarchy emergence in which each individual has incentives to enter into dominant-subordinate or subordinate-dominant relationships (the hawk-dove or dove-hawk combinations shown in Fig. 1). This mechanism also fits remarkably well with psychological evidence revealing that motivated expectations about others' behaviors propel individuals into hierarchical relationships (Tiedens et al., 2007). In a series of studies, Tiedens et al. (2007) show that dominant individuals are motivated to perceive potential partners in a work context as submissive, whereas submissive individuals are motivated to perceive potential partners as dominant. These perceptions of dominance complementarity (the tendency to perceive another individual as different from oneself on dominance) bolster optimism about entering into hierarchical work relationships. Future research can measure expectations about dominance complementarity in the hawk-dove game to test whether it explains why high-testosterone players are more likely to choose the dominance strategy (hawk) and low-testosterone players are more likely to choose the deference strategy (dove).

A third psychological explanation is that high-testosterone individuals may be more willing to harm others to achieve their dominance goal. As shown in Fig. 1, compared to a situation in which Player 1 chooses the dove strategy, a situation in which Player 1 chooses the hawk strategy will lower Player 2's earnings from \$2 to \$1 if Player 2 chooses the dove strategy or from \$4 to \$0 if Player 2 chooses the hawk strategy as well. Indeed, our analyses confirmed that the more

hawk decisions a player made, the lower their partner's earnings were. If high-testosterone individuals were indeed more *motivated* to choose hawk due to their high dominance motivation, they may also have been more *willing* to make hawk choices to achieve their dominance goal even though it caused direct economic harm to their partners. This interpretation fits with the finding that high-testosterone individuals are more willing to harm others in moral dilemmas in order to achieve a desired outcome (Carney and Mason, 2010; see also Arnocky et al., 2016). In contrast, low-testosterone individuals experience greater empathy for others, are less willing to engage in harmful acts toward others, and may be more interested in bonding with others (Wingfield et al., 1990; Mehta et al., 2009; Wright et al., 2012; Ronay and Carney, 2013; Edelman et al., 2014; Ketay et al., 2017), which may all explain why low-testosterone individuals show a preference for deference behavior (dove decisions).

In addition to these psychological explanations related to status and dominance, complementary neural mechanisms may also be involved. More specifically, testosterone's association with decision-making in the hawk-dove game may be explained by activity in neural regions implicated in threat processing (amygdala) as well as self-regulation and impulse control (orbitofrontal cortex). Testosterone enhances amygdala reactivity (Hermans et al., 2008; Gospic et al., 2011; Goetz et al., 2014; Radke et al., 2015), reduces orbitofrontal cortex activity (Mehta and Beer, 2010), and disrupts amygdala-prefrontal cortex connectivity in response to social threat cues (van Wingen et al., 2010; Volman et al., 2011). These neural mechanisms have all been associated with testosterone-dependent aggressive and dominant behaviors (Carré and Olmstead, 2015). Thus, testosterone levels may be related to the dominance versus deference behavioral strategies in the hawk-dove game through some of these same neural mechanisms, a hypothesis that can be tested directly in future research.

The present findings reveal that a person's own basal testosterone level predicted his or her own strategic decisions in the hawk-dove game, but these results open up new avenues for research that examines hormonal configurations within dyads and groups as predictors of collective outcomes. Our analyses that accounted for the interdependent nature of the behavioral data indicate that dyads in which both individuals had high basal testosterone were more likely to end up in financially costly status battles (hawk-hawk combination), whereas dyads in which one individual was high and the other low in basal testosterone were more likely to end up in a social hierarchy (hawk-dove combination). These results imply that groups with more than one high-testosterone individual may experience high levels of status conflict that can undermine individual and collective outcomes, whereas groups that are heterogeneous in basal testosterone levels are more likely to form social hierarchies that improve coordination and foster adaptive collective performance. This hypothesis requires direct testing in future research, but there is some indirect evidence supporting it. For example, dyads and groups with too many high-status individuals have impaired collective performance on tasks requiring coordination due to increased intragroup conflict, whereas status differentiation improves collective performance by improving coordination and reducing conflict (Ronay et al., 2012; Swaab et al., 2014; Wiltermuth et al., 2015; Hildreth and Anderson, 2016; Kilduff et al., 2016). Furthermore, groups in which high-testosterone individuals hold high-status positions and low-testosterone individuals hold low-status positions enjoy high levels of group self-efficacy, a psychological factor that may be involved in group coordination and productivity (Zyphur et al., 2009). Finally, groups with a mix of individuals who are high and low in prenatal testosterone exposure (as indexed by the second to fourth digit ratio) perform well on intergroup decision-making tasks compared to groups with too many individuals with high prenatal testosterone exposure (Ronay et al., 2012). Functional theories propose that a clear status hierarchy has adaptive value for groups by improving group coordination and efficiency, whereas an absence of hierarchy increases conflict, decreases coordination, and negatively impacts group-level performance.

The present results along with the related evidence reviewed here are consistent with these theories. Moreover, these results provide initial support for the hypothesis that the variability in circulating testosterone within a group (having a mix of high and low testosterone individuals) may influence hierarchy emergence, intragroup coordination, and collective performance. Direct tests of this hypothesis await further research.

3.1. Cortisol changes and hawk-dove decisions

Our analyses also revealed a negative association between cortisol changes from before to after the game and the number of hawk choices. That is, individuals who decreased in cortisol tended to choose hawk more often, whereas individuals who increased in cortisol tended to choose dove. This finding aligns with some prior research and theorizing proposing that lower cortisol should be related to social approach behaviors such as dominance, whereas higher cortisol should be related to socially inhibited behaviors such as deference (Terburg et al., 2009). New research points to another psychological mechanism: interpersonal closeness. In a recent study, male dyads were exposed to a stressor or a non-stressful control condition, completed a dyadic interaction task, and then reported their feelings of psychological closeness to their partner (Berger et al., 2016). Cortisol changes were measured before and after the stressful/non-stressful task. Participants who experienced the largest increases in cortisol, independent of whether they were exposed to the stressful or non-stressful control condition, reported greater psychological closeness to their partner compared with participants who experience smaller increases in cortisol or cortisol decreases. Extending these prior results to the present study, individuals who experienced the largest decreases in cortisol may have felt low levels of psychological closeness toward their partner in the hawk-dove game, facilitating a dominance behavioral strategy (but see also Ketay et al., 2017). Future studies can test this hypothesis by including measures of psychological closeness.

The correlational design of our study precludes clear conclusions about causality. Although it is possible that cortisol changes had an influence on hawk-dove decisions, the causal direction may have gone from decisions to cortisol changes instead. Selecting the dominance behavioral strategy (hawk) may have caused cortisol concentrations to decrease, but selecting the deference behavioral strategy (dove) may have caused cortisol concentrations to increase. This pathway from behavior to cortisol changes is consistent with recent experimental evidence indicating that stable dominant positions buffer cortisol stress responses, whereas stable subordinate positions exacerbate cortisol stress responses (Knight and Mehta, 2017). This pathway is also consistent with evidence that acts of aggressive behavior can be rewarding and may reduce cortisol concentrations (Virgin and Sapolsky, 1997; Chester and DeWall, 2016). Future studies that adopt experimental designs will be important for determining causal pathways linking cortisol changes to hawk-dove decisions.

3.2. The dual-hormone hypothesis, task satisfaction, and affect

Some prior studies have shown that testosterone interacts with cortisol to predict status-relevant social behavior (Mehta and Prasad, 2015), but other studies have failed to find this interaction effect and instead have showed direct associations between testosterone or cortisol and social behavior. Our results are consistent with this latter body of evidence. We found independent associations between these two hormones and hawk-dove behavior, but we did not detect any dual-hormone interactions predicting hawk-dove decisions. One clear possibility is that testosterone independently predicts decisions but does not interact with cortisol to predict decisions in the hawk-dove game, as our analyses suggest. Behaviors in the hawk-dove game may have different underlying mechanisms than the behaviors investigated in prior research supporting the dual-hormone hypothesis (e.g.,

confidence in a position of leadership, Mehta and Josephs, 2010; status in teammates and executives, Edwards and Casto, 2013; Sherman et al., 2016; popularity in social networks, Ponzi et al., 2016). But at least two other possibilities should be considered in future work. First, we may have had insufficient statistical power to detect such a dual-hormone interaction on hawk-dove decisions especially if the effect is present in one sex but not the other. Studies that use larger mixed-sex sample sizes may indeed detect a dual-hormone interaction on hawk-dove decisions. Second, a dual-hormone interaction effect on hawk-dove decisions may further depend on other environmental or personality moderators that were not considered in the present study but should be considered in future work (e.g., for a review, see Mehta and Prasad, 2015).

Despite the absence of a dual-hormone interaction on hawk-dove decisions, there was robust support for the dual-hormone hypothesis on self-reported satisfaction in the hawk-dove game. The satisfaction measure consisted of five questions that assessed task enjoyment, satisfaction with earnings, desire to play the economic game again, satisfaction with how one played the game, and liking of one's partner based on how the partner played the game. Our study showed for the first time that basal testosterone was positively related to self-reported satisfaction for individuals *low* in basal cortisol but not for individuals high in basal cortisol, a pattern closely aligned with prior studies supporting the dual-hormone hypothesis (Mehta and Prasad, 2015). This new support for the dual-hormone hypothesis on task-related satisfaction is consistent with the theoretical assertion that reward motivation may be a key mechanism for testosterone and cortisol's joint behavioral effects (e.g., Welker et al., 2015) and opens up new avenues for research on psychological mechanisms of dual-hormone behavioral effects. To date, studies have generally failed to identify psychological mediators of dual-hormone interactions on behavior. The present results point to an important hypothesis that should be tested directly in future research: that psychological factors linked to reward motivation such as task-related satisfaction (as well as dopaminergic neural reward systems such as the ventral striatum) may partially explain the dual-hormone interaction effects on social behavior observed in prior studies (Mehta and Prasad, 2015; Bhanji and Delgado, 2014; Welker et al., 2015).

The dual-hormone interaction was related to satisfaction in the hawk-dove game, but it was not related to general positive or negative affect (measured with the Positive and Negative Affect Schedule, Watson et al., 1988). Instead, there was a weak, non-significant positive association between basal testosterone and positive affect. Even though satisfaction was positively correlated with positive affect and negatively correlated with negative affect, the dual-hormone interaction on satisfaction still remained when controlling for positive or negative affect. This pattern of results indicates that basal testosterone and cortisol are more strongly related to satisfaction in the hawk-dove game than to general positive or negative affect. One plausible explanation is that the task satisfaction measure more closely tapped into the dopaminergic reward system, such as activity in the ventral striatum, that is influenced by testosterone and cortisol concentrations (Packard et al., 1997; Hermans et al., 2010; Op de Macks et al., 2011; Kätsyri et al., 2013; Welker et al., 2015). In agreement with this interpretation, neuroimaging research on competition has shown that ventral striatum responses to wins and losses are correlated with self-reported ratings of overall pleasantness of the win and loss events but not with self-reported positive or negative affect (Kätsyri et al., 2013). A related possibility is that the positive and negative affect scale that we used asked participants to report on their feeling states "right now" but did not specifically ask participants to indicate how they felt when playing the hawk-dove game, when making decisions in the game, or when receiving feedback about partner's decisions. In contrast, the task satisfaction measure asked questions about satisfaction about various aspects of the hawk-dove game ("I enjoyed the game."; "I want to play the game again."). It is possible that modified instructions to target affect during game

play itself will show stronger associations with testosterone and cortisol concentrations.

3.3. Hormones, behavior, and sex/gender

In agreement with prior research and published recommendations (e.g., Josephs et al., 2006; Stanton, 2011; Tackett et al., 2014), our primary analyses standardized basal testosterone concentrations within sex so that high scores indicate high testosterone levels relative to other individuals of the same sex (see also footnote 6). We also conducted follow-up analyses to examine the pattern of results within each sex. Our analyses showed non-significant sex differences in basal testosterone's associations with hawk-dove decisions and basal testosterone's interaction with basal cortisol in predicting satisfaction in the hawk-dove game. This absence of significant sex differences aligns with many prior studies, which also found similar testosterone-behavior associations in males and females (e.g., Josephs et al., 2006; Mehta et al., 2009; Zyphur et al., 2009; Mehta and Josephs, 2010; Carney and Mason, 2010; Edelman et al., 2014; Tackett et al., 2014; Mehta et al., 2015a; Kornienko et al., 2016). Thus, our results taken together with this prior research show that basal testosterone levels predict *within*-sex variation in behavior and do not explain *between*-sex variation in behavior. At the same time, other studies revealed significant effects of testosterone in males and non-significant results in females (e.g., Carré and Olmstead, 2015; Welker et al., 2015). These results in women could indicate that testosterone is truly unrelated to the women's behaviors in these studies (e.g., reactive aggression in the Point Subtraction Aggression Paradigm), but there are other possibilities. For example, greater measurement error in assessing testosterone concentrations in females due to low concentrations may reduce effect sizes in women and thus make it harder to detect significant effects (Welker et al., 2016). Future studies should obtain larger mixed-sex samples and should adopt more accurate methods for determining testosterone concentrations, such as mass spectrometry-based methods, when feasible.

Sex differences in the relationship between cortisol change and decision-making have been documented in some previous studies (e.g., the Iowa Gambling Task, van den Bos et al., 2009). Our primary analyses failed to detect a significant sex difference in the negative association between cortisol change and decision-making in the hawk-dove game. Even though exploratory analyses suggest that the effect may have been stronger in men, this pattern was not significant in all analyses and thus should be interpreted with caution. Future studies with greater statistical power can further explore sex similarities and differences in the relation between cortisol changes and hawk-dove game decisions.

There was some evidence for a sex difference in endocrine responses to the hawk-dove game. Cortisol and testosterone concentrations decreased over the course of the hawk-dove game in women, consistent with circadian decline, but not in men. This pattern suggests that playing the hawk-dove game with another man may have caused men's cortisol and testosterone responses to resist circadian decline. This general pattern resembles sex differences in endocrine reactivity to social-evaluative stressors such as the Trier Social Stress Test (TSST); men tend to show stronger cortisol stress responses to the TSST compared to women (Stephens et al., 2016). The testosterone response pattern in men is also consistent with the challenge hypothesis (Wingfield et al., 1990; Archer, 2006). According to this hypothesis, testosterone levels especially among males should be higher during periods of social challenge (e.g., competition) compared to periods without social challenge (e.g., absence of competition). Because testosterone concentrations are expected to decrease in neutral settings consistent with circadian decline, the pattern of relatively steady testosterone levels in men in the current study may be because of the competitive nature of the hawk-dove game. Nevertheless, the design of our study does not allow us to draw firm causal conclusions about

the influence of the hawk-dove game on hormone fluctuations. Future studies that randomly assign male and female participants to the hawk-dove game or a control task can directly test the causal impact of playing the hawk-dove game on acute changes in steroid hormone concentrations.

The present study investigated hawk-dove decision-making strategies in same-sex pairs. We chose this approach to reduce the influence of mating motives that may be observed in opposite-sex social interactions. Social neuroendocrinology studies have indeed shown that opposite-sex social interactions among heterosexual individuals can elicit different patterns of hormone responses compared to same-sex social interactions (e.g., Roney et al., 2007). Given the prevalence of mixed-sex interactions in modern-day hierarchies (e.g., work organizations), future studies should test whether the hormonal effects we observed in same-sex social interactions extend to opposite-sex interactions.

3.4. Limitations and future directions

The present study investigated naturally occurring hawk-dove decisions in same-sex pairs and used a statistical analysis strategy (the actor-partner interdependence model) to account for the interdependent nature of the data within each pair. With this approach we identified statistical significant effects of a player's own hormone profile on his or her own decision-making strategy over the course of the game. The effect size for basal testosterone's association with the number of dove choices can be approximated by the correlation reported in Table 2 ($r = 0.23$; approximately 5.3% of the variance in the number hawk decisions is explained by basal testosterone levels). This observed effect size is similar to the effect sizes reported in previous research on basal testosterone's direct association with social behavior or decision making (e.g., r 's between 0.21 and 0.29, Slatcher et al., 2011; standardized beta estimate of 0.26, Ronay and Carney, 2013; r 's in the 0.20 to 0.30 range, Turan et al., 2014; $r = 0.11$, Platje et al., 2015; $r = 0.11$, Mehta et al., 2015d; standardized beta estimate of 0.18, van der Meij et al., 2016). At the same time, it is important to acknowledge that a partner's number of hawk decisions was a much stronger predictor of a player's own hawk decisions ($r = 0.65$; McClintock and Liebrand, 1988). Further, there was still substantial variance in a player's choices that could not be explained by hormones or partner choices. Future research should investigate additional psychological and biological factors that predict hawk-dove decisions.

The use of real players improves ecological validity, but the inherent cost is the loss of experimental control. In particular, this study cannot directly address the causal influence of a partner's behavior on one's own behavior and hormone changes, or whether a partner's behavior has a causal effect on the association between one's own hormone profile and one's own decisions. Indeed, an important follow-up question is: To what extent does the positive association between basal testosterone and the tendency to select the dominance behavioral strategy (hawk) vary depending on whether one's partner adopts a highly dominant strategy (selects hawk on all or nearly all rounds of play), a highly deferent strategy (selects dove on all or nearly all rounds of play), or a mixed strategy (e.g., a random strategy or a tit-for-tat strategy)? The moderating effect of partner behavior can be addressed directly in future studies that experimentally manipulate partner decision-making strategies using deception (McClintock and Liebrand, 1988; Rilling et al., 2007, 2008). Future studies can also manipulate other partner characteristics, such as physical dominance versus deference signals or a partner's high or low relative status in a previously established hierarchy, to determine whether these partner features moderate the association between one's own hormone profile and one's own decisions in the hawk-dove game.

These follow-up studies that manipulate partner behavior and characteristics will also be able to address open questions about timing. We failed to observe a robust association between basal testosterone and the hawk-dove choice in the first round of play; rather, this hormonal

effect was detected when examining behavior in all ten rounds of play. In supplemental analyses we report that the hormone-behavior associations did not statistically vary from the first five rounds of play to the second five rounds of play. Nevertheless, the pattern suggests that basal testosterone's positive association with the tendency to choose the dominance strategy (hawk) may have been somewhat stronger in the second five rounds of play compared to the first five rounds of play (albeit not significantly so). Future studies that experimentally manipulate partner decision-making strategies or hold them constant may be able to detect significant time-dependent hormonal effects and identify the underlying mechanisms.

We have argued that social motives implicated in dominance, deference, and the pursuit of status may explain the effect of basal testosterone on choices in the hawk-dove game, but we did not examine these social motives directly. Future research should measure such motives, which likely operate outside of conscious awareness (implicit motives, Schultheiss et al., 2005; Terburg et al., 2012), to understand the psychological mechanisms underlying the hormonal effects we observed. These new studies should also measure financial motives to investigate the interplay between financial and social concerns in the hawk-dove game.

Experimental sessions began in the late morning or afternoon to minimize the effects of circadian fluctuations in hormone levels. Testosterone and cortisol measured around the same time of day are moderately stable across several weeks (Liening et al., 2010), suggesting they are reasonable measures of basal testosterone and cortisol. However, future studies can better estimate basal hormone concentrations by collecting multiple baseline samples. Further, there are diurnal slopes in hormone concentrations, and these diurnal slopes may also explain behavior. Connections between these diurnal rhythms and hawk-dove game decisions should be investigated in future research.

The current research found associations between endogenous hormone concentrations and subsequent decisions, but we cannot be certain that hormones directly caused these behavioral effects. Pharmacology experiments that manipulate hormone concentrations are needed to confirm causality. Such pharmacology studies can also be deployed to study the impact of hormonal configurations not only on individual decisions but on collective outcomes as well. The initial evidence reported in this paper suggests that the presence of two or more individuals with high basal testosterone may lead to costly conflict. We look forward to new research that addresses this and other new questions about hormones and hierarchy processes in dyads and groups.

Author contributions

PHM, RAJ, and MV designed the study; PHM collected the data under the supervision of RAJ; PHM and NMLD analyzed the data; PHM wrote the first draft of the paper, and all authors provided comments on subsequent drafts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yhbeh.2017.03.009>.

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