





## STUDENT AWARDEE PAPER

# Circulating Hormones and Dominance Status Predict Female Behavior during Courtship in a Lekking Species

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**Synopsis** Female competitive behaviors during courtship can have substantial fitness consequences, yet we know little about the physiological and social mechanisms underlying these behaviors—particularly for females of polygynous lek mating species. We explored the hormonal and social drivers of female intersexual and intrasexual behavior during courtship by males in a captive population of Indian peafowl. We investigated whether (1) female non-stress induced circulating estradiol (E2) and corticosterone (CORT) levels or (2) female dominance status in a dyad predicts female solicitation behavior. We also tested whether female circulating E2 and CORT predict dominant females' aggressive behaviors toward subordinate females in the courtship context. Our findings demonstrate that females with higher levels of circulating E2 as well as higher levels of circulating CORT solicit more courtships from males. Dominant females also solicit more courtships from males than subordinate females. Female intrasexual aggressive behaviors during courtship, however, were not associated with circulating levels of E2 or CORT. Overall, we conclude that circulating steroid hormones in conjunction with social dominance might play a role in mediating female behaviors associated with competition for mates. Experimental manipulation and measures of hormonal flexibility throughout the breeding season in relation to competitive and sexual behaviors will be necessary to further examine the link between hormonal mechanisms and female behavior in polygynous lekking systems.

## Introduction

Competitive behaviors can directly influence an individual's access to resources, including territories and mates. Historically, competitive interactions among females and their physiological underpinnings have been understudied compared to the study of these processes in males (Clutton-Brock 2007; Rosvall 2011; Duque-Wilckens and Trainor 2017; Rosvall et al. 2020). In species with conventional sex roles, sexual selection typically drives intrasexual competitive behaviors and ornaments in males, and mate choice behaviors in females (Bateman 1948; Trivers 1972; Emlen and Oring 1977; Kokko and Jennions 2003). Female intrasexual competition, however, confers fitness benefits for the

“winning” female; therefore, female competitive behaviors, which can include both intrasexual aggressive behaviors (e.g., Yasukawa and Searcy 1982; Fernandez-Duque and Huck 2013) and solicitation behaviors directed toward males in the presence of other females (e.g., Eens and Pinxten 1996; Stoinski et al. 2009), play an important role in shaping mating success (Rosvall 2011; Stockley and Bro-Jørgensen 2011). Although underlying mechanisms of competitive behaviors are likely shared between males and females, unique selection pressures shaping the fitness strategies of each sex could drive differences in these mechanisms (Duque-Wilckens and Trainor 2017; Lipshutz and Rosvall 2020, 2021).

Hormones are key mediators of competitive and sexual behaviors due to their pleiotropic effects in response to the dynamic ecological and social environment (Adkins-Regan 2005; Zera et al. 2007). Conclusions on whether hormones stimulate similar effects in both sexes remain unresolved, further highlighting the gap in research focusing on hormonal mechanisms of female competitive and sexual behaviors. In birds, estradiol and corticosterone—steroid hormones that are less commonly studied than testosterone in competitive contexts—could play important roles in female competition (Laredo et al. 2014; Duque-Wilckens and Trainor 2017).

Estradiol, a sex steroid hormone converted from testosterone through a single enzyme, aromatase, can directly affect female competitive behavior during development as well as into adulthood (Bentley et al. 2007; Duque-Wilckens and Trainor 2017; Norris and Carr 2020). Testosterone is produced by the gonad, such that estradiol can then be converted at the level of the gonad, promoting ovulation in vertebrates and production of yolk precursors in birds (Adkins-Regan 2005; Bentley et al. 2007; Norris and Carr 2020). Aromatase is also expressed in the brain, converting testosterone into estradiol to directly affect behaviors. Estradiol plays an important role in solicitation behavior (Moore 1982; Searcy and Capp 1997; Maney et al. 2008). Many studies have used estradiol implants to induce sexual behavior in female birds of socially monogamous species. For example, females red-winged blackbirds (*Agelaius phoeniceus*) treated with exogenous estradiol solicited more than control females (Searcy and Capp 1997). Female song sparrows (*Melospiza melodia*) solicited copulations more frequently during the non-breeding breeding season when implanted with estradiol (Wingfield and Monk 1994). Estradiol also promotes intrasexual aggression in females (Albert et al. 1989; Rubenstein and Wikelski 2005; Pärn et al. 2008; Rosvall et al. 2012; Woodley and Moore 1999b).

Glucocorticoids, including corticosterone, which are produced by the adrenal glands as part of the hypothalamic–pituitary–adrenal axis (HPA) response, play a key role in regulating energy homeostasis, and therefore, also in mediating life-history trade-offs and responses to environmental challenges (McEwen and Wingfield 2003; Crespi et al. 2013). Baseline glucocorticoid levels are expected to be related to energetic demands of seasonal behaviors as well as circadian patterns of foraging and appetite (Crespi et al. 2013). During stressful events, glucocorticoids are rapidly upregulated from baseline levels, therefore, suggesting their crucial role in adjusting the physiological state to an environmental challenge (Landys et al. 2006). Experimental hormonal manipulation studies have also

found that glucocorticoids can both promote and suppress aggressive behavior, typically corresponding with the response to acute vs. chronic administration of glucocorticoids, respectively (Wingfield and Silverin 1986; Mikics et al. 2004; Duque-Wilckens and Trainor 2017). However, glucocorticoids from acute stress can also be antagonistic to testosterone (e.g., in male rufous-winged sparrows; Deviche et al. 2010), which would potentially suppress aggression. Baseline glucocorticoid levels have also been found to be correlated with dominance status and aggressive behaviors (Rohwer and Wingfield 1981; Cavigelli et al. 2003; Summers et al. 2005; Muller et al. 2021), but see (Pravosudov et al. 2003). Additionally, experimental manipulation of mineralocorticoid receptors, which primarily mediate actions of baseline levels of glucocorticoids (Myers et al. 2012), exhibited both acute and long-term effects on aggression in rats (Ruiz-Aizpurua et al. 2013). In females, glucocorticoids and other hormones produced in the HPA axis are often negatively correlated with competitive behaviors (Gammie et al. 2004; Gammie et al. 2005; Stoppelbein et al. 2014; Ode et al. 2015). Baseline glucocorticoid levels can also predict relative fitness of individuals or populations, although patterns are not always consistent (Bonier et al. 2009); therefore, we might expect circulating levels to correlate with behaviors associated with mating success.

The relative importance of estradiol and corticosterone in regulating female behaviors in the context of competition for mates remains largely unknown, as most studies on hormonal mechanisms of female aggression have focused on monogamous species in the context of maternal or territorial defense. Female intrasexual competition for mates, however, has been documented in several species (Yasukawa and Searcy 1982; Slagsvold and Lifjeld 1994; Kvarnemo et al. 1995; Bowler et al. 2002; Bro-Jørgensen 2002; Lewis et al. 2004; Razzoli and Valsecchi 2006; Fernandez-Duque and Huck 2013; Mafra et al. 2020). Female–female competition for mates can be strong even in polygynous species when the breeding season is short, or the operational sex ratio favors females (Forsgren et al. 2004; Rusu and Krackow 2004; Duque-Wilckens and Trainor 2017). Therefore, we investigated the hormonal mechanisms underlying female Indian peafowl (*Pavo cristatus*) behavior in a competitive courtship context.

The Indian peafowl is an ideal study species for investigating hormonal mechanisms of female intrasexual competition because of the complexity of their polygynous lek mating system (Petrie et al. 1992). Lek systems, in which only females provide parental care, are known for strong female mate choice and male intrasexual competition (Höglund and Alatalo 2014). However, males can be choosy and females can be

competitive for mates in lekking species (Trail 1990; Sæther et al. 2001; Bro-Jørgensen 2002). Female–female competition is well-established in Indian peafowl and other lekking species (Petrie et al. 1992; Karvonen et al. 2000; Sæther et al. 2001), but the underlying physiological mechanisms of these behaviors remain poorly understood.

In this study, we measured non-stress induced circulating estradiol and corticosterone levels in peahens in early spring. We then conducted behavioral trials and recorded all solicitation and aggressive behaviors of randomly paired females that were presented with a male. We hypothesized that female dominance status and hormone levels would predict female behavior in a competitive courtship context. We predicted that dominant females would solicit more copulations from the male than subordinates. We also predicted that females with higher circulating levels of estradiol would be more aggressive and would solicit more copulations from the male, whereas females with higher circulating levels of corticosterone would be less aggressive and solicit fewer copulations.

## Materials and Methods

### Animals and facilities

This study was conducted in College Station, Brazos County, TX, USA (30°37'40.717"N, 96°20'3.864"W) using a population of captive adult peafowl (*P. cristatus*; 24 peahens and 12 peacocks) during the 2018 breeding season (March–May). All birds were originally captured from feral populations in Florida and California between 2009 and 2012. They were housed in an outdoor enclosure (18.3 × 24.4 × 2.1 m) and provided food and water *ad libitum*. Individuals were identified using a metal band on one leg and a plastic band on the other leg. Within this captive population, males defend display arenas and court females; captive females form social hierarchies, copulate with males, and lay eggs. We remove eggs immediately after they are laid to prevent the captive flock from increasing in size.

### Blood collection and hormone analysis

We collected blood (0.5 mL) from all peahens ( $n = 24$ ) between 8 AM and 10 AM on April 18, 2018. To minimize disturbance to the flock, we lured a peahen from the main enclosure using food into a separate room (6.2 × 6.3 × 2.1 m) that was not visible to other flock members. We collected a blood sample within 3 min of when a female entered the separate room. Blood was collected from the brachial wing vein using a 25-gauge needle attached to a 1-mL syringe. We

then released her into another isolated room (18.3 × 6.2 × 2.1 m) within the enclosure that was separate from the flock to avoid luring the same female more than once. We repeated this process until each peahen was sampled. Circulating hormone levels were not significantly correlated with either latency to sample after the female entered the sampling room (linear models, E2:  $\beta_1 = 0.0004$ ,  $R^2 = -0.06$ ,  $P = 0.64$ ; CORT:  $\beta_1 = 0.002$ ,  $R^2 = -0.08$ ,  $P = 0.81$ ) or order of sampling (linear models, E2:  $\beta_1 = -0.006$ ,  $R^2 = 0.19$ ,  $P = 0.07$ ; CORT:  $\beta_1 = -0.05$ ,  $R^2 = 0.08$ ,  $P = 0.17$ ); therefore, we did not further consider these factors in our analyses. After collecting blood samples from all individuals, the birds were returned to the main enclosure. The samples were centrifuged, and plasma was separated from the red blood cells. All plasma samples were stored in a  $-20^\circ\text{C}$  freezer and subsequently shipped on dry ice to Indiana University for hormone analysis.

We determined non-stress induced circulating levels of estradiol (E2) and corticosterone (CORT) in peahens using 50 and 10  $\mu\text{L}$  of plasma, respectively. Steroids were extracted three times from plasma using a diethyl ether. Following extraction, hormones were assayed using ELISA kits (E2: #ADI-900–174, Enzo Life Sciences, Ann Arbor, MI, USA; CORT: #501,320, Cayman Chemical, Ann Arbor, MI, USA). Parallelism and extraction efficiency were validated for both assays using a pool of peahen plasma. We found that peahen plasma collected during the breeding season had high fat content even following extraction, which prevented initial parallelism validation of the assay. We centrifuged the pooled sample at 5000 rcf for 15 min and then siphoned plasma off the top of the fat using a 100- $\mu\text{L}$  Hamilton syringe prior to the extractions, similar to previous studies that measured hormones in high-fat milk (Butler and Des Bordes 1980; Sullivan et al. 2011; Petruccio et al. 2019). This method allowed for proper validation of the assay. We, therefore, used this method on all individual samples prior to diethyl ether extraction.

Samples were randomized across two plates for each assay. Coefficients of variance were calculated from a plate standard (i.e., a pool of extracted plasma) that was run three times in duplicate across each plate. Coefficients of variance were as follows: E2:  $n = 2$  plates, intraplate variability = 2.5 and 5.5%, inter-plate variability = 6.0%; CORT:  $n = 2$  plates, intra-plate variability = 1.7 and 0.8%, inter-plate variability = 1.2%.

### Courtship trials

To examine the relationship between circulating hormones and courtship behavior, we observed female–female interactions in the presence of a male during

the breeding season (i.e., May 13–15, 2018, ~1 month after blood collection) between 7:00 AM and 12:00 PM. Males and females were separated for 1 week prior to the start of the trials to maximize courtship behaviors during the trials and eliminate any effects of recent mating history on courtship behavior. The dominance relationships between females before they were separated from the males were the same as those observed during the trials. The females were housed within one room of the enclosure ( $18.3 \times 6.2 \times 2.1$  m), while the males were separated within another room of the enclosure ( $18.3 \times 18.3 \times 2.1$  m); the females and males could hear but not see each other. Trials were conducted in another room of the enclosure ( $6.2 \times 6.3 \times 2.1$  m) that was visually isolated from the rest of the flock. Cameras (Swann SWPRO 535CAM security cameras; Swann Security Systems, Santa Fe Springs, CA, USA) were mounted in each corner of the trial room; the videos were synchronized and recorded using a DVR (4-channel HD DVR; Night Owl Security Products LLC, Naples, FL, USA). During the trials, the experimenter (ADE) monitored the trials out of view of the birds through another camcorder (DCR-SR40; Sony Corp, Tokyo, Japan) set up in the room.

We ran nine trials, in which two females were randomly selected (using a random number generator) from the flock of 24 peahens and then placed in the trial room and allowed to freely interact with one another for 10 min prior to the introduction of a randomly selected male (the “pre-trial period”). Each female was used in only one trial. In this pre-trial period, we recorded the dominance interactions within the dyad. We recorded each time a female performed a known dominance behavior toward the other female in the dyad. These dominance behaviors included: (1) displacing (dominant walks or runs toward subordinate and subordinate moves away), (2) pecking (dominant’s beak quickly comes into contact with subordinate), and (3) hopping (dominant jumps on top of subordinate and subordinate moves away) (Earl et al. 2022). We then introduced the male to the trial room and all individuals were allowed to freely interact for 1 h. Six different males were used for these trials and a given male was used in up to two trials (at least a day lapsed between trials involving the same male). Each male displayed throughout the trial. After the 1-h trial, the birds were returned to their respective rooms. Two trials were aborted (and therefore excluded from the analysis) because the females did not interact with one another in the pre-trial period such that the females’ dominance relationship could not be confirmed. In all other trials, the dominance relationships between each dyad in the trial room were clear because only one individual within the dyad performed dominance

behaviors directed toward the other (i.e., subordinate individuals did not challenge dominant individuals in this one on one setting). Additionally, the dominance relationships between each dyad in the trial room for this study were consistent with the dominance order of the full flock determined several months prior in March 2018 (Earl et al. 2022), which confirmed the stability of the hierarchy in this flock.

We analyzed the videos of the trials ( $n = 7$ ) (QuickTime Player 10.4; Apple Inc., Cupertino, CA, USA) and recorded the number of courtships solicited by each peahen (“solicited courtships”), including successful courtships (i.e., those that resulted in the male mounting the female) and unsuccessful courtships (i.e., those in which the female approached the male, the male performed a hoot-dash display (Petrie et al. 1992), but the female avoided copulation). We combined the successful and unsuccessful courtships into one count because successful copulations only consisted of 59% of solicited courtships (total successful copulations and failed copulations:  $n = 29$ ,  $n = 20$ , respectively). We also recorded female–female aggression via counting and then summing the number of female-aggressive displays by a given peahen toward the other peahen in the trial within 1.5 m of the displaying male. We used the same ethogram of dominance displays for evaluating female–female aggression as we used for the pre-trial period.

### Statistical analysis

We tested whether a female’s non-stress induced hormone levels and dominance status within the dyad (categorical variable, “dominant” or “subordinate”) predicted her behavior (i.e., solicited courtships, aggressive displays) in a competitive courtship context. All statistical analyses were conducted in R (version 4.0).

Hormone values (E2 and CORT) were scaled using the `scale()` function in R, so that slopes of linear models were comparable across results for the models that included one hormone as a fixed effect. For solicited courtships, we built five generalized linear mixed effects models (GLMMs) that included one of the following fixed effects: hormone levels only (i.e., E2 or CORT, defined as  $\beta_1$ ), dominance status only (defined as  $\beta_2$ ), or both terms and their interaction (defined as  $\beta_3$ ). All models included 14 females (subordinate:  $n = 7$ , dominant:  $n = 7$ ). We chose to use interactions between hormone levels and dominance status because of the expected relationship between steroid hormones and dominance status observed in both males and females across vertebrate taxa during the breeding season, in which dominant individuals have higher E2 levels (Creel et al. 1997; Carlson et al. 2004; Renn et al.



**Table 1** Model selection for solicited courtships using AICc, where candidate models are ranked by  $\Delta$ AICc and Akaike weight ( $w_i$ ) alongside the number of estimated parameters ( $k$ ) and log likelihood

Model	$k$	log likelihood	$\Delta$ AICc	$w_i$
~E2 + (1  Male ID)	3	-27.76	0	0.38
~dominance status + (1  Male ID)	3	-27.98	0.43	0.306
~CORT + (1  Male ID)	3	-28.24	0.95	0.236
~(1  Male ID)	2	-31.76	4.68	0.036
~E2 * dominance status + (1  Male ID)	5	-26.06	5.7	0.022
~CORT * dominance status + (1  Male ID)	5	-26.18	5.93	0.02

All models included a random factor of the trial male's ID.

2012; O'Connell et al. 2013) and higher CORT levels (Cavigelli et al. 2003; Carlson et al. 2004; Goymann and Wingfield 2004; Mooring et al. 2006; Creel et al. 2013). We did not include a model with both E2 and CORT because these hormones were correlated with each other (linear model,  $\beta = 0.06$ ,  $p = 0.02$ ), as females with higher levels of E2 also had higher levels of CORT, resulting in collinearity in the model with an interaction between E2 and CORT ( $VIF > 2$ ). We used a Poisson distribution in each model because the number of solicited courtships was right-skewed count data. We considered two possible random effects for each model: Male ID (because one male was used for two of the final trials) and dyad ID (because behavioral data were non-independent due to behavioral testing in dyads). Due to a limited sample size, we were unable to include more than one random effect in each model. Therefore, we compared two null models with the random effects, Male ID and dyad ID in an information theoretic framework using Akaike's information criterion (AICc) corrected for small sample sizes. The model with male ID as the random effect was the top model, such that we used this null model in further model comparisons. However, because the model that included dyad ID as the random effect was within 2  $\Delta$ AICc ( $\Delta = 0.18$ ) (Burham and Anderson 2002), we confirmed that model selection and results were similar when including dyad ID in the model as a random factor rather than male ID. We then compared the fixed-effects models and null model in an information theoretic framework using AICc, considering all models within 2  $\Delta$ AICc of the top model to be competitive (Burham and Anderson 2002). We confirmed that the residuals were dispersed as expected under each of the fitted models, using the *testDispersion()* function from the R package DHARMA v0.4.5. (Hartig 2020). We tested whether the number of aggressive displays performed was predicted by circulating hormone levels (i.e., E2 or CORT) within dominant individuals only because no subordinate females exhibited aggressive displays toward dominant females during the courtship trials.

Aggressive behaviors were normally distributed; therefore, we modeled aggressive displays with a linear mixed model (LMM) and included male ID as a random effect. We also confirmed that dispersion of the residuals was normal for all models.

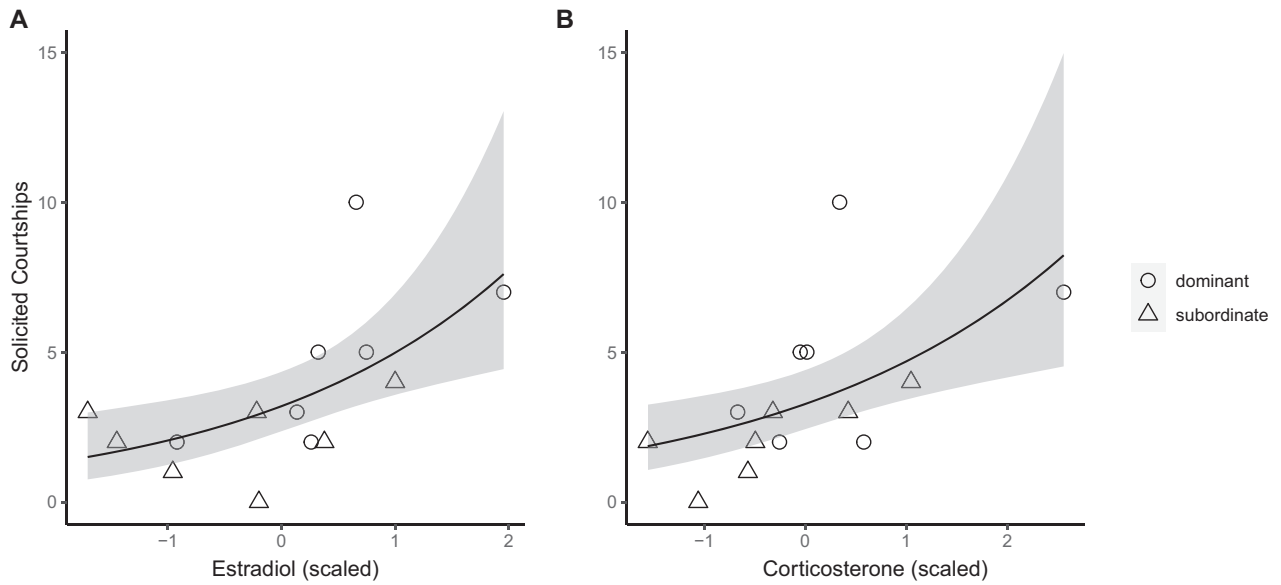
## Results

### Solicited courtship

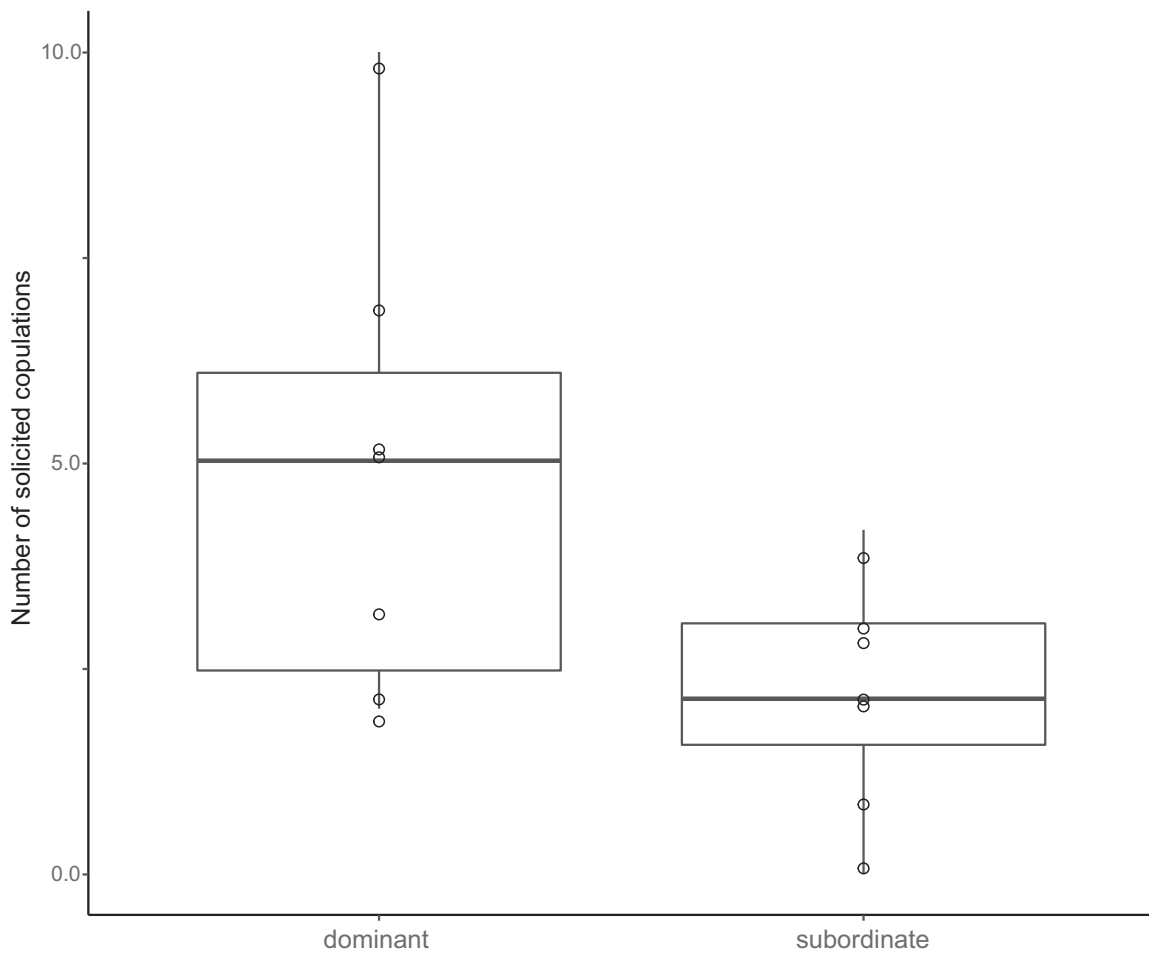
Model comparison revealed that the model that included E2 as the only fixed effect was the best model ( $w_i = 0.380$ ). We also report results from models that included female dominance status or CORT, as they were both strongly supported ( $< 1$   $\Delta$ AICc), but models with the interaction between hormone levels and dominance status were not competitive (see Table 1). Females solicited courtship from males significantly more when they had higher circulating levels of E2 (Fig. 1A:  $\beta_1 = 0.45$ ,  $P = 0.005$ , 95% CI [0.14, 0.76]) or higher circulating levels of CORT (Fig. 1B:  $\beta_1 = 0.39$ ,  $P = 0.009$ , 95% CI [0.10, 0.68]). Dominant females also solicited courtship from males more than subordinate females (Fig. 2: dominant:  $4.9 \pm 1.1$  solicitations, subordinate:  $2.1 \pm 0.5$  solicitations,  $\beta_2 = -0.82$ ,  $P = 0.008$ , 95% CI [-1.42, -0.21]). The random effect, Male ID, explained very little variation in solicitation behaviors across individuals in any of the models (E2: estimated  $\sigma^2 = 0.02$ ; CORT: estimated  $\sigma^2 = 0.05$ ; Dominance status: estimated  $\sigma^2 = 0.08$ ).

### Intrasexual aggression

The number of aggressive displays performed by a dominant female, directed at the subordinate female during the courtship trial, was not correlated with her circulating levels of E2 ( $\beta_1 = -1.20$ ,  $P = 0.706$ , 95% CI [-10.75, 8.35]) or CORT ( $\beta_1 = 2.68$ ,  $P = 0.322$ , 95% CI [-4.86, 10.22]). The random effect, Male ID, explained more variation in aggressive behaviors across dominant individuals than the fixed effects in both models (E2 model: estimated  $\sigma^2 = 44.67$ ; CORT model: estimated  $\sigma^2 = 30.86$ ).



**Fig. 1** The number of times females solicit male courtship in a competitive courtship context is predicted by both circulating (A) estradiol ( $\beta_1 = 0.45, P = 0.005, 95\% \text{ CI } [0.14, 0.76]$ ) and (B) corticosterone levels ( $\beta_1 = 0.39, P = 0.009, 95\% \text{ CI } [0.10, 0.68]$ ), regardless of their dominance status within the trial dyad.



**Fig. 2** Female dominance status within a trial dyad predicts female behavior in a competitive courtship context. Dominant females solicit male courtship significantly more often than subordinate females ( $\beta_2 = -0.82, P = 0.008, 95\% \text{ CI } [-1.42, -0.21]$ ).

## Discussion

We investigated the hormonal mechanisms underpinning female courtship behavior, and competitive behavior in a courtship context, for a lekking species. In support of our hypothesis, we found that hormone levels predicted female behavior in a courtship context. More specifically, non-stress induced circulating levels of two steroid hormones, E2 and CORT, were correlated with female solicitation behavior in both dominant and subordinate peafowl. As we predicted, peahens with higher concentrations of E2 solicited more courtships from peacocks. Counter to our prediction, peahens with higher CORT levels also solicited more (rather than less) courtships from peacocks. Additionally, neither E2 nor CORT concentrations predicted the number of aggressive displays by dominant peahens toward subordinate peahens. These results suggest that in peahens, E2 and CORT may both play a role in mediating intersexual solicitation behavior, but not intrasexual aggressive behavior in a competitive courtship context. Alternatively, it is possible that E2 and CORT are correlates of another hormonal or social phenotype that we did not measure that directly influences intersexual solicitation behavior. In this study, we only found correlations between hormones sampled at one time point and female behaviors in the competitive courtship context, such that it is difficult to assign the directionality between the link observed. Experimental manipulation of E2 and CORT would be necessary to determine if circulating steroid hormones are mediating behaviors associated with mate competition in a polygynous system.

One limitation of our study is the time lapse (i.e., 1 month) between collecting blood samples and the courtship behavior trials. Hormone levels fluctuate daily and within a season, but there is also evidence that E2 peaks and remains elevated during the early breeding season, or the courtship phase in birds (Wingfield and Farner 1978; Williams 1992). Baseline CORT levels have been found to exhibit significant, but low repeatability (Schoenemann and Bonier 2018; Taff et al. 2018). Circulating hormone levels closer to the time of the trials might exhibit stronger relationships with female solicitation and aggressive behaviors, but we believe it is notable that circulating levels at the start of the breeding season are correlated with behaviors in the breeding season. Future studies should sample hormones at multiple time points to account for endocrine flexibility, as individual variation in endocrine response to dynamic social interactions could play an important role in mediating behaviors (Grindstaff et al. 2022).

Independent of circulating hormone concentrations, dominant females solicited more courtships from males than subordinate females solicited. This result supports our prediction, as well as previous findings that more dominant peahens solicit courtships from peacocks more often than subordinate peahens do in a feral population (Petrie et al. 1992). Our results, therefore, corroborate Petrie's (1992) suggestion that dominant peahens monopolize preferred males by repeatedly engaging them in courtship interactions (Petrie et al. 1992).

## Hormonal mechanisms of solicitation behavior

We found that females with higher concentrations of E2 solicited more courtship from males. This is consistent with a large body of evidence from observational and experimental studies demonstrating a positive relationship between E2 and female mating behavior. For example, free living female Lapland longspurs (*Calcarius lapponicus*) given subcutaneous implants of E2 were more likely to engage in courtship or incubation begging toward males than control females given empty implants or not given an implant (Hunt and Wingfield 2004). Additionally, the frequency of solicitations by females toward males was highest after estradiol levels were highest during the fertile phase of the ovarian cycle in Sichuan golden monkeys (*Rhinopithecus roxellana*) (Yan and Jiang 2006).

On the other hand, the relationship between female mating behavior and CORT is highly understudied. CORT levels increase during breeding in many species (Rubenstein and Wikelski 2005) due to the increased energetic demands of breeding (Wingfield and Kitaysky 2002). However, if and how CORT levels affect individual fitness and adaptive behaviors (e.g., competitive behaviors) tend to be context dependent. According to the "CORT-adaptation hypothesis," CORT levels should be positively associated with fitness if elevated CORT helps individuals cope with challenging life history stages (Bonier et al. 2009; Vitousek et al. 2018). For example, in tree swallows (*Tachycineta bicolor*), females with experimentally enlarged broods had both higher baseline CORT levels and higher fledging success than females with reduced broods (Bonier et al. 2011). In our study, females who solicited more courtships from males had higher non-stress induced CORT, which could be explained by a relationship between higher baseline CORT levels and higher reproductive success.

Alternatively, the "CORT-fitness hypothesis" predicts that individuals with higher levels of CORT will likely experience lower fitness outcomes, as this might be

associated with exposure to chronic stress (Cyr and Romero 2007; Bonier et al. 2009; Vitousek et al. 2018). For example, in wild European starlings (*Sturnus vulgaris*), females who were experimentally subjected to chronic stress had lower total non-stress induced CORT and lower free non-stress induced CORT, as well as lower reproductive success compared to unstressed control females (Cyr and Romero 2007). Differences in non-stress induced CORT levels in our study could also be related to exposure to chronic stress. Because dominant and subordinate females were housed together in a flock, subordinates may experience chronic stress due to stressful social interactions (e.g., aggression from dominant individuals), resulting in lower levels of non-stress induced CORT (Creel et al. 2013). Exposure to chronic stress could also suppress solicitation behavior in subordinate females (Young et al. 2006).

Non-stress induced CORT levels can also reflect an inter-individual variation in activity and effort during the breeding season. For example, studies of multiple avian species have demonstrated that, within limits, elevated non-stress induced CORT can promote parental care (Bonier et al. 2009; Crossin et al. 2012; Ouyang et al. 2013; Patterson et al. 2014). Higher levels of CORT can also mobilize energy for mate guarding (Ancona et al. 2010; Girard-Buttoz et al. 2014). In peafowl, peahens may solicit repeated copulations from peacocks in order to guard preferred males from other females, which could reduce intrasexual competition through a less costly behavior than physical aggression between females (Petrie 1992). Mate guarding and repeated copulations could also reduce exposure to sexually transmitted infections. Therefore, if elevated CORT levels mobilize peahens to mate guard by soliciting repeated copulations, then higher non-stress induced CORT levels might be adaptive in peahens during breeding. However, we can only speculate about the underlying causes of our finding that non-stress induced CORT levels are positively correlated with solicitation behavior in peahens, as we have neither experimentally manipulated the environment or reproductive success of individuals in this study. Future studies might gain a better understanding of the relationship between CORT regulation and peahen mating behavior by measuring the acute stress response in addition to baseline levels.

While we have interpreted these data as a demonstration of female solicitation behavior being driven by female hormone levels, it is also important to consider that male choice may be influenced by female hormone levels that alter female attractiveness (Puts et al. 2013; Higham et al. 2021) or influenced by female reproductive pheromones which can alter male behavior (LeMaster and Mason 2002) and may be

under hormonal control. Thus, male preference could be affected by female hormone levels and could play a role in these interactions. Future studies could test whether males preferentially display toward females with higher levels of circulating hormones.

### Intrasexual aggression

We found that neither circulating E2 nor CORT levels were related to the number of aggressive behaviors presented by a dominant female within a peahen dyad. These results might suggest that other hormonal mechanisms are stronger drivers of aggressive behaviors in peahens. For example, testosterone (T) and progesterone (P) are related to female aggression and dominance in other species (Goymann et al. 2008; O'Connell et al. 2013; Adreani et al. 2018).

Most previous research on the role of hormones in mediating female intrasexual aggression has focused on testosterone (T). Testosterone, a steroid hormone, is well known to regulate aggression and dominance status in male vertebrates (Soma 2006). Similarly, T likely plays an important role in female competition (Rosvall et al. 2020), as evidenced by positively correlated T levels and territorial aggression, and defense across taxa (Desjardins et al. 2006; Ross and French 2011; Renn et al. 2012; George and Rosvall 2018). However, there are also numerous cases in which T is either not correlated or negatively correlated with competitive behaviors in females (Elekovich and Wingfield 2000; Davis and Marler 2003; Rubenstein and Wikelski 2005; Goymann et al. 2008). In addition to negative effects of T experienced by males (i.e., metabolic costs and immunosuppression), high levels of T can delay reproductive timing and inhibit parental care in females (Jawor et al. 2006; Gerlach and Ketterson 2013). Therefore, selection on T and aggression in females could be decoupled, such that T is not elevated throughout the breeding season (Jawor et al. 2006). We were unable to validate a T ELISA with our samples, due to conflicts with high fat content, but future studies could investigate the role of T in both female solicitation and aggression in a competitive courtship context in peahens.

Other steroid hormones, such as E2, could therefore regulate female competitive behaviors when T levels are low and may play an important role throughout the breeding season (Woodley and Moore 1999a, 1999b; Rubenstein and Wikelski 2005; Pärn et al. 2008; Duque-Wilckens and Trainor 2017; Rosvall et al. 2020). Compared to other steroid hormones, including T and E2, even fewer studies have evaluated the role of CORT in female–female aggression. In one study in mountain



spiny lizards, T and E2 likely promoted female aggression, while CORT likely suppressed female aggression (Woodley and Moore 1999a). We, however, did not find support for a relationship between steroid hormones and intrasexual aggression.

Physiological correlates of stress, such as circulating CORT levels, can also reflect the costs of behaviors associated with social status. For example, dominant individuals in less stable social groups, particularly when hierarchies are being established or when hierarchical reorganization occurs, tend to have higher physiological indices of stress due to the physical and psychological costs of maintaining their rank (Sapolsky 2005). Higher levels of glucocorticoids in dominant individuals can be associated with the number of aggressive interactions they initiate, whereas higher glucocorticoid levels in subordinate individuals can be associated with the number of aggressive attacks directed toward them (Cavigelli et al. 2003; Goymann and Wingfield 2004). Therefore, we cannot exclude the possibility that CORT levels in peahens reflect interactions in the flock, rather than acting as a mediator of aggression or sexual behaviors.

Alternatively, feather CORT could be a better predictor of stress levels that influence female competitive behavior toward other females (Robertson et al. 2017). Because CORT is deposited during feather growth, this measure better indicates HPA activity over a longer duration, and is more often repeatable than circulating blood CORT levels (Taff et al. 2018). Feather CORT is likely to be particularly relevant if female aggressive behavior has a relationship with chronic stress, because CORT in feathers is an integrated, long-term measure of avian stress physiology (Bortolotti et al. 2008; Fairhurst et al. 2013). Additionally, peahen feather ornamentation reflects dominance status within the female hierarchy, such that feather CORT could better reflect long-term dominance status as well (Earl et al. 2022).

### Future directions

Both the hypothalamic–pituitary–gonadal (HPG) axis and the HPA axis, responsible for E2 and CORT production, respectively, are complex signaling pathways that integrate hormones, receptors, carrier proteins, and enzymes (Adkins-Regan 2005; Bentley et al. 2007; Norris and Carr 2020). Therefore, selection may act on many different aspects of both the HPG and the HPA axis to shape variation in female intrasexual aggression, which should be considered in future studies (Adkins-Regan 2005). For example, CORT or E2 might play a role in peahen intrasexual aggression through differences in tissue sensitivity to hormones rather than circulating hormone levels (Allen et al. 2010; O'Connor et al.

2013). It is also possible that behavior and hormone concentrations from captive peahens differ from those observed in the wild. Ultimately, to fully understand the proximate mechanisms of variation in female sexual solicitations toward males and female–female aggression, future studies should investigate these traits in wild populations, as well as experimentally manipulate hormone levels to observe how this influences female courtship behavior.

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### Supplementary data

Supplementary data available at *ICB* online.

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