PLASTICITY IN REPRODUCTIVE PHENOTYPES REVEALS STATUS-SPECIFIC CORRELATIONS BETWEEN BEHAVIORAL, MORPHOLOGICAL, AND PHYSIOLOGICAL SEXUAL TRAITS

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Reproductive success is determined by a complex interplay between multiple sexual traits that promote mate acquisition and, following copulation, provide control over paternity. The intensity of sexual competition that individuals experience often fluctuates, and here we investigate how this influences the expression of reproductive traits and their relationships. We show in the fowl, *Gallus gallus,* that males of different social status, which experience different intensities of sexual competition, before and after copulation, have different reproductive phenotypes. Dominant males are more vigilant, feed less, and have larger sexual ornaments than subordinate males. Experimentally manipulating social status revealed that these differences were phenotypically plastic, indicating multiple sexual traits were dependent on the social environment. We integrated these data with previous published findings on changes in sperm numbers and velocity to show that relationships between traits were different for males when they were dominant and when they were subordinate. Furthermore, when males switched status a complex array of negative and positive correlations between the degree traits changed was observed. Our results suggest that variation in the intensity of sexual competition generates reversible plasticity in reproductive phenotypes and that relationships between sexual traits may be variable and influence the evolution of reproductive strategies.

KEY WORDS: Phenotypic plasticity, reproductive strategies, sexual selection, social status.

Sexual selection acts prior to copulation, on the ability of individuals to outcompete rivals (intrasexual selection) and obtain sexual partners (intersexual selection) (Darwin 1871; Andersson 1994). It is well established that intra- and intersexual selection are potent evolutionary forces giving rise to a wide variety of behavioral, morphological, and physiological traits (Andersson 1994; Andersson and Simmons 2006). In many species females are promiscuous and intrasexual selection continues after copulation in the form of sperm competition (Parker 1970, 1998; Wedell et al. 2002; Snook 2005). Females may bias the outcome of sperm competition generating intersexual selection through the process of cryptic female choice (Thornhill 1983; Eberhard 1996). Fertilization success is therefore determined by the expression of, and interactions between, multiple reproductive traits that are under intra- and intersexual selection operating before and after copulation (Birkhead and Møller 1998; Andersson and Simmons 2006; Chenoweth and Blows 2006).

The factors regulating the expression of sexual traits and the way they covary have crucial implications for how reproductive strategies evolve (Chenoweth and Blows 2006). Because resources

are often finite, investment in one trait can theoretically limit investment in others (Emlen 2001; Stearns 2004). In promiscuous systems it is predicted that investment in gaining copulations will reduce resources allocated to securing fertilizations, such as sperm production, generating negative relationships between traits under pre- and postcopulatory selection (Parker 1983, 1998). However, the expression of trade-offs in investment may be masked by individual "quality." For example, if sexual traits are condition dependent, individuals in better condition may be able to invest more in all traits (Simmons and Kotiaho 2002; Hine et al. 2004; Birkhead et al. 2006), leading to positive relationships between traits and the erosion of additive genetic variance in "condition" (Fisher 1930; Falconer 1989). Nevertheless, when resources become limited and trade-offs between traits are exposed, disruptive selection may ensue promoting the evolution of alternative reproductive strategies (Gross 1996).

Alternative reproductive strategies have evolved in a diverse range of taxa and typically arise where individuals in disfavored mating roles compensate for reduced copulation success by investing more in traits that confer a fertilization advantage (Forsyth and Alcock 1990; Clark and Galef 1995; Lank et al. 1995; Parker 1998; Sinervo and Zamudio 2001; Vladić and Järvi 2001). In situations in which the frequency that individuals occupy different mating roles is low and negative genetic covariance underpins trade-offs between traits, alternative reproductive strategies may become canalized and regulated by genetic polymorphisms (alternative strategies), which is known to occur in some species (Lank et al. 1995; Sinervo and Lively 1996). Conversely, individuals may switch mating roles across space and/or in time and the expression of genotypes may change accordingly leading to phenotypically plastic alternative reproductive strategies (conditional strategy) (Gross 1996; Cornwallis and Birkhead 2006; Rudolfsen et al. 2006; Pizzari et al. 2007). Plasticity may arise in both trait expression and the way traits covary, which may be favored by selection leading to dynamic investment in traits according to environmental conditions (Via 1993; Roff 1997). Alternatively individuals may be constrained in the expression of their traits and phenotypic changes may result from an inability to cope with environmental variation (Via 1993; Roff 1997). Where phenotypic plasticity is elevates fitness directional selection will favor the evolution of plasticity, reducing variation in gene by environment interactions (Via and Lande 1985). However, variation may be maintained when levels of plasticity are negatively correlated to mean phenotype (Lynch and Gabriel 1987). Therefore, establishing whether reproductive strategies are fixed or phenotypically plastic; how plasticity influences the expression and relationships between traits; and determining the mechanisms underlying the maintenance of plasticity, are all crucial to understanding the processes influencing sexual strategies.

The aims of this study were threefold: (1) to examine how males in favored and disfavored mating roles, as determined by their social status, invest in different sexual traits that influence copulation success; (2) to experimentally manipulate male mating roles to quantify levels of phenotypic plasticity in different traits and establish whether plasticity varies among males and according to the absolute size of their traits; and (3) to quantify the phenotypic correlations between sexual traits when males are in favored and disfavored mating roles and to examine the relationships between changes in traits when male mating role is manipulated.

To investigate aims 1–3 we used the fowl, *Gallus gallus,* an emerging model for the study of sexual selection (Pizzari et al. 2002). The fowl is highly promiscuous with multiple males copulating with multiple females generating intense sexual selection both before and after copulation (Pizzari et al. 2002; Cornwallis and Birkhead 2007). Male social status mediates access to females placing dominant and subordinate males in favored and disfavored mating roles respectively, which are exposed to different intensities of pre- and postcopulatory sexual competition (Cheng and Burns 1988; Pizzari et al. 2002). Although dominance hierarchies are generally stable, males can change status both within and between breeding seasons (Collias and Collias 1996; Cornwallis and Birkhead 2006). The copulation success of males is dependent on a number of behavioral and morphological traits, but the relationship between these traits and whether dominant and subordinate males differ in their reproductive phenotypes is unclear. Males perform a wide variety of behaviors including vigilance, feeding, resting, preening, dust bathing, and nest-showing. Male vigilance provides females with direct benefits (Pizzari 2003) and increases the likelihood that males detect and interrupt rival males' copulations (Cheng and Burns 1988; Artiss and Martin 1995). Preening and dust bathing reduce ectoparasites and maintain feather condition and along with feeding and resting are likely to be important in determining body condition. Nest-showing is a display whereby males scrape a hollow in the ground (nest) and utter a low-pitched repetitive call that attracts females and often results in females laying in the nest (Wood-Gush 1989). The exact function of this nest-showing is unknown, but it may enable males to monitor female fecundity. Male copulation success is also determined by morphological traits, namely body mass, which influences the outcome of male–male competition, and comb size, a condition-dependent ornament that is a target of female choice (Ligon et al. 1990; Zuk et al. 1995; Parker and Ligon 2003). After copulation, fertilization success is determined predominantly by the number of sperm males inseminate relative to competitors and by the velocity of sperm (Martin et al. 1974; Wishart and Palmer 1986; Dziuk 1996; Froman and McLean 1996). The overall reproductive success of male fowl is therefore influenced by the interplay between behavior, morphology, and ejaculate traits.

Materials and Methods

STUDY POPULATION

We studied a population of fowl similar to red junglefowl, *G. gallus*, (Harrison 1987; Schütz and Jensen 2001) at Tovetorp Zoological Field Station, University of Stöckholm during April to July 2002 and May to August 2003. Males were randomly assigned to pairs and kept in aviaries (6 × 6 m). Male social hierarchies were determined by observing aggressive interactions, which in all pairs were stable with aggression being unidirectional (see Cornwallis and Birkhead 2007 for further details).

INVESTMENT IN TRAITS BY DOMINANT AND SUBORDINATE MALES

Measurement of behavioral traits

The behavior of males ($n = 26$) was recorded by conducting 15-min focal watches on each pair at three different times—morning (0700 h to 0930 h), noon (1200 h to 1430 h), and evening (1600 h to 1730 h)) during most days throughout the breeding season (*n* watches = 1320, average per male = 50). During each watch the time each male spent vigilant, feeding, preening, resting, dust bathing, and nest-showing were recorded. To verify that data from watches conducted during morning, noon, and evening were representative of dominant and subordinate males' behavior throughout the day, a set of watches was conducted whereby each group was watched for 15 min every hour from sunrise (c. 0430 h), until roosting (c. 2030 h) on two separate occasions in 2002, once at the start of the season and once midway through the season. There was no significant difference in the amount of time dominant and subordinate males were observed performing different behaviors when watched throughout the day and when watched during morning, noon, and evening (behavior × social status × watch type, $F_{5,157} = 1.29$, $P = 0.27$. See Table A1 for full list of terms and details).

Variation in the amount of time dominant and subordinate males spent conducting different behaviors was analyzed using a general linear mixed model (GLMM) with social status and type of behavior as fixed factors; comb size, body mass, body size (see measurement of morphological traits), and time of measurement (weeks since start of breeding season) as covariates; and year and male nested within group nested within behavior as random factors (for full list of terms see Table A4). The response variable was the average time males spent performing different behaviors during periods between morphological measurements (every two weeks) and only data on males before they changed status or that remained the same status throughout the breeding season were used in the analysis.

Measurement of morphological traits

Male comb size, body mass, and body size were measured every two weeks using methods described in Cornwallis and Birkhead 2007. We analyzed variation in comb size and body mass using GLMMs with social status as a fixed factor; body mass (in analysis of comb size only), body size, and time of measurement as covariates; and male nested within group and year as random factors (for full list of terms see Table A5).

Measurement of physiological traits

The total number of sperm ejaculated by males and sperm swimming velocity were measured, which both predict fertilization success in the fowl (Wishart and Palmer 1986; Froman and McLean 1996). These data were collected as part of another study with different aims (Cornwallis and Birkhead 2007), but here we use these data to examine the relationships between ejaculate traits and behavioral and morphological traits. It was beyond the scope of a single paper to present all information obtained and there is no overlap between the studies. Full details of the way sperm numbers and velocity were measured can be found in Cornwallis and Birkhead (2007), but in brief, natural ejaculates were collected from sexually rested males until they became sexually satiated. The number of sperm in each ejaculate was counted and sperm velocity (average path velocity: VAP) was measured. The cumulative number of sperm a male ejaculated on a given day and the change in sperm velocity over successive copulations were used in analyses. The change in sperm velocity over successive copulations was calculated for each male as the slope of sperm velocity versus copulation order derived from a GLMM (see Cornwallis and Birkhead 2007 for further details). Under natural conditions males continually acquire copulations, but dominant males copulate more frequently than subordinate males (Pizzari et al. 2003). Therefore the total number of sperm males produce and changes in sperm velocity over successive copulations are likely to be good indicators of a male's fertilization success over time and these parameters differ between dominant and subordinate males (see Cornwallis and Birkhead 2007 for details).

PHENOTYPIC PLASTICITY IN TRAITS: MANIPULATION OF SOCIAL STATUS

Social status was experimentally manipulated midway through each breeding season by placing two dominant males together, causing one male to decrease in status, and two subordinate males together, resulting in one male increasing in status (see Cornwallis and Birkhead 2007 for details). After the manipulation, groups were left for one week before their behavior was monitored and two weeks before morphological and ejaculate traits were measured. Sixteen males changed status, eight of which occupied a dominant position during the first half of the breeding season followed by a subordinate position, and eight males that were initially subordinate and then became dominant. As males changed status in different directions (dominant to subordinate and subordinate to dominant) it was possible to assess the effect of previous social

experience on the expression of traits. However, to control for the effect of winning or losing a fight and to assess seasonal changes in traits without the complication of males changing status, we examined whether males that switched pairs, but remained the same status, exhibited changes in traits. We found that males that were paired with a new male, but remained the same status, did not exhibit any changes in their behavior, comb size, or body mass (Tables A2 and A3). Therefore data on males that remained the same status were included in the analyses examining differences in investment in traits across dominant and subordinate males (see Tables A4 and A5 for details).

We analyzed plasticity in behavior, comb size, and body mass using GLMMs on data collected from males before and after they changed social status. The fixed effects entered into models are the same as those in the analyses of differences between dominant and subordinate males (see above), but the direction that males changed status (1 = dominant to subordinate, 2 = subordinate to dominant) was entered as a fixed factor and the time (weeks) since status changed was entered as a covariate. The random effects included in models were used to quantify variation among males in plasticity. The random factors in analysis of behavior were defined as male identity, male identity × behavior, and male identity × behavior × status and in the analyses of comb size and body mass were male identity and male identity × social status (for full list of terms entered in to models see Tables A6 and A7). Furthermore, we examined changes in all traits simultaneously (behavior, comb size, body mass, sperm number, and sperm velocity) to assess: (1) if plasticity in traits was linked to absolute trait expression, (2) whether certain traits were more plastic than others, and (3) whether there was variation in plasticity among males across all traits. We analyzed plasticity in all traits simultaneously using a GLMM with change in trait expression when male status was manipulated (dominant value minus subordinate value) as the response variable, trait (vigilance, feeding, comb, sperm number, and change in sperm velocity over successive copulations) was entered as a fixed factor, mean size of trait (trait value when dominant + trait value when subordinate/2) as a covariate, and male identity and male identity × trait as random factors. Absolute changes in traits and average size of traits were mean-centered to standardize the scale of data across traits. Of the 16 males that changed status only information on the total number of sperm produced and sperm velocity over successive copulations was available for 11 males from Cornwallis and Birkhead (2007) as it was not possible to collect three or more ejaculates (minimum needed to calculate slope of sperm velocity over successive copulations) from the remaining males.

CORRELATIONS BETWEEN TRAITS

We first analyzed whether correlations between traits were different for males when they were dominant and when they

were subordinate using GLMMs, taking each trait as the response variable in turn (e.g., one model for each trait: time spent vigilant, time spent feeding, comb size, number of sperm produced, sperm velocity over successive copulations) and entering the remaining four traits as covariates, social status as a fixed factor, and male identity as a random factor. We tested whether the relationships between traits changed when males were dominant and when they were subordinate by fitting interaction terms between social status and each covarying trait. Secondly, we examined whether changes in traits (dominant value minus subordinate value) when male social status was manipulated were related using partial correlations, controlling for changes in all other traits. In all analyses traits were standardized by mean-centering. Due to restricted sample size only traits that systematically changed when male social status was manipulated were entered into the analyses, which included time spent vigilant, time spent feeding, comb size, number of sperm produced, and sperm velocity over successive copulations.

STATISTICAL METHODS

Analyses were performed in SAS version 9.1 (Littell et al. 2006). The significance of fixed effects (factors and covariates) in GLMMs was examined using Wald type adjusted F statistics and the effect with the highest P value was sequentially dropped until only significant terms ($P < 0.05$) remained (Crawley 2002). The Kenward and Roger (1997) method for calculating denominator degrees of freedom was used, which is specifically designed for analyzing unbalanced repeated measures data with models that contain multiple random effects (Kenward and Roger 1997; Littell et al. 2006). The significance of random effects was assessed using log-likelihood ratio tests (LRTs) (Self and Liang 1987). Specific differences between factor levels (e.g., different behaviors) were identified using least squares (LS) means post hoc tests.

Results
INVESTMENT IN TRAITS BY DOMINANT AND SUBORDINATE MALES

The behavior of dominant and subordinate males differed markedly (Behavior × status: $F_{5,38} = 24.64, P < 0.0001$; Fig. 1A; Table A4) with dominant males being more vigilant, but feeding, preening, and resting less than subordinate males (Fig. 1). As the breeding season progressed both dominant and subordinate males increased the amount of time they spent feeding and to a lesser extent decreased their vigilance (behavior × time: $F_{5,204} = 5.03$, $P = 0.0002$. Table A4). After controlling for the effects of social status, male comb size and body mass were also related to the time spent performing certain behaviors. Comb size was significantly and positively correlated with time spent vigilant (comb size × behavior: $F_{5,58} = 4.63, P = 0.001$. Table A4). Similarly, body mass was significantly and positively correlated with vigilance
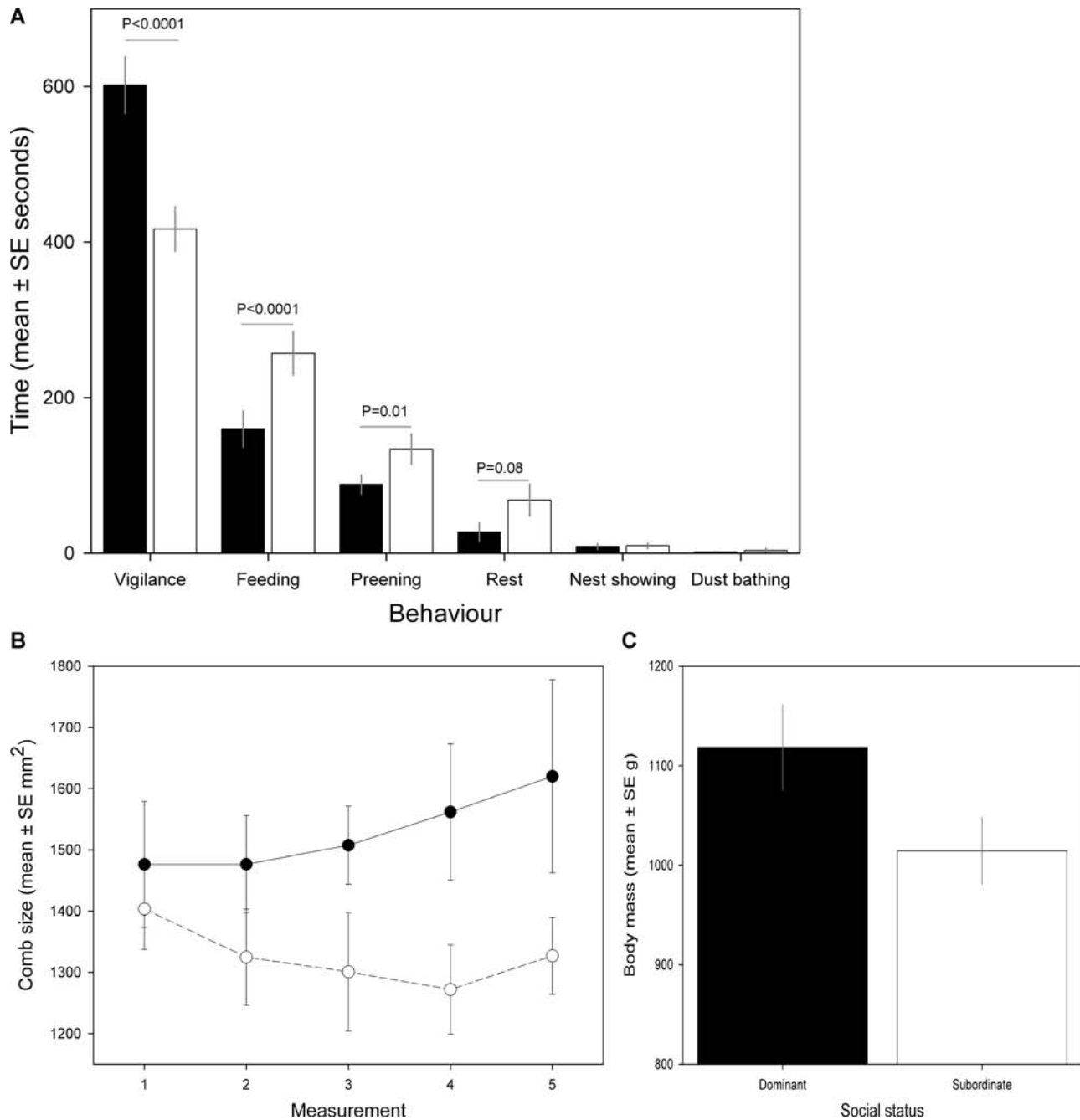
Figure 1. The behavioral and morphological traits of dominant (black) and subordinate (white) males. *P* values represent LS means tests from the GLMM. (A) Dominant males were more vigilant, but fed, preened, and rested less than subordinate males. (B) Repeated measurement of dominant and subordinate males' comb sizes from time since pairs were established (time of measurement 1 = start of season, each increment thereafter = 2 weeks). The comb size of dominant males increased over time whereas the combs of subordinate males decreased in size. (C) The body mass of dominant and subordinate males. Males that became dominant were heavier than subordinate males, but body mass did not changed after male hierarchies were established.

and was significantly negatively related to the amount of time spent feeding (body mass × behavior: $F_{5,58} = 2.63$, $P = 0.03$. Table A4). Although somewhat paradoxical, this negative relationship between body mass and feeding may be driven by males in better condition requiring less time feeding.

Dominant and subordinate males also differed in their morphological traits. At the start of the breeding season, soon after males were paired together, the comb size of dominant and subordinate individuals did not differ significantly. However, as the season progressed, the comb size of dominant males increased

whereas that of subordinate males decreased (status $\times$ time: $F_{1,71} = 16.65$, $P = 0.0001$. Fig. 1B. Table A5). This indicates that comb size did not predict social status when unfamiliar males encountered each other, but rather that comb size was dependent upon the length of time a male experienced a particular social rank. Comb size was also significantly positively correlated with body size ($F_{1,36} = 15.07$, $P = 0.0004$. Table A5) and body mass after controlling for body size ($F_{1,36} = 5.74$, $P = 0.02$. Table A5), indicating that comb size was condition dependent to some extent. Body mass was also linked to social status with dominant males being heavier than subordinates ($F_{1,19} = 9.87$, $P = 0.005$. Fig. 1. Table A5). However, in contrast to comb size, the relationship between body mass and social status was not dependent upon the length of time males were paired (status $\times$ time: $F_{1,69} = 0.89$, $P = 0.35$. Table A5), suggesting that body mass was important in determining social status, but was not influenced by social rank. Unsurprisingly, body size was positively correlated to body mass, but this was different for dominant and subordinate males. The slope of the relationship between body size and body mass was significantly greater for dominant males than for subordinate males (status $\times$ body size: $F_{1,19} = 10.58$, $P = 0.004$. Table A5), revealing that the body mass of subordinate males was less constrained by body size in comparison to dominant males.

PHENOTYPIC PLASTICITY IN TRAITS

When social status was experimentally manipulated, behavior changed significantly. Males became more vigilant and fed less when they were dominant compared with when they were subordinate (behavior $\times$ status: $F_{5,65} = 27.59$, $P < 0.0001$. Fig. 2. Table A6). Although there was variation among males in the amount of time they allocated to different behaviors (male $\times$ behavior: LRT $= 10.80$, df $= 1$, $P = 0.001$. Table A6), males did not differ in their behavioral plasticity when they changed social status (male $\times$ status $\times$ behavior: LRT $= 0.20$, df $= 1$ $P = 0.65$. Table A6). Furthermore, there were no consistent differences among males in their behavior across social contexts: there was no relationship between a male's behavior, vigilance, or feeding when he was dominant and when he was subordinate (Fig. 2). As in the previous analysis of behavior (Table A4), there was a significant interaction between comb size and behavior (behavior $\times$ comb size: $F_{5,82} = 3.16$, $P = 0.01$. Table A6) due to comb size being positively correlated with vigilance ($P < 0.001$), but not to other behaviors ($P > 0.05$).

Comb size was phenotypically plastic with respect to social status. Males had larger combs when they were dominant than when they were subordinate (status: $F_{1,13} = 8.24$, $P = 0.01$. Fig. 2. Table A7). In contrast, body mass did not systematically change when social status was manipulated (status: $P = 0.13$. Fig. 2. Table A7). A significant amount of variation in comb size and body mass was attributable to differences among males (comb size: $P <$

0.0001. body mass: $F_{1,15} = 0.60$, $P < 0.0001$. Table A7). There also appeared to be consistent differences among males across social contexts, with comb size and body mass of males when they were dominant being significantly and positively correlated with when they were subordinate (Fig. 2). Furthermore, there was significant variation among males in the plasticity of their combs and body mass with some males exhibiting greater changes in these traits than others (comb size: male $\times$ status; LRT $= 5.20$, df $= 1$, $P = 0.02$. Body mass: male $\times$ status; LRT $= 14.42$, df $= 1$, $P = 0.0001$. Table A7). These results indicate that males varied in the amount their morphological traits changed when social status was manipulated, but that only comb size systematically changed significantly increasing with social status.

The time lapsed since status was manipulated and the direction that males changed status (dominant to subordinate vs. subordinate to dominant) had no effect on any behavioral or morphological trait examined (Table A6 and A7). This indicates that traits changed within two weeks (time to first measurement), and that prior social experience did not influence plasticity in behavior, comb size, or body mass. When examining whether plasticity was related to trait expression across all traits (vigilance, feeding, comb size, total number of sperm produced, and sperm velocity over successive copulations) it was evident that absolute trait size was not associated with levels of plasticity (size of trait: $F_{1,46} = 0.23$, $P = 0.63$. Table A8) and this relationship did not differ across traits (size of trait $\times$ trait: $F_{4,46} = 1.54$, $P = 0.21$, Table A8). Also, males did not vary in how plastic they were across all traits (male: LRT $= 0.00$, df $= 1$, $P > 0.05$, Table A8) or between different traits (male $\times$ trait: LRT $= 0.00$, df $= 1$, $P > 0.05$, Table A8). However, there were significant differences in the degree to which different traits changed in response to switches in social status (trait: $F_{4,42} = 15.34$, $P < 0.0001$). Ejaculate traits (total number of sperm produced and sperm velocity over successive copulations) exhibited the greatest changes; behavioral traits (amount of time spent vigilant and feeding) varied to a lesser extent; and morphological traits (comb size) displayed the least change (Fig. 3, Table A8). Differences in plasticity between behavioral, morphological, and physiological traits suggest that these different classes of traits may be more or less flexible or have a greater propensity to be influenced by changes in the social environment.

CORRELATIONS BETWEEN TRAITS

There was a complex set of relationships between the different traits, some of which spanned across social environments. Vigilance and feeding rates were negatively related and comb size was positively correlated with the number of sperm males produced, irrespective of whether males were dominant or subordinate (Table 1). However, there were a number of significant changes in relationships among traits when males were dominant and when they were subordinate. Time spent vigilant and
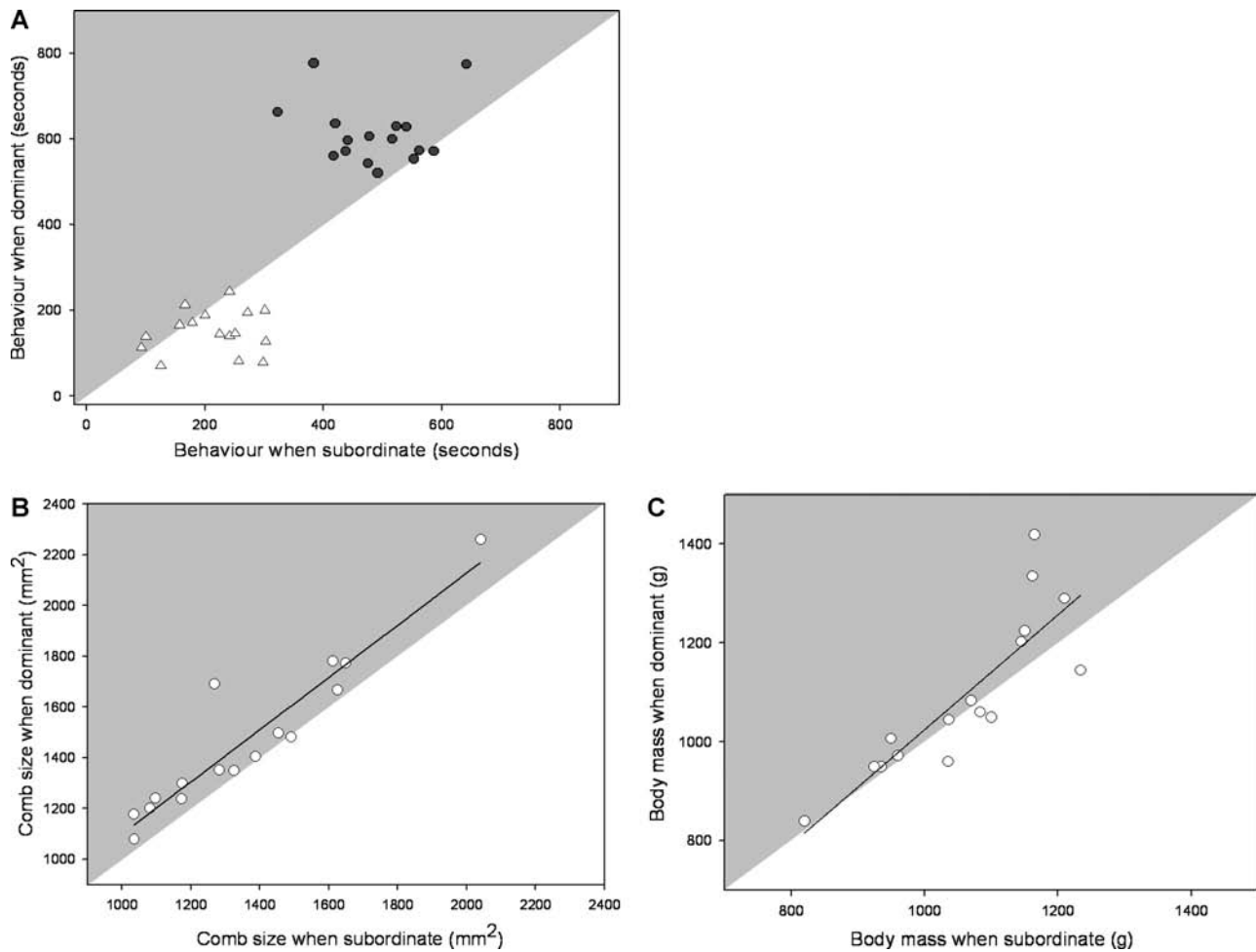
Figure 2. Phenotypic plasticity in behavioral and morphological traits. Points represent individual males. Gray areas indicate where males had greater trait values when they were dominant (y-axis) whereas the white areas represent cases in which males had greater traits values when they were subordinate (x-axis). Lines of best fit are presented for significant correlations. (A) Change in behavior when male status was manipulated. When males were dominant they were more vigilant (dark circles: LS means $P < 0.001$) and fed less (white triangles: LS means $P < 0.001$) relative to when they were subordinate. The amount of time males spent vigilant and feeding when dominant was unrelated to the when they were subordinate (Pearson's correlations: Vigilance, $r = -0.06$, $N = 16$, $P = 0.84$; feeding, $r = 0.11$, $N = 16$, $P = 0.69$) (B) Change in comb size when male status was manipulated. Males increased their comb size when they were dominant relative to when they were subordinate. There were consistent differences between males in their comb sizes with the size of a male's comb when he was dominant being highly correlated to that when he was subordinate (Pearson's correlation: $r = 0.94$, $N = 16$, $P < 0.0001$). (C) Body mass when males were dominant and when they were subordinate. Male body mass did not significantly change when social status was manipulated and was related across different social ranks: body mass when males were dominant was correlated with their mass when subordinate (Pearson's correlation: $r = 0.85$, $N = 16$, $P < 0.0001$).

feeding was negatively related to comb size when males were dominant, but positively correlated when males were subordinate (Table 1). Furthermore, when males were dominant, the degree to which their sperm velocity declined over successive copulations was negatively related to the time they spent feeding and the number of sperm they produced, but positively related to comb size (Table 1). When males became subordinate these relationships were reversed (Table 1). Overall, negative relationships between traits, perhaps representative of trade-offs in investment between traits, were more apparent when males were dominant (Table 1).

Examining correlations between the amount that traits changed when social status was manipulated revealed both negative and positive relationships between traits. The change in the amount of time males spent vigilant was negatively related to changes in time spent feeding, the number of sperm males produced, and the amount that males' sperm velocity declined over successive copulations (Table 1). However, there was a tendency for changes in vigilance to be positively correlated with changes in comb size, and for comb size to be positively related to the number of sperm males produced (Table 1). There were also negative
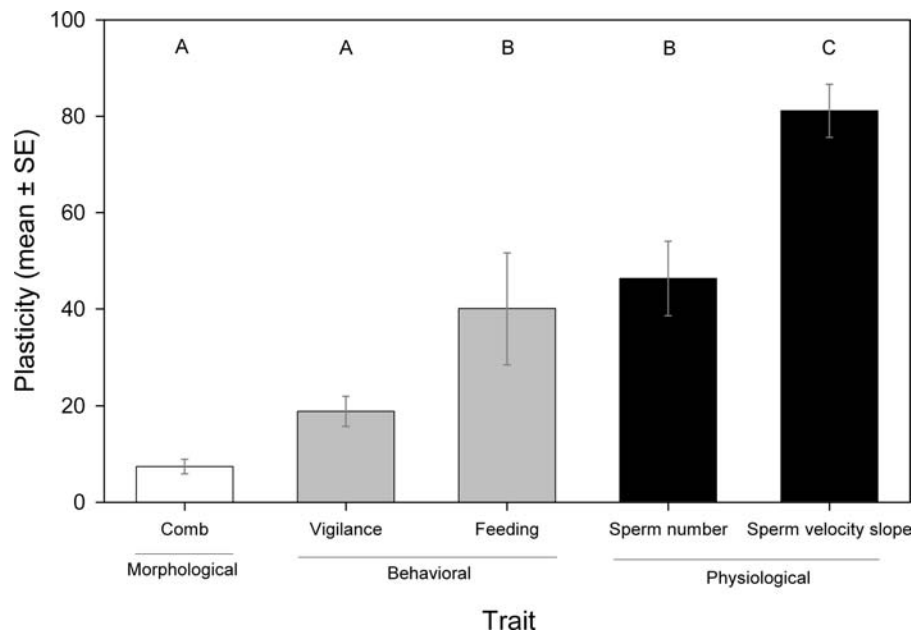
Figure 3. The level of phenotypic plasticity in behavioral, morphological, and physiological traits. Plasticity was calculated as the absolute amount that traits changed when social status was manipulated (dominant value – subordinate value). Changes were standardized across traits by mean centering. Letters represent significant differences between bars ($P < 0.01$) determined by LS means from a GLMM.

correlations between changes in sperm velocity, the time males spent feeding, and the number of sperm produced (Table 1). These relationships were apparent only when partial correlations were calculated, which controlled for all other traits. When bivariate correlations were examined only weak relationships between traits were evident, highlighting that relationships between traits may remain hidden unless investment in other traits is taken into account.

Discussion

Reproductive success is dependent upon multiple sexual traits subject to varying intensities of pre- and postcopulatory sexual competition over space and time (Andersson 1994). It has been unclear how individuals regulate the expression of, and the relationships between, sexual traits in response to changing intensities of sexual competition and the mechanisms that might underpin such responses. We show that variation in the social environment, which determines the intensity of pre- and postcopulatory sexual competition, leads to changes in the reproductive phenotypes of males. Variation among males in the amount their traits changed was limited however, indicating that the potential for further evolution of plasticity, at least at the phenotypic level, may be restricted. In contrast, there was substantial variation among males in the absolute expression of their traits and our results suggest that this was independent of variation in plasticity, but might be maintained by trade-offs between multiple sexual traits.

Previous studies have highlighted how different intensities of pre- and postcopulatory sexual selection can shape the evo-

lution of reproductive biology and the way trade-offs between sexual traits can influence reproductive success (Andersson and Simmons 2006; Chenoweth and Blows 2006). Studying species with alternative reproductive strategies has illustrated that the fitness of males in favored and disfavored mating roles is mediated by the differential expression of multiple traits (Moczek and Emlen 2000; Zamudio and Sinervo 2000; Gage et al. 2004). Despite reproductive success being influenced by many sexual traits, most studies have usually focused on a few traits at any one time (Chenoweth and Blows 2006). It is unclear from such studies how investment in the suite of sexual traits that determine reproductive success may be influenced by varying intensities of pre- and postcopulatory sexual selection. In the present study we simultaneously examined six behavioral traits, two morphological traits, and two physiological traits. Consistent with previous research, we found that in general males in favored mating roles, as determined by social status, invested more in traits that promote copulation success than males in disfavored mating roles, which in some respects, produced more competitive ejaculates (Cornwallis and Birkhead 2007). The traits we examined have been shown to be under intra- and intersexual selection and/or important in determining condition (Rowe and Houle 1996).

In line with previous work, we found that the outcome of male–male competition was determined by body mass, but once dominance hierarchies were established somatic investment by dominant and subordinate males was similar (Ligon et al. 1990; Parker et al. 2002). In contrast, when males became dominant they increased investment in vigilance and the size of their combs,

Table 1. Relationships between different traits when males were dominant, when they were subordinate, and between the amount traits changed when males changed social status. Partial variances along the diagonal, partial covariances in the upper triangle, and partial correlations in the lower triangle.

Trait / Analysis	Vigilance Dominant	Vigilance Subordinate	Vigilance Change	Feeding Dominant	Feeding Subordinate	Feeding Change	Comb size Dominant	Comb size Subordinate	Comb size Change	Sperm number Dominant	Sperm number Subordinate	Sperm number Change	Sperm velocity Dominant	Sperm velocity Subordinate	Sperm velocity Change
Vigilance	0.005	0.009	0.02	−0.009	−0.02	−0.05	−0.004	0.01	0.005	0.007	−0.02	−0.04	−0.006	0.001	−0.05
Feeding	−0.48*,[2] (0.69)[1]	−0.57	−0.93 (0.01)[3]	0.07	0.11	0.15	−0.008	0.04	0.01	0.02	−0.04	−0.11	−0.04	0.01	−0.14
Comb size	−0.28 (0.02)	0.67	0.79 (0.06)	−0.17 (0.01)	0.58	0.63 (0.18)	0.03	0.03	0.02	0.07	0.04	0.01	0.05	−0.006	0.01
Sperm number	0.13 (0.19)	−0.53	−0.88 (0.02)	0.10 (0.75)	−0.23	−0.74 (0.09)	0.58** (0.98)	0.49	0.86 (0.03)	0.50	0.23	0.13	−0.20	0.01	−0.11
Sperm velocity[4]	−0.29 (0.16)	0.07	−0.91 (0.01)	−0.52 (0.04)	0.21	−0.91 (0.01)	0.86 (0.01)	−0.16	0.74 (0.09)	−0.92 (0.02)	0.14	−0.80 (0.05)	0.10	0.05	0.16

Note: Separate GLMMs were performed for each trait (mean centered) with the remaining four traits as covariates (mean centered), social status as a fixed factor and male identity as a random to identify: [1] differences in the relationships between traits when males were dominant and when they were subordinate tested by fitting interactions between each covarying trait and social status (P values are presented in parentheses in the dominant column), and [2] relationships between traits that were independent of social status indicated by a significant main term of trait and no significant interaction between trait and social status (*P<0.05, **P<0.01, **P<0.01 presented in the dominant column).

[3] Figures in parentheses in the change column are P values from partial correlations controlling for changes in all other traits.

[4] Sperm velocity is the slope of sperm velocity over successive copulations calculated for each male using the parameter estimates from a GLMM of sperm velocity vs. copulation order (covariate) and social status (fixed factor) with male identity as a random factor (see Cornwallis and Birkhead 2007 for details).

which may be advantageous as vigilance enables males to monitor and disrupt the copulation attempts of rival males and comb size is a target of female choice (Artiss and Martin 1995). Furthermore, females may be attracted to vigilant males as it reduces their need for scanning for predators leaving more time for foraging (Ligon and Zwartjes 1995; Zuk et al. 1995; Fusani et al. 1997; Pizzari 2003). The reproductive benefits that males gain from being more vigilant and having larger combs may be lower for subordinate males than dominants because investing in traits that attract females are unlikely to result in more copulations due to dominant males interrupting mating attempts (Collias and Collias 1996; Johnsen et al. 2001). Moreover, vigilance is likely to be costly as it detracts from other activities, which are important in maintaining energetic budgets and body condition (Fritz et al. 2002; Willisch and Ingold 2007). Expressing a large comb may also be costly as it is condition dependent and can attract aggression from other males (Zuk et al. 1995; Parker and Ligon 2002). Sexual selection may therefore favor subordinate males that minimize the costs of vigilance and maintaining large combs when access to females is restricted by dominant males. Furthermore, reduced investment in traits that attract females when males are in disfavored mating roles may allow energetic reserves to be redirected to traits, such as sperm velocity, which combat higher risks of sperm competition (Froman et al. 2002; Rudolfsen et al. 2006; Pizzari et al. 2007). Alternatively, the smaller combs of subordinate males and reduced level of vigilance may not be selectively favored and represent an inability to cope with the environment.

Consistent with previous research (Stockley and Seal 2001), our results highlight the importance of the social environment in determining reproductive phenotypes. Phenotypic plasticity in sexual traits is expected to evolve when traits have a state-specific optima, individuals commonly experience different environments, and there is variation in gene by environment interactions (Via and Lande 1985; Lynch and Gabriel 1987; Roff 1997). In the fowl dominant and subordinate males experience different intensities of pre- and postcopulatory sexual competition leading to different phenotypic optima for traits and males often switch social status (Collias and Collias 1996; Pizzari et al. 2002). Nevertheless at the phenotypic level there was little variation among males in the amount their traits changed with respect to social status. This suggests that plasticity may have been under strong selection in the past and that further evolution of plasticity may be limited. Although plasticity was generally consistent among males, levels of plasticity were broadly different between behavioral, morphological, and physiological traits. This indicates that different components of the male reproductive phenotype are more labile than others and that certain traits may be more responsive or sensitive to environmental variation.

In contrast to low variation in plasticity, there were large differences in absolute body mass and comb size between males, both

within and across different social positions. Consistent differences between males in the amount of sperm they produce have also been found in this study population (Cornwallis and Birkhead 2007). This suggests there are inherent differences between males in their morphology and physiology, possibly due to genetic differences, an idea that is consistent with artificial selection experiments in domestic fowl that have demonstrated these traits are heritable (body mass: (Tufvesson et al. 1999), comb size: (Von Schantz et al. 1995), sperm production: (Etches 1996)). Given that body mass, comb size, and sperm production are heritable and likely to be under selection, it is unclear why variation persists in these traits. Theoretically, variation in traits may be maintained by negative relationships between plasticity and the mean expression of traits, resulting in individuals with more exaggerated traits being less flexible (Via and Lande 1985; Lynch and Gabriel 1987). However, we found no relationship between plasticity and absolute trait expression and previous work has in fact found that individuals with greater trait expression were more plastic (Garland and Kelly 2006).

Variation in sexual traits may be maintained by trade-offs (Stearns 2004) and empirical research has revealed negative relationships between a number of sexual traits (Pitnick 1996; Levitan 2000; Hosken 2001; Simmons and Emlen 2006). Despite this substantial body of work it has been unclear how individuals invest in multiple traits simultaneously and whether correlations between traits change with environmental conditions. Our results show that when multiple traits were examined together a variety of negative and positive associations between traits became apparent and that relationships between traits were dependent on the social environment. When male social status was manipulated the correlations between traits that influence copulation success and fertilization success changed. When males increased in social status the negative relationships between vigilance and comb size became more pronounced and increases in sperm production were associated with declines in sperm velocity. Furthermore, the interaction between traits mediating copulation success and fertilization success was altered. Comb size became more positively correlated with sperm velocity when males were dominant in comparison to when they were subordinate. Overall, negative relationships between traits were more evident when males were dominant, compared with when they were subordinate; suggesting that trade-offs in investment between traits may be more pronounced when males are in favored mating roles and generally increase the absolute expression of their traits.

Examining the degree to which changes in traits were correlated when male social status was manipulated, further supports the idea that a number of negative and positive relationships exist between traits. The change in the amount of time males spent vigilant was negatively correlated with change in the number and velocity of sperm males produced and there was also a negative

association between changes in sperm numbers and sperm velocity. However, the change in the number of sperm males produced was positively correlated with comb size, and comb size was positively correlated to changes in vigilance. The links between changes in traits may provide some insight into the complex mechanisms underlying phenotypic plasticity. The number of sperm males produce is dependent on the activity of the Leydig and Sertoli cells within the testes, which produce testosterone (Johnson 1991; Kirby and Froman 2000). Comb size and vigilance have been shown to be dependent on testosterone levels (Ligon et al. 1990; Fusani et al. 1997; Kirby and Froman 2000). The social-status-specific expression of vigilance, comb size, and sperm production may therefore be regulated by the central nervous system responding to social cues that result in a hormonal cascade that influences testicular function and the release of testosterone.

Although our results should be interpreted with caution due to the small sample size, this study suggests that variation in reproductive phenotypes may, to some extent, be maintained by negative relationships between traits under pre- (comb size and vigilance) and post- (sperm number and velocity) copulatory sexual selection. These results have important implications for our understanding of the evolution of reproductive strategies and begin to highlight how the interplay between different sexual traits across fluctuating social conditions may act to maintain variation in reproductive traits. It now remains for the exact fitness payoffs of phenotypic plasticity in different traits to be quantified.

ACKNOWLEDGMENTS

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Supplementary Material

The following supplementary material is available for this article:

Table S1. General linear mixed model of the time (seconds) that dominant and subordinate males allocated to performing different behaviors during watches that were conducted throughout the day (continuous) and watches that were carried out during morning, noon, and evening (focal).

Table S2. General linear mixed model of the differences in behavior that occurred before and after males were paired with another male (before/after), but did not change status.

Table S3. General linear mixed model of the differences in morphological traits (comb size and body mass) that occurred before and after males were paired with another male, but did not change status.

Table S4. General linear mixed model of the time (seconds) that dominant and subordinate males allocated to performing different behaviors.

Table S5. General linear mixed models of differences in morphological traits (comb size and body mass) between dominant and subordinate males.

Table S6. General linear mixed model of the changes in behavior that occurred when male social status was manipulated.

Table S7. General linear mixed model of the changes in morphological traits (comb size and body mass) that occurred when male social status was manipulated.

Table S8. General linear mixed model of variation in the absolute changes that occurred in different traits (mean centered).

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