Ethology

Seizing the Opportunity: Subordinate Male Fowl Respond Rapidly to Variation in Social Context

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Abstract

Dominance affects mating and reproductive success in many group-living species. Potential mechanisms include subordinates being inherently less attractive and social constraints imposed by dominant individuals. To test the former possibility, we measured morphology in 45 male fowl, *Gallus gallus*, prior to group formation. Males were then assigned to social groups (three males and three females in each). None of the measured traits predicted subsequent social status, suggesting that subordinates were not inherently unattractive. We then manipulated social constraints in each group to test if subordinates were socially constrained. We removed either the alpha (experimental) or the gamma male (control) for 40 min and observed the effect on the beta male's reproductive behavior. Controls accounted for putative group size and disturbance effects, and ensured that the only difference between treatments was the relative dominance of the remaining male. In each trial, we measured the beta male's courtship effort and his mating success, as well as his proximity to females and to the remaining male. Results show that social context did not affect mating success, but had a significant impact on courtship behavior. Beta males courted significantly more often when they had exclusive access to a female, as opposed to when another male was nearby. Furthermore, their courtship effort was higher if the nearby male was a fellow subordinate, as opposed to the dominant male. We conclude that both the proximity and social status of nearby males affects, either directly or indirectly, the courtship efforts of subordinate male fowl.

Introduction

Mating and reproductive success are not distributed randomly among individuals in many species (Darwin 1871). Instead, an individual's success is often determined by its ability to compete with rivals of the same sex for mates and to attract those mates directly (Andersson 1994). In systems exhibiting high reproductive skew (e.g. Le Boeuf 1974), the majority of individuals are either inferior competitors, unattractive mates, or both. It is hence not uncommon in these systems for individuals to employ different reproductive strategies (e.g. satellite behavior, Arak 1988; sexual mimicry; Gross & Charnov 1980; Hanlon et al. 2005). These may be fixed throughout an individual's lifetime (e.g. Shuster & Wade 1991; Sinervo & Lively 1996), or phenotypically plastic, varying as a function of intrinsic (e.g. somatic growth, Jacob et al. 2007) and contextual factors (e.g. residency effects, Kummer et al. 1974).

In group-living animals, the social environment can be critical. In general, there is a strong relationship between dominance rank and mating frequency (DeFries & McClearn 1970; Griffin et al. 2003; but see Hogg & Forbes 1997). However, despite socially dominant individuals monopolizing access to the opposite sex, subordinates of virtually every group-living species achieve a limited degree of reproductive success. In superb fairy-wrens (*Malurus cyaneus*), for example, subordinate males intercept females that are in search of dominant extragroup mates. By so parasitizing the sought-after dominant males, subordinates usurp over one-fifth of all extragroup paternity (Double & Cockburn 2003). Similarly, subordinate male meerkats (*Suricata suricatta*) are not permitted to mate within their own social groups (Griffin et al. 2003), but they achieve appreciable paternity by prospecting for receptive females from other territories (Young et al. 2007). As subordinates of most social species constitute the population majority, it is important to understand their alternative reproductive strategies (Double & Cockburn 2003; Young et al. 2007).

A critical question regarding dominance-dependent reproductive strategies is 'what determines social rank?' This can be problematic because it is often difficult to disentangle causes from consequences. For example, individuals could possess inherent and immutable phenotypic differences that form the basis of differential social status. This is the case in male side-blotched lizards (*Uta stansburiana*), in which dominance and dominance-dependent reproductive strategies are heritable and hence genetically constrained (Sinervo & Lively 1996). Alternatively, the effects of social status may actually generate behavioral, morphological and physiological differences between individuals (Drummond & Osorno 1992; Cornwallis & Birkhead 2008). The probability of winning contests, for example, can be independent of fighting ability, depending instead on whether contestants have won or lost their previous encounters (winner/loser effects: Chase et al. 1994; Hsu & Wolf 1999). Similarly, dominant individuals may condition subordinates to lose following their initial confrontation (suppression hypothesis: Drummond & Osorno 1992). Other factors, such as age (Jacob et al. 2007), association with dominant individuals (Cristol 1995), parental status (de Waal 1991), residency effects (Koivula et al. 1993), and resource-holding potential (Parker 1974), may also affect social status.

Male fowl, *Gallus gallus*, are ideal for exploring dominance and dominance-related reproductive traits. They establish pronounced social hierarchies marked by intrasexual aggression and differential access to females, food and territory (Schjelderup-Ebbe 1935; Guhl & Warren 1946; Graves et al. 1985; Pizzari 2003). A male's dominance is also an excellent predictor of his long-term mating success, accounting in one study for over a third of the observed variation in copulation rate (Wilson et al. 2008). Furthermore, there is clear evidence that social status has a causal effect on reproductive phenotypes. Experimentally increasing a male's social status increased his vigilance behavior and the size of his sexual ornament, (Cornwallis & Birkhead 2008), both of which are positively related to his reproductive success (Zuk et al. 1990, 1995; Pizzari 2003; Wilson et al. 2008).

The aim of this study was to characterize the conditional sexual strategies of subordinate male fowl. We began by measuring several morphological traits from 45 males prior to group formation. Males were then assigned in trios to one of 15 social groups to test if any of the measured traits predicted subordinate social status and, hence, whether subordinates were inherently different from their dominant counterparts. Once groups established a stable social structure, we examined the subordinate males under four experimentally controlled social situations. These were designed to manipulate the immediate social constraints imposed by dominant males, while maintaining the social status of individual group members. In each situation, we recorded the subordinates' mating success and courtship behavior to test for context-dependent plasticity in reproductive effort. Specifically, we were interested in whether the reproductive efforts of subordinate males were fixed as a function of their social status, or whether they were instead variable, changing as a function of the social environment.

Methods

General Methods

We studied 15 social groups of fowl at Macquarie University, Sydney, Australia during the 2005/2006 and 2006/2007 Austral breeding seasons (November–February). Consistent with the social structure described for natural populations (Collias et al. 1966), each group contained three males and three females. Individuals that had been housed together during the previous month were not placed into the same social group. Finally, to preserve independence among data (Machlis et al. 1985), individuals were used in only one group (i.e. 45 males and 45 females in total).

Birds came from a population that had been interbreeding freely for several generations. They were originally derived from golden Sebrights, a strain that has not been artificially selected for rapid growth or egg production and that, although morphologically distinct from ancestral red junglefowl, shares a most similar behavioral repertoire (Wilson et al. 2008). These fowl habituate readily to humans, are tolerant of experimental manipulations, and have been used successfully in a series of studies of animal communication and sexual selection (Evans & Marler 1992, 1994; Evans et al. 1993; Evans & Evans 1999, 2007; Wilson & Evans 2008; Wilson et al. 2008).

Groups were established by simultaneously releasing the six birds into one of four outdoor aviaries (10 × 20 m). These were constructed of 1-cm^2 nylon mesh (A&A Contract Services, Queensland, Australia), which afforded birds an unobstructed view of their surroundings. Each aviary contained food, water, shelter from the sun, friable earth for dustbathing, and a coop fitted with perches for roosting. Following their initial release, we monitored birds for signs of stress or despotism. Initial aggression typically lasted less than 1 min, always less than 3 min and never resulted in injury. We also ensured that every bird was permitted to roost inside the coop at night.

New groups were given 1 wk to acclimatize to their new surroundings and to establish a stable social structure. To determine each male's social status, we observed each group for 20 min/d during the final 3 d of acclimatization and scored all male-male interactions. Displacements were scored when two males were within 1 m of each other and the movement of the displaced male (defined by taking at least one step away) occurred within 1 s of the other male's approach. 'Alpha' status was assigned to the male that was never displaced, 'gamma' status to the male that was always displaced, and 'beta' status to the male that was displaced by the alpha male and which displaced the gamma male. In all groups, every possible dyadic interaction was observed and displacements within dyads were exclusively unidirectional (i.e. hierarchies were perfectly linear; Landau's index of linearity: $h = 1$ for all groups; Martin & Bateson 1993). The 15 beta males became the subjects of our group manipulations.

Morphology

To test whether morphological traits predicted subsequent social status, we obtained standard morphometric measures from each male immediately before group formation. At this time, males had been housed individually in indoor cages containing a single female companion for 4 wk. Housing males individually for this period relieves suppression caused by previous subordinate status and ensures that their behavior (e.g. crowing rate) and morphology (e.g. comb size) are indistinguishable from that of dominant males residing in social groups (Parker & Ligon 2002; Parker et al. 2002). This was important because it allowed us to test for traits that are predictive of social status, without the confounding effects of status-dependent phenotypic suppression.

We weighed each male using a Pesola spring scale (accurate to the nearest 10 g) and a cloth bag and measured the length of his right tarsus to the nearest 1 mm. Body condition was estimated from the unstandardized residuals derived by regressing body weight against tarsus length. We also photographed each male in right side profile against a ruled background using a Canon EOS 300 digital camera (6.5 megapixels resolution). From the photographs, we measured the size of the fleshy red ornaments on each male's head using NIH ImageJ software (version 1.33u). Specifically, we measured the length of the comb and the combined surface areas of the comb, wattles, ear lappets and red facial skin. Finally, we measured the reflectance spectra of the comb and hackle feathers of a subset of 33 males using a USB Miniature Fiber Optic Spectrometer (Ocean Optics Inc, Dunedin, FL, USA). Reflectance was measured at four randomly selected locations on each structure relative to a white WS-1 diffuse reflectance standard (reflectivity >99%; wavelength range: 200–1100 nm) using a two-fiber probe. Illumination was provided by a MINI-D2T miniature deuterium tungsten light source (Ocean Optics Inc; peak-to-peak stability: 0.3% from 200 to 850 nm). Measurements were taken using OOIBase32 spectrometer operating software at 0.37-nm increments. For each structure, we calculated the mean reflectance of each 10-nm interval between 350 and 700 nm. This range corresponds to the complete spectral sensitivity of fowl (Prescott & Wathes 1999). For each male, the resulting mean reflectance curve for each structure was then standardized, such that the lowest value obtained a score of zero and the highest value a score of one. These standardized mean reflectance values were used in statistical analyses.

Group Manipulations

We manipulated the beta male's social environment by temporarily removing the alpha male (experimental treatment). Our intent was to relieve the beta male of any physical constraints imposed by the dominant male, and to provide him with an opportunity to adjust the expression of courtship and mating behavior. However, removing a group member may simulate a predator event. It also changes the group's size, which is known to influence behavior in other species (e.g. Grand & Dill 1999). To control for these putative disturbance and group size effects, we included a control treatment in which the gamma male was instead removed. The only difference between control and experimental trials was thus the relative status of the remaining male.

Each beta male was observed in each treatment on three separate days (i.e. a total of six observation days per beta male) over a 2-wk period. The sequence of observation sessions was assigned at random, but with the constraint that the same treatment could not be applied to a given male on two consecutive days. Because as many as four groups could be established at any one time, we observed each group at one of four different times throughout the day. These began at sunrise, 1 h after sunrise, 2 h before sunset and 1 h before sunset to coincide with the periods of peak activity in fowl. To minimize diel variation, a given male was always observed at the same time of day.

Trials began by removing either the alpha male or the gamma male from the rest of the group. To avoid the disturbance that would be caused by chasing the male and catching him in a net, we simply ushered him to the end of the aviary and confined him behind a curtain constructed of green shade cloth. This blocked 70% of light transmission, was acoustically transparent, and enclosed an area measuring 10 × 3 m. It allowed the removed male to interact visually and vocally with the rest of the group, but prevented him from physically interfering with them. Following separation, the group was given 15 min to acclimate to the new conditions, after which the beta male was observed for 40 min. We released the removed individual immediately following the observation session.

Our method of separating males was intended to simulate a male simply wandering away from the group, perhaps to defend his territory or to court another female, as opposed to one being chased, captured and completely removed. Importantly, this method permitted continuous visual and vocal contact between males, which is sufficient for maintaining stable social relationships between fowl (Mench & Ottinger 1991). Furthermore, removals lasted for only 55 min. This removal duration is similar to that used in studies by Cornwallis & Birkhead (2006, 2007), in which males exhibited status-specific patterns of sperm allocation following at least 30 min of separation from their flockmates. Consistent with Mench & Ottinger (1991), we did not observe any overt aggression following the release of any male, suggesting that social status was indeed maintained throughout the group manipulations.

During each 40 min session, an observer sat at the end of the aviary opposite the curtain and scored the beta male's behavior using JWATCHER event recording software (version 1.0; Blumstein & Daniel 2007) running on a Macintosh laptop computer. Behaviors of interest included copulations and courtship waltzes. Copulations were defined as the male grasping a female's comb or hackle feathers with his mandibles and climbing onto her back with both feet (Guhl et al. 1945). Courtship waltzing was defined as the male circling in close proximity around a female, while simultaneously lowering his outer wing and scratching his outer foot and spur through the lowered primaries (see detailed descriptions in Guhl et al. 1945; Kruijt 1961, 1963). Behaviors were considered as discrete events when separated by an interval of more than 5 s. The observer also continually tracked the subject's social state, which was scored as 'exclusive access to hens' when he was within 1 m of at least one female and not the other male, as 'shared access to hens' when he was within 1 m of at least one female and the other male, and as 'no access to hens' when he was beyond 1 m from the nearest female. We defined 'access to hens' as the 1 m radius surrounding females because this is the area in which males perform courtship waltzes. Our observations of dominance interactions during the acclimatization period indicated that this was also the area from which dominant males actively excluded subordinates. Finally, all displacements resulting from male–male interactions were noted so that changes in social status could be detected. However, dominance hierarchies were completely stable; no changes in social status occurred in any group throughout the experiment.

Statistical Analysis

We tested for differences in morphology and age as a function of social status using Kruskal-Wallis tests (n = 45). Reflectance data were not conducive to such analyses in their original format, so we first summarized the overall variation contained in each structure's mean reflectance curve using a principal components analysis (see Mennill et al. 2003). For each structure, the 35 mean reflectance values (10 nm each) were entered as variables and the 33 males from which reflectance data were obtained were entered as observations. Unrotated factor scores were generated from the mean reflectance curves of each male's comb and hackle feathers, and these were then compared across alpha, beta and gamma males using Kruskal–Wallis tests. A total of four orthogonal factors were generated from the comb, which together accounted for 96% of the variation contained in its original 35 measures. Similarly, three orthogonal factors were generated from the hackle feathers, which together accounted for 94% of the original variation in hackle feather reflectance. The alpha value for all tests was 0.05 and all tests were two-tailed.

For both control and experimental treatments, we calculated the total number of copulations and courtship waltzes performed by each beta male (n = 15). However, these behaviors occur only when a male is in proximity to a female, so we also calculated the total time spent by beta males in each of the relevant social states (i.e. exclusive access or shared access to a hen). There were hence four social situations in which mating and courtship waltzing could occur: shared access to a hen with the alpha male removed, exclusive access to a hen with the alpha male removed, shared access to a hen with the gamma male removed, and exclusive access to a hen with the gamma male removed. We used JWatcher's conditional events algorithm to determine the number of copulations and courtship waltzes performed in each of these four social states, then calculated rates by dividing each value by the total time spent in the respective state. Friedman tests were used to compare the total time spent in each social state, as well as the state-specific rates of both mating and courtship waltzing across the four social situations. Where an overall model was significant, we conducted four planned pairwise comparisons using Wilcoxon signed ranks tests. Overall experimentwise error rate was controlled using the sequential Bonferroni method (Holm 1979; Rice 1989). Planned tests compared the two social states within each treatment, as well as the two treatments within each social state.

Results

We found no evidence that initial morphology predicted social status. None of the 13 morphological variables, including age, weight, tarsus length, body condition, comb length, surface area of the ornament, comb reflectance (principal components 1–4) and hackle feather reflectance (principal components 1–3), differed significantly between alpha, beta and gamma males (Kruskal–Wallis tests: all $p \geq 0.09$; Table 1).

Our relatively brief experimental manipulations of social constraints did not significantly affect the amount of time that beta males spent in each of the four social states (Friedman test: $\chi^2 = 3.00$, $p = 0.39$, n = 15; Fig. 1a), or their copulation rates (Friedman test: $\chi^2 = 0.99$, $p = 0.80$, n = 15; Fig. 1c).

Table 1: Morphology of 45 male fowl. Characteristics were compared as a function of subjects' eventual social status using Kruskal–Wallis tests

Variable	Alpha male Mean (SE)	Beta male Mean (SE)	Gamma male Mean (SE)	X^2	p-value
Age (mo)	25 (4.4)	29 (4.9)	35 (5.3)	1.51	0.47
Weight (g)	1179 (34.7)	1146 (35.8)	1131 (36.3)	0.48	0.79
Tarsus length (mm)	76 (0.9)	77 (1.5)	77 (1.0)	0.15	0.93
Body condition (g)	31 (33.6)	−11 (34.3)	−21 (33.9)	0.64	0.73
Comb length (mm)	71 (2.1)	72 (2.6)	66 (3.0)	2.02	0.37
Ornament area (mm^2)	2892 (92.8)	2981 (136.4)	2559 (124.1)	4.91	0.09
Comb reflectance					
PC1 (×1000)	94 (448.1)	−90 (235.8)	−4 (181.1)	2.13	0.35
PC2 (×1000)	−325 (235.5)	138 (276.8)	187 (378.0)	4.70	0.10
PC3 (×1000)	271 (425.8)	−250 (165.7)	−21 (261.7)	1.23	0.54
PC4 (×1000)	93 (268.0)	233 (336.9)	−326 (297.7)	1.24	0.54
Plumage reflectance					
PC1 (×1000)	−71 (279.7)	−9 (374.6)	80 (266.8)	0.29	0.87
PC2 (×1000)	−195 (149.2)	122 (373.4)	73 (351.3)	0.04	0.98
PC3 (×1000)	180 (284.4)	−129 (244.8)	51 (380.8)	0.70	0.70

Mean and standard errors (SE) are provided for each social rank. Reflectance values were derived from a subset of 33 males. See text for details of how the principal components (PC) summarizing reflectance were derived. Body condition was estimated from unstandardized residuals derived by regressing body weight against tarsus length.

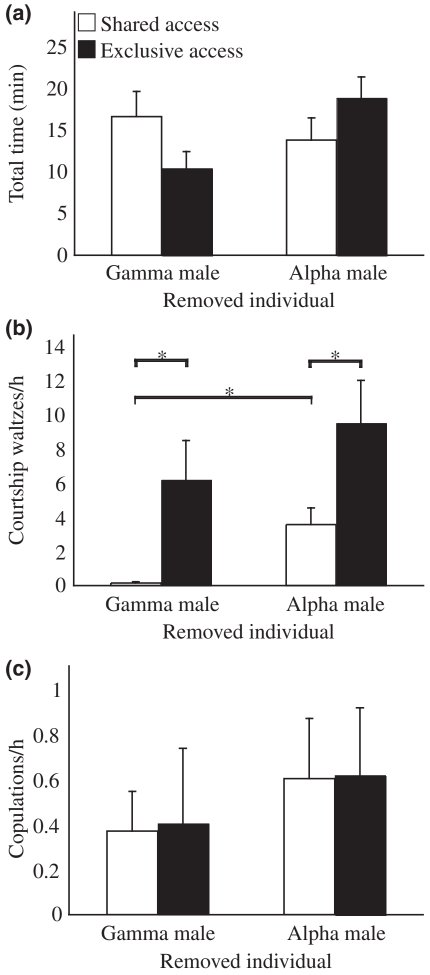

Fig. 1: Reproductive behavior of 15 subordinate male fowl. Shown for four social situations are (a) the total time spent in each social situation, and, within each social situation, (b) the rate of courtship waltzing and (c) the rate of copulations. Graphs present mean values + 1 standard error. Statistically significant Wilcoxon signed ranks tests are denoted by an asterisk (alpha is 0.05; experimentwise error rate controlled using the sequential Bonferroni method). Note differences in the ordinate scale.

Manipulations did, however, profoundly affect the beta males' rates of courtship waltzing (Friedman test: $\chi^2 = 23.88$, $p < 0.01$, $n = 15$; Fig. 1b). In both experimental and control treatments, beta males performed significantly more courtship waltzes per hour when their access to a hen was exclusive, as opposed to shared with the remaining male (Wilcoxon signed ranks tests: experimental treatment, $Z = -2.39$, $p = 0.02$, $n = 15$; control treatment, $Z = -3.18$, $p < 0.01$, $n = 15$). Furthermore, when the beta male's access to a female was shared with the remaining male, his rate of courtship waltzing was significantly higher if his companion was a fellow subordinate (Wilcoxon signed ranks test: $Z = 2.85$, $p < 0.01$, $n = 15$). Together, these results indicate that both the proximity and the social status of the remaining male affected the beta male's courtship effort (Fig. 1b).

Discussion

We studied facultative variation in the sexual behavior of male fowl, a species in which mating and reproductive success are highly dependent upon social status (Guhl & Warren 1946). Prior to group formation, we quantified several aspects of male morphology and showed that none of the measured traits predicted subsequent subordinate status. We then manipulated the social environment of subordinate males and showed that their courtship behavior differed substantially across the four social contexts.

Our failure to detect morphological differences between males as a function of their subsequent social status appears at first to contrast markedly with previous studies, which have consistently reported larger ornaments among dominant males (Graves et al. 1985; Ligon et al. 1990; Parker et al. 2002). This may be explained, however, by the finding that ornament size changes as a function of social status (Zuk & Johnsen 2000). For example, the ornaments of males that are experimentally made subordinate shrink, while those of males that are made dominant grow (Zuk & Johnsen 2000; Cornwallis & Birkhead 2008). Furthermore, the ornament size of subordinate and dominant individuals diverges as a direct function of time spent in their respective social ranks (Cornwallis & Birkhead 2008). In this study, we measured morphology prior to group formation, following a 4-wk period in which males were housed individually and without competition from other males. Our results are therefore consistent with the idea that morphological differences are not conducive to differential social status, but, rather, that they are generated as a result of ongoing dominance interactions. Future studies exploring the basis of differential social status should hence focus on other factors, such as hormone levels (e.g. testosterone titre, Beehner et al. 2006) and the genetic basis and heritability of dominance (de Waal 1991; Cristol 1995; Sinervo & Lively 1996).

Manipulating social constraints did not affect copulation rates among beta males. This could reflect low statistical power caused by a limited sample size and short observation sessions. Alternatively, it could reflect female control over copulations (Zuk et al. 1990; Pizzari 2001). Females are known to mate preferentially with dominant males, and will even utter distress calls that attract the alpha when mounted forcibly by a subordinate (Pizzari 2001). It is therefore possible that beta males attempted to mate more frequently when given the opportunity to do so, but that uncooperative females thwarted their attempts.

In contrast to their mating success, male courtship behavior was strongly affected by group manipulations. Beta males courted most frequently when they had exclusive access to a female, which is consistent with previous observations of unmanipulated groups of fowl (Johnsen et al. 2001). Furthermore, when the beta males' access to a female was shared with another male, their rate of courtship was higher if the other male was also a subordinate. It remains unclear from these results, however, whether beta males increased their courtship effort in the absence of the alpha male, or whether they decreased their courtship behavior in the absence of the gamma male. It also remains unclear whether males were responding directly to the removal of other males, or whether they were responding to possible changes in female behavior that could have resulted from our experimental manipulations. Nevertheless, these findings demonstrate that both the proximity and social status of nearby males affects, either directly or indirectly, the reproductive efforts of subordinate males. This could be critical, as dominant males interfere with the mating attempts of subordinates (Pizzari 2001). By courting predominantly when the dominant male is distant, it is possible that subordinate individuals increase their likelihood of copulating successfully while minimizing their probability of being punished. We conclude that subordinate males are not inherently less motivated than their dominant counterparts, but, rather, that their reproductive behavior is affected by the presence of nearby males. Furthermore, subordinates' reproductive behavior is highly plastic and changes remarkably quickly in response to changes in the social environment.

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