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**Title** Seizing the opportunity: subordinate male fowl respond rapidly to variation in social context

**Running title** Social constraints affect courtship effort in fowl

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1 **Abstract**

2

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

21

## 22 **Introduction**

23  
24 Mating and reproductive success are not distributed randomly among individuals in many  
25 species (Darwin 1871). Instead, an individual's success is often determined by its ability to  
26 compete with rivals of the same sex for mates and to attract those mates directly (Andersson  
27 1994). In systems exhibiting high reproductive skew (e.g., Le Boeuf 1974), the majority of  
28 individuals are either inferior competitors, unattractive mates, or both. It is hence not  
29 uncommon in these systems for individuals to employ different reproductive strategies (e.g.,  
30 satellite behavior, Arak 1988; sexual mimicry; Gross & Charnov 1980; Hanlon et al. 2005). These  
31 may be fixed throughout an individual's lifetime (e.g., Shuster & Wade 1991; Sinervo & Lively  
32 1996), or phenotypically plastic, varying as a function of intrinsic (e.g., somatic growth, Jacob et  
33 al. 2007) and contextual factors (e.g., residency effects, Kummer et al. 1974).

34  
35 In group-living animals, the social environment can be critical. In general, there is a strong  
36 relationship between dominance rank and mating frequency (DeFries & McClearn 1970; Griffin  
37 et al. 2003; but see Hogg & Forbes 1997). However, despite socially dominant individuals  
38 monopolizing access to the opposite sex, subordinates of virtually every group-living species  
39 achieve a limited degree of reproductive success. In superb fairy-wrens (*Malurus cyaneus*), for  
40 example, subordinate males intercept females that are in search of dominant extragroup mates.  
41 By so parasitizing the sought-after dominant males, subordinates usurp over one fifth of all  
42 extragroup paternity (Double & Cockburn 2003). Similarly, subordinate male meerkats (*Suricata*  
43 *suricatta*) are not permitted to mate within their own social groups (Griffin et al. 2003), but they

44 achieve appreciable paternity by prospecting for receptive females from other territories (Young  
45 et al. 2007). As subordinates of most social species constitute the population majority, it is  
46 important to understand their alternative reproductive strategies (Double & Cockburn 2003;  
47 Young et al. 2007).

48  
49 A critical question regarding dominance-dependent reproductive strategies is 'what  
50 determines social rank?' This can be problematic because it is often difficult to disentangle  
51 causes from consequences. For example, individuals could possess inherent and immutable  
52 phenotypic differences that form the basis of differential social status. This is the case in male  
53 side-blotched lizards (*Uta stansburiana*), in which dominance and dominance-dependent  
54 reproductive strategies are heritable and hence genetically constrained (Sinervo & Lively 1996).  
55 Alternatively, the effects of social status may actually generate behavioral, morphological, and  
56 physiological differences between individuals (Drummond & Osorno 1992; Cornwallis &  
57 Birkhead 2008). The probability of winning contests, for example, can be independent of  
58 fighting ability, depending instead on whether contestants have won or lost their previous  
59 encounters (winner/loser effects: Chase et al. 1994; Hsu & Wolf 1999). Similarly, dominant  
60 individuals may condition subordinates to lose following their initial confrontation (suppression  
61 hypothesis: Drummond & Osorno 1992). Other factors, such as age (Jacob et al. 2007),  
62 association with dominant individuals (Cristol 1995), parental status (de Waal 1991), residency  
63 effects (Koivula et al. 1993), and resource holding potential (Parker 1974), may also affect  
64 social status.

65

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

76  
77 Our goal in the present study was to characterize the conditional sexual strategies of  
78 subordinate male fowl. We began by measuring several morphological traits from 45 males  
79 prior to group formation. Males were then assigned in trios to one of 15 social groups to test if  
80 any of the measured traits predicted subordinate social status and, hence, whether  
81 subordinates were inherently different from their dominant counterparts. Once groups  
82 established a stable social structure, we examined the subordinate males under four  
83 experimentally controlled social situations. These were designed to manipulate the immediate  
84 social constraints imposed by dominant males, while maintaining the social status of individual  
85 group members. In each situation, we recorded the subordinates' mating success and courtship  
86 behavior to test for context-dependent plasticity in reproductive effort. Specifically, we were  
87 interested in whether the reproductive efforts of subordinate males were fixed as a function of

88 their social status, or whether they were instead variable, changing as a function of the social  
89 environment.

90

91

## 92 **Methods**

93

### 94 *General Methods*

95 We studied 15 social groups of fowl at Macquarie University, Sydney, Australia during the  
96 2005/2006 and 2006/2007 Austral breeding seasons (November - February). Consistent with the  
97 social structure described for natural populations (Collias et al. 1966), each group contained  
98 three males and three females. Individuals that had been housed together during the previous  
99 month were not placed into the same social group. Finally, to preserve independence among  
100 data (Machlis et al. 1985), individuals were used in only one group (i.e., 45 males and 45  
101 females in total).

102

103       Birds came from a population that had been interbreeding freely for several generations.

104 They were originally derived from golden Sebrights, a strain that has not been artificially  
105 selected for rapid growth or egg production and that, although morphologically distinct from  
106 ancestral red junglefowl, shares a very similar behavioral repertoire (Wilson et al. 2008). These  
107 fowl habituate readily to humans, are tolerant of experimental manipulations, and have been  
108 used successfully in a series of studies of animal communication and sexual selection (Evans &

109 Evans 1999, 2007; Evans & Marler 1992, 1994; Evans et al. 1993; Wilson & Evans 2008; Wilson  
110 et al. 2008).

111  
112       Groups were established by simultaneously releasing the six birds into one of four outdoor  
113 aviaries (10 x 20 m). These were constructed of 1-cm<sup>2</sup> nylon mesh (A&A Contract Services,  
114 Queensland, Australia), which afforded birds an unobstructed view of their surroundings. Each  
115 aviary contained food, water, shelter from the sun, friable earth for dustbathing, and a coop  
116 fitted with perches for roosting. Following their initial release, we monitored birds for signs of  
117 stress or despotism. Initial aggression typically lasted less than one minute, always less than  
118 three minutes, and never resulted in injury. We also ensured that every bird was permitted to  
119 roost inside the coop at night.

120  
121       New groups were given one week to acclimatize to their new surroundings and to  
122 establish a stable social structure. To determine each male's social status, we observed each  
123 group for 20 min per day during the final three days of acclimatization and scored all male-male  
124 interactions. Displacements were scored when two males were within 1 m of each other and  
125 the movement of the displaced male (defined by taking at least one step away) occurred within  
126 1 s of the other male's approach. 'Alpha' status was assigned to the male that was never  
127 displaced, 'gamma' status to the male that was always displaced, and 'beta' status to the male  
128 that was displaced by the alpha male and which displaced the gamma male. In all groups, every  
129 possible dyadic interaction was observed and displacements within dyads were exclusively  
130 unidirectional (i.e., hierarchies were perfectly linear; Landau's index of linearity:  $h = 1$  for all

131 groups; Martin & Bateson 1993). The 15 beta males became the subjects of our group  
132 manipulations.

133

#### 134 *Morphology*

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

144

145 We weighed each male using a Pesola spring scale (accurate to the nearest 10 g) and a  
146 cloth bag and measured the length of his right tarsus to the nearest 1 mm. Body condition was  
147 estimated from the unstandardized residuals derived by regressing body weight against tarsus  
148 length. We also photographed each male in right side profile against a ruled background using a  
149 Canon EOS 300 digital camera (6.5 megapixels resolution). From the photographs, we measured  
150 the size of the fleshy red ornaments on each male's head using NIH ImageJ software (version  
151 1.33u). Specifically, we measured the length of the comb and the combined surface areas of the  
152 comb, wattles, ear lappets, and red facial skin. Finally, we measured the reflectance spectra of



153 the comb and hackle feathers of a subset of 33 males using a USB Miniature Fiber Optic  
154 Spectrometer (Ocean Optics, Inc., Dunedin, FL, U.S.A.). Reflectance was measured at four  
155 randomly selected locations on each structure relative to a white WS-1 diffuse reflectance  
156 standard (reflectivity: >99%; wavelength range: 200-1100 nm) using a two-fiber probe.  
157 Illumination was provided by a MINI-D2T miniature deuterium tungsten light source (Ocean  
158 Optics, Inc; peak-to-peak stability: 0.3% from 200 to 850 nm). Measurements were taken using  
159 OOIBase32 spectrometer operating software at 0.37-nm increments. For each structure, we  
160 calculated the mean reflectance of each 10-nm interval between 350 and 700 nm. This range  
161 corresponds to the complete spectral sensitivity of fowl (Prescott & Wathes 1999). For each  
162 male, the resulting mean reflectance curve for each structure was then standardized, such that  
163 the lowest value obtained a score of zero and the highest value a score of one. These  
164 standardized mean reflectance values were used in statistical analyses.

165

### 166 *Group Manipulations*

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

174 The only difference between control and experimental trials was thus the relative status of the  
175 remaining male.

176

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

185

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

195

196           Our method of separating males was intended to simulate a male simply wandering away  
197 from the group, perhaps to defend his territory or to court another female, as opposed to one  
198 being chased, captured, and completely removed. Importantly, this method permitted  
199 continuous visual and vocal contact between males, which is sufficient for maintaining stable  
200 social relationships between fowl (Mench & Ottinger 1991). Furthermore, removals lasted for  
201 only 55 min. This removal duration is similar to that used in studies by Cornwallis & Birkhead  
202 (2006, 2007), in which males exhibited status-specific patterns of sperm allocation following at  
203 least 30 minutes of separation from their flockmates. Consistent with Mench & Ottinger (1991),  
204 we did not observe any overt aggression following the release of any male, suggesting that  
205 social status was indeed maintained throughout the group manipulations.

206  
207           During each 40 min session, an observer sat at the end of the aviary opposite the curtain  
208 and scored the beta male's behavior using JWatcher event recording software (version 1.0;  
209 Blumstein & Daniel 2007) running on a Macintosh laptop computer. Behaviors of interest  
210 included copulations and courtship waltzes. Copulations were defined as the male grasping a  
211 female's comb or hackle feathers with his mandibles and climbing onto her back with both feet  
212 (Guhl et al. 1945). Courtship waltzing was defined as the male circling in close proximity around  
213 a female, while simultaneously lowering his outer wing and scratching his outer foot and spur  
214 through the lowered primaries (see detailed descriptions in Guhl et al. 1945; Kruijt 1961, 1963).  
215 Behaviors were considered as discrete events when separated by an interval of more than five  
216 seconds. The observer also continually tracked the subject's social state, which was scored as  
217 'exclusive access to hens' when he was within 1 m of at least one female and not the other

218 male, as 'shared access to hens' when he was within 1 m of at least one female and the other  
219 male, and as 'no access to hens' when he was beyond 1 m from the nearest female. We defined  
220 'access to hens' as the 1 m radius surrounding females because this is the area in which males  
221 perform courtship waltzes. Our observations of dominance interactions during the  
222 acclimatization period indicated that this was also the area from which dominant males actively  
223 excluded subordinates. Finally, all displacements resulting from male-male interactions were  
224 noted so that changes in social status could be detected. However, dominance hierarchies were  
225 completely stable; no changes in social status occurred in any group throughout  
226 the experiment.

227

#### 228 *Statistical Analysis*

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

240 of the original variation in hackle feather reflectance. The alpha value for all tests was 0.05, and  
241 all tests were 2-tailed.

242

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

260 **Results**

261  
262 We found no evidence that initial morphology predicted social status. None of the 13  
263 morphological variables, including age, weight, tarsus length, body condition, comb length,  
264 surface area of the ornament, comb reflectance (principal components 1 - 4), and hackle feather  
265 reflectance (principal components 1 - 3), differed significantly between alpha, beta, and gamma  
266 males (Kruskal-Wallis tests: all  $P \geq 0.09$ ; Table 1).

267  
268 Our relatively brief experimental manipulations of social constraints did not significantly  
269 affect the amount of time that beta males spent in each of the four social states (Friedman test:  
270  $\chi^2 = 3.00$ ,  $P = 0.39$ ,  $N = 15$ ; Fig. 1a), or their copulation rates (Friedman test:  $\chi^2 = 0.99$ ,  $P = 0.80$ ,  $N$   
271  $= 15$ ; Fig. 1c). Manipulations did, however, profoundly affect the beta males' rates of courtship  
272 waltzing (Friedman test:  $\chi^2 = 23.88$ ,  $P < 0.01$ ,  $N = 15$ ; Fig. 1b). In both experimental and control  
273 treatments, beta males performed significantly more courtship waltzes per hour when their  
274 access to a hen was exclusive, as opposed to shared with the remaining male (Wilcoxon signed  
275 ranks tests: experimental treatment,  $Z = -2.39$ ,  $P = 0.02$ ,  $N = 15$ ; control treatment,  $Z = -3.18$ ,  
276  $P < 0.01$ ,  $N = 15$ ). Furthermore, when the beta male's access to a female was shared with the  
277 remaining male, his rate of courtship waltzing was significantly higher if his companion was a  
278 fellow subordinate (Wilcoxon signed ranks test:  $Z = 2.85$ ,  $P < 0.01$ ,  $N = 15$ ). Together, these  
279 results indicate that both the proximity and the social status of the remaining male affected the  
280 beta male's courtship effort (Fig. 1b).

281

282 **Discussion**

283  
284 We studied facultative variation in the sexual behavior of male fowl, a species in which mating  
285 and reproductive success are highly dependent upon social status (Guhl & Warren 1946). Prior  
286 to group formation, we quantified several aspects of male morphology and showed that none of  
287 the measured traits predicted subsequent subordinate status. We then manipulated the social  
288 environment of subordinate males and showed that their courtship behavior differed  
289 substantially across the four social contexts.

290  
291 Our failure to detect morphological differences between males as a function of their  
292 subsequent social status appears at first to contrast markedly with previous studies, which have  
293 consistently reported larger ornaments among dominant males (Graves et al. 1985; Ligon et al.  
294 1990; Parker et al. 2002). This may be explained, however, by the finding that ornament size  
295 changes as a function of social status (Zuk & Johnsen 2000). For example, the ornaments of  
296 males that are experimentally made subordinate shrink, while those of males that are made  
297 dominant grow (Zuk & Johnsen 2000; Cornwallis & Birkhead 2008). Furthermore, the ornament  
298 size of subordinate and dominant individuals diverges as a direct function of time spent in their  
299 respective social ranks (Cornwallis & Birkhead 2008). In our study, we measured morphology  
300 prior to group formation, following a four-week period in which males were housed individually  
301 and without competition from other males. Our results are therefore consistent with the idea  
302 that morphological differences are not conducive to differential social status, but, rather, that  
303 they are generated as a result of ongoing dominance interactions. Future studies exploring the

304 basis of differential social status should hence focus on other factors, such as hormone levels  
305 (e.g., testosterone titre, Beehner et al. 2006) and the genetic basis and heritability of dominance  
306 (de Waal 1991; Cristol 1995; Sinervo & Lively 1996).

307  
308         Manipulating social constraints did not affect copulation rates among beta males. This  
309 could reflect low statistical power caused by a limited sample size and short observation  
310 sessions. Alternatively, it could reflect female control over copulations (Zuk et al. 1990; Pizzari  
311 2001). Females are known to mate preferentially with dominant males, and will even utter  
312 distress calls that attract the alpha when mounted forcibly by a subordinate (Pizzari 2001). It is  
313 therefore possible that beta males attempted to mate more frequently when given the  
314 opportunity to do so, but that uncooperative females thwarted their attempts.

315  
316         In contrast to their mating success, male courtship behavior was strongly affected by  
317 group manipulations. Beta males courted most frequently when they had exclusive access to a  
318 female, which is consistent with previous observations of unmanipulated groups of fowl  
319 (Johnsen et al. 2001). Furthermore, when the beta males' access to a female was shared with  
320 another male, their rate of courtship was higher if the other male was also a subordinate. It  
321 remains unclear from these results, however, whether beta males increased their courtship  
322 effort in the absence of the alpha male, or whether they decreased their courtship behavior in  
323 the absence of the gamma male. It also remains unclear whether males were responding  
324 directly to the removal of other males, or whether they were responding to possible changes in  
325 female behavior that could have resulted from our experimental manipulations. Nevertheless,



326 these findings demonstrate that both the proximity and social status of nearby males affects,  
327 either directly or indirectly, the reproductive efforts of subordinate males. This could be critical,  
328 as dominant males interfere with the mating attempts of subordinates (Pizzari 2001). By  
329 courting predominantly when the dominant male is distant, it is possible that subordinate  
330 individuals increase their likelihood of copulating successfully while minimizing their probability  
331 of being punished. We conclude that subordinate males are not inherently less motivated than  
332 their dominant counterparts, but, rather, that their reproductive behavior is affected by the  
333 presence of nearby males. Furthermore, subordinates' reproductive behavior is highly plastic  
334 and changes remarkably quickly in response to changes in the social environment.

335

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337

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

variable	<u>alpha male</u>		<u>beta male</u>		<u>gamma male</u>		$\chi^2$	P-value
	mean	(SE)	mean	(SE)	mean	(SE)		
age (months)	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 <sup>2</sup> )	2892	(92.8)	2981	(136.4)	2559	(124.1)	4.91	0.09
comb reflectance								
PC1 (x 1000)	94	(448.1)	-90	(235.8)	-4	(181.1)	2.13	0.35
PC2 (x 1000)	-325	(235.5)	138	(276.8)	187	(378.0)	4.70	0.10
PC3 (x 1000)	271	(425.8)	-250	(165.7)	-21	(261.7)	1.23	0.54
PC4 (x 1000)	93	(268.0)	233	(336.9)	-326	(297.7)	1.24	0.54
plumage reflectance								
PC1 (x 1000)	-71	(279.7)	-9	(374.6)	80	(266.8)	0.29	0.87
PC2 (x 1000)	-195	(149.2)	122	(373.4)	73	(351.3)	0.04	0.98
PC3 (x 1000)	180	(284.4)	-129	(244.8)	51	(380.8)	0.70	0.70

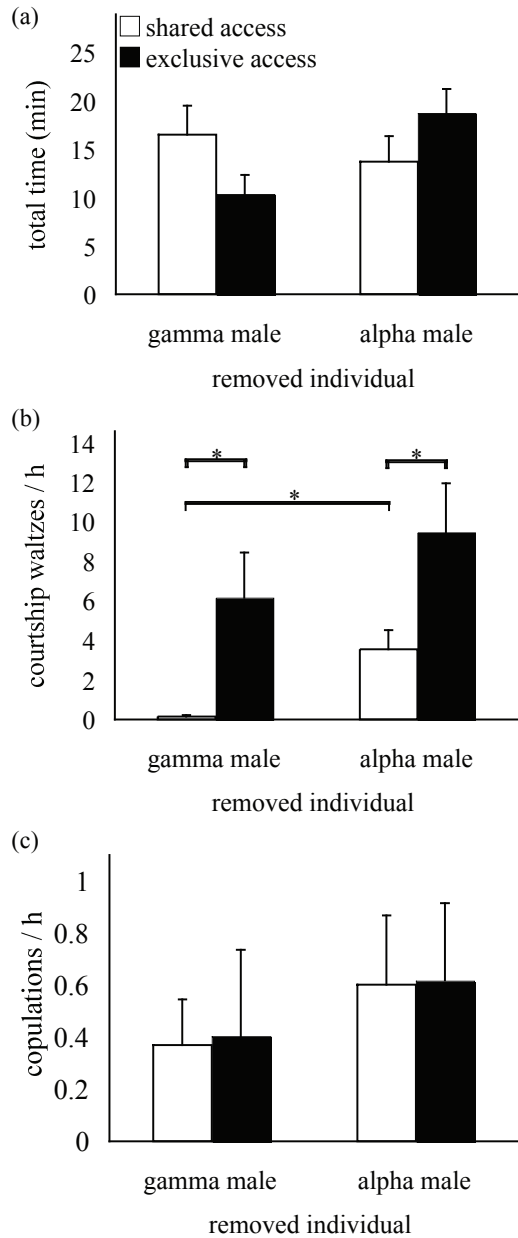
Means and standard errors (SE) are provided for each social rank. Reflectance values were

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.

Figure 1



**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.