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SOCIAL DOMINANCE, MALE BEHAVIOUR AND MATING IN MIXED-SEX FLOCKS OF RED JUNGLE FOWL

by

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Summary

In mixed-sex flocks of red jungle fowl (*Gallus gallus*), both males and females form dominance hierarchies, and male-male aggression and female choice can influence mating success. If females prefer the dominant male, there is no conflict between intra- and inter-sexual selection. We studied captive flocks consisting of two males and three females. In 1998, dominant males had larger combs than subordinate males in most flocks, while in 1999, comb size did not differ between dominant and subordinate males. The dominant male crowed more and performed more wing flaps than the subordinate male, but both males performed an equal number of tidbits and waltzes. The dominant male obtained more copulations than the subordinate male. When the dominant male had the larger comb, females of all ranks preferred to mate with and associated with the dominant male. When the subordinate male had the larger comb, primary and secondary females mated with the dominant male while tertiary females mated more often with the subordinate male, and female association with a male did not predict mating. Males with large combs are preferred by females and tend to become dominant, but females seem to prefer males with large combs even when these males are subordinate.

Introduction

Sexual selection can cause the evolution of traits not favoured through natural selection (Darwin, 1871; Andersson, 1994). Males compete for

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access to females, and when a male's ability to compete is enhanced, his reproductive success may increase (Wingfield, 1984). Females are usually the more choosy sex, and female choice can cause the evolution of male ornamental traits (Andersson, 1994). Male ornaments that attract females and a male's ability to dominate other males tend to be condition dependent and females should choose to mate with males that win in aggressive encounters (Berglund *et al.*, 1996). For example, female pied flycatchers (*Ficedula hypoleuca*) prefer to pair with males that have high quality territories and bright plumage, and bright males hold better territories (Alatalo *et al.*, 1990; Sætre *et al.*, 1994). A male's ability to dominate other males and female choice both seem important in determining male mating success, and in the pied flycatcher, there seems to be no conflict between inter- and intra-sexual selection. On the other hand, females may prefer to mate with subordinate males when traits selected by male-male competition do not reflect male quality (Qvarnström & Forsgren, 1998). Male cockroaches (*Nauphoeta cinerea*) release pheromones that function in determining social dominance and in female choice (Moore & Moore, 1999). The component of the pheromone that influences female choice differs from the component that confers social status, suggesting that females should at times prefer to mate with subordinate males.

Staged mate choice trials eliminate interactions among males and allow the investigation of female choice. When presented with dead stuffed males, female yellowhammers (*Emberiza citrinella*) prefer to associate with older males that also have brighter feathers (Sundberg, 1995). Female guppies (*Poecilia reticulata*) presented with video images of males prefer to associate with those that have brighter colours and perform more vigorous courtship displays (Kodric-Brown & Nicolletto, 1997). In the Japanese quail (*Coturnix japonica*), female association with a male predicts her mating preference (White & Galef, 1999). In other studies (Zuk *et al.*, 1990b, 1995a; Sætre *et al.*, 1994), nest building or copulations with a male are used to indicate mate choice, but the males are prevented from interacting and females not allowed to assess quality by watching males in aggressive encounters.

In the wild, males interact with each other and females choose mates among the options she has available. When males and females are allowed to interact, social dominance can affect mating and the patterns are more complex than in staged mate choice trials. In mixed-sex groups of guppies, the sexual behaviour of the subordinate male is suppressed and male-male

aggression seems important in determining the pattern of copulations (Bruce & White, 1995). Male dominance affects mating success and courtship displays in ring-necked pheasants (*Phasianus colchicus*), with dominant males inhibiting the displays of subordinate males (Mateos & Carranza, 1999). The association of female guppies with a male in staged mate choice trials predicts mating patterns after the males and females are allowed to interact, and females prefer to mate with dominant males (Kodric-Brown, 1993). Mating patterns depend on female choice and the ability of dominant individuals to enforce their interests on subordinates. Studies of mate choice usually investigate variation among male ornaments and assume that all females have the same preferences in mating or in their association with males. If there are costs to the female of searching for a high quality male (Real, 1990), females in poor condition or of low rank may not be able to pay these costs and may therefore be less choosy.

Red jungle fowl (*Gallus gallus*) are native to south-east Asia and live in mixed sex flocks that have a dominant male, one or more subordinate males and several females (Collias & Collias, 1967). In the free-ranging population at the San Diego Zoo in California, USA, both males and females form dominance hierarchies (Collias & Collias, 1996). The dominant male is usually at least two years old and mate guards the receptive females in the flock. All females lay eggs, but dominant females are more likely than subordinate females to have their young survive to be recruited into the reproductive population (Collias *et al.*, 1994). In aggressive encounters between males, those with a large comb are likely to win over males with a small comb suggesting that comb size is an indicator of fighting ability (Graves *et al.*, 1985; Ligon *et al.*, 1990). Male red jungle fowl have multiple ornaments and perform vocal and visual displays. They have bright feathers on their head, neck, back and tail, bright red fleshy combs and wattles, bright red eyes, and sharp spurs that function in male-male combat. In mate choice trials, females prefer to copulate with the males that have the larger and brighter comb, although in some experiments, eye colour and hackle feather colour explain some of the variance in male mating success (Zuk *et al.*, 1990b, 1995a). Female red jungle fowl do not seem to use male crows and wingflaps in mate choice, and only waltz displays that are performed immediately prior to copulation are associated with male mating success (Zuk *et al.*, 1995b). McBride *et al.* (1969) studied the behaviour of feral domestic fowl (*Gallus gallus*). The hens usually stay in close proximity to

the dominant male and subordinate males spend most of their time at the periphery of the flock. Subordinate males crow more than dominant males (McBride *et al.*, 1969), while in free-ranging flocks of red jungle fowl, dominant males crow more (Collias & Collias, 1996). Females that wander away from the dominant male are chased by subordinate males and may copulate with them (McBride *et al.*, 1969).

In this study, we explore interactions among male and female red jungle fowl in captive mixed-sex flocks. First, we investigate the relationship between morphology and dominance in males and how dominance can affect male behaviour. Social dominance can have an effect on male displays associated with mating, and the presence of the dominant male may inhibit the subordinate male and thus reduce his reproductive success. Second, we investigate the relationship between female association with the males and copulations to determine to what degree association can be used to predict female mating preferences. Studies often use association as a measure of mate choice, but rarely investigate the validity of this assumption. Finally, we investigate the effect of female rank on patterns of association and copulation with the males, and we investigate if the relative sizes of the comb in dominant and subordinate males plays a role in mating patterns. Low ranking females may be less choosy than dominant females, or interactions between the males may affect which male the females mate with. If the dominant male has the smaller comb, females should prefer to mate with the subordinate male (Zuk *et al.*, 1990b) and the outcome of this male-female conflict depends on the ability of the dominant male to mate guard.

Methods

Our population of red jungle fowl originated from the free-ranging population at the San Diego Zoo in California, USA (Zuk *et al.*, 1995a). During June of 1997 and 1998, we collected fertilized eggs from our population and hatched the young in incubators and kept the chicks indoors in commercial brooders for the first six weeks of their lives. We then moved the chicks outside and kept them in large communal cages in flocks of up to 80 birds. When they were approximately five months old, the males began to fight with each other, and we separated the birds into male-female pairs and housed them in smaller cages (1 m high, 2 m wide, 1 m deep). At all times the birds had free access to both food and water.

During the breeding season when the birds were nine to eleven months old, we formed mixed sex flocks consisting of two males and three females. Immediately before we placed the males in their flocks, we used digital calipers to measure their comb and tarsus to the nearest 0.1 mm and we used a digital scale to measure their mass to the nearest 1.0 g. We

had also used this method for measuring comb length in the years between 1993 and 1997. The birds for each flock were chosen randomly such that none of the males and females had been housed with each other or in adjacent cages. In 1998, we kept the flocks in large cages (2 m high, 2 m wide and 5 m deep) with ten fixed perches at different heights to allow subordinates the opportunity to escape when chased by dominant birds. We also provided a small area (approximately 1 m²) in which it was possible for the subordinate male to hide. In 1999, we doubled the space available to each flock by cutting two openings in the plywood between adjoining cages, and by leaving the wall as a partition, we allowed the birds an opportunity to occupy an area visually isolated from the dominant male.

All females were given one numbered metal band and an equal number of yellow plastic bands as identification. One female had both bands on her right leg, one had both on the left leg and the last female had one band on each leg. The males were banded either on their right or left leg. We observed aggressive interactions among females and assigned dominance ranks based on winners and losers of these encounters. A female was scored as winning an encounter if she pecked her opponent in the head or initiated the motion of a peck and her opponent ran away. In 1998, we had 96 dyads in 32 flocks, and a total of 889 interactions among females. The dominant female won 887 of the encounters, and for the two dominant females that lost one encounter with a subordinate, one had 25 wins and the other had 3 wins over the subordinate female. In one dyad, the females did not interact and we were unable to determine their relative status. In 1999, we had 78 dyads in 26 flocks, and a total of 434 interactions among females, and the dominant female won all of the encounters. Because female red jungle fowl have a peck right and the subordinate female rarely attacks (Wood-Gush, 1971), we determined dominance based on one interaction in some dyads. On the following day, we added the two males to each flock and we observed them as they fought for dominance. In most cases, the dominant male persistently harassed the subordinate by chasing him around the cage. If the dominant male continued attacking the subordinate male to the point where escape was not possible, we removed the males and did not include data from these flocks in our analysis. When male interactions were more subtle, we observed pecks and displacements to determine male status.

Between days five and fifteen we observed behaviour in the flocks. The duration of our observations were in part determined by the weather, and in a few flocks, the death of one of the birds caused us to cease observation. In 1998, the median observation time for the flocks was 2 hours and 30 minutes (two flocks were observed for a period of only 30 minutes), and during this time we recorded the identity of the males and females that copulated. We scanned the flocks every two minutes and recorded the association between males and females. If a female was within 50 cm (pecking distance) of a male at the time of the scan, we scored her as associating with that male. Otherwise, we scored her as being away from the males. The percentage of time a female spent alone or in association with the dominant or subordinate male was determined by dividing each category by the total number of scans.

In 1999, the median observation time was 8 hours per flock (shortest observation time 1 hour and 20 minutes), and during that time we recorded the identification of copulating males and females. We also recorded whether the copulation was solicited by the female (female crouches before the male mounts) or forced (the male grabs the feathers on the back of the female's head before she crouches), and we recorded interference by the other male (attacking the other male). During our continuous observations, we recorded male behaviour as well as recording if the males were in the same or opposite halves of the cage. We recorded the following behaviours:

- (1) **Crowing:** a loud call that functions in the maintenance of dominance and as an advertisement of location (McBride *et al.*, 1969).
- (2) **Wing flaps:** the males bring their wings together over their back making a clapping sound. This behaviour also functions in the maintenance of social dominance (McBride *et al.*, 1969).
- (3) **Tidbits:** the male picks up an item from the ground (sometimes food), shakes it and then drops it. Females often approach the male after this display, and tidbitting is a behaviour associated with courtship feeding (Stokes, 1971).
- (4) **Waltzes:** the male approaches the female from the side while shaking his lowered wing (lateral display). Females sometimes respond by soliciting a copulation, and females rarely solicit if the male does not perform a waltz (Zuk *et al.*, 1995b).
- (5) **Crouch-scratch:** The male crouches down and scratches the earth.

We also did a scan of the members of the flock every four minutes and recorded their position. We recorded which birds were in the right and left halves of the cage and whether the females were within 50 cm of one or both males (association).

We used discriminant analysis to compare the morphology of dominant and subordinate males while accounting for correlations among the morphological traits. We used paired *t*-tests to investigate the differences in the frequency of behaviour between dominant and subordinate males. We calculated the frequency of each behaviour by dividing the total number of times it was observed by observation time. We used paired *t*-tests to investigate changes in male behaviour when the two males were in the same versus when they were in separate halves of the cage. In our scans, we recorded the location of both males, and this allowed us to calculate the percentage of time the males spent in the same half of the cage. Using this value, we calculated the time spent together and apart, and since we recorded the relative locations of the males for each behaviour we could calculate the frequency of each behaviour when males were together and in separate halves of the cage. We used a binomial test to compare the number of times females copulated with dominant and subordinate males, and we used a *G*-test with Williams' correction to investigate if male and female rank affected copulations. We combined primary and secondary females in 1998 and used a Fisher's exact test to investigate this relationship in the flocks where the subordinate male had the larger comb because of a small sample size. We used a two-way ANOVA with female rank and the relative comb sizes of the males as variables to investigate differences in female association with males. We used a paired *t*-test to investigate differences in the amount of time females spent in association with the dominant and subordinate males, first in flocks in which the dominant male had the larger comb and then in flocks in which the subordinate male had the larger comb. Finally, we used a binomial test to investigate how well female association with a male predicted which male she copulated with.

Results

Male comb size

Comb size in males seemed to differ between 1998 and 1999. The maximum comb length was 113.8 mm in 1998 and 103.4 mm in 1999 and the minimum

TABLE 1. *Comb length (mm) of males in our study population (mean \pm 1 SE) between 1993 and 1999*

Year	Comb length	N
1993 (a)	88.7 \pm 1.51	35
1994 (a)	90.0 \pm 1.42	65
1995 (a)	87.5 \pm 1.25	52
1996 (a)	89.4 \pm 1.23	51
1997 (a)	91.6 \pm 1.03	58
1998 (a)	90.4 \pm 0.94	80
1999 (b)	81.7 \pm 1.10	66

A difference ($p < 0.05$) in a Tukey's post-hoc test with uneven sample size is indicated by the letters after the year ($F_{6,400} = 8.34$, $p < 0.001$).

was 71.0 mm and 53.4 mm. Mean comb length for both dominant and subordinate males was greater than 90.0 mm in 1998, while in 1999, mean comb length for both groups was less than 83.0 mm. We looked at comb length in our population between 1993 and 1999 to investigate if this difference was within the normal variation among years. Comb length in males varied among years ($F_{6,400} = 8.34$, $p < 0.001$), but this difference was caused entirely by the males having smaller combs in 1999 (Table 1).

Male behaviour

In 1998, dominant males had larger combs than subordinate males, and there was a tendency for dominant males to be larger (Table 2). The dominant male had the larger comb in 22 of 32 flocks. In 1999, dominant and subordinate males did not differ significantly in comb length, tarsus length or mass (Table 2). In 1999, dominance rank affected male displays in mixed-sex flocks of red jungle fowl (Fig. 1). The dominant males crowed more and performed more wing flaps than subordinate males. However, the frequency of tidbits, waltzes and crouch-scratches (courtship behaviour) did not differ between dominant and subordinate males. The cages were partitioned, and the subordinate male could display while out of sight of the dominant male. The frequency of behaviours displayed by the dominant male did not change depending on whether the subordinate male was absent or in the same half of the cage (Fig. 2). However, the behaviour of the subordinate male changed when he was away from the dominant male (Fig. 2). Subordinate males crowed more and directed more waltzes towards the females when the dominant male was absent.

TABLE 2. *Differences in the morphology of dominant and subordinate males from 37 flocks in 1998 and 29 flocks in 1999*

	Dominant	Subordinate	r^*
1998			
Discriminant analysis: $F_{3,70} = 3.16, p < 0.05$			
Comb (mm)	96.1 \pm 1.2	90.3 \pm 1.4	0.99
Tarsus (mm)	93.1 \pm 0.7	91.7 \pm 0.8	0.42
Mass (g)	1290 \pm 30	1238 \pm 31	0.39
1999			
Discriminant analysis: $F_{3,50} = 0.35, NS$			
Comb (mm)	81.5 \pm 1.7	82.5 \pm 1.8	0.31
Tarsus (mm)	92.5 \pm 0.9	91.4 \pm 1.0	-0.83
Mass (g)	1186 \pm 23	1153 \pm 30	-0.82

The values are means \pm one SE.

r^* is the correlation of each variable with the first canonical axis.

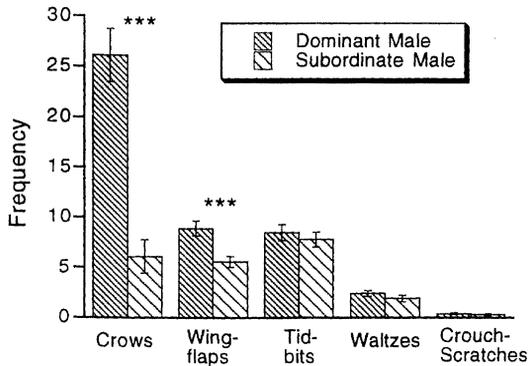


Fig. 1. The mean frequency of behaviours (\pm 1 SE) for male red jungle fowl in 23 flocks, each consisting of two males and three females. *** indicates $p < 0.001$ in a paired t -test comparing the dominant and subordinate males.

Association and copulation

In 1998, when the dominant male had the larger comb, female association predicted which male she copulated with. Of the 31 females seen copulating with a male in these flocks, 24 copulated with the male they associated with, and 7 copulated with the other male ($z = 3.44, p < 0.001$). This pattern was no longer present when the subordinate male had the larger comb. Of the 12 females seen copulating with a male in these flocks, 7 copulated with the

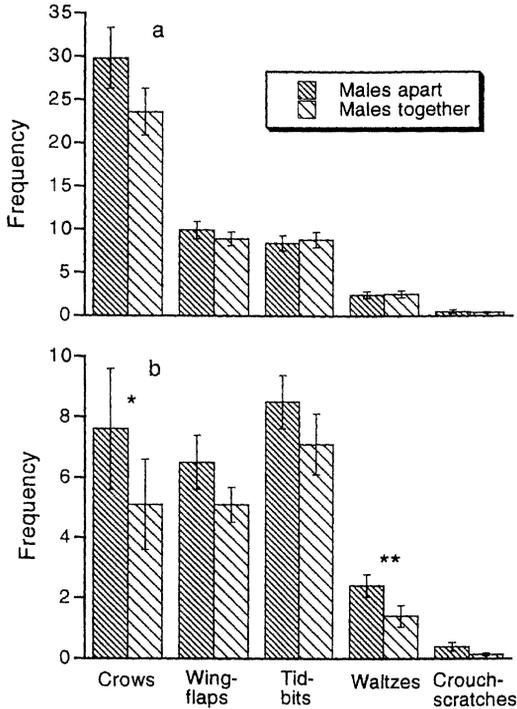


Fig. 2. The mean frequency of behaviours (± 1 SE) for (a) dominant males and (b) subordinate males in 23 flocks when the males were in opposite halves of the cage *versus* when both were present in the same section of the cage. * indicates $p < 0.05$ and ** indicates $p < 0.01$ in a paired t -test.

male they associated with and 5 copulated with the other male (NS). In 1999, female association with a male did not predict which male she preferred copulating with ($z = 1.56$, NS).

Dominance and mating

In 1998, almost half of the 96 females were observed copulating with a male, and many were seen copulating more than once. During our observations, 31 females copulated once, ten females copulated twice, and three females copulated more than twice. Of the 13 females with multiple copulations, only one copulated with both males and was scored as not having a mating preference. In 1999, 43 of 69 females were observed copulating with one or both males. Eleven females copulated only once during our observations, and the remaining females were observed copulating between two and seven

times. Of these 32 females, 23 were seen copulating with only one male, while the remaining nine females copulated with both males. Four females copulated an equal number of times with both males and were scored as having no mating preference. Four females were subjected to a total of five forced copulations. All female ranks were represented, and all five forced copulations were committed by subordinate males. We observed two cases in which the dominant male interrupted the subordinate male during a copulation, and in one case, the subordinate male made an unsuccessful attempt at interrupting the dominant male.

The dominant male obtained more copulations than the subordinate male. In 1998, of the 43 females that we observed copulating with only one male, 34 copulated with the dominant male and nine with the subordinate male ($z = 4.50$, $p < 0.001$). In 1999, 28 females preferred copulating with the dominant male and eleven preferred the subordinate male ($z = 2.85$, $p < 0.005$). Female rank affected copulations, and in 1998, the pattern depended on the relative comb size of dominant and subordinate males. When the dominant male had the larger comb, females of all ranks copulated with the dominant male ($G_{\text{adj}} = 0.18$, $df = 1$, NS, Fig. 3). When the subordinate male had the larger comb, the primary and secondary females copulated with the dominant male while the tertiary females copulated more often with the subordinate male ($p < 0.05$, Fig. 3). In 1999, female rank also affected the pattern of copulations (Fig. 4). The primary and tertiary females copulated almost exclusively with the dominant male, while the secondary females were as likely to copulate with the subordinate male.

In 1998, both the dominance status of the males and relative male comb size influenced female association with the males, and females of all dominance ranks showed the same pattern of association (Fig. 5). In a two-way ANOVA with the percentage of time spent with the dominant and subordinate male as the dependent variables, rank did not explain variation among females in their association with males (Rao's $R_{4,174} = 0.85$, NS), but relative male comb size did affect female association (Rao's $R_{2,87} = 5.06$, $p < 0.01$). When the dominant male had the larger comb, females of all ranks spent more time associating with him than with the subordinate male ($t = 5.51$, $df = 65$, $p < 0.001$). When the subordinate male had the larger comb, the females associated equally with both males ($t = 0.39$, $df = 29$, NS). In 1999, female rank did not affect their association with dominant and subordinate males (Rao's $R_{4,126} = 0.83$, NS), and in a paired t -test, females

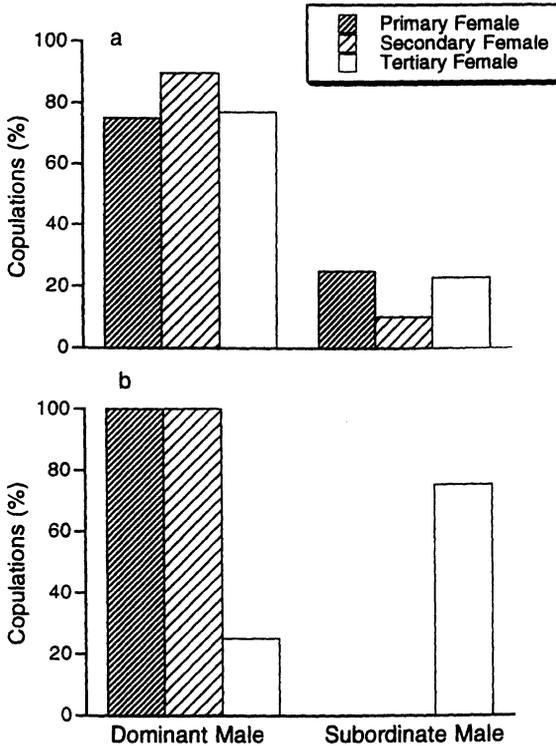


Fig. 3. The percentage of copulations for females of various ranks with the dominant and subordinate males in 1998. (a) 22 flocks in which the dominant male had the larger comb (sample size: primary = 8, secondary = 10, tertiary = 13). (b) 10 flocks in which the subordinate male had the larger comb (sample size: primary = 5, secondary = 2, tertiary = 4).

associated equally with both males ($t = 1.11$, $df = 66$, NS). Similarly, female rank did not affect the time spent in the same section of the cage as the dominant male ($F_{2,66} = 0.15$, NS), and the females did not prefer the portion of the cage occupied by the dominant male ($t = 0.78$, $df = 67$, NS).

Discussion

Differences in comb length between years

Between 1993 and 1998, comb length remained constant among the males in our population of red jungle fowl. Although 1999 differed from the other years, the males did not have abnormal combs. The difference in the ranges

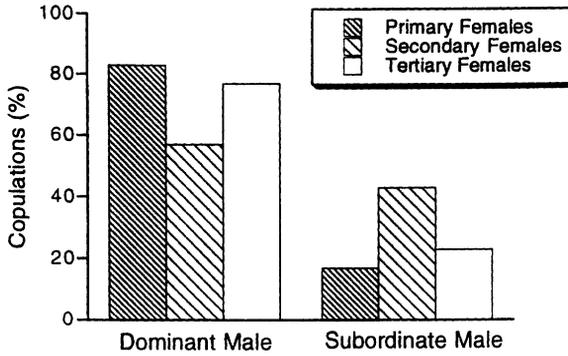


Fig. 4. The percentage of females of various ranks that mated with the dominant and subordinate males in 1999 (sample size: primary = 12, secondary = 14, tertiary = 13).

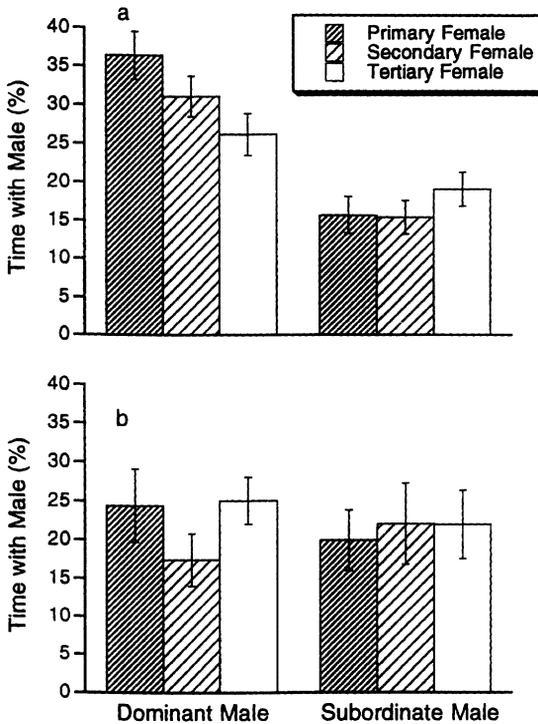


Fig. 5. The percentage of time females of various ranks spent associating with the dominant and subordinate males in 1998. (a) 22 flocks in which the dominant male had the larger comb. (b) 10 flocks in which the subordinate male had the larger comb.

and means in 1998 and 1999 indicates that comb size was reduced by approximately 1.0 cm in 1999, and most males had combs that were within the range seen in other years. Comb size and colour in male red jungle fowl is condition dependent (Zuk *et al.*, 1990b). It is possible that the difference in comb size was caused by a change in the environment, although our protocol for raising the birds remained unchanged. In red jungle fowl, females prefer to mate with males that have larger redder combs, but do not seem to use comb size in mate choice when both males have small combs (Zuk *et al.*, 1990a). Because male comb size affects both dominance and female choice (Ligon *et al.*, 1990; Zuk *et al.*, 1990b), we do not make comparisons between the two years of our study, and we only discuss mating patterns relative to male comb size for 1998.

Male dominance and behaviour

When we placed two male red jungle fowl in a cage, they would usually fight until one was defeated. At other times, one male would immediately run away, and in both cases, losers remained subordinate to winners throughout the experiment. As in earlier studies (Graves *et al.*, 1985; Ligon *et al.*, 1990), in 1998, males with large combs tended to become dominant. Ligon *et al.* (1990) found that tarsus length contributed to dominance, but in this study, tarsus length and mass were less important than comb size in determining social dominance. Comb size is correlated with testosterone levels (Zuk *et al.*, 1995a) and the increase in testosterone levels during a fight affects the outcome (Johnsen & Zuk, 1995). In addition, dominant male red jungle fowl have higher hematocrit levels than subordinate males (Zuk & Johnsen, 2000). High hematocrit allows a higher maximum oxygen consumption and increased stamina in a prolonged fight (Chappell *et al.*, 1997). In 1999, most of the males in our population had small combs. Our results suggest that when the comb is small in both males, relative comb size does not reflect competitive ability.

The dominance relationship between the males affected their behaviour. The dominant male performed more crows and wing flaps than the subordinate male. Both of these behaviours are noisy and they are thought to function in advertising the male's location to the members of his flock and to neighbouring flocks as well as helping to maintain dominance relationships within a flock (McBride *et al.*, 1969). The high rate of crowing and wing

flaps in dominant males is consistent with these proposed functions. The dominant male could be displaying to maintain his position in the flock. The subordinate male, whose crowing rate is higher when away from the dominant male, may be inhibited in the presence of the dominant male and he may be announcing his location to the females when away from the flock.

The males court the females equally but the subordinate males have less success in obtaining copulations. Males perform tidbits that entice the female to approach and they waltz in an attempt to solicit a copulation. Of these behaviours, only the frequency of the waltz is associated with mating success in staged mate choice trials (Zuk *et al.*, 1995b). Tidbitting does not seem to be associated with mating success, but it may have to be performed as part of the mating ritual to entice the female into the male's proximity. The equal overall rate of courtship behaviours in dominant and subordinate males suggests that dominance does not affect the male's investment in courting females. On the other hand, dominant males seem to inhibit this behaviour in the subordinate male, and the subordinate male may pursue a strategy of courting females away from the flock. In this study, the flocks were kept in a confined area, and this may have affected our results. Further work with free-living birds is needed. The pattern of crowing in our study is consistent with the higher rate in dominant male red jungle fowl at the San Diego Zoo (Collias & Collias, 1996), but in feral domestic fowl, subordinates on the periphery of the flock crow more (McBride *et al.*, 1969).

Association and mating preferences

Studies that investigate female choice often use female association with a male as an indicator of mating preferences (Tobias & Hill, 1998; Waas & Wordsworth, 1999). When an isolated female guppy is presented with two males, she prefers to associate with the male that has the higher display rate, and when the fish are released into a common tank, the females mate with the male they associated with earlier (Kodric-Brown, 1993). Our results suggest caution when using association between males and females to measure female choice. In 1998, when the dominant male had the larger comb, association with a male predicted which male the female would copulate with. Females associated with and copulated with the dominant male. There was no discernable pattern in flocks where the subordinate male had the larger comb, and in 1999, female association with a male did not predict

the pattern of copulations. In the Japanese quail, female association predicts which male she copulates with in staged mate choice trials (White & Galef, 1999). When male and female red jungle fowl are allowed to interact freely, association does not always predict copulations, and it seems that a conflict between the interests of males and females can disrupt the pattern between association and copulation.

Copulations and association with the females

In both years, the dominant male gained most of the copulations with the females in his flock, and when the subordinate male copulated, it was most often with a subordinate female. This pattern is similar to that seen in the free-ranging population at the San Diego Zoo where females copulated most often with the dominant male, but would occasionally copulate with a subordinate male (Collias & Collias, 1996). The dominant male may inhibit the subordinate male from attempting copulations, as suggested by the decrease in waltzes performed by the subordinate in the presence of the dominant male and the two cases of interference with a subordinate male's copulation attempt. If the dominant male is limited by the number of females he can effectively mate guard, he should give up guarding paternity first in females of lower rank that have lower reproductive value. In 1998, subordinate males copulated with the tertiary females, and in 1999, they copulated with secondary females. This suggests that the dominant male did not have the ability to guard all females.

In some of the 1998 flocks, the reproductive interests of the females and the dominant males coincide. The male should try to fertilize all eggs. The female should try to mate with the higher quality male, and female red jungle fowl prefer to mate with males that have larger red combs (Zuk *et al.*, 1990b, 1995a). When the dominant male had the larger comb, females of all ranks spent more time associating with the dominant male and they also copulated with him. In ten of the flocks, the subordinate male had the larger comb, and if the females used comb length in mate choice, they should have preferred to mate with the subordinate male. The primary and secondary females copulated with the dominant male and the tertiary females copulated with the male with the larger comb. If the dominant females preferred the dominant male because they had direct evidence of his quality, we would expect the same pattern of association as in the flocks where the dominant

male had the larger comb. On the contrary, dominant females did not spend more time with the dominant male. This suggests that in these captive flocks, the females preferred the male with the larger comb, but that male-male aggression was more important than female choice in determining male mating success.

Berglund *et al.* (1996) argue that male ornaments that function in mate choice are also signals of male competitive ability. Females should prefer to mate with dominant males because they are in good condition and there is no conflict between intra- and inter-sexual selection. When the dominant male had the larger comb, all females copulated and associated more with the dominant male, but females did not seem to prefer the dominant male when the subordinate male had the larger comb. Qvarnström & Forsgren (1998) suggest that sometimes females will prefer to mate with subordinate males. Our data support this hypothesis. When the subordinate male had the larger comb, tertiary females copulated with the subordinate males and all females associated equally with both males. In red jungle fowl, the interests of dominant males and females sometimes coincide, sometimes they do not. The question does not seem to be whether females always prefer dominant or subordinate males, but to what degree there is conflict between the sexes, and how the social interactions influence the outcome of this conflict.

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