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Effects of male dominance and courtship display on female choice in the ring-necked pheasant

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Abstract Male traits and behaviours acting in mate choice and intrasexual competition are expected to be congruent. When studying their evolution, this often makes it difficult to differentiate between these two components of sexual selection. Studies are therefore needed on mate choice in conjunction with the role of displays and dominance. We present the results from two experiments conducted to investigate the effects of male dominance and courtship displays on female choice in the ring-necked pheasant, *Phasianus colchicus*, controlling for differences in morphological male traits. We found: (1) different courtship behaviours had different effects on female choice: females were mainly attracted by the feeding courtship behaviour, while another courtship display (the lateral display) was effective in producing the copulation-acceptance response by the females; (2) subordinate males performed the courtship behaviour before females less frequently than dominant males, and females reinforced intrasexual selection by choosing dominant males, and (3) subordinate males in visual contact with a dominant became less attractive to females. The results support the idea (armament-ornament model) that female pheasants may benefit from using traits selected in male-male competition as clues for mate choice.

Key words Sexual selection · Courtship behaviour · Female mate choice · Male-male competition · *Phasianus colchicus* · Ring-necked pheasant

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Introduction

In the study of sexual selection, it is often difficult to differentiate between the effects of male-male competition and female preferences on male reproductive success. As some models predict, some traits acting in either of the two contexts are expected to be congruent (Andersson 1982; Hamilton and Zuk 1982; West-Eberhard 1983; Kodric-Brown and Brown 1984; Bradbury and Davis 1987). In addition, in several species, courtship and ritual threats share common features and in both cases males exhibit the same enlarged sexual traits. Therefore, it is also difficult to make a clear distinction between morphological male traits and behaviour, and sexual displays directed to females or to rivals. Recently, Berglund et al. (1996) have presented an extension of the indicator model of sexual selection that combines inter- and intrasexual mechanisms to account for the evolution of traits with this dual function: the armament-ornament model. According to this model, sexual characters of dual utility evolve primarily through male-male competition, and females benefit by subsequently using the information contained in these signals to select high-quality males. Morphological male traits may depend on phenotypic male condition (condition-dependent cost), but their use in sexual display may also depend on the results of social interaction (social control of deception), so traits used in contests may be more honest than traits used purely in mate choice (Berglund et al. 1996).

Males of most polygynous species of birds have multiple ornaments and complex displays whose function is just beginning to be explored (Møller and Pomiankowski 1993; Borgia 1995; Andersson and Iwasa 1996; Gibson 1996; Omland 1996). Therefore, it has been stressed that any realistic explanation of the evolution of traits associated with courtship and male-male competition must be able to account for this complexity. More work is needed, especially on mate choice in conjunction with the importance of displays and dominance (e.g. Kodric-Brown 1993; Zuk et al. 1995).

Male ring-necked pheasants, *Phasianus colchicus*, have multiple dimorphic traits: a pair of tarsus spurs, long tail, bright and coloured plumage, a periorbicular red tissue, which can be swollen by blood irrigation up to twice its normal size in a process that can be either momentary or maintained (the wattle), and two tufts of feathers about 2 cm long over the head, which are often raised during the mating season to resemble a pair of small 'ears' (the ear tufts). Field studies on this species have shown a polygynous mating system. Males defend mating territories and do not contribute to parental care (Taber 1949; Lachlan and Bray 1976; Ridley and Hill 1987). Territory acquisition and defence are based on agonistic interactions (threats, direct attacks and long-duration fights), and territory maintenance is based on a territorial display (the wattle display: wattle and ear tufts erected) which is costly and highly related to dominance (Mateos and Carranza 1997). As a consequence, between 15 and 50% of males are reported as not obtaining a territory, behaving as satellite individuals with low reproductive expectations during the current breeding season (Lachlan and Bray 1976; Cramp and Simmons 1980; Ridley and Hill 1987; Biadi and Mayot 1990). Most of these floating males are usually young, though sexually mature (Hiatt and Fisher 1947; Cramp and Simmons 1980; Göransson 1984), and include some low-weight adults (Hill and Robertson 1988). Hence, it seems likely that direct intrasexual competition should be an important component of male reproductive success, and non-territorial males are expected to be subordinate to territorial ones (Hill and Robertson 1988; Biadi and Mayot 1990; but see Grahn et al. 1993a). However, while some authors maintain that females prefer dominant males, which can contribute to vigilance while females feed in open habitats (Ridley and Hill 1987), others find no relationship between male social rank and reproductive success, measured as the number of females in their harems (Göransson et al. 1990; Grahn et al. 1993b).

We have some evidence for a relationship between male contest and female preference based on field and experimental studies that show a dual function in both contexts for some morphological male traits (von Schantz et al. 1989; Göransson et al. 1990; Mateos and Carranza 1995, 1996, 1997), but no study has attempted to test female preference for male courtship behaviour and dominance controlling for the differences in morphological variables (but see Grahn et al. 1993a, 1993b).

In male pheasants, as in other Galliformes (e.g. *Gallus gallus*: Zuk et al. 1990; *Lagopus mutus*: Holder and Montgomerie 1993), head ornaments are structures whose role largely depends on the behaviour of their carriers: the size of wattle and ear tufts is correlated with the frequency with which they are used in displays, the length of ear tufts can be perceived only if they are erected, and wattle size depends on the degree of inflation (Mateos and Carranza 1997). Dominance has been reported to be correlated with some morphological traits (e.g. tail length and weight: von Schantz et al. 1989; spur length: Mateos and Carranza 1996; ear tuft length and wattle size: Mateos and Carranza 1997), but the most significant differences between dominant and subordinate males are in behaviour. Dominant males perform ritual threats and the wattle display more frequently than subordinate males (Mateos and Carranza 1997; Mateos and Illanes 1997).These behaviours are reliable signals of status and are used by males when assessing each other during agonistic encounters (Mateos and Carranza 1997). In field conditions, territorial males perform the courtship behaviours to females while satellite males try to obtain copulations by coercion (see reviews in Cramp and Simmons 1980; Hill and Robertson 1988).

Here, we report the results of two mate choice experiments with captive ring-necked pheasants designed to study the interaction between male dominance, courtship display and female choice of different male behaviours. We were particularly interested in how the courtship behaviour affects female choice, whether some displays are more effective than others in attracting females, and in which moment of the mating interaction are they performed. We also wanted to determine if male display is influenced by the dominance relationship between stimuli males and if courtship display by subordinates is inhibited by the visual presence of dominant males.

Methods

Subjects

We used 23 males and 40 females hatched on a commercial farm in Spain in April–May 1989 from different reproductive harems. The commercial chicks are derived from the free-ranging European population and, at present, birds in Europe are the result of cross-breeding between several subspecies (Cramp and Simmons 1980; Hill and Robertson 1988; Biadi and Mayot 1990). The study was performed in an experimental area at the University of Extremadura, Spain. In October 1989, the subjects were introduced into two aviaries with the sexes separated. The aviaries consisted of two outdoor enclosures of 10 × 6 m, 2.5 m high (1 m of wall and 1.5 m of wire mesh). The ground was covered with sand and small gravel, with areas of shadow, shelter places, branches for perching and areas with fine sand for care of plumage. The animals were fed ad libitum by automatic troughs which delivered commercial feed for pheasants. Their diet was complemented by fresh plants (*Urtica* sp. and *Cichorium intybus*) and a mixture of wheat and oats scattered directly on the ground. All individuals were vaccinated against Newcastle disease, avian pox and Pullorum disease. Faeces were periodically collected and checked for parasites (coccidia, nematodes and cestodes), and the affected individuals were treated.

We marked males and females with an individual combination of colour rings for identification. When we began the mate choice trials in the spring of 1990, all animals were 1 year old and sexually mature, but they had no prior breeding experience.

Dominance measurement

From December 1989 to May 1992, agonistic interactions between males were monitored daily. The agonistic interactions recorded were displacing, pecking, chasing and threatening (Walk threat, Peck threat and Lateral strut in Hill and Robertson 1988). We observed the males for periods of 30–60 min, throughout the day, seasons and years. At least two periods of observation were carried out daily, one in the morning (from dawn to noon) and another in the afternoon (from noon to dusk). The size of the aviary allowed simultaneous observation of all individuals, and we assume that every dyadic interaction that took place during observation periods was recorded. We noted 10,624 interactions, for which we recorded the identity of both aggressor and recipient, and the outcome of the encounter. Most interactions occurred out of the context of direct competition for resources, but they were consistent among those occurring at feeding and drinking sites, perches or sand baths.

We calculated dominance rank periodically (every 3 months) because dominance relationships changed over time, especially at the beginning of each new breeding season (February–March) (Mateos and Illanes 1997). We calculated dominance by using the cardinal index of Clutton-Brock (ICB) which takes into account the success of opponents, so that the rank of an individual is determined by the ranks of the defeated individuals and the ranks of those individuals defeating him (Clutton-Brock et al. 1979; Boyd and Silk 1983). There was no effect of band colour on male-male interactions (Mateos and Carranza 1996, 1997).

Mate choice

Experiment 1

In the spring of 1990, we chose six pairs of males from the aviary. For each pair, we selected a dominant and a subordinate male matched in morphological features, i.e. the variables did not differ significantly between dominant and subordinate male (Table 1). We also ensured that the dominant member of the pair did not consistently show larger values for the majority of traits: in three pairs, dominants were larger for more morphological measurements, in two pairs, the subordinate were larger, and in one pair, the number of traits with larger values was the same for both members (Wilcoxon test: $T = 5, n = 5, P > 0.05$).

The experimental arena consisted of one outdoor enclosure of 6 × 9 × 1.3 m, with a ceiling net of white cotton. The area was free of vegetation and the soil was natural terrain covered by a layer of sand. We randomly placed males of each pair into two round wire cages (1 m diameter) at both corners of one side of the arena, and a cloth screen (1.5 m long) placed between the two cages created an individual area around each, so that the males could not see each other. We allowed four females to choose between the dominant and the subordinate of each pair, the males being swapped between the cages (each male received two females at the right cage and two at the left) to prevent possible position effects. The female was placed in a wooden cage (50 × 50 × 50 cm), with a wire door, centred on the side opposite the male cages, so females could observe both stimuli males at the same time, and which could be opened by an observer from a hidden position. Each female was placed in the cage for 5 min before release and was then observed continuously for 15 min, recording her behaviour and spatial position. We assumed that a female had made a choice when she stayed more than 75% of the time close to one of the males (in his individual area) and performed before him at least one, typically several, copulation solicitation (i.e. squats and associated behaviours). We used 6 male pairs (12 different males) four times each and 24 different females (4 females per male pair). So there were four trials per male pair and we had six independent sets of trials. Each female was used only once, randomly chosen from the 40 females in the aviary.

Experiment 2

In spring of 1991, we carried out another mate choice experiment with the same experimental design, but in this case we removed the cloth screen placed between the two stimuli males so they could now see each other. The six male pairs were different from those in experiment 1, although they were chosen using the same criteria. Thus, dominant and subordinate males were matched in morphological features (Table 2), and they did not differ in the number of traits with larger values: in two pairs dominants were larger for more morphological measurements, in three pairs the subordinate ones were larger, and in one pair both members showed the same number of traits with larger values (Wilcoxon test: $T = 6, n = 5, P > 0.05$). For this experiment, we also used 24 females in total, randomly chosen from the aviary.

Both experiments were carried out in the late afternoon, corresponding to the second peak in the circadian activity rhythm of the species (Cramp and Simmons 1980). More detailed information on receptive behaviour, motivation of females and validity of the criteria used in mate choice trials has been reported elsewhere (Mateos and Carranza 1995).

Male behaviour

For each trial, we also recorded the behaviour of males, since the female was placed in the cage to the end of the trial (20 min in total). Those trials in which the female did not leave the cage, or in which she did not make a clear choice between the males, were not included in the analysis of female preferences, although they were included in the analysis of male behaviour.

We recorded the following male behaviours. (1) Sexual inactivity: the males do not show any behaviour recognizable as sexual activity, and they exhibit the concealed wattle display (wattles and ear tufts down). (2) Wattle display: wattles inflated and the ear tufts erected. (2a) Crowing-call: the males in wattle display perform a very loud call, sudden, thick-voiced, and harsh. This call is followed by a brief loud wing-drumming sound and is audible up to 2 km away (Cramp and Simmons 1980). (2b) Escaping behaviour: the

Table 1 Characteristics considered for matching males in experiment 1 [*Wattle colour* chroma scores (level of saturation with red pigment) evaluated with the Munsell colour system, *Black points* width of black tufts in the wattle (measured after the experiment), *Dominance index* square root and logarithmic transformation of the cardinal index (ICB)]. Statistical analysis involved a paired *t*-test for six pairs of males and a two-tailed *P*

Variable	Mean ± SE		*t*	*P*
	Dominant males	Subordinate males		
Weight (g)	1408 ± 64	1417 ± 43	0.191	> 0.05
Tarsus length (cm)	9.51 ± 0.12	9.42 ± 0.09	0.736	> 0.05
Tail length (cm)	15.66 ± 1.20	14.66 ± 1.38	0.612	> 0.05
Spur length (cm)	1.28 ± 0.09	1.15 ± 0.11	0.669	> 0.05
Wattle size (cm)	4.20 ± 0.29	4.01 ± 0.04	0.599	> 0.05
Wattle colour	11.00 ± 0.44	10.66 ± 0.66	0.415	> 0.05
Black points (mm)	0.92 ± 0.03	0.89 ± 0.03	0.628	> 0.05
Ear tuft length (cm)	1.80 ± 0.10	1.75 ± 0.08	0.46	> 0.05
Dominance index	0.77 ± 0.10	0.19 ± 0.03	7.012	< 0.001

Table 2 Characteristics considered for matching males in experiment 2 [*Wattle colour* chroma scores (level of saturation with red pigment) evaluated with the Munsell colour system, *Black points* width of black tufts in the wattle *Dominance index* square root and logarithmic transformation of the cardinal index (ICB)]. Statistical analysis involved a paired *t*-test for six pairs of males and a two-tailed *P*

Variable	Mean ± SE		*t*	*P*
	Dominant males	Subordinate males		
Weight (g)	1383 ± 84	1358 ± 32	0.439	>0.05
Tarsus length (cm)	9.41 ± 0.13	9.53 ± 0.06	0.704	>0.05
Tail length (cm)	18.00 ± 3.56	21.00 ± 1.31	0.725	>0.05
Spur length (cm)	1.35 ± 0.11	1.31 ± 0.11	0.158	>0.05
Wattle size (cm)	4.33 ± 0.10	4.03 ± 0.05	1.885	>0.05
Wattle colour	11.33 ± 0.42	11.16 ± 0.40	0.222	>0.05
Black points (mm)	0.93 ± 0.04	0.86 ± 0.05	0.725	>0.05
Ear tuft length (cm)	1.73 ± 0.12	1.60 ± 0.11	1.195	>0.05
Dominance index	0.60 ± 0.11	0.33 ± 0.03	2.987	<0.05

males, in wattle display, peck the cage, knock it with their legs or try to run towards the females. (3) Courtship behaviour: the typical courtship behaviour as described in the literature of the species (Cramp and Simmons 1980; Hill and Robertson 1988). (3a) Ritual approach: the male in wattle display, with his head held high, walks with short steps towards the female. It is typically accompanied by a call described as "conversational-croon". (3b) Tid-bitting: this is a ritualistic courtship feeding behaviour. The males, in crouching posture with raised tail, indicate a food source with jerky up-and-down movements of the head. It is usually accompanied by a characteristic sound called the "tid-bitting-call". (3c) Lateral display: similar to lateral threat. The male turns his side to the female, and shows his sexual traits extended: head drawn in and held low with erected head ornaments (ear tufts raised, and wattles swollen), body feathers fluffed out, tail and back feathers shifted towards the female, nearer wing drooped (often so that tips of primaries scrape the ground), tail spread and vibrating so that an audible sound is produced.

Statistical analysis

To maintain the pairwise design of the experiments, we calculated differences between males of each pair for the behavioural variables measured. Data were subjected to non-parametric tests with the null hypothesis that there is no association between status and male behaviour (for the comparison of the behaviour of dominant and subordinate males of each pair, $n = 6$) and that there is no association between male behaviour and mate choice (for the comparison of the behaviour of chosen and rejected males in each pair, $n = 6$). For each male, we have considered the number of times (trials) he performed any of the above described behaviours with respect to the total number of trials he was in (this total being the same for both males in a pair). We performed analyses separately for three periods during the trials: (1) during the 5 min when the females were within the cages, before they were released: pretrial viewing period; (2) prechoice period: from the moment when the female was released until she clearly approached one of the males; (3) postchoice period: the time in which the female stayed within a male area.

Some behaviours (e.g. courtship after the female choice) could be performed with higher or lower intensity, but we used presence/absence of a given behaviour during a trial as a more conservative criterion than the comparison of mean times or any other estimate of behavioural intensity.

We also made further parametric tests to investigate the success of each male's behaviour in obtaining female choices. First, we computed the relative frequency with which a male performed the different behaviours (number of trials each male performed a behaviour divided by the number of trials he was in). Data were arcsine square root transformed to improve the parametric criteria in the analysis (Zar 1984). Second, we calculated the male success as the ratio between the number of trials in which he was chosen, plus one, divided by the number of trials in which he was rejected, plus one. This ratio was used as the dependent variable in a regression analysis, for what it was ln transformed (Agresti 1984).

Results

Experiment 1

In two trials females did not leave the cage, and in another two trials there was no clear choice of either of the males. Among 20 valid choices, 12 were for the dominant and 8 for the subordinate male. For the six male pairs, dominant males were chosen in 2.00 ± 0.25 trials (mean ± SE, $n = 6$) out of the 4 they were in, and subordinate males were chosen in 1.33 ± 0.49 trials ($n = 6$) (Wilcoxon test: $T = 2.50$, $n = 4$, $P > 0.05$).

Behaviour of dominant and subordinate males

During the 24 pretrial viewing periods, there were no behavioural differences between dominant and subordinate males. For the six male pairs, dominant males showed the wattle display in 3.16 ± 0.65 trials ($n = 6$) out of the 4 they were in, and subordinate males showed the wattle display in 2.33 ± 0.76 trials ($n = 6$) (Wilcoxon test: $T = 1$, $n = 3$, $P > 0.05$). During the 22 prechoice periods (24 trials minus the 2 trials in which females did not leave the cage), dominant males were in courtship behaviour in 11 trials (1.83 ± 0.54) while in only one case was the subordinate male in courtship behaviour at this time (0.16 ± 0.16), (Wilcoxon test: $T = 0$, $n = 5$, $P = 0.062$). In six trials, four out of six dominant males performed the lateral display immediately after the female was released.

When females were in a male area, during the 20 postchoice periods, dominant males courted before females in 10 trials from 12 in which they were chosen (9 times with the lateral display), while the rejected subordinate males were inactive or in wattle display with escaping behaviours. By contrast, subordinate males only courted in 4 trials out of 8 in which they were chosen, and only one male performed the lateral display, while the rejected dominant males, in 4 trials, continued with the ritual approach, even producing the crowing-call in 2 trials.

Female preference for male behaviour

During the pretrial viewing period, chosen and rejected males did not differ significantly in behaviour. For the six male pairs, in 1.83 ± 0.47 trials ($n = 6$) chosen males had shown the wattle display, but in 2.50 ± 0.22 trials ($n = 6$) the rejected males did so also (Wilcoxon test: $T = 0$, $n = 2$, $P > 0.05$). All males that performed the ritual approach and the courtship feeding behaviour during the prechoice period were later chosen by the females. However, the four individuals (in six trials) that readily performed the lateral display when the female was released were always rejected. Thus, the courtship behaviour as a whole (including the lateral display) did not appear to be significantly related to female choice (0.83 ± 0.40 choices for males in courtship behaviour, 1.00 ± 0.36 rejections for males in courtship behaviour; Wilcoxon test: $T = 4$, $n = 4$, $P > 0.05$). During the postchoice period, when the female was in a male area, chosen males performed the lateral display and the tid-bitting in more trials than rejected males (Fig. 1a). However, at this time, the lateral display did not produce rejection but squatting by the female.

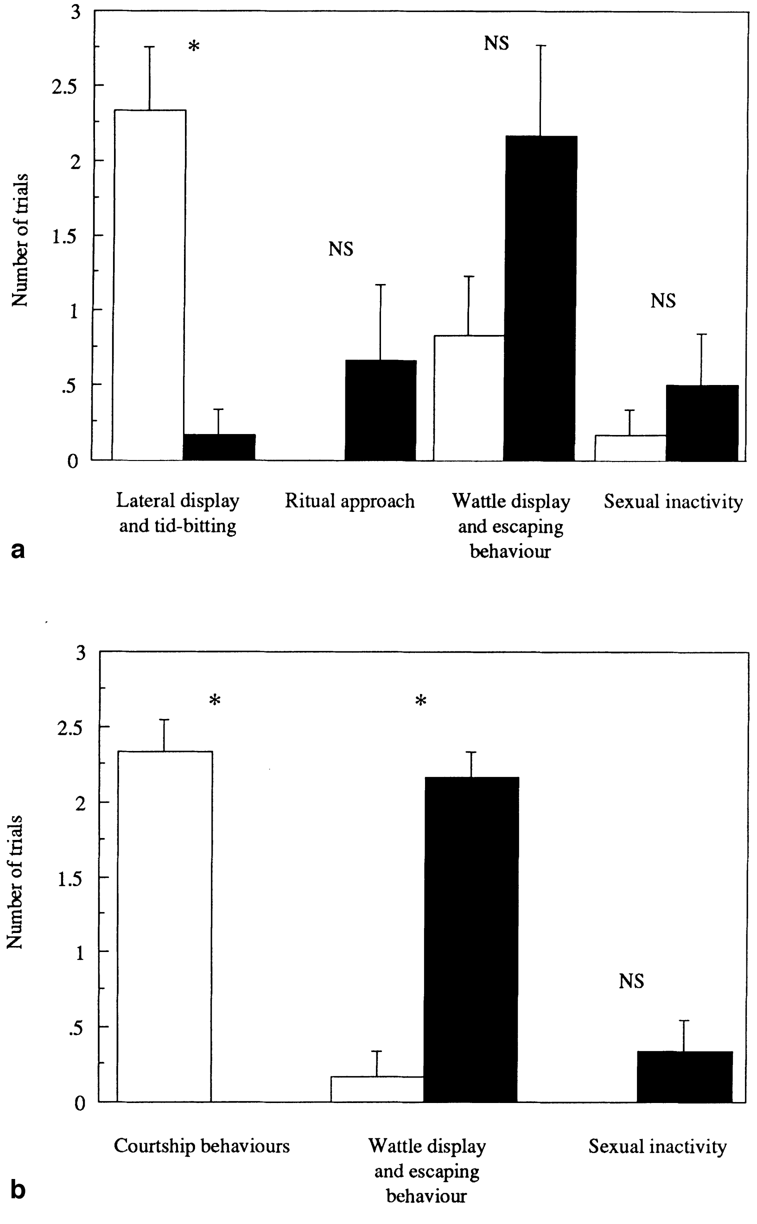

Fig. 1 Behaviour of chosen and rejected males during the postchoice period [*open bars* number of trials (mean + SE) for chosen males; *filled bars*: number of trials (mean + SE) for rejected males]. **a** Experiment 1. Chosen males performed the lateral display and the tid-bitting courtship behaviour in more trials than rejected males (Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$). **b** Experiment 2. Chosen males performed the courtship behaviours before females (Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$), while the rejected males performed escaping behaviour in wattle display (Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$)

Experiment 2

In two trials, the females did not leave the cage, and in seven trials there was either no choice or the females stayed with both males (in such cases, they usually first visited the dominant male or spent more time close to him). Out of 15 clear choices, 13 were for the dominant male and only 2 for the subordinate (2.16 ± 0.16 choices for the dominant male of each pair, 0.33 ± 0.21 choices for the subordinate male of each pair; Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$).

Behaviour of dominant and subordinate males

When males could see each other, only dominants showed the wattle display during the 24 pretrial viewing periods (2.50 ± 0.71 trials for dominant males, 0.00 ± 0.00 trials for subordinate males; Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$). During the prechoice period (22 trials), dominant males also had a higher frequency of courtship behaviour than subordinate males (2.50 ± 0.56 trials for dominant males in courtship behaviour, 0.16 ± 0.16 trials for subordinate males; Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$); but in this experiment, dominant males performed the ritual approach and the courtship feeding behaviour in 14 trials and only once performed the lateral display. During the postchoice period (15 trials), all chosen dominant males performed the lateral display before the females (in 9 trials together with other courtship behaviours) and only one out of two chosen subordinate males did so.

Female preference for male behaviour

Individuals that showed the wattle display during the pretrial viewing period were later chosen by the females in 9 out of 15 clear choices (mean: 1.50 ± 0.42) and rejected in only one case (mean: 0.16 ± 0.16; Wilcoxon test: $T = 0$, $n = 5$, $P = 0.062$). Males that performed courtship behaviour during the prechoice period were also chosen more often (mean: 1.83 ± 0.30 choices for males in courtship behaviour, 0.16 ± 0.16 rejections for males in courtship behaviour; Wilcoxon test: $T = 0$, $n = 6$, $P = 0.031$). When males performed the ritual approach and the courtship feeding behaviour (in 73% of trials), they were always chosen. However, and following the results from experiment 1, the only male that performed the lateral display just after the female left the cage was rejected by her. Finally, during the postchoice period, chosen males performed the courtship behaviour in 14 out of 15 trials (in 12 trials, the lateral display), while the rejected males performed escaping behaviour or remained sexually inactive (Fig. 1b).

Parametric analyses

Despite the differences, there is some consistency between the two experiments: dominant and subordinate males differ significantly in the frequency of courtship display during the pre- and postchoice periods (Fig. 2), and the different displays were consistent in tending to produce the same response by the females. Therefore, to obtain a clearer perspective on the relationship between the male success and courtship behaviour, we made further analyses with all the males from both experiments ($n = 24$). First, the different male behaviours and displays, both vocal and visual, were grouped using a factor analysis (principal-components analysis). Then, we used a multiple regression analysis to investigate the relationships between the grouped variables and the success obtained by each male.

During the prechoice period, the factor analysis grouped male behavioural variables into three factors: factor 1 – tid-bitting and the ritual approach, with their typical sounds – explaining 40% of the variance after oblique transformation; factor 2 – wattle display and

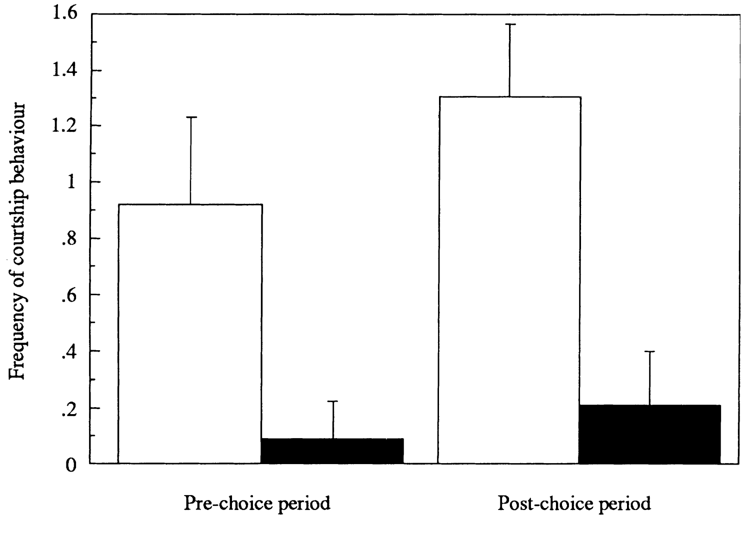

Fig. 2 Mean relative frequency (+SE) of courtship behaviour for all males (experiment 1 and 2, $n = 24$). Relative frequency was the number of trials each male performed the courtship behaviour divided by the number of trials in which he participated. Data were arcsine square root transformed (*open bars* dominant males; *filled bars* subordinate males). Two-tailed paired t-test: $df = 11$, $t = 5.03$, $P < 0.001$ for the prechoice period; $df = 11$, $t = 6.76$, $P < 0.001$ for the postchoice period

escaping behaviour, both negatively associated with sexual inactivity −34% of the variance, and factor 3 – crowing-call and lateral display −25% of the variance. The multiple regression analysis performed with the factor scores as independent variables and the ratio of success obtained by each male revealed that the behaviours associated with mate choice were tid-bitting and the ritual approach: factor 1 (Table 3, Fig. 3a). Because at this time (prechoice period), females were not in male areas, the results indicate that behavioural differences between males were not affected by female choice. Moreover, the results were consistent between experiments, although in experiment 1, the significance level was not reached because of the low number of trials in which males performed this kind of display (relationship between male success and frequency of tid-bitting plus ritual approach: $r = 0.42$, $n = 12$, $P > 0.05$ for experiment 1; $r = 0.68$, $n = 12$, $P = 0.01$ for experiment 2).

Male behaviours performed during the postchoice period were grouped into three factors: factor 1 – lateral display and tid-bitting, both negatively associated with escape behaviour – explaining 49% of the variance; factor 2 – ritual approach negatively associated with wattle display −30% of the variance, and factor 3 – sexual inactivity −20% of the variance. Multiple regression analysis performed with the factor scores and the ratio of success obtained by each male, showed that the only behaviours associated with female choice at this time were those grouped in factor 1 (Table 4, Fig. 3b). A simple regression between each of the three behaviours associated with factor 1 and the male success was significant in all three cases. However, the lateral display was the main behaviour associated with the immediate presence of females (relationship between male success and lateral display: $r = 0.84$, $n = 24$, $P < 0.01$; relationship between male success and tid-bitting: $r = 0.50$, $n = 24$, $P < 0.05$; relationship between male success and escape behaviour: $r = -0.59$, $n = 24$, $P < 0.05$). The results remained significant when the experiments were analysed separately (relationship between male success and frequency of lateral display plus tid-bitting: $r = 0.83$, $n = 12$, $P < 0.001$ for experiment 1; $r = 0.92$, $n = 12$, $P < 0.001$ for experiment 2).

Table 3 Multiple regression analysis of the behaviour during the prechoice period by all males (experiment 1 and 2) with the ratio of success obtained by each male as the dependent variable. Independent variables are the factor scores obtained from a principal-components analysis of male behaviours (*Factor 1* tid-bitting and ritual approach, with their typical sounds; *Factor 2* wattle display and escape behaviour, negatively associated with sexual inactivity; *Factor 3* lateral display and crowing-call). Multiple $r = 0.62$ ($r^2 = 0.387$, $n = 24$, $P = 0.01$)

Variable	Coefficient	*t*	*P*
Constant	0.017	–	–
Factor 1	0.493	3.08	0.005
Factor 2	−0.223	1.39	0.177
Factor 3	−0.052	0.32	0.746

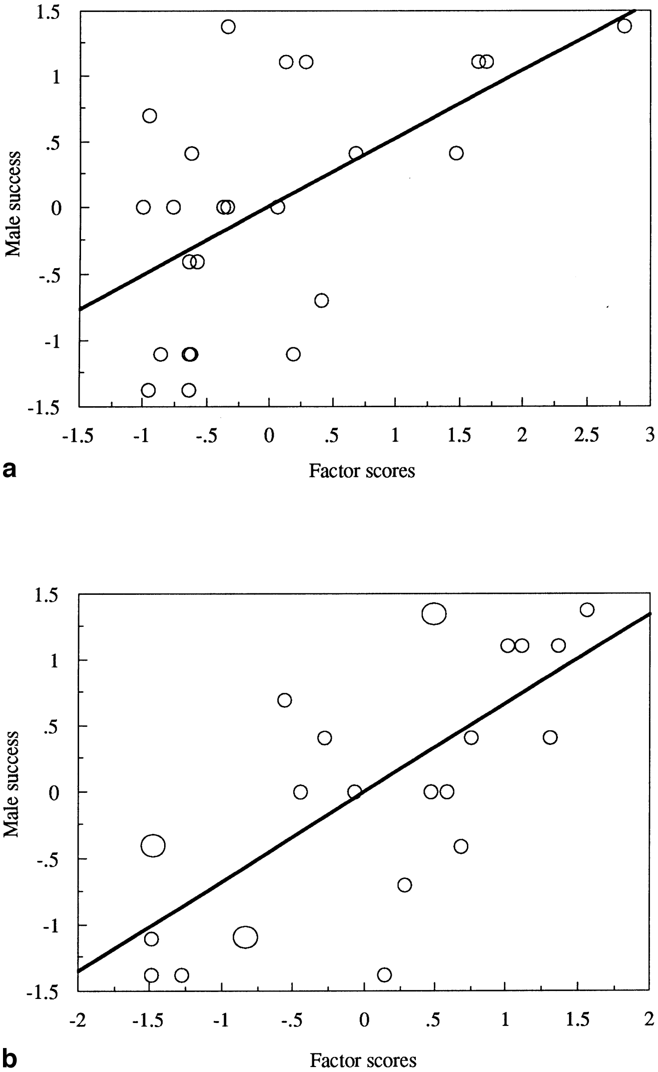

Fig. 3 Relationship between male success and factor scores for all males. Male success was the ratio between the number of trials in which he was chosen, plus one, divided by the number of trials in which he was rejected, plus one (ln transformed). **a** Prechoice period. Factor scores are based on frequency of tid-bitting and ritual approach, with their typical sounds; $Y = 0.517X + 0.017$, $r^2 = 0.33$, $n = 24$, $P < 0.01$. **b** Postchoice period. Factor scores are based on frequency of lateral display and tid-bitting, both negatively associated with escape behaviour; $Y = 0.677X - 1.97\text{E}^{-21}$, $r^2 = 0.509$, $n = 24$, $P < 0.001$

Table 4 Multiple regression analysis of the behaviour during the postchoice period by all males (experiment 1 and 2) with the ratio of success obtained by each male as the dependent variable. Independent variables are the factor scores obtained from a principal-components analysis of male behaviours (*Factor 1* lateral display and tid-bitting negatively associated with escape behaviours, *Factor 2* ritual approach negatively associated with wattle display, *Factor 3* sexual inactivity). Multiple $r = 0.78$ ($r^2 = 0.61$, $n = 24$, $P < 0.001$)

Variable	Coefficient	*t*	*P*
Constant	-8.01E^{-21}	–	–
Factor 1	0.666	4.99	0.0001
Factor 2	0.272	2.04	0.054
Factor 3	−0.112	0.84	0.408

Discussion

Previous experimental studies with the ring-necked pheasant have indicated that mate choice by females may be based on traits which are correlated with male condition and viability, such as tail length, ear tuft length, and presence of brush-shaped black feathers (mean diameter 0.9 mm) distributed throughout the wattle surface (Geis and Elbert 1956; Mateos and Carranza 1995) or spur length (von Schantz et al. 1989; but see Mateos and Carranza 1996). Some of these traits have a dual utility since spurs are used in male-male encounters (Davison 1985; Hill and Robertson 1988; Grahn et al. 1993b) and head ornaments function as reliable signals of status (Mateos and Carranza 1997).

Our results here provide evidence that courtship behaviours performed by male pheasants also affect female choice. During the prechoice period, the displays associated with female attraction were the ritual approach with conversational-croon and, mainly, the courtship feeding behaviour together with the tid-bitting call.We observed a close temporal relationship (likely cause effect) between the performance of such behaviours and the decision of the female to move directly to the male. In contrast, females rejected those males that immediately and from a long distance exhibited the lateral display.

The origin and function of tid-bitting in Galliformes have been investigated in detail by Stokes (1971) and Stokes and Williams (1971). According to these authors, and the results in this study, while behaviours such as lateral display in pheasants or waltzing in the red jungle fowl (Zuk et al. 1990) precede the female squats and facilitate mounting, the tid-bitting and associated calling serve as powerful stimuli for a hen to approach the displaying male and keep close to him. This behaviour resembles the feeding behaviour of the female to her chicks, and its ritualized use in courtship feeding may have evolved from monogamous ancestors with biparental care (Stokes 1971; Stokes and Williams 1971). In fact, cases of male parental care in the absence of the female have been reported for the common pheasant (see review in Cramp and Simmons 1980). In the red jungle fowl, however, Zuk et al. (1990, 1995) did not find differences in the tid-bitting behaviour between chosen and unchosen males. There are important differences in the mating systems between these species (e.g. territoriality in the pheasant may have favoured a signal which, emphasized by a long tail, might contribute to signalling feeding location), but also, as indicated by these authors, the experimental designs in mate choice tests may account for the differences between studies (Zuk et al. 1990). In our case, the non-random selection of male pairs of different status and similar morphology has emphasized the behavioural differences between them, allowing us to identify female preferences for such behaviours.

Field studies on pheasants show that the lateral display, very similar to lateral strut, is more frequent at the beginning of the breeding season and initially produces the withdrawal of the female (Cramp and Simmons 1980; Hill and Robertson 1988; Biadi and Mayot 1990). In experiment 1, four dominant males (in six trials) performed the lateral display immediately after the females were released. During the prechoice period, this behaviour elicited rejection by the females. However, during the postchoice period, males could promote the squatting behaviour of females by using the lateral display; perhaps, as several authors have suggested, by exploiting the physiological effect of tonic immobility produced in the females (Ridley 1981; Davison 1983).

On the other hand, results show that mate choice may reinforce the effects of intrasexual selection since in both experiments displaying males were also dominant in male-male interactions. During the pretrial viewing period, subordinate males performed the wattle display only when they did not see the dominant male (experiment 1) but never in his presence (experiment 2). In the second experiment, female choice for dominant males was significant. Hence, our experimental design also allows us to infer that subordinate males become less attractive to females when they are in visual contact with a dominant, perhaps because the display in subordinates is inhibited by the presence of dominant males (Stokes and Williams 1971). Our pheasants were 1 year older in the second experiment, so the different results at this time might have been affected by the age factor. However, as already discussed, the different male behaviours consistently tended to produce the same response by the females in both experiments, and no change in mate choice criteria by juvenile and adult females has been reported (Grahn and von Schantz 1994).

These results provide support for the armament-ornament model for the evolution of traits of dual utility (Berglund et al. 1996) which predicts that "... a male may try to display more of the signal when other males are absent, and reduce signal conspicuousness in the presence of other males because the expression of sexual characters is a compromise between attracting females and being punished by other males." Mate choice trials carried out by Hillgarth (1990) with pheasants can be interpreted in the same way: when females were allowed to choose between groups of four males that were in visual contact, a significant difference was found in favour of those males that exhibited the wattle display during the prerelease period.

The wattle display is a signal of status that may be related to the quality of the male, but its reliability is socially controlled (Mateos and Carranza 1997). For this reason, wattle size of an isolated male does not reliably reflect his status, and females did not discriminate between males on the basis of this trait (Mateos and Carranza 1995). Field studies show that subordinate or satellite males did not perform the wattle display in the presence of dominants, but they did so in the presence of females (Cramp and Simmons 1980; Hill and Robertson 1988; Biadi and Mayot 1990). Hence, social control of deception may be used by females to ensure that a courting male is the real owner and not a short-term intruder (Berglund et al. 1996). Furthermore, displaying a dominant status during the whole mating period is costly, both socially and physiologically (Mateos and Carranza 1997), and there is increased mortality associated with territoriality (Grahn 1993). Males that display more vigorously are dominants and more resistant to parasites (Hillgarth 1990). So, signalling a dominant or territorial status constitutes a reliable signal of condition also directed to females (Kodric-Brown and Brown 1984).

So far, studies on sexual selection in the ring-necked pheasant suggest that, as in other species (e.g. Kodrick-Brown 1993), female choice is based on several characters that reflect the quality or condition of the bearer, and that their relative importance depends on a suite of factors affecting the decision-making process by females, including the outcome of male-male encounters. Traits and sounds involved in the display are used by territorial males to signal their condition, to attract females and to keep away rivals (Ridley and Hill 1987; Biadi and Mayot 1990). Other male traits may be clues used by females to exercise mate choice at a short distance (Mateos and Carranza 1995; von Schantz et al. 1989), while certain behaviours, such as the lateral display, might also function to facilitate copulation. Therefore, it is possible that different cues operate at different stages of the choice process with temporally distinct functions, as has recently been suggested (Borgia 1995; Gibson 1996).

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