THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1348

Indirect partner choice through manipulation of male behaviour by female fowl, *Gallus gallus domesticus*

Tommaso Pizzari

Evolutionary Ecology Group, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK (t.pizzari@sheffield.ac.uk)

The direct and indirect consequences of female copulatory behaviour for copulation success have seldom been quantified. In feral fowl, most copulations were forced by males and copulation success was determined by two factors. First, female differential resistance and solicitation directly affected copulation success and were displayed non-randomly with respect to male social status. Second, another female copulatory behaviour, the distress call, had an indirect effect on both copulation success and the quality of copulation partners. Distress calls triggered male attention to a copulation, which increased the probability of higher-ranking males than the copulating male disrupting the copulation and inseminating the calling female. Females preferentially uttered distress calls when mounted by low-ranking males. Both copulation resistance and distress calling influenced copulation success, but only distress calling increased the probability of copulation disruption by other males. Consistent with the effect of direct selection, differential distress calling indirectly biased copulation success in favour of dominant males. Female fowl may thus ameliorate the effect of male sexual coercion by manipulating male behaviour.

Keywords: indirect female choice; copulation calls; sexual selection; intersexual conflict

1. INTRODUCTION

The conflict between the reproductive interests of males and females (Bateman 1948; Trivers 1972; Parker 1979) can lead to the evolution of sexually antagonistic traits (Rice 1984, 1996; Chapman *et al.* 1995; Holland & Rice 1998). Although females can directly bias copulation success in favour of individual males through copulation solicitation and resistance (Andersson 1994; Eberhard 1998), males often constrain female choice of copulation partners (Thornhill 1980; Clutton-Brock & Parker 1995; Gowaty & Buschhaus 1997; Parker 1998). Hence, females have traditionally been considered to be at the losing end of the sexual conflict, playing a relatively passive role in sexual selection (Cunningham & Birkhead 1998; Hrdy 1999). However, when female copulatory behaviour is constrained by males, females may influence the likelihood of being inseminated by individual males by manipulating male sexual behaviour (Cox & LeBoeuf 1977; Kuester & Paul 1992; Fisher & Brown 1993; Poston 1997). Partner selection may then result from male–male competition over insemination induced by female behaviour, a process which Wiley & Poston (1996) refer to as indirect partner selection.

One potential way by which females may manipulate male sexual behaviour is through copulation calls (Montgomerie & Thornhill 1989; Semple 1998). It has been suggested that females utter copulation calls to signal their sexual receptivity and by so doing promote competition between males, which may indirectly select socially dominant males or males in good condition (Montgomerie & Thornhill 1989; Semple 1998). By advertising sexual receptivity, a female may also copulate with more than one partner, thus triggering intrasexual competition in the form of sperm competition (Davies *et al.* 1996; Semple 1998), through which females may obtain one or more direct and indirect benefits (Birkhead & Parker 1997; Jennions & Petrie 2000). The function of female copulation calls may be to manipulate male sexual behaviour and allow females to maximize partner quality, before or after copulation, particularly in systems where the direct selection of copulation partners is relatively costly to females. However, the extent to which females can actually control copulation indirectly is unknown, as is the adaptive function of many female vocalizations (Langmore 1998).

Female feral fowl, *Gallus gallus domesticus*, can select copulation partners directly, through solicitation and resistance (Etches 1996; Pizzari & Birkhead 2000) and they also produce a call often associated with copulation, the distress call (Collias 1987; Thornhill 1988). Due to its tight association with copulation (Thornhill 1988), the distress call may influence male sexual behaviour and allow for indirect partner selection. The aim of this study was to test the extent to which female fowl can determine copulation success: (i) directly, through differential solicitation and resistance; and (ii) indirectly, through differential distress calling.

2. METHODS

(a) *Study population*

I studied a feral population of domestic fowl of a breed morphologically and behaviourally very close to the red junglefowl, *Gallus gallus* (Harrison 1987; Pizzari 1999), at the research station of the University of Stockholm (Sweden) from April to July 1998 and from April to July 1999. The study population was free ranging, unconstrained in the forest and meadows surrounding the research station and comprised 13 adult males and 21 adult females in 1998 and, in 1999, ten males and 13 females which were different from the previous year (Pizzari

© 2001 The Royal Society
Received 21 July 2000 *Accepted* 2 October 2000

1999). In both years, males belonged to different age classes. Male social hierarchy was described as a linear rank order derived from the outcome of pairwise interactions (Clutton-Brock *et al.* 1979; see Pizzari (1999) for details).

(b) *Data collection*

The birds were fully habituated and most copulations were observed at $\leqslant 5$ m distance. The behavioural sequence leading to a copulation has been extensively described in the domestic fowl (Guhl 1962; Wood-Gush 1971; Etches 1996). A copulation was defined as solicited by the female when she crouched in front of the male. Copulations where the male forcefully mounted the female in the absence of female solicitation were regarded as forced. A copulation was resisted if the female avoided the male or lowered the tail once the male had mounted her. A female passively accepted a copulation when she raised the tail to facilitate cloacal contact following mounting. Copulation attempts were behaviourally successful when cloacal contact was observed directly or when it was assumed to occur when the male's tail was lowered over the female's cloaca. The copulatory behaviour of female fowl was recorded in 30-min observation periods of randomly chosen focal females and through *ad libitum* behavioural observations (Altmann 1974; Slater 1978).

For every copulation observed, I recorded (i) whether the female produced the distress call; (ii) the presence of other males within a 10-m radius around the copulating pair; (iii) whether any of them attempted to interrupt the interaction after the distress call; and (iv) if so, the outcome of such disruption.

(c) *Playback experiment*

The aim of this experiment was to test whether the distress call elicited male response. As controls I used the contentment call (Collias 1987) and the post-oviposition cackling call (Collias 1987; Pizzari & Birkhead 2001). The contentment call is usually produced in response to temporary inaccessibility of commodities such as food, roosting and nesting sites (Collias 1987; Pizzari 1999; see also Konishi 1963; Wood-Gush & Gilbert 1969; Wood-Gush 1971). Neither control calls are linked to male sexual behaviour (Wood-Gush & Gilbert 1969; Wood-Gush 1971; Pizzari & Birkhead 2001). In 1998 and 1999, I recorded distress and contentment calls and post-oviposition cackling with an Audiotronics® 252 tape-recorder (North Hollywood, CA, USA) and a AKG® D222 microphone (Vienna, Austria), within 5 m of the bird. The call of a single female was played back for 10 min through the tape-recorder speakers, when birds were dust-bathing and resting, and thus less likely to move. In the case of the distress call, I played back a series of calls for the same length of time within the range of the distress-call frequency naturally occurring in the population, and therefore the treatment provided a stimulus within the natural range. The experiment was conducted between 09.00 and 16.30, at the time of day that was within the range of natural occurrence of all three vocalizations. Calls were played back when females were not producing either vocalization. The tape recorder was placed at least 5 m from the birds. I recorded the location of all visible birds before the playback, and allocated them to three zones from the recorder: (i) 5–10 m, (ii) 10–20 m, and (iii) > 20 m. Throughout the playback and for 5 min afterwards I also recorded the number of males that moved between zones towards the recorder (male attraction) and the number of males that ceased their activity to assume a vigilant position facing the recorder (male attention). To reduce the pseudoreplication I used the voice of ten, seven and ten females for the distress call, the post-oviposition cackling and the contentment call, respectively. To prevent birds from habituation I did not use the same call on successive days.

(d) *Data analysis*

The mean values of copulation behaviours for individual combinations of males and females (dyads) were averaged for individual females. To assess the effect of both female resistance and distress calling on copulation success and copulation disruption, I considered only females that had copulated with at least five males. Data from 1998 and 1999 were pooled when no significant difference was detected between years. Values are expressed as median + range when data were analysed non-parametrically and as mean ± s.e. when analysed parametrically. All analyses were performed with v. 6.1.3 of the SPSS statistical package (Norušis 1994).

3. RESULTS

Copulations were more likely to be forced on females than to be solicited by them (median number forced per female, $1998=36.5+82.0$, $1999=63.0+110.0$; median number solicited per female, $1998=0.5+3.0$, $1999=1.0+10$; 1998, Wilcoxon $T=0.00$, females $n=20$, $p<0.001$; 1999, Wilcoxon $T=0.00$, females $n=13$, $p=0.001$) and females resisted significantly more copulation attempts than they accepted (median resisted copulation attempts, $1998=18.5+46.0$, $1999=40.0+87.0$; median unresisted, $1998=6.0+23.0$, $1999=13.0+28.0$; 1998, Wilcoxon $T=0.00$, females $n=20$, $p<0.0001$; 1999, Wilcoxon $T=0.00$, females $n=13$, $p=0.001$).

(a) *Direct selection*

The probability of copulation success was significantly higher when a copulation was either solicited or passively accepted than when it was resisted by a female (mean probability of copulation success (1998, 1999) when solicited, 1.0 + 0.67, 1.0 + 0.40; passively accepted, 0.78 + 0.05, 0.4 + 0.50; resisted, 0.09 + 0.30, 0.09 + 0.15; Friedman ANOVA, 1998, $\chi^2_2=15.06$, females $n=10$, $p=0.0005$; 1999, $\chi^2_2=12.28$, females $n=7$, $p=0.002$). I analysed the probability of copulation success in relation to female copulation behaviour (resistance and passive acceptance, too few cases for solicitation) in the absence of the potential indirect effect of the distress call. Copulation success was significantly higher when females did not resist (median probability of success, 0.87 + 1.00) a copulation than when they did (0.00 + 1.00, Wilcoxon $T=1.00$, females $n=16$, $p=0.0027$).

The proportion of copulations solicited by females was significantly higher for males from the top (mean probability of solicitation, 0.07 ± 0.03) rather than the bottom half of the hierarchy (0.01 ± 0.01, status $F_{1,22}=7.28$, $p=0.01$, year $F_{1,22}=2.66$, $p=0.12$; figure 1*a*). Consistent with this general trend, individual females were more likely to solicit copulations from males of the top rather than the bottom half of the social hierarchy (median probability of solicitation to high- versus low-ranking males, 0.17 + 0.6 versus 0.00 + 0.06, Wilcoxon $T=3.00$, $p=0.0005$, females $n=23$). Females resisted most copulations (mean proportion (%) of resisted copulations by

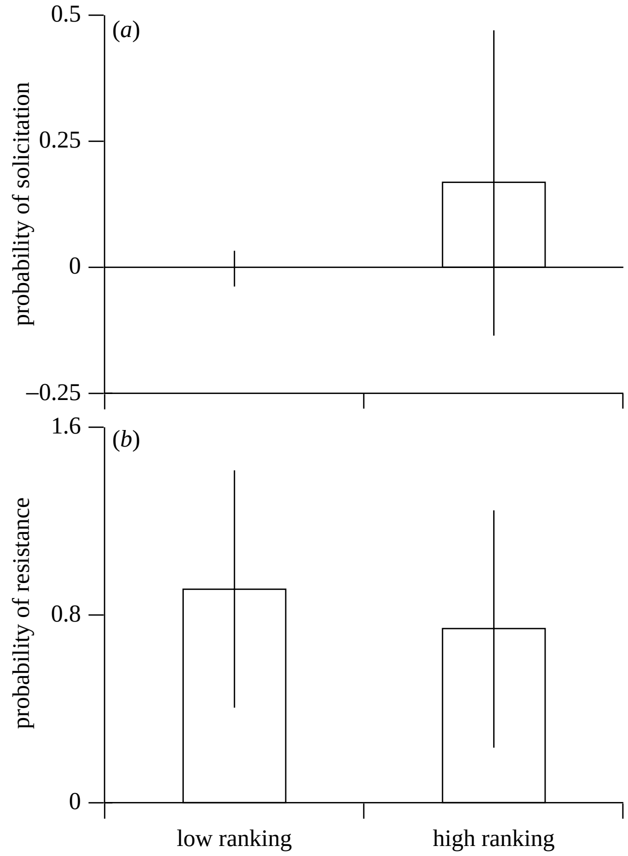

Figure 1. Relationship between male social status and the median probability of (*a*) female copulation solicitation (Wilcoxon $T = 3.00$, females $n = 5$, $p = 0.0005$), and (*b*) female resistance to copulation (Wilcoxon $T = 123.00$, females $n = 31$, $p = 0.024$). Vertical bars represent range.

individual females, 72.8 ± 2.35) with a tendency to resist more copulations from the bottom rather than from the top half of the hierarchy (median probability of resistance from high- versus low-ranking males, 0.74 + 1.00 versus 0.91 + 1.00, Wilcoxon $T = 123.00$, $p = 0.024$, females $n = 31$; figure 1*b*).

(b) *Indirect selection*

When resisting a copulation, individual females were more likely to utter the distress call than when copulations were passively accepted or solicited (median probability of distress call when copulation resisted, accepted and solicited, 0.88 + 0.38, 0.79 + 0.92, 0.00 + 0.00, Friedman ANOVA, $\chi^2_2 = 33.63$, $p < 0.0001$, females $n = 21$).

When attempting to copulate, males approached females from behind with raised hackles (T. Pizzari, personal observation; Etches 1996). A female would resist a male as soon as she detected (measured as the female initiation of male avoidance) him approaching. Approaches that were detected closer than one male body length (BL) from the female were significantly more successful than approaches detected further away (median copulation success when approach < 1 versus > 1 BL, 0.17 + 0.36 versus 0.00 + 0.00, Wilcoxon $T = 0.00$, $p = 0.003$, females $n = 12$). I recorded whether females were more likely to utter the distress call when males were detected close (< 1 BL) rather than far (> 1 BL). Females were more likely to utter the distress call when an approaching male was detected close (median probability of distress call when male detected < 1 versus > 1 BL, 1.00 + 0.21 versus 0.17 + 1.00, Wilcoxon $T = 0.00$, $p < 0.005$, females $n = 11$).

Females were more likely to utter the distress call when mounted by bottom- rather than by top-ranking males (median frequency of distress call when copulating with bottom versus top males = 0.91 + 1.0 versus 0.74 + 1.0, Wilcoxon $T = 55.0$, $p = 0.0003$, females $n = 32$; figure 2*a*). Copulation disruption by neighbouring males was more likely when females uttered the distress call than when they did not (mean probability of copulation disruption with versus without distress call, 0.87 + 0.44 versus 0.33 + 1.00, Wilcoxon $T = 2.00$, $p < 0.0001$, females $n = 27$; figure 2*b*). Males that disrupted a copulation were more likely to be dominant over the copulating males than males that witnessed but did not disrupt a copulation (mean difference between the status of highest-ranking male witnessing a copulation and the status of the copulating male when the witnessing male did versus did not disrupt the copulation, 0.95 ± 0.06 versus 0.24 ± 0.09, Wilcoxon $T = 0.00$, $p = 0.0001$, females $n = 21$; figure 2*c*). Copulation success was significantly lower when copulations were disrupted (median probability of success with versus without disruption, 0.20 + 0.39 versus 0.80 + 0.87, Wilcoxon $T = 0.00$, $p < 0.0001$, females $n = 33$; figure 2*d*). Disrupting males often copulated with the disrupted female: overall, as a result of copulation disruption females copulated with the disrupter in 20% of cases. Averaged for individual dyads, this meant that each female had an average probability of 0.17 (± 0.03) of copulating with the disrupter.

(i) *Playback experiment*

Males were significantly more likely to move towards the tape-recorder when the distress call was played than when the control calls were played ($\chi^2_2 = 22.16$, $p < 0.0001$, $n_1 = n_2 = n_3 = 10$ where n represents the experimental trials for each call). Similarly, male attention was significantly more likely to be triggered by the distress call than by the two control calls ($\chi^2_2 = 22.82$, $p < 0.0001$, $n_1 = n_2 = n_3 = 10$). In 60% (six out of ten) of the trials when the distress call was played some males walked up to the recorder. All cases involved exclusively the top-ranking male (with the exception of one instance when one low-ranking male joined the top-ranking male). The effect of calls could be mediated by the distance at which males were from the tape recorder, as males may be more likely to respond to a call when closer to the tape-recorder. However, the mean proportion of males at the three zones did not vary significantly between calls (5–10 m, distress call = 19.78 ± 10.3, cackling = 7.78 ± 7.78, contentment call = 16.89 ± 5.91; 10–20 m, distress call = 23.43 ± 9.64, cackling = 13.43 ± 3.89, contentment call = 20.00 ± 13.33; > 20 m, distress call = 56.72 ± 9.78, cackling = 78.49 ± 8.46, contentment call = 63.11 ± 11.73; Kruskal–Wallis, $n_1 = n_2 = n_3 = 10$; 5–10 m, $\chi^2_2 = 0.957$, $p = 0.620$; 10–20 m, $\chi^2_2 = 2.97$, $p = 0.226$; > 20 m, $\chi^2_2 = 0.14$, $p = 0.931$).

(c) *Relative importance of direct and indirect selection*

Three female behaviours played a role in partner choice because they were differentially displayed

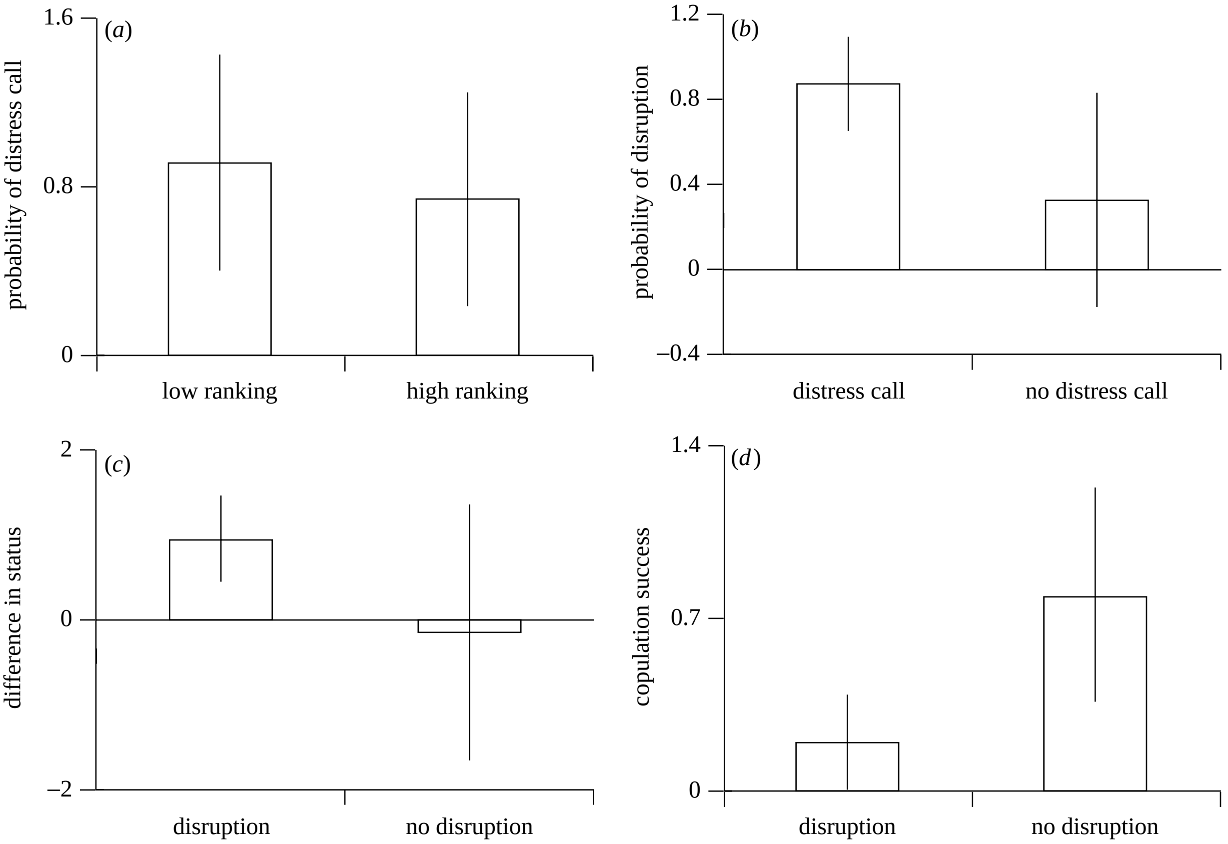

Figure 2. Effect of distress calling on copulation success. (*a*) Median probability of distress calling with low- and high-ranking copulation partners (Wilcoxon $T = 55.0$, females $n = 32$, $p = 0.0003$). (*b*) Probability of a copulation being disrupted when the distress call was and was not uttered (Wilcoxon $T = 2.00$, females $n = 27$, $p < 0.0001$). (*c*) Difference in status between the highest-ranking male witnessing a copulation and the copulating male (witnessing − copulating) when the former disrupted the copulation and when he did not (Wilcoxon $T = 0.00$, females $n = 21$, $p = 0.0001$). (*d*) Copulation success with and without copulation disruption (Wilcoxon $T = 0.00$, females $n = 33$, $p < 0.0001$).

Table 1. *Analysis of variance for angular-transformed (a) mean copulation success (1998, 1999) and (b) copulation disruptions*

(MS, mean squares.)

source	d.f.	MS	*F*	*p*
(*a*)				
resistance	1, 1	2.547, 1.283	26.93, 15.02	0.0001, 0.0001
distress call	1, 1	0.964, 0.796	10.19, 9.32	0.002, 0.003
male status	1, 1	0.218, 0.342	2.30, 4.01	0.132, 0.050
female	15, 7	0.117, 0.073	1.23, 0.86	0.261, 0.546
error	99, 60	0.095, 0.085	—	—
total	117, 70	0.127, 0.140	—	—
(*b*)				
resistance	1	0.035	0.247	0.620
distress call	1	10.578	73.648	0.0001
male status	1	2.660	18.519	0.0001
female	28	0.165	1.148	0.289
error	180	0.144	—	—
total	211	0.207	—	—

according to male quality and influenced the outcome of copulation: (i) direct copulation solicitation; (ii) direct copulation resistance; and (iii) the distress call. Because copulation solicitation was relatively rare, it was difficult to quantify its effect on copulation success. Therefore, I assessed the relative importance of resistance and distress call in determining variation in two measures of copulation outcome: (i) copulation success and (ii) copulation disruption, which had the effect of both reducing the success of the current copulation and resulting in a copulation with a male of higher rank (see § 3(b)). Both female resistance and the distress call explained a significant proportion of the variation in copulation success between individual males and females (table 1*a*). In addition, the distress call but not resistance explained a significant proportion of the variation in the probability of disruption, particularly of low-ranking males (table 1*b*).

4. DISCUSSION

Female fowl directly selected dominant copulation partners. Indirect partner selection through differential distress calling also occurred and contributed significantly to the bias in copulation success in favour of males of high rank. Resistance to copulation and the distress call appeared to influence copulation outcome in two different ways. Female resistance directly decreased the success of a copulation, while the distress call increased the probability of a copulation being disrupted when males more dominant than the copulating male were present. Compared to resistance, distress calling was a less efficient (although possibly also less costly) way to avoid an insemination. Distress calling also increased partner quality by promoting copulations from males of relatively high rank, allowing females to exert a significant control over the selection of copulation partners. However, the fact that females were more likely to distress call when males were too close to be avoided suggests that distress calling may also be associated with some costs, possibly due to the attraction of other males.

Although female fowl showed a preference for high-ranking copulation partners, a high degree of copulation resistance was maintained across the entire male social hierarchy, suggesting that some conflict may occur between optimal copulation frequency for males and females. Because sperm competition is intense in this system, it is adaptive for males to defend paternity by copulating frequently (Parker 1984). Frequent copulation may, on the other hand, be costly to females regardless of the quality of the copulation partner (Sheldon 1993; Chapman *et al.* 1995; Partridge & Hurst 1998). In the case of the fowl, copulation costs may derive from pathogens transferred with semen which may contain faecal material (T. Pizzari, personal observation) and physical injuries which may have lethal consequences (Pizzari 1999). Nevertheless, due to female preference for dominant males intersexual conflict is exacerbated between females and low-ranking males.

It has been suggested that copulation calls may indirectly select for partner quality by manipulating male sexual behaviour (Montgomerie & Thornhill 1989; Semple 1998). Some evidence for female manipulation of male sexual behaviour to increase partner quality has been observed in some taxa (Thornhill & Alcock 1983). Female Northern elephant seals, *Mirounga angustirostris*, utter loud copulation calls which trigger male–male competition over copulation, thereby favouring copulations from the most dominant males (Cox & LeBoeuf 1977). When courted, female black grouse, *Tetrao tetrix*, approach other males thereby triggering fights between males, which reveal their relative status (Hovi *et al.* 1995). Similarly, copulation calls of female macaques, *Macaca sylvanus*, attract the attention of surrounding males and can result in dominant males copulating with the calling females (Semple 1998). As far as I am aware, the results of the present study provide the first quantitative evidence that indirect mate choice can be an important part of intersexual selection. The evolution of indirect mechanisms of sexual selection is of particular relevance in the fowl mating system, where the costs of directly resisting copulation by females can sometimes be lethal or sublethal (Pizzari 1999).

I am grateful to T. R. Birkhead for help during the study and C. K. Cornwallis for technical assistance. I am especially grateful to N. Andbjer, A. Bylin and particularly S. Jakobsson for providing facilities at the study site, and to T. R. Birkhead, B. J. Hatchwell, F. M. Hunter and M. Petrie for useful comments on earlier drafts of the manuscript. I was supported by a Patrick & Irwin Packington Fellowship (University of Sheffield) when carrying out the study.

REFERENCES

Altmann, J. 1974 Observational study of behaviour. *Behaviour* **49**, 227–267.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Bateman, A. 1948 Intra-sexual selection in *Drosophila*. *Heredity* **2**, 349–368.

Birkhead, T. R. & Parker, G. A. 1997 Sperm competition and mating systems. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 121–145. Oxford, UK: Blackwell.

Chapman, T., Liddle L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. 1995 Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**, 241–244.

Clutton-Brock, T. H. & Parker, G. A. 1995 Sexual coercion in animal societies. *Anim. Behav.* **49**, 1345–1365.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–225.

Collias, N. E. 1987 The vocal repertoire of the red junglefowl: a spectrographic classification and the code of communication. *Condor* **89**, 510–524.

Cox, C. J. & LeBoeuf, B. J. 1977 Female incitation of male competition: a mechanism of mate selection. *Am. Nat.* **111**, 317–335.

Cunningham, E. J. A. & Birkhead, T. R. 1998 Sex roles and sexual selection. *Anim. Behav.* **56**, 1311–1322.

Davies, N. B., Hartley, I. R., Hatchwell, B. & Langmore, N. E. 1996 Female control of copulations to maximise male help: a comparison of polygynandrous alpine accentors, *Prunella collaris*, and dunnocks, *P. modularis*. *Anim. Behav.* **51**, 27–47.

Eberhard, W. G. 1998. Female roles in sperm competition. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 91–116. London: Academic Press.

Etches, R. J. 1996 *Reproduction in poultry*, 1st edn. Wallingford, UK: CAB International.

Fisher, R. B. & Brown, P. S. 1993 Vaginal secretions increase likelihood of intermale aggression in Syrian hamsters. *Physiol. Behav.* **54**, 213–214.

Gowaty, P. A. & Buschhaus, N. 1998 Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy. *Am. Zool.* **38**, 207–225.

Guhl, A. M. 1962 The behaviour of chickens. In *The behaviour of domestic animals* (ed. E. S. E. Hafez), pp. 491–530, London: Baillière, Tindall & Cox.

Harrison, B. 1987 Den Svenska dvärghönan. Part II. *Sven. Rasf. Tidskrift* **1**, 12–14.

Holland, B. & Rice, W. R. 1998 Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 17.

Hovi, M., Alatalo, R. V. & Siikamaki, P. 1995 Black grouse leks on ice: female mate sampling by incitation of male competition. *Behav. Ecol. Sociobiol.* **37**, 283–288.

Hrdy, S. B. 1999 *Mother nature. Natural selection and the female of the species*. London: Chatto & Windus.

Jennions, M.D. & Petrie, M. 2000 Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**, 21–64.

Konishi, M. 1963 The role of auditory feed-back in the vocal behaviour of the domestic fowl. *Zeitschrift Tierpsychol.* **20**, 349–367.

Kuester J. & Paul A. 1992 Influence of male competition and female mate choice on male mating success in barbary macaques (*Macaca sylvanus*). *Behaviour* **120**, 192–217.

Langmore, N. E. 1998 Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* **13**, 136–140.

Montgomerie, R. & Thornhill, R. 1989 Fertility advertisement in birds: a means of inciting male–male competition? *Ethology* **81**, 209–220.

Norusis, J. M. 1994 *SPSS 6.1 base system user's guide*. Chicago, IL: SPSS.

Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.

Parker, G. A. 1984 Sperm competition and the evolution of animal mating strategies. In *Sperm competition and the evolution of animal mating systems* (ed. R. L.Smith), pp. 1–60. Orlando, FL: Academic Press.

Parker, G. A. 1998 Sperm competition and the evolution of ejaculates: towards a theory base. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 3–54. London: Academic Press.

Partridge, L. & Hurst, L. D. 1998 Sex and conflict. *Science* **281**, 2003–2008.

Pizzari, T. 1999 Reproductive strategies in feral fowl, *Gallus gallus*. PhD thesis, University of Sheffield, UK.

Pizzari, T. & Birkhead, T. R. 2000 Female feral fowl eject sperm of subdominant males. *Nature* **405**, 787–789.

Pizzari, T. & Birkhead, T. R. 2001 For whom does the hen cackle? The adaptive function of post-oviposition cackling. *Anim. Behav.* (In the press.)

Poston, J. P. 1997 Mate choice and competition for mates in the boat-tailed grackle. *Anim. Behav.* **54**, 525–534.

Rice, W. R. 1984 Sex chromosomes and the evolution of sexual dimorphism. *Evolution* **38**, 735–742.

Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234.

Semple, S. 1998 The function of barbary macaque copulation calls. *Proc. R. Soc. Lond.* B **265**, 287–291.

Sheldon, B. C. 1993 Sexually transmitted disease in birds: occurrence and evolutionary significance. *Proc. R. Soc. Lond.* B **239**, 491–497.

Slater, P. J. B. 1978 Data collection. In *Quantitative ethology* (ed. P. W. Colgan), pp. 7–24. New York: Wiley.

Thornhill, R. 1980 Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.* **28**, 52–59.

Thornhill, R. 1988 The jungle fowl hen's cackle incites male competition. *Verh. Dtsch. Zool. Ges.* **81**, 145–154.

Thornhill, R. & Alcock, J. 1983 *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press.

Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine–Atherton.

Wiley, R. H. & Poston, J. 1996 Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.

Wood-Gush, D. G. M. 1971 *The behaviour of the domestic fowl*. Alton, UK: Nimrod Press.

Wood-Gush, D. G. M. & Gilbert, A. B. 1969 Oestrogen and the pre-laying behaviour of the domestic hen. *Anim. Behav.* **17**, 586–589.