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Female mate preferences and subsequent resistance to copulation in the mallard

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In the majority of socially monogamous bird species, females solicit or accept copulations from males other than their partner. Females may gain direct benefits from extrapair males, such as greater access to resources, or indirect genetic benefits that will influence the future success of their offspring. However, one group of birds appears to be the exception to this general rule; in the wildfowl (Anseriformes), all extrapair copulations appear to be resisted by females. It has been suggested that resistance behavior may be a strategy to allow females a greater choice of mates, either at the precopulatory level (to promote choice of copulation partner) and/or the postcopulatory level (to promote multiple mating to increase their choice of sperm). This paper examines the function of female resistance behavior in one of the dabbling ducks, the mallard (*Anas platyrhynchos*). Observations on a marked population of wild mallard and experiments with captive birds found that although females showed a strong preference for particular males that are the first to molt into their breeding plumage, male attractiveness did not influence female responses to pair or extrapair copulation attempts. Female resistance decreased the likelihood that copulation attempts would end in successful insemination. The findings did not support the hypothesis that females resist copulations to promote female choice and the reasons why waterfowl may benefit from avoiding all extrapair copulations are discussed. *Key words: Anas platyrhynchos*, forced copulation, good genes, mallard, mate choice, resistance. *[Behav Ecol 14:326–333 (2003)]*

In the majority of bird species that form monogamous pairbonds, both males and females may seek copulations with individuals other than their social partner (for review, see Bradbury and Davies, 1987; Gowaty, 1985; Westneat et al., 1990). Males are assumed to benefit primarily from the potential to father more offspring; females may gain direct benefits from these extra copulations, such as greater access to resources (Hunter and Davis, 1998), and/or indirect genetic benefits for their offspring. This has been supported by the observation that preferred males (Møller, 1994; Norris, 1993; Petrie, 1994; but see Cunningham and Russell, 2000; Gil et al., 1999) and extrapair males (Hasselquist et al., 1996; Kempenaers et al., 1992, 1997; Sheldon et al., 1997) appear to father more successful offspring. Yet, despite this apparent advantage, there are some breeding systems in which females actively resist all extrapair copulation attempts. In many cases, males appear to be able to restrain females and force them to copulate, often despite extreme female resistance (for examples, see Berger, 1983 [mammals]; Farr, 1980 [fish]; McKinney et al., 1983, 1984 [birds]; Olsson, 1995 [reptiles]; Smuts and Smuts, 1993 [primates]; and Thornhill, 1980 [insects]).

Female resistance to all extrapair copulation attempts would seem paradoxical in light of the current emphasis on the benefits to females of extrapair mating. Hence, it has been assumed that the function of resistance is avoidance of unwanted copulations, either to avoid costs associated with copulation (such as disease, injury, or punishment from partner) or to avoid fertilization by a low-quality or incompatible partner. However, it has also been suggested that resistance could be a strategy to promote mate choice, whereby females are resisting initial copulation attempts to facilitate greater choice of extrapair copulation partners (Cristoleit, 1929). If the function of female resistance behavior is to promote female choice, it has the potential to operate at two levels: (1) the precopulatory level and (2) the postcopulatory level.

At the precopulatory level, resistance may allow females to fully assess the males with which they can choose to copulate, for example, by assessing the best male during a chase, comparing the potential extrapair partner to their own partner, or allowing females to gain copulations from other males without incurring punishment from their partner. Resistance behavior may also be selected for through indirect choice (Wiley and Poston, 1996): The winner of the chase will have sons that are also successful at forcing copulations and produce more offspring than other males.

Alternatively, at the postcopulatory level, resistance may function to attract other males to the vicinity when a copulation is about to occur, thereby allowing the female to copulate with more than one extra male at the same time. This could either allow selection or rejection of sperm from particular males or promote sperm competition within the reproductive tract so that the most competitive sperm or sperm from the most compatible male successfully fertilizes her eggs. Resistance as a strategy arguments generally assume genetic benefits can be gained from copulating with additional or preferred males.

The aim of this paper is to examine mate choice and the function of subsequent female resistance to copulation in the mallard (*Anas platyrhynchos*). Female mallard form monogamous pair bonds and would seem a likely candidate to benefit from extrapair copulations. First, females appear to exhibit strong mate choice on the basis of male traits alone, and males provide no paternal care to the offspring (Cramp and Simmons, 1977). Second, populations tend to be strongly male biased, so variance in male reproductive success is likely to be large because some males do not acquire a partner (Grant and Grant, 1987; Lack, 1954; Møller, 1992). Yet, female mallards frequently appear to have copulations forced upon them by males other than their partner, resulting in extrapair

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offspring (Burns et al., 1980; Evarts and Williams, 1987). This may be facilitated by the possession of an intromittent organ by males, an extremely unusual feature in birds, occurring in only 3% of all species (King, 1981).

To assess the function of female resistance, it is important to look both at which males are attempting to force copulations and how females respond to different males. If those males attempting extrapair copulations are of a lower quality, then a general strategy of resistance to extrapair copulations could be beneficial to females. High-quality males, for example, may be paired to high-quality females and may concentrate more on mate guarding than seeking extrapair copulations with females of lower quality. If, however, all males attempt extrapair copulations, and resistance is functioning to promote female choice, we might expect to see preferred males being more successful in gaining copulations.

The first part of this study examines the behavioral responses of females to forced copulation by males that have been ranked for female preference. The second part of the study examines male and female responses to different extrapair copulation partners in a wild population of marked mallard.

METHODS

Female preferences and responses to forced copulation in a captive population of mallard

Female preferences and ranking of males

A group of 10 female and 13 male mallards was obtained from Chatsworth Pheasantries in October 1995. All birds were 10-week-old premolt mallards and had hatched on the same day. Birds were ringed and individually wing-tagged and housed in a large flight pen incorporating free running water. Male and female morphometrics and the percentage of breeding plumage that males exhibited were recorded at regular intervals over the pairing period until the following spring.

Female preferences can be assessed directly from their pairing behavior. Three displays unambiguously indicate female preference at a given time (Lorenz, 1951; Omland, 1996a,b): (1) inciting, (2) head pumping, and (3) copulation (Lorenz, 1951). The inciting display involves the female swimming toward her preferred male while jerking her head backward and forward over her wing and making characteristic clucking noises, usually in the direction of less preferred males and competing females (Lorenz, 1951). The head-pumping display is a mutual courtship display of males and females. Pairs move away from other birds and, directing their display toward each other, move the head and neck up and down in unison. This display also precedes pair copulations (Lorenz, 1951). Pairing copulations are preceded by females indicating their willingness to copulate by adopting the receptive position; females lie flat in the water to allow the male to mount. No transfer of sperm occurs during these autumn copulations as the reproductive systems of both sexes remain regressed until the breeding season in spring. These displays can be quantified and used to assess mate choice directly so that males can be ranked for female preference (Cunningham, 1997; Omland, 1996a,b). This female preference is repeatable between different groups of females (Cunningham and Russell, 2000).

Over the autumn pairing period, observations of 1-h duration were performed regularly and all pairing displays, male displays, aggressive interactions, their participants, and their outcomes were recorded by ad libitum sampling onto a Dictaphone. Males were ranked independently by a number of possible measures of female preference, including pairing order and the number of females preferring a particular male, to confirm all possible measures of female preference were in agreement.

Female responses to pair and extrapair copulations by males of different rank

When pairs had formed and male rank had been established, birds were housed, in their pairs, in individual pens. Each pair had access to natural nesting cover and a stretch of free running stream. The breeding cycles of the birds were synchronized by allowing them to lay a first clutch of eggs, then removing them from all the females at the start of the experiments. Mallards often lose clutches of eggs through predation and can lay at least four replacement clutches within a season (Cunningham, 1997). Each female then underwent two trials; one examined the female's response to extrapair copulation attempts by males ranked higher than her partner, the other examined the female's response to extrapair copulation attempts by males ranked lower than her partner.

In each trial, females were placed, on their own, in a separate experimental flight pen measuring 24 × 8 × 2m containing a 24-m stretch of stream 2-m wide. The extrapair male was introduced into the pen and their responses recorded on video for a period of 1 h or until copulation occurred. The following measures of male and female responses were later scored from the video by two independent observers who did not know the ranks of the birds involved: (1) time taken for males to initiate a copulation, (2) time taken for males to achieve intromission once the female had been caught, (3) duration of intromission, (4) female response to copulation attempts; female resistance was ranked on a scale of zero to five, and (5) presence or absence of female vocalizations during extrapair copulation attempts.

At the end of the trial, the birds were returned to their partner in their individual pen. Pair males were excluded when females underwent each trial, as they are likely to attempt to dislodge the extrapair male from the female, both prolonging the copulation attempt and risking injury to the female. Removal of the pair male also prevented differences in mate guarding ability of partners influencing female responses. To control for changes in female receptivity over the laying period, five of the ten females were placed with more attractive males for their first trial and five with less attractive males, then vice versa for their second trial. Trial one was conducted on day 1 of their laying cycle, trial two on day 5 of the laying cycle. Females generally lay 9–13 eggs in a single clutch (Cramp and Simmons, 1977). All trials were conducted at the same time of day to control for any circadian rhythm in female receptivity.

All pairs were also observed continuously between dawn and dusk from the period just before the onset of laying, until the end of the female laying cycle including the period that the trials were conducted (24 April to 13 May). All behaviors associated with copulation were recorded ad libitum on to Dictaphone.

Female responses to copulation in a wild population of mallard

A population of wild mallard was studied on Chatsworth Estate, North Derbyshire, England (53°15′ N, 1°35′ W), between 1994 and 1997. Over the 3-year study, 119 birds were caught and individually marked with a numbered leg ring and a pair of soft, numbered wing tags, allowing birds to be identified on water when leg rings were out of sight. Biometrics (body weight, wing length, bill length, tarsus length) were recorded to the nearest millimeter. All birds were caught between November and March, before breeding commenced, in order to minimize any disturbance to breeding behavior. The study site was monitored daily between March and July in 1995, 1996, and 1997 during which the presence, location, and breeding status of all marked birds encountered were recorded.

In one breeding season, focal sampling periods of 1 h, divided into 4-min blocks, were used to collect data on randomly selected pairs. Observations were conducted spanning the period of dawn to dusk (between 0400 and 2230 h) and distributed evenly throughout the day. In order to examine how females respond to extrapair behavior by different males, the following behaviors were recorded:

(1) Extrapair copulation behavior: Extrapair male, pair male, and female responses to all extrapair attempts and the outcome of any attempt. Forced copulation attempts are defined as chases where the male was actively attempting to catch hold of the female. Forced copulation was considered successful when intromission of the phallus was observed.
(2) Pair copulation behavior: All copulation attempts by pair males, whether they were resisted or not resisted, and whether they were successful.
(3) Female chases: The identity of all birds, male and female responses, and the outcome of the chase.
(4) Aggressive interactions: The identity of the participants involved, the degree of escalation categorized as (a) no contact (b) contact, or (c) fight, and the winner of all interactions.
(5) Displays: Pairing displays performed by extrapair males, pair males or females.
(6) Nonpair approaches: The identity of any approaching non-pair bird and pair male and female response.
(7) Intra-pair distance: The distance between the male and female was estimated every 4 min. Categories of less than 0.5 m, 0.5–1 m, 1–5 m, 5–10 m, 10–20 m, 20–50 m, and more than 50 m were used.
(8) Nearest neighbor identity and distance: The identity of all birds within a 50-m radius of the focal pair was recorded every 4 min. Categories of less than 0.5 m, 0.5–1 m, 1–5 m, 5–10 m, 10–20 m, 20–50 m, and more than 50 m were used. Distance was measured from the female of the pair when pairs separated.
(9) Time alone: The amount of time the female was left unguarded and, if known, the location and activity of the absent partner.

RESULTS

Female preferences and responses to copulations in a captive population of mallard

Ranking of males
Males were initially ranked according to the order in which they paired. The first male to pair was assigned a rank of one and was considered to be of higher rank than males that took longer to pair who were assigned ranks up to 10. Other possible measures of female preference agreed with the ranking position: More females directed pairing displays at high ranking males compared to lower ranking males (Figure 1a) and females displayed at a higher frequency toward higher ranking males (Figure 1b).

Once females had paired, it was observed that there was a trend for females to have displayed only at higher ranking males than their eventual partner (Wilcoxon signed ranks test, $T^+ = 30$, $p = .07$). Of 10 females, eight displayed at more than one male. Out of 97 pairing displays by these eight females, only two by the same female were directed at a lower ranking male. Both these occasions were when the female's partner had displayed with another female and were directed at the next highest ranking male.

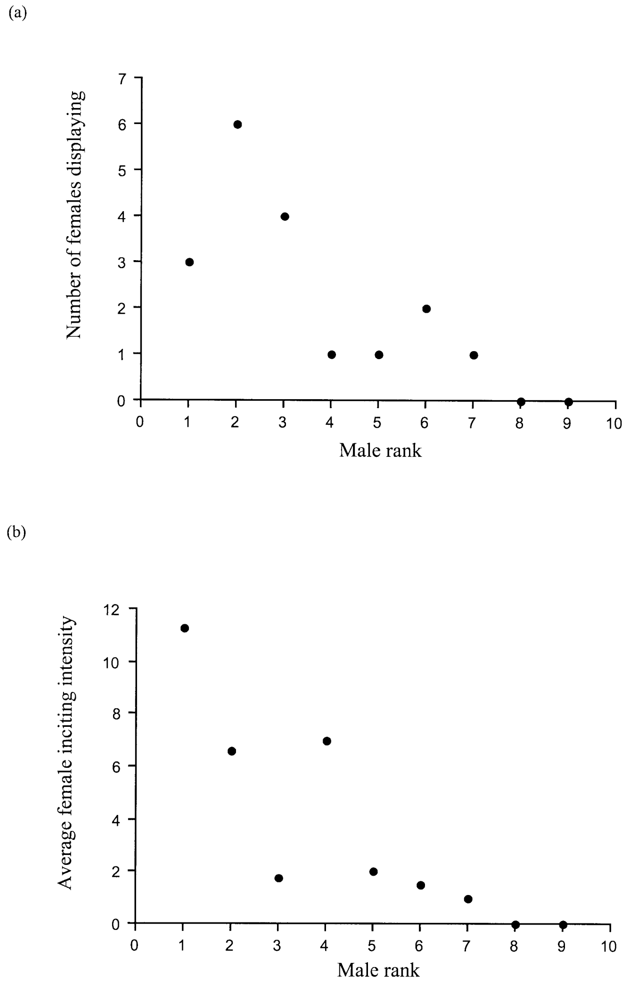

Figure 1
The relationship between male rank (defined as the order of pairing) and (a) the number of females that directed pairing displays at the ranked male ($r_s = -0.86$, $n = 9$, $p = .015$) and (b) the average rate at which females directed pairing displays at the ranked male ($r_s = -0.91$, $n = 9$, $p = .01$).

Correlates of male rank
Male rank was related to the timing of molt into and out of breeding plumage but did not correlate with male body size, body condition, display rate, or dominance rank (Table 1). High ranking males had the highest percentage of breeding plumage amongst the group at the onset of pairing (Figure 2a) and maintained their breeding plumage for longer (Figure 2b).

Responses to forced extrapair copulation
Males attempted an extrapair copulation in 18 out of 20 trials. The two males that did not attempt to force a copulation were of higher rank than the female's partner but there was no difference between high and low ranking males in whether they attempted a forced copulation (Fisher exact test, $p = .23$, power = .31).

All extrapair copulation attempts were resisted by females. Measures of female effort correlated strongly between observers ($r_s = 0.89$, $n = 16$, $p = .0006$). There was no difference in how hard females tried to resist males of different rank (Wilcoxon matched-pairs test: $T = 6$, $n = 7$

Table 1

Summary of Spearman rank correlations between male rank and male trait recorded

Male trait	r_s	p
Male body size (tarsus length)	0.381	.31
Male body condition	0.0003	.99
Male dominance rank	0.18	.66
Male display rate	−0.468	.18
Percentage breeding plumage		
Onset of pairing	−0.92	.008
End of breeding	−0.73	.038

Moult score at the onset of breeding remains a significant trend after Bonferroni corrections for multiple tests establishing a rejection level of 0.008 at 95% confidence limits and 0.017 for 90% confidence limits (n = 9).

pairs, p = .402; $\bar{x}_{\text{higher}}$ = 2, 95% confidence interval [95%CI] 1.5 to 3.5, $\bar{x}_{\text{lower}}$ = 2.5 95%CI$_{\text{lower}}$ 1.5 to 4). Nor did females differ in their vocalization rate during forced copulation attempts by high and low ranking males (McNemar change test χ^2 = 1, df = 1, $p > .30$).

All initiated copulation attempts resulted in successful intromission. There was no difference between high and low ranking males in the time they took to initiate a copulation with each female (Wilcoxon matched-pairs test: T = 15, n = 7 pairs, p = .93; $\bar{x}_{\text{higher}}$ = 156, 95%CI 15 to 369, $\bar{x}_{\text{lower}}$ = 91, 95%CI$_{\text{lower}}$ 49 to 402). Once females were caught there was no difference in the time taken for high and low ranking males to achieve intromission with each female (Wilcoxon matched-pairs test: T = 13, n = 7 pairs, p = .93, $\bar{x}_{\text{higher}}$ = 16, 95%CI 12 to 37.5, $\bar{x}_{\text{lower}}$ = 16, 95%CI$_{\text{lower}}$ 12 to 34) nor any difference in how long intromission took with each female, i.e. the length of time required for successful sperm transfer (Wilcoxon matched-pairs test: T = 10, n = 7 pairs, p = .99, $\bar{x}_{\text{higher}}$ = 2, 95%CI 1.75 to 5.8, $\bar{x}_{\text{lower}}$ = 3, 95%CI$_{\text{lower}}$ 1.8 to 14).

Post-forced copulation pair copulatory behavior

Pairs were observed from dawn to dusk over the study period for a total of 272 h. During this time, 119 pair copulation initiations were observed, 58.8% (n = 70) of which culminated in successful intromission. Of the 119 observed pair copulation initiations, 31.9% (n = 38) were resisted by females and 68.1% (n = 81) were not resisted. Of the 38 pair copulation initiations resisted by 10 females, 36.8% (n = 14) resulted in copulation, and of 81 not resisted, 69.1% (n = 56) resulted in copulation. Resistance behavior significantly reduced the likelihood of successful intromission (paired t test: t = −3.97, n = 10 females, p = .005).

In the 3 days that followed each trial, there was a tendency for females to resist a higher proportion of pair copulations following a forced copulation by a high ranking male than following a low ranking male (Figure 3a). However, this was because there was a trend for lower ranking males to attempt more pair copulations than high ranking males (r_s = 0.68, n = 8, p = 0.07; Figure 3b) leading to higher levels of female resistance. Overall, there was no difference in the actual number of successful copulations that followed copulations with high and low ranking extrapair males (Wilcoxon signed-rank test, W = 1, n = 9, p = 1.00, $\bar{x}_{\text{higher}}$ = 1, 95%CI 0 to 4.5, $\bar{x}_{\text{lower}}$ = 1, 95%CI$_{\text{lower}}$ 0.5 to 2.5; Figure 3c).

Female responses to copulation in a wild population of mallard

Counts of marked and unmarked birds around the study site indicated that a minimum of 67% (n = 119) of the population within the study area was marked over the three year period.

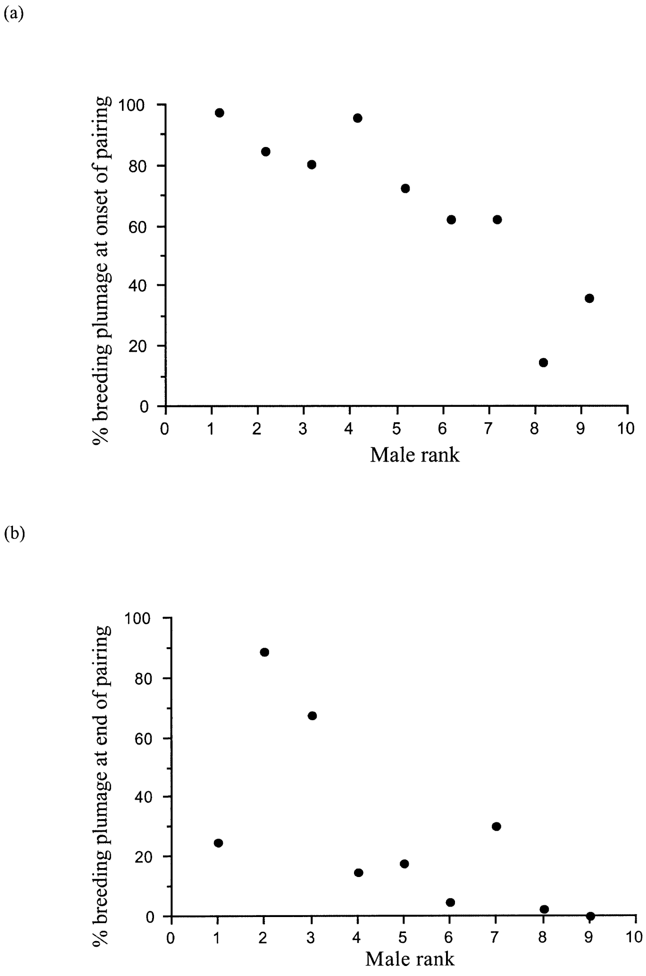

Figure 2
The relationship between male rank and (a) the percentage of breeding plumage that males had developed by the onset of pairing (r_s = −0.929, n = 9, p = .0086) and (b) the percentage of breeding plumage males retained at the end of breeding (r_s = −7.33, n = 9, p =.038).

Pairing status of birds involved in extrapair copulations

As the sex ratio in the adult population of mallards tends to be biased toward males, some males remain unpaired during the breeding season. Pairing status and pair bonds were generally maintained between years: of 18 pairs in which both individuals were marked and survived to the following breeding season, 17 pairs remained together for all subsequent breeding attempts over the three years. The exception occurred when a female switched mate within a breeding season after her partner developed an infection of the phallus. In all cases (five out of five), trios were maintained. Unpaired males also tended to remain unpaired between years; six out of seven of unpaired males that were caught in 1995 remained unpaired, for both the following seasons, and of the two surviving unpaired birds caught in 1996, neither paired in 1997.

Because pairing status is generally maintained between years, with unpaired males failing to gain a mate as they get older, we can assume that paired males are preferred males and that unpaired males are less preferred males. Over the three year study period, 75% of males were paired (n = 51)

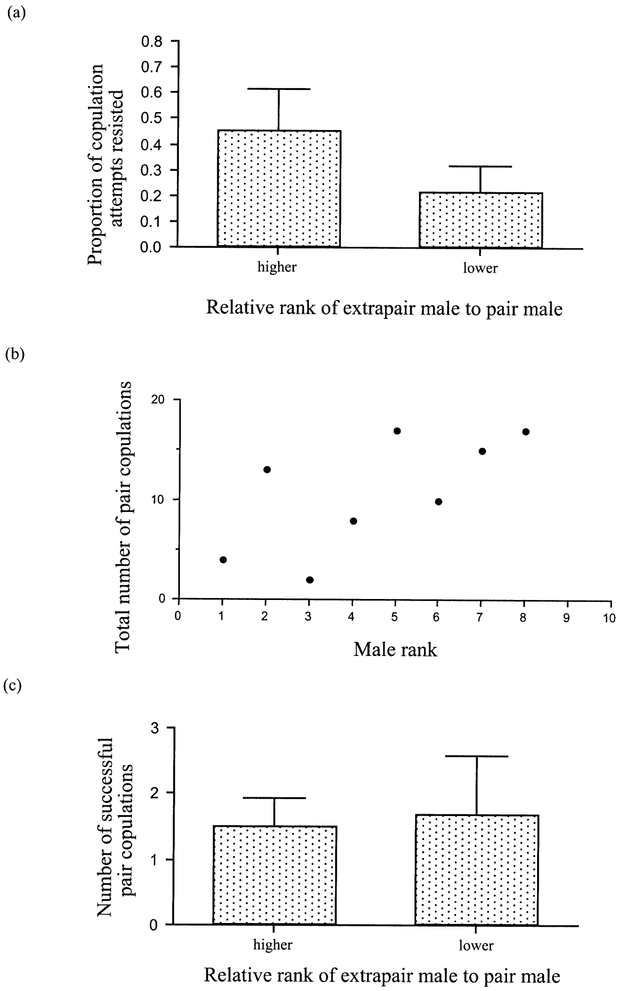

Figure 3
The effect of relative male rank on (a) the proportion of pair copulations resisted by females following a forced copulation by high and low ranking males, (b) the number of pair copulations attempted, and (c) the actual number of pair copulations that were successful.

and 25% of males were unpaired ($n = 17$). There was no difference in the frequency of forced copulation attempts by paired and unpaired males ($n = 2$ trio males, 10 paired males, 7 unpaired males, χ^2 of partnered versus unpartnered males, $\chi^2 = 1.04$, df = 1, $p > .05$). There appeared to be no difference in relative success of copulations achieved by partnered and unpaired males but there was not enough power to conclude if this was a consequence of the small sample size or a true reflection of their relative success (five out of 12 paired males and 3 out of 7 unpaired males successfully forced a copulation). Unpaired males were smaller ($t = 2.23$, df = 22, $p = .04$) and in significantly poorer condition than paired males ($t = 3.1$, df = 22, $p = .007$). However, there was no significant difference in body weight, tarsus length, bill length or wing length between birds participating in forced extrapair copulations and the rest of the population, or between birds participating in successful and unsuccessful forced extrapair copulation attempts (Tables 2 and 3).

Numbers of males involved in extrapair copulations

Of the 21 forced copulation attempts observed, 66.7% ($n = 14$) involved a single extrapair male, 28.6% ($n = 6$) involved two extrapair males and 4.7% ($n = 1$) involved three extrapair males attempting to copulate with the female.

Table 2

Comparisons of morphometric traits of males observed in forced copulation attempts (a) with those not observed in forced copulation attempts (b)

Characteristic	t	Mean ± SE	p	95% CI
Weight	0.565	1186 ± 31.1(a)	.58	1114 to1258
		1163 ± 18.4(b)		1116 to 1210
Wing length	0.932	286 ± 2.2(a)	.37	280.5 to 290.8
		283 ± 1.6(b)		278.7 to 287.0
Tarsus length	−0.117	115 ± 3.1(a)	.91	107.5 to 121.9
		115 ± 2.3(b)		109.2 to 121.1
Bill length	0.490	52.6 ± 0.77(a)	.63	50.8 to 54.3
		51.9 ± 1.3(b)		48.6 to 55.1

Of 17 attempts observed to their outcome, 58.8% ($n = 10$) were successful and 47.2% ($n = 7$) were unsuccessful. Of the attempts that were successful, 80% ($n = 8$) of forced extrapair copulation attempts resulted in intromission by a single male and 20% ($n = 2$) resulted in intromission by two males. In none of these cases was the pair male observed to copulate with the female, despite always being present as the extrapair copulation took place.

Patterns of resisted pair copulations

Females did not accept all pair copulations attempts. Of the pair copulations observed ($n = 10$), 30% of pair copulations were resisted. Two out of the three resisted copulations did not result in successful copulation whereas five out of five unresisted copulations resulted in intromission.

The effect of mate guarding behavior on extrapair copulations

Male mate guarding effort was calculated as the mean distance between males and their partner over the period females were estimated to be fertile. There was no correlation between mate guarding distance and frequency of successful forced copulation attempts on a female partner ($r_s = 0.1$, $n = 14$, $p = .70$). The rate of forced copulations successfully targeted on his partner was not correlated with male dominance rank ($r_s = -0.03$, $n = 14$, $p = .90$).

Males pursuing a mixed reproductive strategy may leave their females unguarded, allowing other males copulatory access to their partners. However, there was no correlation between the rate at which males were involved in female chases and the number of chases his partner received ($r_s = 0.15$, $n = 14$, $p = .60$). Females were rarely seen alone, apart from early in the morning around the period of egg laying. At this time, pair males appeared to sit and wait for females at a nearby site to which females would later return.

Table 3

Comparison of characteristics of males who were involved in successful (a) and unsuccessful (b) forced copulation attempts

Characteristic	t	Mean ± SE	p	95% CI
Weight	−0.96	1160 ± 58(a)	.365	975 to 1344
		1217 ± 30(b)		1139 to 1293
Wing length	−0.757	283 ± 3.4(a)	.471	272.7 to 294.3
		287 ± 2.6(b)		280.1 to 293.3
Tarsus length	−0.467	114 ± 4.4(a)	.653	99.9 to 12.1
		117 ± 4.3(b)		105.9 to 128.1
Bill length	−0.957	51.5 ± 0.48(a)	.366	49.9 to 53.0
		52.9 ± 1.14(b)		50.6 to 55.9

DISCUSSION

Female mallard show a strong preference for particular males; preferred males developed their breeding plumage earlier and maintained it for longer than less preferred males but did not differ in body size, condition, dominance rank or display activity from less preferred males. All males, regardless of rank, were equally likely to attempt extrapair copulations, all of which were resisted, and were equally likely to succeed in gaining extrapair copulations. Female resistance decreased the likelihood that copulation attempts would end in successful insemination and male rank did not appear to influence either male responses to forced copulation opportunities or female responses to either pair or extrapair copulation attempts. High ranking males tended to copulate at a lower frequency with their partners than low ranking males.

Observations on a marked population of wild mallard showed that pairing status was maintained between years and that unpaired male generally remained unpaired from year to year. Unpaired males were smaller and in significantly poorer condition than paired males at the start of the breeding season. Paired and unpaired males were equally likely to attempt extrapair copulations and equally likely to succeed in achieving copulations. The likelihood of attempting to force a copulation, or the likelihood of successfully forcing a copulation, were not correlated with any male morphometric traits. Mate guarding behavior did not appear to influence the rate at which forced extrapair copulations were attempted on a female. Forced copulation attempts resulted in successful copulations by a single male in 80% of cases.

Do females resist copulations to incite competition between males?

Precopulatory choice

If female mallard resist extrapair copulation attempts to promote pre-copulatory competition, the predicted outcome of extrapair copulation attempts would be that females copulate with preferred males. The findings of this study were not consistent with this prediction.

Field data demonstrated paired and unpaired males were equally likely to participate in forced copulation attempts and equally likely to be successful. In captive studies, female preferences for particular males did not influence their responses to extrapair copulation attempts. Males of high and low rank were equally likely to attempt extrapair copulations and equally likely to be successful in gaining extrapair copulations. All attempted copulations resulted in successful intromission, including those by males of lower rank than their partner. Furthermore, males of different rank did not differ in either the time they took to initiate copulation or to achieve copulation, suggesting this effect is not due to differences in males in their ability to force copulations.

Female incitement of competition has been suggested to be an important mechanism by which females may benefit in several species. In the dunnock (*Prunella modularis*) females incite competition by copulating with both alpha and beta males. However, in this case, the female gains directly as both potential fathers provision the offspring (Davies, 1985; Hatchwell and Davies, 1992). In the bearded tit (*Panurus biarmicus*), females appear to initiate long chases between males in their nesting area, apparently to test the fitness of potential extrapair copulation partners (Hoi, 1997). However, females appear to be able to control copulations in this species and chases were initiated by high ranking females who might be expected to have the least to gain from extrapair copulations to obtain good genes for their offspring. One species in which incitement between males does result in copulation by males of high rank is the northern elephant seal, (*Mirounga angustirostris*). When subordinate males approach females and attempt to copulate, females call loudly to attract the attention of a more dominant male who usually succeeds in displacing the subordinate male to copulate with the female himself (Cox and LeBoeuf, 1977). However, whether the main function of incitement is to gain a copulation from a high ranking male or avoid injury by a low ranking male is unclear since young, inexperienced males often injure females during copulations (LeBoeuf and Mesnick, 1991a,b). It has been assumed that if indirect benefits are important, females should choose males of high genetic quality as a partner and that these same males should be involved in extrapair copulation attempts (Kempenaers et al., 1992; Møller, 1994). However, females may choose a male partner on different criteria and seek good genes from other, extrapair males if direct benefits do not correlate in males with genetic benefits. This may seem more likely where pair males provide direct fitness benefits in the form of parental care. However, to test this possibility, a longer term study looking at the relative success of pair and extrapair offspring would be required.

Postcopulatory choice

If females are inciting competition to promote post-copulatory competition, by encouraging multiple copulations to promote sperm competition within the reproductive tract, the predicted outcome of forced copulation attempts would be that females attract the attention of, and successfully copulate with, several males and that female reproductive success would increase with her number of copulation partners.

In the mallard, field data suggested that forced copulation attempts resulted in insemination by a single male in 80% (n = 10) of cases. This is in contrast to a study by Barash (1977) who observed 71% (n = 89) of forced extrapair copulations to involve more than one male. However, Barash's study was not conducted on a wild population and did not distinguish between successful and unsuccessful attempts (McKinney et al., 1978). There was no evidence that females may use vocalizations to attract more preferred males to join a forced copulation attempt (Montgomerie and Thornhill, 1989); in experimental studies, females were no more likely to vocalize to attract competitors when being chased by a low ranking male.

Whether a 20% chance of copulating with an extra-male is enough to promote costly resistance behavior to incite sperm competition would depend on the extent of the genetic benefits to be gained from extrapair copulations. However, a number of other pieces of evidence suggest that post-copulatory choice is unlikely to be the function of female resistance. Firstly, both parts of the study suggested that resistance behavior significantly reduced the likelihood of successful copulation, rather than promote further copulations. Second, this hypothesis assumes that (1) males differ in their sperm characteristics and fertilizing ability, and (2) that offspring benefit either because males with winning sperm are males of high heritable genetic quality or males with high heritable sperm quality. It would therefore predict sperm phenotype to be a reliable indicator of some type of quality, and that females should be repeatable in their choice of sperm in the same way that you would predict that females are repeatable in their choice of mate. We have found, in other studies, that when the same group of females was repeatedly inseminated over several different clutches, with identical sperm mixtures, females did not consistently select or utilize the same type of sperm (Cunningham and Cheng, 1999).

Why then do females prefer particular males yet avoid all extrapair copulations?

Female mallard may benefit from avoiding extrapair copulations if copulations are costly and/or females choose to pair with males primarily for direct benefits that would not translate into benefits for extrapair females.

First, this study has shown that high ranking males show a trend toward copulating at a lower frequency than lower ranking males. This may be an advantage in this particular species as the possession of an intromittent organ may be more likely to transfer venereal pathogens than birds where sperm isn't placed inside the body, including pathogens that may not always be associated with sexual transmission in other groups (Hamilton, 1990; Sheldon, 1993). Disease and parasite transmission have been reported to account for up to 87% of mortality in wild populations of wildfowl (Stout and Cornwell, 1976) and evidence of a phallus infection was observed in the study population. Many pathogens important in domestic wildfowl show an increase in prevalence with copulation frequency (Stipkovits et al., 1986) and their virulence is often determined by the relative levels of pathogen present (Wobeser, 1981). Sub-lethal effects of sexually transmitted diseases are common and often have a greater detrimental effect on females than males (Wobeser, 1981); in domesticated wildfowl for example, venereal disease can cause reduced female weight, fertility and egg production (Marius-Jestin et al., 1987; Stipkovits et al., 1986).

This increased risk of sexually transmitted diseases may not only make extrapair copulations more costly but be one reason females prefer particular males. High ranking males may be better able to carry the large metabolic cost of the large testes mass required for a strategy of low copulation frequency as paired males were consistently in better condition. Furthermore, we have found from further studies that the single most important factor determining both viability traits and male attractiveness in the mallard is hatch date (first versus second clutches; Cunningham and Russell, 2000). This is governed by whether or not first clutches are predated. Early hatched males are also the first males to molt into their breeding plumage and this study has also shown that females show a strong preference for particular males who molt into their breeding plumage first and maintain their breeding condition for longer. These males do not have to partition energy between growth and reproduction unlike their later hatched counterparts. They therefore have a much longer period when they can put energy into reproduction after growth has been completed. It would be interesting to examine the effects of male rank, body condition and early hatching on sperm production to investigate this possibility further.

If preferred males are in better condition, they are also likely to be the most effective in defending a feeding area for a female to feed. Males defend transient feeding sites around females during the egg laying and incubation period. This study found that mate guarding was not an effective strategy in preventing forced copulations and females paired to dominant males were no more likely to escape forced copulation attempts than those of less dominant males. Mate guarding was also observed to occur during incubation when the female is off the nest but no longer fertile. Mate guarding may actually be functioning to defend a feeding area for a female, to enable her to build up the large energy reserves she needs for egg production. Onset of molt has also been found to be an important predictor of extrapair mating success in superb fairy wrens (*Malarus cyaneus*; Mulder and Magrath, 1994) and may be a signal of male quality as onset becomes earlier with age and body condition.

In conclusion, female mallard appear to be resisting copulations in order to avoid copulation rather than facilitate mate choice. This may be because males are chosen on the basis of the direct benefits they provide and any genetic benefits for offspring to be gained from copulating with preferred males are likely to be small and/or uncorrelated with preferences for social mates. Furthermore, the costs of extra copulations are likely to be higher than in other species of bird due to the increased risk of disease transmission. This may be why costly resistance behavior by females persists rather than the passive acceptance of extrapair copulations that can be so beneficial to males.

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REFERENCES

Barash DP, 1977. Sociobiology of rape in mallards (*Anas platyrhynchos*): responses of the mated male. Science 197:788–789.

Berger J, 1983. Induced abortion and social factors in wild horses. Nature 303:59–61.

Bradbury JW, Davies NB, 1987. Relative roles of inter- and intra- sexual selection. In: Sexual selection: testing the alternatives (Bradbury JW and Andersson MB, eds). Chichester, UK: Wiley; 143–163.

Burns JT, Cheng KM, McKinney F, 1980. Forced copulation in captive mallards. 1. Fertilization of eggs. Auk 97:875–879.

Christoleit E, 1929. Uber das Reihen der Enten. Beitr Fortpfl Biol Vögel 5:45–53.

Cox CJ, LeBoeuf BJ, 1977. Female incitation of male competition; a mechanism of mate selection. Am Nat 111:317–335.

Cramp S, Simmons KEL, 1977. Handbook of birds of Europe, the Middle East and North Africa: birds of the Western Palearctic. Oxford: Oxford University Press.

Cunningham EJA, 1997. Forced copulation and sperm competition in the mallard (*Anas platyrhynchos*) (PhD thesis). Sheffield, UK: University of Sheffield.

Cunningham EJA, Cheng KM, 1999. Biases in sperm use in the mallard: no evidence for selection by females based on sperm genotype. Proc R Soc Lond B 266:905–910.

Cunningham EJA, Russell AF, 2000. Egg investment is influenced by male attractiveness in the mallard. Nature 404:74–77.

Davies NB, 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. Anim Behav 33:628–648.

Evarts S, Williams CJ, 1987. Multiple paternity in a wild population of mallards. Auk 104:597–602.

Farr JA, 1980. Social behaviour patterns and determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study of the effects of intermale competition, female choice and sexual selection. Behaviour 74:38–91.

Gil D, Graves J, Hazon N, Wells A, 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286:126–128.

Gowaty PA, 1985. Multiple parentage and apparent monogamy in birds. Ornithol Monogr 37:11–21.

Grant BR, Grant PR, 1987. Mate choice in Darwin's finches. Biol J Linn Soc 32:247–270.

Hamilton WD, 1990. Mate choice near or far. Am Zoo 30:341–352.

Hasselquist D, Bensch S, von Schantz T, 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature 381:229–232.

Hatchwell BJ, Davies NB, 1992. An experimental study of mating competition in monogamous and polyandrous dunnocks, *Prunella* *modularis*: II. Influence of removal and replacement experiments. Anim Behav 43:610–622.

Hoi H, 1997. Assessment of the quality of copulation partners in the monogamous bearded tit. Anim Behav 53:277–286.

Hunter FM, Davis LS, 1998. Female Adelie penguins acquire nest material from extra-pair males after engaging in extra-pair copulations. Auk 115:526–528.

Kempenaers B, Verheyen GR, Dhondt AA, 1997. Extrapair paternity in the blue tit *Parus caeruleus*: female choice, male characteristics, and offspring quality. Behav Ecol 8:481–492.

Kempenaers B, Verheyen GR, Van de Broeck M, Burke T, Van Broeckhoven CV, Dhondt AA, 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature 357:494–496.

King AS 1981. Phallus. In: Form and function in birds (King AS, McLelland J, eds). London: Academic Press; 107–147.

Lack D, 1954. The natural regulation of animal numbers. Oxford: Clarendon Press.

LeBoeuf BJ, Mesnick SL, 1991a. Sexual behaviour of male northern elephant seals: I. Lethal injuries to adult females. Behaviour 116:142–162.

LeBoeuf BJ, Mesnick SL, 1991b. Sexual behaviour of male northern elephant seals: II. Female response to potentially injurious encounters. Behaviour 117:262–280.

Lorenz K, 1951. Comparative studies on the behaviour of the Anatinae. Avic Mag 57:157–182.

Marius-Jestin V, Le Menec M, Thibault E, Moisan JC, L'Hospitalier R, 1987. Normal phallus flora of the gander. Vet Med B 34:67–78.

McKinney F, Barrett J, Derrickson SR, 1978. Rape among mallards. Science 201:281–282.

McKinney F, Cheng KM, Bruggers DJ, 1984. Sperm competition in apparently monogamous birds. In: Sperm competition and the evolution of animal mating systems (Smith RL, ed). Orlando: Academic Press; 523–545.

McKinney F, Derrickson SR, Mineau P, 1983. Forced copulation in waterfowl. Behaviour 86:250–294.

Møller AP, 1992. Frequency of female copulations with multiple males and sexual selection. Am Nat 139:1089–1101.

Møller AP, 1994. Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow. Proc Nat Acad Sci USA 91:6929–6932.

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

Mulder RA, Magrath MJL, 1994. Timing of prenuptial molt as a sexually selected indicator of male quality in superb fairy-wrens (*Malurus* cyaneus). Behav Ecol 5:393–400.

Norris K, 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major.* Nature 362:537–539.

Olsson M, 1995. Forced copulation and costly female resistance behavior in the Lake Eyre Dragon *Ctenophorus maculosus.* Herpetologica 51:19–24.

Omland KE, 1996a. Female mallard mating preferences for multiple male ornaments. I. Natural variation. Behav Ecol Sociobiol 39: 353–360.

Omland KE, 1996b. Female mallard mating preferences for multiple male ornaments II. Experimental variation. Behav Ecol Sociobiol 39:361–366.

Petrie M, 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 371:598–599.

Sheldon BC, 1993. Sexually transmitted diseases in birds: occurrence and evolutionary significance. Phil Trans R Soc B 339:491–497.

Sheldon BC, Merila J, Qvarnstrom A, Gustafsson L, Ellegren H, 1997. Paternal genetic contribution to offspring condition predicted by size of a male secondary sexual character. Proc R Soc Lond B 264:297–302.

Smuts BB, Smuts RW, 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. Adv Stud Behav 22:1–63.

Stipkovits L, Varga Z, Czifra G, Dobos-Kovacs M, 1986. Occurrence of mycoplasmas in geese infected with inflammation of the cloaca and phallus. Av Path 15:289–299.

Stout IJ, Cornwell GW, 1976. Nonhunting mortality of fledged North American waterfowl. J Wild Manag 40:681.

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

Westneat DF, Sherman PW, Morton ML, 1990. The ecology and evolution of extra-pair copulations in birds. Curr Ornith 7:331–369.

Wiley RH, Poston J, 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. Evolution 50:1371–1381.

Wobeser G, 1981. Diseases of wild waterfowl. New York: Plenum Press.