Stockholm University

This is a published version of a paper published in *American Naturalist*.

Citation for the published paper:

Lovlie, H., Pizzari, T. (2007)

"Sex in the Morning or in the Evening? Females Adjust Daily Mating Patterns to the Intensity of Sexual Harassment"

American Naturalist, 170(1): E1-E13

URL: <http://dx.doi.org/10.1086/518180>

Access to the published version may require subscription.

Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:su:diva-65777>

<http://su.diva-portal.org>

Sex in the Morning or in the Evening? Females Adjust Daily Mating Patterns to the Intensity of Sexual Harassment

Hanne Løvlie^{1,*} and Tommaso Pizzari^{2,†}

1. Department of Zoology, Stockholm University, 10691 Stockholm, Sweden;

2. Edward Grey Institute of Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom

Submitted August 18, 2006; Accepted January 10, 2007;
Electronically published May 22, 2007

ABSTRACT: Selection on males to mate at a higher rate than females often results in male harassment of females and counteracting female responses. When the reproductive value of copulation changes over time, these mating strategies are expected to be time dependent. Here, we demonstrate that variation in the intensity of male harassment leads to drastic changes in female daily mating patterns. In feral populations of fowl *Gallus gallus domesticus*, male harassment is intense, particularly in the evening when inseminations are most likely to result in fertilization. We experimentally manipulated the intensity of male harassment through similar-sized groups of different sex ratios. Male mating propensity was always higher than females', particularly in male-biased groups and in the evening, when males were closer to and more likely to approach females. Females counteracted male harassment by escalating resistance to mating and—crucially—by shifting their daily mating pattern: in strongly female-biased groups with relaxed sexual harassment, females solicited sex in the evening, while in male-biased groups, they solicited sex in the morning, thus avoiding harassment in the evening. Together, these results indicate that intersexual conflict may occur not only over mating rates but also over when in the day to copulate.

Keywords: sex ratio, optimal copulation time, polyandry, mating rates, sexual conflict, *Gallus*.

Because they have higher potential reproductive rates, males may vary more than females in number of mating partners, leading to more intense intrasexual selection on male mating rates (Bateman 1948; Trivers 1972; Parker

1979; Andersson 1994; Arnqvist and Nilsson 2000; Shuster and Wade 2003). This divergence in male and female optima may generate sexual conflict over mating (Parker 1970b, 1979, 2006; Arnqvist and Rowe 2005) and the evolution of sex-specific mating strategies, such as male sexual harassment of females and counteracting female strategies (Parker 1979, 2006; Clutton-Brock and Parker 1995; Arnqvist and Rowe 2005). Each sex operates as the evolving social environment driving the evolution of the other sex (Moore and Pizzari 2005), and the mating strategies of males and females are expected to change plastically according to varying selective pressures from the social environment.

Selection on male mating is expected to be strong in male-biased populations, where more intense male competition leads to a higher male reproductive skew (Holland and Rice 1999; Martin and Hosken 2004). Furthermore, because of their higher potential reproductive rate, males will outnumber females available for reproduction at any given time, further increasing the opportunity of sexual selection through male competition and the intensity of sexual harassment (Emlen and Oring 1977; Clutton-Brock and Parker 1995; Shuster and Wade 2003). While much research has focused on the evolutionary conflict arising between the sexes over mating rates, relatively few studies have explicitly considered that in many species the reproductive value of a copulation will change over time (but see Parker 1970a), and the interaction between male and female mating strategies is therefore likely to be time dependent. First, selection on further mating is likely to vary as a function of the cumulative mating rate (Parker 1970b). This may be particularly important for females, for which optimal mating rate is likely to be relatively low. Therefore, selection on female mating may progressively decline over time as she accumulates sufficient sperm reserves to fertilize her eggs (e.g., see Head and Brooks 2006), while male mating propensity, being less time dependent, is expected to remain constantly high. Second, the fitness pay-offs associated with an insemination may change over the day in relation to changes in the probability that an insemination will result in fertilization due to physiological

* E-mail: hanne.lovlie@zoologi.su.se.

† E-mail: tommaso.pizzari@zoo.ox.ac.uk.

Table 1: Number of male-initiated copulation attempts to which individual female fowl were exposed in 18 free-ranging groups of different sex ratios

Response variable and factors	Least squares means $\pm$ SE	df	F	P
No. male-initiated copulations ($N_{\text{copulations}}$ /females):				
Days 1–4:				
Observation day	d1: $4.08 \pm .3$; d2: $3.31 \pm .25$; d3: $3.31 \pm .25$; d4: $3.02 \pm .23$; d1 vs. d2, d3;** d1 vs. d4***	3, 752	9.43	<.0001
Group sex ratio	2M : 8F: $1.78 \pm .17$; 4M : 6F: $3.79 \pm .38$; 6M : 4F: $5.84 \pm .71$; 2M : 8F vs. 4M : 6F, 6M : 4F;*** 4M : 6F vs. 6M : 4F: $P = .06$	2, 752	33.69	<.0001
Observation duration		1, 752	150.86	<.0001
Time of day ^a		1, 749	.93	.3358
Female laying status ^a		1, 749	2.17	.1411
Group sex ratio $\times$ time of day ^a		2, 749	1.78	.1697
Days 2–4:				
Group sex ratio	2M : 8F: $1.57 \pm .16$; 4M : 6F: $3.2 \pm .35$; 6M : 4F: $5.35 \pm .7$; 2M : 8F vs. 4M : 6F, 6M : 4F;*** 4M : 6F vs. 6M : 4F*	2, 538	30.21	<.0001
Time of day	a.m.: $2.66 \pm .2$; p.m.: $3.37 \pm .25$	1, 538	18.51	<.0001
Observation duration		1, 538	72.63	<.0001
Female laying status ^a		1, 536	1.27	.2609
Group sex ratio $\times$ time of day ^a		1, 536	1.87	.1545

Note: $N_{\text{groups}} = 18$, $N_{\text{females}} = 58$. Asterisks indicate significant post hoc tests presented.

^a Significant terms after stepwise removal of nonsignificant terms.

* $P \leq .05$.

** $P \leq .001$.

*** $P \leq .0001$.

changes associated with the oviposition cycle and/or daily patterns in sperm competition risk and intensity. Unfortunately, temporal variation in mating strategies on such a fine scale is seldom considered by evolutionary studies of mating behavior. The study of mating strategies is crucial to understand the evolution of polyandry, sexual conflict over mating, sexual segregation, reproductive isolation, and the mechanisms of postcopulatory sexual selection. However, failing to consider time dependence of mating strategies may provide a partial or distorted view. Here, we adopt an experimental approach to reveal time-dependent variation in male and female mating behavior with important effects on mating rates within and across groups of feral fowl *Gallus gallus domesticus*.

In free-ranging populations of feral fowl, as in their wild ancestor, the red jungle fowl (Fumihito et al. 1994), both sexes are sexually promiscuous because of some degree of mating propensity by males and females (McBride et al. 1969; Thornhill 1988; Etches 1996). Males often coerce females into copulation (McBride et al. 1969; Thornhill 1988; Collias and Collias 1996; Jones et al. 2001; Pizzari 2001). Female fowl often resist forced copulations directly; however, resistance is costly (Pizzari 2001), and female strategies to control copulation indirectly have also been described (Pizzari and Birkhead 2000; Pizzari 2001). Female propensity to mate is influenced by previous copu-

lation history. A succession of four copulations typically reduces female propensity to solicit and increases female resistance to mating in the three following days, and this inhibition of female promiscuity is mediated by the stimulus associated with male mounting (Løvlie et al. 2005). In addition, following insemination, sperm are stored in the female sperm storage tubules from which sperm are lost at a constant rate. On average, the insemination of a large ejaculate results in females having sufficient sperm to fertilize eggs for the following 14 days (Warren and Kilpatrick 1929; Etches 1996; Pizzari et al. 2004). Therefore, a sexually rested hen is expected to be particularly prone to mating if she ovulates in the next 14 days; however, she is expected to resist mating progressively more over successive copulations as sperm accumulate in her sperm storage tubules. Oviposition occurs in the first half of the day (Etches 1996) and peaks in the middle of the day (Christensen and Johnston 1977; Johnson 2000; Pizzari and Birkhead 2001). Inseminations occurring a few hours before and after oviposition have limited fertilizing efficiency (Moore and Byerly 1942; Parker 1945; Johnston and Parker 1970; Christensen and Johnston 1977) relative to inseminations in the evening (natural matings: Graewski and Scott 1943; Parker 1945; artificial inseminations: Moore and Byerly 1942; Parker 1945; Christensen and Johnston 1977). Therefore, the evening corresponds

Figure 1: Daily patterns of male mating behavior. Individual females were exposed to more male-initiated copulations (average number of male-initiated copulation attempts/h for each female) in more male-biased sex ratios ($F = 30.21$, $df = 2, 538$, $P < .0001$; 2M : 8F vs. 4M : 6F, $P \leq .0001$; 2M : 8F vs. 6M : 4F, $P \leq .0001$; 4M : 6F vs. 6M : 4F, $P \leq .05$) and in the evening (filled symbols) compared with the morning (open symbols; $F = 18.51$, $df = 1, 538$, $P < .0001$). Data points are group means, and vertical bars are group SE.

to an optimal copulation time because by copulating at this time, a female can minimize the number of copulations required to fertilize her eggs while maximizing fertilization success. However, males are also selected to inseminate hens in the evening, leading to more intense sexual harassment at this time of day (Pizzari and Birkhead 2001). We tested the idea that this daily pattern of costs and benefits associated with copulation leads to daily patterns in interacting male and female mating strategies. We experimentally manipulated the intensity of sexual coercion through fowl groups of similar size but different sex ratio to (i) analyze daily patterns of male sexual harassment across different sex ratios and (ii) measure how daily patterns in female mating propensity changed in relation to male sexual harassment.

Methods

Study Population

We studied a population of free-ranging feral fowl at Tovetorp research station (Stockholm University, Sweden) in August–September 2003, May–July 2004, and July–August 2005 (population size: 63–84; sex ratio: 0.9–0.71 males : females). This population is of an old Swed-

ish breed (Harrison 1987) similar to the red jungle fowl in morphology, behavior, and social structure (Pizzari and Birkhead 2001; Schütz and Jensen 2001). Birds were individually marked and fully habituated to human presence; thus, observations were conducted at a close range (≤ 5 m) without disturbing the birds' natural behaviors. All birds used were sexually mature (≥ 8 months; Etches 1996) and sexually rested before each experimental trial through physical—but not visual or acoustic—isolation from members of the opposite sex: females for 14 days to ensure that female sperm storage tubules were sperm depleted (see above) and males for a minimum of 2 days to ensure replenished sperm supplies (Parker et al. 1942).

Sex Ratio Manipulation Experiment

The aim of this experiment was to manipulate variation in the intensity of male sexual harassment by changing the sex ratio of groups of similar size. We set up three sex ratio treatments—(i) two males and eight females (2M : 8F), (ii) four males and six females (4M : 6F), and (iii) six males and four females (6M : 4F)—with six replicate groups for each treatment (total number of females: 58; total number of males: 39). Both group size and sex

Table 2: Male mating propensity determined through experimental exposure to a soliciting female in free-ranging fowl groups

Response variable and factors	Least squares means $\pm$ SE	df	F	P
Latency (s) to first male attracted:				
Group sex ratio	2M : 8F: 30.96 $\pm$ 7.13; 4M : 6F: 33.22 $\pm$ 7.48; 6M : 4F: 11.32 $\pm$ 3.84; 2M : 8F vs. 6M : 4F, 6M : 4F**	2, 83	4.77	.0109
Time of day	a.m.: 58.26 $\pm$ 8.39; p.m.: 8.82 $\pm$ 2.99	1, 83	27.82	<.0001
Observation day ^a		3, 78	.96	.4149
Group sex ratio $\times$ time of day ^a		2, 78	.11	.8989
No. males attracted to a presented female ($N_{\text{males}}/\text{group}$):				
Group sex ratio	2M : 8F: 1.8 $\pm$.15; 4M : 6F: 2.7 $\pm$.19; 6M : 4F: 4.69 $\pm$.28; 2M : 8F vs. 4M : 6F; ** 2M : 8F vs. 6M : 4F, 6M : 4F***	2, 83	47.56	<.0001
Time of day	a.m.: 2.55 $\pm$.14; p.m.: 3.16 $\pm$.16	1, 83	10.06	.0021
Observation day ^a		3, 78	.85	.4722
Group sex ratio $\times$ time of day ^a		2, 78	.20	.8197

Note: $N_{\text{groups}} = 12$. Asterisks indicate significant post hoc tests presented.

^a Significant terms after stepwise removal of nonsignificant terms.

** $P \leq .001$.

*** $P \leq .0001$.

ratios are within the natural range observed in populations of feral fowl and red jungle fowl (group size range: 2–15; sex ratio range: 0.17–4 males : females; McBride et al. 1969; Sullivan 1991; Collias and Collias 1996). In general, however, groups of red jungle fowl are slightly female biased (Sullivan 1991; Collias and Collias 1996). In particular, we avoided extremely male-biased sex ratios (e.g., 2F : 8M) because such treatments would have been of limited biological relevance and could have jeopardized female welfare. The operational sex ratio (OSR) of a group was measured by monitoring the oviposition cycle of individual hens through the administration of lipid dyes and the assignment of egg maternity (see Pizzari et al. 2003; Løvlie et al. 2005). We considered a female reproductively active if she produced at least one egg during an experimental trial and/or in the following 14 days (Warren and Kilpatrick 1929; Etches 1996). Males were always considered reproductively active since previous studies indicated that males are unlikely to become completely sperm depleted even under unnaturally high copulation rates (Pizzari et al. 2003). The experimental manipulation of sex ratio significantly changed the OSR of a group, with OSR being on average male biased in male-biased groups and female biased in female-biased groups ($F = 48.29$, $df = 2, 18$, $P < .0001$). Following the establishment of a group on the morning of day 1, one of us (H. Løvlie) observed the behavior of the group for 4 successive days (days 1–4) for a total of 533 h of observation. Copulation rate typically peaks in the evening and may show a smaller peak in the morning (Upp 1928; McBride et al. 1969; Craig and Bhagwat 1974; Cheng and Burns 1988; this population: Pizzari and Birkhead 2001), and groups were observed at both these times.

The timing of morning observations was standardized over the breeding season by starting when the first female left the roost. The morning peak in copulations typically occurs after all birds leave the roost and spread out to forage on invertebrates (H. Løvlie and T. Pizzari, unpublished data; see also McBride et al. 1969). When the morning copulation peak is over, birds cluster around the roost again to preen, dust bath, and lay eggs (Collias and Collias 1967; McBride et al. 1969; Pizzari and Birkhead 2001). Since copulatory activity is reduced at the onset of oviposition (Pizzari and Birkhead 2001), morning observations ended when females started displaying oviposition behaviors and vocalizations associated with oviposition (Etches 1996; Pizzari and Birkhead 2001). Over the breeding season, morning observations started at 3:30–6:00 a.m. and terminated at 7:30–8:45 a.m., lasting on average 204.4 min (range 107–279 min). Similarly, evening observations started after oviposition (Pizzari and Birkhead 2001) and terminated when the last bird in the group went to roost. Over the breeding season, evening observations started at 4:00–5:00 p.m. and terminated at 7:30–9:15 p.m., lasting on average 223.1 min (range 145–315 min).

In each observation, every copulation and copulation attempt observed was recorded. Copulations were recorded as initiated by the female if the female crouched in front of the male and actively solicited the mating (i.e., “solicited copulation”; Etches 1996; Pizzari 2001; Løvlie et al. 2005). All copulations not solicited by the female were male initiated. Female behavior was scored on a resistance gradient from 1 to 5 (1: female solicits a copulation, no resistance; 2: male approaches female from behind with raised hackles and female encourages mounting by crouching; 3: male approaches, female pas-

Figure 2: Daily patterns of male mating propensity. *A*, Time (s) taken to attract the first male to the experimental presentation of a soliciting female. Latency was shorter in more male-biased sex ratios ($F = 4.77$, $df = 2, 83$, $P = .0109$; 2M : 8F vs. 6M : 4F, $P \leq .001$; 2M : 8F vs. 6M : 4F, $P \leq .001$) and in the evening (filled symbols) compared with the morning (open symbols, $F = 27.82$, $df = 1, 83$, $P < .0001$). *B*, Number of males in a group that were attracted to the presented female increased in more male-biased sex ratios ($F = 47.56$, $df = 2, 83$, $P < .0001$; 2M : 8F vs. 4M : 6F, $P \leq .001$; 2M : 8F vs. 6M : 4F and 6M : 4F, $P \leq .0001$) and in the evening ($F = 10.06$, $df = 1, 83$, $P = .0021$). Data points are group means, and vertical bars are group SE.

sively accepts copulation; 4: male runs after and grabs female, female initially resists before finally accepting copulation; 5: female resists until insemination occurs or male abandons the female; see Løvlie et al. 2005 for a similar scoring system). Copulation was recorded as resisted by a female if ranked as 4 or 5 on the female resistance score and as successful if the male lowered his train over the female's cloaca, enabling insemination. Temporal variation in mating behavior may be mediated by changes in spatial group distribution. We therefore monitored changes in group distribution every 15 min during each observation by recording the distance of ev-

ery individual from all other members of the group to the nearest 0.5 m. This allowed us to measure (i) the distance of a female from the closest male and (ii) the mean distance of a female from all males in the group.

Male Mating Propensity Experiment

We studied variation in male mating propensity by experimentally quantifying male sexual attention to a soliciting female (only in 2003 and 2004). In each observation period of each sex ratio trial, an unfamiliar female (i.e., not from the focal group) was presented at a place within

Table 3: Variation in intersexual spatial distribution in free-ranging fowl groups with different sex ratios

Response variable and factors	Least squares means $\pm$ SE	df	F	P
Mean distance (m) from all males:				
Days 1–4:				
Observation day	d1: 4.92 $\pm$.24; d2: 3.32 $\pm$.19; d3: 3.53 $\pm$.19; d4: 3.8 $\pm$.2; d1 vs. d2, d3, d4;*** d2 vs. d4*	3, 752	16.07	<.0001
Group sex ratio	2M : 8F: 4.1 $\pm$.19; 4M : 6F: 3.38 $\pm$.19; 6M : 4F: 4.12 $\pm$.27; 2M : 8F vs. 4M : 6F;* 4M : 6F vs. 6M : 4F*	2, 752	4.26	.0144
Time of day	a.m.: 6.81 $\pm$.23; p.m.: 2.18 $\pm$.11	1, 752	465.76	<.0001
Group sex ratio $\times$ time of day ^a		2, 750	1.18	.3081
Days 2–4:				
Group sex ratio	2M : 8F: 3.52 $\pm$.23; 4M : 6F: 2.81 $\pm$.22; 6M : 4F: 4.03 $\pm$.37; 2M : 8F vs. 4M : 6F;* 4M : 6F vs. 6M : 4F*	2, 537	4.59	.0106
Time of day	a.m.: 6.35 $\pm$.29; p.m.: 1.84 $\pm$.11	1, 537	454.79	<.0001
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 5.85 $\pm$.39, p.m.: 2.12 $\pm$.19;*** 4M : 6F, a.m.: 5.25 $\pm$.41, p.m.: 1.51 $\pm$.17;*** 6M : 4F, a.m.: 8.36 $\pm$.74, p.m.: 1.94 $\pm$.24***	2, 537	4.96	.0073
Distance (m) to nearest male:				
Days 1–4:				
Observation day	d1: 1.16 $\pm$.09; d2: .59 $\pm$.06; d3: .65 $\pm$.06; d4: .61 $\pm$.06; d1 vs. d2, d3, d4***	3, 752	29.26	<.0001
Group sex ratio	2M : 8F: 1.76 $\pm$.13; 4M : 6F: .59 $\pm$.06; 6M : 4F: .37 $\pm$.05; 2M : 8F vs. 4M : 6F, 6M : 4F;*** 4M : 6F vs. 6M : 4F*	2, 752	70.36	<.0001
Time of day	a.m.: 1.24 $\pm$.09; p.m.: .42 $\pm$.04	1, 752	203.67	<.0001
Group sex ratio $\times$ time of day ^a		2, 750	1.82	.1627
Days 2–4:				
Group sex ratio	2M : 8F: 1.49 $\pm$.31; 4M : 6F: .5 $\pm$.12; 6M : 4F: .31 $\pm$.09; 2M : 8F vs. 4M : 6F;** 2M : 8F vs. 6M : 4F***	2, 537	46.42	<.0001
Time of day	a.m.: 1.04 $\pm$.08; p.m.: .31 $\pm$.04	1, 537	120.90	<.0001
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 2.25 $\pm$.48, p.m.: .99 $\pm$.22;*** 4M : 6F, a.m.: .88 $\pm$.2, p.m.: .29 $\pm$.08;*** 6M : 4F, a.m.: .71 $\pm$.18, p.m.: .14 $\pm$.06***	2, 537	5.12	.0063

Note: $N_{\text{groups}} = 18$. Asterisks indicate significant post hoc tests presented.

^a Significant terms after stepwise removal of nonsignificant terms.

* $P \leq .05$.

** $P \leq .001$.

*** $P \leq .0001$.

the home range of the focal group that was randomly selected a priori. The female was presented in a soliciting position (Pizzari et al. 2003) for 5 min or until all males in the group were attracted to her within 0.5 m. We recorded (i) the time elapsed to attract the first male and (ii) the overall number of males attracted to the presented female. Because they were conducted in the morning and evening of each successive day of each sex ratio trial, these male mating propensity trials tested time-dependent changes in the probability of males approaching a female and thus in the intensity of sexual harassment to which a soliciting female is exposed in a given sex ratio.

Statistical Analysis

We analyzed daily variation in mating behavior and intersexual spatial distribution through a series of gener-

alized linear mixed models (GLMMs) that controlled for the effect of different social factors, with stepwise deletion of nonsignificant terms, Poisson error distribution, log link function because of the skewed error distribution, and adjusted sum of squares. Sex ratio (i.e., 2M : 8F, 4M : 6F, 6M : 4F), female oviposition status (i.e., whether a female laid at least one egg during a trial or in the following 14 days), observation day (i.e., day 1–4), and time of day (i.e., morning vs. evening), and the interaction between sex ratio and time of day were entered as fixed factors, while observation duration (i.e., the duration of each observation in the morning and in the evening) was entered as covariate. Year (i.e., 1–3), group identity (i.e., 1–18), and female identity were entered as random factors. In these analyses, one response value is entered for each female for a given observation for all the four successive observation days; thus, eight values

Figure 3: Daily patterns in intersexual spatial distribution. The mean distance of a female to all males in a group was minimized at the intermediate sex ratio (4M : 6F, sex ratio: $F = 4.26$, $df = 2,752$, $P = .0144$; 2M : 8F vs. 4M : 6F, $P \leq .05$; 4M : 6F vs. 6M : 4F, $P \leq .05$) and in the evening (*filled symbols*) compared with the morning (*open symbols*; $F = 465.76$, $df = 1,752$, $P < .0001$). Data points are group means, and vertical bars are group SE.

were entered in the analysis for each female in each group, giving a total of 864 observations and the total degrees of freedom ranging between 601 and 752. However, because some females were utilized in multiple groups, female identity was defined as the subject within the analysis, which identifies the unit on which repeated measures are taken, preventing pseudoreplication of individual females represented over successive days and in different groups. The GLMMs used to analyze the male mating propensity experiment were similar to the other GLMMs in that they had stepwise deletion of nonsignificant terms, Poisson error distribution, log link function because of the skewed error distribution, and adjusted sum of squares. Sex ratio (i.e., 2M : 8F, 4M : 6F, 6M : 4F), observation day (i.e., day 1–4), time of day (i.e., morning vs. evening), and the interaction between sex ratio and time of day were entered as fixed factors. Year (i.e., 1–2) and group identity (i.e., 1–12) were random effects. Group was defined as subject within the analysis, and one value per group for each time of day and over the four observation days was entered in the analysis (i.e., eight values per group), giving a total of 96 observations and the total degrees of freedom between 78 and 83. First, we tested variation in the intensity of male sexual harassment through a GLMM, with the total number of male-initiated copulation attempts (i.e., all successful and unsuccessful copulation attempts, with the exception of copulations solicited by females, from all males in a

group) directed at each individual female in a group as the response variable.

Second, we explored the mechanisms underlying time-dependent variation in intensity of sexual harassment. To this end, we investigated temporal variation in the male-female spatial distribution through two separate GLMMs, each analyzing a different response variable: (i) distance of each female of a group to nearest male and (ii) the average distance of a female from all the males in a group. Similarly, we used the male mating propensity experiment trials to investigate variation in male attraction to a soliciting female, measured as (i) latency to attraction of the first male and (ii) number of males attracted to the presented female as response variables in two separate GLMMs. We also investigated temporal changes in female propensity to (i) solicit and (ii) resist copulation. We tested (i) with a GLMM analyzing the variance in the number of copulations solicited by each individual female to any male in a group. Similarly, we tested (ii) with two separate GLMMs analyzing variation in (a) the number of copulations resisted by each female of a group and (b) the average resistance score of all copulations in which each individual female was involved. We analyzed female solicitation or resistance in relation to male sexual attention by entering the total number of copulation attempts involving a female during an observation as a covariate. All analyses were performed in SAS, 2002–2003.

Table 4: Female solicitation in free-ranging groups of fowl

Response variable and factors:	Least squares means $\pm$ SE	df	F	P
No. copulations solicited ($N_{\text{copulations}}$ /female):				
Days 1–4:				
Observation day	d1: .33 $\pm$.05; d2: .14 $\pm$.02; d3: .08 $\pm$.01; d4: .07 $\pm$.01; d1 vs. d2, d3, d4;*** d2 vs. d3;* d2 vs. d4**	3, 748	47.72	<.0001
Group sex ratio	2M : 8F: .2 $\pm$.03; 4M : 6F: .12 $\pm$.02; 6M : 4F: .08 $\pm$.02; 2M : 8F vs. 4M : 6F, 6M : 4F**	2, 748	6.84	.0011
Time of day	a.m.: .15 $\pm$.02; p.m.: .1 $\pm$.02	1, 748	12.44	.0003
Female laying status	Laying: .16 $\pm$.02; nonlaying: .09 $\pm$.02	1, 748	5.51	.0192
Group sex ratio $\times$ time of day	2M : 8F, a.m.: .17 $\pm$.03, p.m.: .24 $\pm$.04;* 4M : 6F, a.m.: .19 $\pm$.04, p.m.: .08 $\pm$.02;*** 6M : 4F, a.m.: .11 $\pm$.03, p.m.: .06 $\pm$.02*	2, 748	15.59	<.0001
No. copulation attempts		1, 748	105.91	<.0001
Observation duration ^a		1, 747	.51	.4762
Days 2–4:				
Group sex ratio	2M : 8F: .1 $\pm$.02; 4M : 6F: .05 $\pm$.01; 6M : 4F: .05 $\pm$.02; 2M : 8F vs. 4M : 6F;* 2M : 8F vs. 6M : 4F: P = .06	2, 535	2.78	.0631
Female laying status	Laying: .1 $\pm$.02; nonlaying: .04 $\pm$.013	1, 535	6.04	.0154
Group sex ratio $\times$ time of day	2M : 8F, a.m.: .05 $\pm$.01, p.m.: .2 $\pm$.04;*** 4M : 6F, a.m.: .05 $\pm$.02, p.m.: .05 $\pm$.02; 6M : 4F, a.m.: .09 $\pm$.03, p.m.: .03 $\pm$.01**	3, 535	14.42	<.0001
No. copulation attempts		1, 535	47.41	<.0001
Time of day ^a		1, 534	.00	.9844
Observation duration ^a		1, 534	1.88	.1707

Note: N_{groups} = 18, N_{females} = 58. Asterisks indicate significant post hoc tests presented.

^a Significant terms after stepwise removal of nonsignificant terms.

* $P \leq .05$.

** $P \leq .001$.

*** $P \leq .0001$.

Results

Male Sexual Harassment

Overall, males showed a higher mating propensity than females and initiated 92% of all observed copulations ($n = 3,569$). Females were exposed to more intense male sexual harassment in groups with more males (table 1; fig. 1). This effect was entirely due to the effect of sex ratio per se and not to individual males having a higher mating propensity with increasing competition in groups with more males, because the number of male-initiated copulations per male did not increase significantly across sex ratios but in fact decreased slightly in the male-biased sex ratio (sex ratio: $F = 3.15$, $df = 2, 497$, $P = .044$; least squares means $\pm$ SE: 2M : 8F = 6.23 ± 1.06 ; 4M : 6F = 5.52 ± 0.69 ; 6M : 4F = 4.21 ± 0.46 ; post hoc: 2M : 8F vs. 4M : 6F: $P = .52$; 2M : 8F vs. 6M : 4F: $P = .034$; 4M : 6F vs. 6M : 4F: $P = .049$). The number of male-initiated copulations was highest on day 1 of a trial, indicating that sexual harassment was most intense when females were sexually novel to the males and males were sexually rested (table 1). The removal of day 1 from the analysis to control for this

sexual novelty effect revealed a time of day effect in days 2–4. Male propensity to copulate was significantly higher in the evening (table 1; fig. 1), and the male mating propensity experiment indicated that males were more rapidly attracted and more males were attracted to the experimentally presented female in the evening within each sex ratio treatment (table 2; fig. 2). Consistent with these results, males were closer to females in the evening than in the morning within each sex ratio treatment (table 3; fig. 3).

Together, these results show that females are exposed to more intense harassment when initially introduced to sexually rested males and particularly in the evening, when males are closer to females and more eager to copulate. Consequently, soliciting in the evening attracts more male attention and is more likely to elicit male harassment than soliciting in the morning, particularly in male-biased groups. We next investigated the way this temporal variation in male harassment influenced female mating behavior.

Female Mating Behavior

Females solicited proportionally fewer and resisted proportionally more copulations in less female-biased sex ratios

Table 5: Female resistance in copulations in free-ranging groups of fowl

Response variable and factors	Least squares means $\pm$ SE	df	F	P
No. copulations resisted ($N_{\text{copulations}}$ /females):				
Days 1–4:				
Observation day	d1: 1.5 $\pm$.09; d2: 1.95 $\pm$.1; d3: 2.02 $\pm$.11; d4: 1.8 $\pm$.1; d1 vs. d2, d3, d4;*** d3 vs. d4*	3, 748	10.07	<.0001
Group sex ratio	2M : 8F: 1.16 $\pm$.08; 4M : 6F: 2.05 $\pm$.13; 6M : 4F: 2.49 $\pm$.19; 2M : 8F vs. 4M : 6F, 6M : 4F;*** 4M : 6F vs. 6M : 4F*	2, 748	32.38	<.0001
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 1.21 $\pm$.09, p.m.: 1.1 $\pm$.09; 4M : 6F, a.m.: 1.93 $\pm$.14, p.m.: 2.19 $\pm$.15;* 6M : 4F, a.m.: 2.75 $\pm$.23, p.m.: 2.26 $\pm$.19*	3, 748	4.22	.0057
Observation duration		1, 748	16.08	<.0001
No. copulation attempts		1, 748	564.14	<.0001
Time of day ^a		1, 747	1.28	.2589
Female laying status ^a		1, 747	.52	.4697
Days 2–4:				
Group sex ratio	2M : 8F: 1.15 $\pm$.085; 4M : 6F: 1.97 $\pm$.14; 6M : 4F: 2.33 $\pm$.2; 2M : 8F vs. 4M : 6F, 6M : 4F***	2, 535	21.74	<.0001
Time of day	a.m.: 1.87 $\pm$.09; p.m.: 1.61 $\pm$.09	1, 535	7.81	.0054
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 1.26 $\pm$.11, p.m.: 1.04 $\pm$.095, $P = .07$; 4M : 6F, a.m.: 1.89 $\pm$.16, p.m.: 2.04 $\pm$.16; 6M : 4F, a.m.: 2.76 $\pm$.27, p.m.: 1.96 $\pm$.19***	2, 535	7.40	.0007
Observation duration		1, 535	7.28	.0072
No. copulation attempts		1, 535	471.56	<.0001
Female laying status ^a		1, 534	.17	.6785
Average resistance score:				
Days 1–4:				
Observation day	d1: 3.16 $\pm$.06; d2: 3.58 $\pm$.07; d3: 3.77 $\pm$.07; d4: 3.75 $\pm$.07; d1 vs. d2, d3, d4;*** d2 vs. d3, d4*	3, 601	27.42	<.0001
Group sex ratio	2M : 8F: 3.32 $\pm$.06; 4M : 6F: 3.55 $\pm$.07; 6M : 4F: 3.82 $\pm$.09; 2M : 8F vs. 4M : 6F: $P = .07$; 2M : 8F vs. 6M : 4F;*** 4M : 6F vs. 6M : 4F*	2, 601	12.38	.0001
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 3.46 $\pm$.08, p.m.: 3.2 $\pm$.07;** 4M : 6F, a.m.: 3.54 $\pm$.09, p.m.: 3.55 $\pm$.09; 6M : 4F, a.m.: 3.84 $\pm$.11, p.m.: 3.8 $\pm$.11	3, 601	3.69	.0118
Time of day ^a		1, 598	5.43	.0201 ^b
Female laying status ^a		1, 598	2.53	.1125
Observation duration ^a		1, 598	2.00	.1573
No. copulation attempts ^a		1, 598	.25	.6206
Days 2–4:				
Group sex ratio	2M : 8F: 3.44 $\pm$.06; 4M : 6F: 3.69 $\pm$.07; 6M : 4F: 3.92 $\pm$.09; 2M : 8F vs. 4M : 6F;* 2M : 8F vs. 6M : 4F;*** 4M : 6F vs. 6M : 4F*	2, 413	11.70	<.0001
Time of day	a.m.: 3.79 $\pm$.06; p.m.: 3.57 $\pm$.06	1, 413	11.51	.0008
Group sex ratio $\times$ time of day	2M : 8F, a.m.: 3.7 $\pm$.08, p.m.: 3.21 $\pm$.07;*** 4M : 6F, a.m.: 3.75 $\pm$.09, p.m.: 3.62 $\pm$.09; 6M : 4F, a.m.: 3.93 $\pm$.11, p.m.: 3.93 $\pm$.11	2, 413	6.24	.0034
Female laying status ^a		1, 410	.53	.4684
Observation duration ^a		1, 410	.00	.9631
No. copulation attempts ^a		1, 410	.47	.4916

Note: $N_{\text{groups}} = 18$, $N_{\text{females}} = 58$. Asterisks indicate significant post hoc tests presented.

^a Significant terms after stepwise removal of nonsignificant terms.

^b The term is nonsignificant in the final model.

* $P \leq .05$.

** $P \leq .001$.

*** $P \leq .0001$.

Figure 4: Daily pattern of female mating behavior. Females showed a tendency to solicit fewer copulations (average number of solicitations/h for each female) in more male-biased sex ratios ($F = 2.78$, $df = 2, 535$, $P = .0631$; $2M : 8F$ vs. $4M : 6F$, $P \leq .05$; $2M : 8F$ vs. $6M : 4F$, $P = .06$). Importantly, females solicited more copulations in the morning (*open symbols*) than in the evening (*filled symbols*) in the most female-biased groups ($2M : 8F$) and reversed this trend in male-biased groups ($6M : 4F$), while there was no difference in solicitation rate in groups of the intermediate sex ratio ($4M : 6F$, sex ratio $\times$ time of day: $F = 14.42$, $df = 3, 535$, $P < .0001$). Data points are group means, and vertical bars are group SE.

(tables 4, 5). Importantly, female behavior was strongly time dependent. Females, like males, had a higher propensity to mate when initially introduced to males following sexual rest. Females solicited about five times more copulations and also resisted male-initiated copulations less in the first than in the last day of a trial (tables 4, 5). We further investigated the daily pattern of variation in female mating behavior by excluding day 1 from the analysis. The removal of day 1 from the analysis revealed that the daily pattern of female mating behavior changed with the sex ratio of a group. In the most female-biased sex ratio (i.e., $2M : 8F$), females solicited most copulations in the evening, but in the male-biased sex ratio (i.e., $6M : 4F$), they solicited most copulations in the morning, while no daily mating pattern was evident in the intermediate sex ratio (i.e., $4M : 6F$; table 4; fig. 4).

Together, these results indicate time-dependent variation in female mating behavior across different sex ratios. In male-biased groups, females not only solicit proportionally fewer copulations but also shift the time of solicitation from the optimal time in the evening to the morning, possibly to avoid intense sexual harassment.

Discussion

The results of this study reveal that male sexual harassment influences not only the level of female mating propensity

but also the daily pattern of female mating behavior. The result that sexual harassment is more intense with more males in a population is intuitive and consistent with previous studies, mostly of invertebrates (e.g., Holland and Rice 1999; Martin and Hosken 2004; Crudgington et al. 2005; Kraaijeveld et al. 2005; Le Galliard et al. 2005; Wigby and Chapman 2005; Head and Brooks 2006). However, it is important to note that a drastic increase in sexual harassment intensity was observed as the group sex ratio changed from $2M : 8F$ to $4M : 6F$, indicating that populations do not need to be male biased for females to be exposed to intense sexual harassment. Intense harassment with more males in a population may be explained by two non-mutually exclusive mechanisms: (i) the effect of sex ratio per se (i.e., a female is exposed to more males) and (ii) increased propensity to mate of individual males because of more intense intrasexual competition. The results of this study indicate that in the fowl, changes in male mating behavior across different sex ratios are mostly determined by the effect of sex ratio per se. One potential explanation of this result is that while the mating propensity of individual males may increase with more males in a population, male interference and inhibition may also increase as more males compete over fewer copulation opportunities. This mechanism may be particularly relevant for social species such as the fowl, where socially dominant males are able to interrupt or altogether inhibit

the sexual investment of subordinate males (e.g., Koyama and Kamimura 2000; Pizzari 2001).

The mating behaviors of males and females were strongly dependent on two different temporal effects: (i) cumulative time of exposure to members of the opposite sex following sexual rest and (ii) time of day. Within each sex ratio, both males and females were more eager to copulate when first exposed to each other following sexual rest, and their mating propensity declined over successive days (or following the first day). This pattern may be driven by two factors. First, copulations at the beginning of a reproductive event may have higher reproductive value for males. In other words, the function of cumulative rate of male reproductive success over successive copulations may be curvilinear and approach a horizontal asymptote, so first copulations increase male reproductive success more than subsequent copulations. This may happen because copulation depletes the sperm reserves of a male. Male fowl would need approximately 48 h of sexual rest to replenish their extragonadal sperm reserves completely (Parker et al. 1942). It is therefore plausible that over the 4-day trial, sperm depletion may have reduced ejaculate size and the fitness payoffs of subsequent copulations. Second, reproductively available females need to secure sufficient sperm supplies to fertilize each of their eggs, and high mating rates in the first days of the trial may have been triggered by a relatively high mating propensity of reproductively active females (Løvlie et al. 2005). However, as females accumulate copulations, their mating propensity rapidly declines (Løvlie et al. 2005). While males need to mate with the same females to protect their paternity, female resistance may make this progressively more difficult over time, leading to time-dependent patterns of divergence in male and female propensity to mate.

A similar system occurs in several Diptera, where some male seminal fluid peptides transiently reduce female receptivity to subsequent males (Chapman 2001). In the Mediterranean fruit fly *Ceratitis capitata*, the interaction between male-induced refractoriness following mating and male sexual harassment for mating resulted in females experiencing a higher mating rate 3–4 days following exposure to males (Kraaijeveld et al. 2005). Importantly, in groups where the sex ratio was biased fivefold in favor of males, female mating rates were higher than in groups with more even sex ratios (Kraaijeveld et al. 2005). Similarly, Head and Brooks (2006) found that female guppies (*Poecilia reticulata*) were exposed to more intense sexual harassment in male-biased groups than in female-biased groups. This difference was not due to changes in the behavior of individual males but to higher numbers of males. Importantly, Head and Brooks (2006) observed that male mating propensity changed over successive days in nonlinear patterns. The mating propensity of female gup-

pies, on the other hand, declined sharply over successive days.

Importantly, mating dynamics showed distinct daily patterns driven by the fact that the probability that an insemination results in fertilization is highest at least 4 h following oviposition and thus typically in the evening (Moore and Byerly 1942; Parker 1945; Johnston and Parker 1970; Christensen and Johnston 1977). In light of this, it seems puzzling that female fowl should solicit in the morning. This study sheds light on the adaptive significance of this female mating behavior. We show that female fowl plastically adjust the timing of solicitation to the level of sexual harassment of a group. In the most female-biased groups, sexual harassment is relatively low, and females can optimize copulation time by mating in the evening. However, in male-biased groups, females actively shift solicitation time to the morning, thus reducing sexual harassment and increasing the probability of insemination by the targeted male. Starting the day with the sperm of the preferred male may enable female fowl to retain some control over paternity and—simultaneously—become more independent from costly copulations in the evening, when sexual harassment is intense. On the other hand, the fact that inseminations in the morning may have reduced fertilizing efficiency may mean that females may have to remate to “top up” their sperm reserves more frequently than if they copulated in the evening. Alternatively, the endocrine control of female solicitation behavior may be partly decoupled from securing sperm for fertilization.

Mating benefits other than fertilization may occur under relaxed sexual harassment that promote mating at sub-optimal times. For example, in primate societies, females often encourage mating outside their fertile period, which may spread confidence in paternity across more males and thus convey benefits to the young (reviewed in Ziegler 2007). Male fowl provide females with courtship feeding, although the extent to which this potential direct benefit is associated with female solicitation remains unclear (Pizzari 2003). We also detected interactions between two temporal effects: cumulative exposure to members of the opposite sex over successive days and time of day. The effect of time of day became apparent only when the first day was excluded from the analysis. This is due to the fact that trials started in the morning of day 1. While males would normally initiate copulations mostly in the evening (Pizzari and Birkhead 2001), the first exposure of sexually novel partners in the morning masked the daily copulation pattern on day 1, resulting in above average mating rates in the morning. The removal of day 1 revealed a strong daily pattern with an evening peak in the subsequent days.

The temporal patterns of mating behaviors have important implications for the operation of sexual selection. In socially monogamous birds, females may preferentially

invest in young fathered by high-quality extra-pair partners by timing extra-pair copulations so that these are more likely to fertilize the first eggs of a clutch, which may contain more resources for the embryo and/or hatch earlier in species with hatching asynchrony (Magrath 1990; Krist et al. 2005). Similarly, female kittiwake (*Rissa tridactyla*) eject inseminations early in the season, possibly to avoid fertilization by old sperm that may impair offspring viability (Wagner et al. 2004). Finally, in the green-veined butterfly *Pieris napi*, oviposition occurs in the middle of the day, and males prefer virgin females but harass both virgin and mated females. This results in virgin females mating over the whole day but most frequently earlier in the morning, while mated females remated mainly in the afternoon. Remating later in the day may reduce the cost of male harassment because of interruption of oviposition (Forsberg and Wiklund 1989). Counteracting mating strategies by males and females may be indicative of intersexual conflict over mating rates (Arnqvist and Rowe 2005). This study indicates that the intensity of this potential intersexual conflict over mating varies drastically across successive days and particularly within days. Considering such temporal effects is critical to understanding intersexual dynamics and coevolutionary arms races.

Acknowledgments

We are grateful to A. Öhman for taking care of the birds; S. Jakobsson for support and facilities at Tovetorp; C. Camolese, R. Dean, A. Halvarsson, M. Jaakola, and L. Jääskeläinen for help in the field year 2005; R. McLeery and the rest of the Edward Grey Institute for discussions; and M. Jennions and two anonymous reviewers for excellent comments. H. Løvlie was supported by a departmental PhD studentship, and T. Pizzari was supported by grants from the Natural Environment Research Council, the Royal Society, and the Nuffield Foundation.

Literature Cited

- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.
- Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60: 145–160.
- Arnqvist, G., and L. Rowe. 2005. Sexual conflict. Princeton University Press, Princeton, NJ.
- Bateman, A. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.
- Chapman, T. 2001. Seminal fluid-mediated fitness traits in *Drosophila*. *Heredity* 87:511–521.
- Cheng, K. M., and J. T. Burns. 1988. Dominance relationship and mating behavior of domestic cocks: a model to study mate-guarding and sperm competition in birds. *Condor* 90:697–704.
- Christensen, V. L., and N. P. Johnston. 1977. Effect of time of day of insemination and the position of the egg in the oviduct on the fertility of turkeys. *Poultry Science* 56:458–462.
- Clutton-Brock, T. H., and G. A. Parker. 1995. Sexual coercion in animal societies. *Animal Behaviour* 49:1345–1365.
- Collias, N. E., and E. Collias. 1967. A field study of the red jungle fowl in north-central India. *Condor* 69:360–386.
- . 1996. Social organization of a red jungle fowl, *Gallus gallus*, population related to evolution theory. *Animal Behaviour* 51:1337–1354.
- Craig, J. V., and A. L. Bhagwat. 1974. Agonistic and mating behaviour of adult chickens modified by social and physical environments. *Applied Animal Ethology* 1:57–65.
- Crudgington, H. S., A. P. Beckerman, L. Brustle, K. Green, and R. R. Snook. 2005. Experimental removal and elevation of sexual selection: does sexual selection generate manipulative males and resistant females? *American Naturalist* 165(suppl.):S72–S87.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Etches, R. J. 1996. Reproduction in poultry. CAB International, Oxford.
- Forsberg, J., and C. Wiklund. 1989. Mating in the afternoon: time-saving in courtship and remating by females of a polyandrous butterfly *Pieris napi* L. *Behavioral Ecology and Sociobiology* 25: 349–356.
- Fumihito, A., T. Mityake, S. I. Sumi, M. Takada, S. Ohno, and N. Kondo. 1994. One subspecies of the red jungle fowl (*Gallus gallus gallus*) suffices as the matriarchic ancestor of all domestic chickens. *Proceedings of the National Academy of Sciences of the USA* 91: 12505–12509.
- Gracowski, J. J., and H. M. Scott. 1943. The influence of time of mating on fertility. *Poultry Science* 22:264–265.
- Harrisson, B. 1987. Den svenska dvärghönan. II. Svensk Rasfäderfäförbundets Tidskrift 1:12–14.
- Head, M. L., and R. Brooks. 2006. Sexual coercion and the opportunity of sexual selection in guppies. *Animal Behaviour* 71:515–522.
- Holland, B., and W. R. Rice. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proceedings of the National Academy of Sciences of the USA* 96:5083–5088.
- Johnson, A. L. 2000. Reproduction in the female. Pages 569–596 in G. Causey Whittow, ed. *Sturkie's avian physiology*. Academic Press, London.
- Johnston, N. P., and J. E. Parker. 1970. Effect of time of oviposition in relation to insemination on fertility in chicken hens. *Poultry Science* 49:325–327.
- Jones, E. K. M., N. B. Prescott, P. Cook, R. P. White, and C. M. Wathes. 2001. Ultraviolet light and mating behaviour in domestic broiler breeders. *British Poultry Science* 42:23–32.
- Koyama, S., and S. Kamimura. 2000. Influence of social dominance and female odor on sperm activity of male mice. *Physiology and Behavior* 71:415–422.
- Kraaijeveld, K., B. I. Katsoyannos, M. Stavrinides, N. A. Kouloussis, and T. Chapman. 2005. Mating in wild females of the Mediterranean fruit fly, *Ceratitis capitata*. *Animal Behaviour* 69:771–776.
- Krist, M., P. Nádvořík, L. Uvírová, and S. Bures. 2005. Paternity covaries with laying and hatching order in the collared flycatcher *Ficedula albicollis*. *Behavioral Ecology and Sociobiology* 59:6–11.
- Le Galliard, J.-F., P. S. Fitze, R. Ferriere, and J. Clobert. 2005. Sex ratio bias, male aggression, and population collapse in lizards.

- Proceedings of the National Academy of Sciences of the USA 102: 18231–18236.
- Løvlie, H., C. K. Cornwallis, and T. Pizzari. 2005. Male mounting alone reduces female promiscuity in the fowl. *Current Biology* 15: 1222–1227.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biological Reviews of the Cambridge Philosophical Society* 65:587–622.
- Martin, O. Y., and D. J. Hosken. 2004. Reproductive consequences of population divergence through sexual conflict. *Current Biology* 14:906–910.
- McBride, G., I. P. Parer, and F. Foenander. 1969. The social organisation and behaviour of the feral domestic fowl. *Animal Behavior Monographs* 2:125–181.
- Moore, A. J., and T. Pizzari. 2005. Quantitative genetic models of sexual conflict based on interacting phenotypes. *American Naturalist* 165(suppl.):S88–S97.
- Moore, O. K., and T. C. Byerly. 1942. Relation of time of insemination to percent fertility. *Poultry Science* 21:253–255.
- Parker, G. A. 1970a. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). V. The female's behaviour at the oviposition site. *Behaviour* 37:140–168.
- . 1970b. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45:525–567.
- . 1979. Sexual selection and sexual conflict. Pages 123–166 in M. S. Blum and N. A. Blum, eds. *Sexual selection and reproductive competition in insects*. Academic Press, New York.
- . 2006. Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:235–259.
- Parker, J. E. 1945. Relation of time of day of artificial insemination to fertility and hatchability of hen's eggs. *Poultry Science* 24:314–317.
- Parker, J. E., F. F. McKenzie, and H. L. Kempster. 1942. Fertility in the domestic fowl. *Missouri Agricultural Experiment Station Research Bulletin* 347:3–50.
- Pizzari, T. 2001. Indirect partner choice through manipulation of male behaviour by female fowl, *Gallus gallus domesticus*. *Proceedings of the Royal Society B: Biological Sciences* 268:181–186.
- . 2003. Food, vigilance, and sperm: the role of male direct benefits in the evolution of female preference in a polygamous bird. *Behavioral Ecology* 14:593–601.
- Pizzari, T., and T. R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. *Nature* 405:787–789.
- . 2001. For whom does the hen cackle? the function of post-oviposition cackling. *Animal Behaviour* 61:601–607.
- Pizzari, T., C. K. Cornwallis, H. Løvlie, S. Jakobsson, and T. R. Birkhead. 2003. Sophisticated sperm allocation in male fowl. *Nature* 426:70–74.
- Pizzari, T., H. Løvlie, and C. K. Cornwallis. 2004. Sex-specific, counteracting responses to inbreeding in a bird. *Proceedings of the Royal Society B: Biological Sciences* 271:2115–2121.
- Schütz, K. E., and P. Jensen. 2001. Effects of resource allocation on behavioural strategies: a comparison of red junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. *Ethology* 107:753–765.
- Shuster, S. M., and M. J. Wade. 2003. *Mating systems and strategies*. Princeton University Press, Princeton, NJ.
- Sullivan, M. S. 1991. Flock structure of red junglefowl. *Applied Animal Behaviour Science* 30:381–386.
- Thornhill, R. 1988. The jungle fowl hen's cackle incites male competition. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 81:145–154.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine-Atherton, Chicago.
- Upp, C. W. 1928. Preferential mating in fowls. *Poultry Science* 7: 225–232.
- Wagner, R. H., F. Helfenstein, and E. Danchin. 2004. Female choice of young sperm in a genetically monogamous bird. *Proceedings of the Royal Society B: Biological Sciences* 271:S134–S137.
- Warren, D. C., and L. Kilpatrick. 1929. Fertilization in the domestic fowl. *Poultry Science* 8:237–256.
- Wigby, S. L., and T. Chapman. 2005. Sex peptide causes mating costs in female *Drosophila melanogaster*. *Current Biology* 15:316–321.
- Ziegler, T. E. 2007. Female sexual motivation during non-fertile periods: a primate phenomenon. *Hormones and Behavior* 51:1–2.

Associate Editor: Allen J. Moore
 Editor: Monica A. Geber