



The evolution of female sexuality

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Females in monogamous species tend to be more sexually active than females in species with other mating systems. In this paper we consider the possibility that female sexuality has evolved because more sexually active females have received more male assistance. We develop a model in which there is no direct cue available to males indicating whether the female is fertile. Instead males might respond to female behaviour as an indirect cue. The latter could favour increased female sexuality if males tend to stay longer with more sexually active females. Our results show that female sexual behaviour can have a significant impact on social behaviour and that sexually active females and sexual behaviour outside fertile periods can evolve under some circumstances. We end with a discussion of theories of the evolution of female sexuality. We believe that theories based on male assistance fit empirical findings better than theories based on variation in male genetic quality.

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In the majority of species female receptivity is confined to a short period and the majority of females copulate only once or a few times per breeding attempt (see e.g. [Butler 1974](#); [Crews 1975](#); [Thornhill & Alcock 1983](#); [Hrdy & Whitten 1986](#); [Ridley 1988](#)). A low number of copulations allows for fertilization to occur without waste of time and energy and females reduce the risk of being predated or infected with contagious diseases. However, females of many bird and mammal species engage in more sexual behaviour than would be necessary if the sole function of copulating were fertilization. Copulations may even occur regularly when fertilization is impossible or unlikely ([Cheng et al. 1981](#); [Birkhead & Møller 1992](#)).

Perhaps surprisingly, many examples of high female sexual activity are found in species in which males and females form pairs and cooperate in reproduction (social monogamy). In birds, females of socially monogamous species are generally more 'sexually active' than females in species with other mating systems (see e.g. [Lumpkin 1983](#); [Birkhead et al. 1987](#); [Birkhead & Møller 1992](#)). For instance, ospreys, *Pandion haliaetus*, which are socially monogamous, attempt to copulate 160 times on average

(43% of these copulations are successful) over a 14-day period during each breeding attempt ([Birkhead & Lessells 1988](#)). Furthermore, females may frequently take the initiative to copulate and the sexual interest is not solely directed towards the male partner ([Birkhead & Møller 1992](#)). A similar link between sexuality and monogamy can be seen in some mammals. Examples include humans and other socially monogamous primates ([Hrdy & Whitten 1986](#); [Dixon 1998](#)), rodents ([Carter & Lowell 1993](#); [Gubernick & Nordby 1993](#)) and porcupines, *Hystrix indica* ([Sever & Mendelssohn 1988](#)). While sexual receptivity in birds is mainly confined to the period prior to egg laying, sexual activity in monogamous mammals may also occur during pregnancy and even after conception ([Hrdy & Whitten 1986](#); [Sever & Mendelssohn 1988](#)). Extended female sexual activity also occurs in some nonmonogamous group-living primates ([Hrdy & Whitten 1986](#); [Dixon 1998](#)). Scattered examples of high sexual activity can also be found among invertebrates. Very few invertebrates can be labelled socially monogamous, but copulation frequency is sometimes high in species where males associate with females and assist them in reproduction (burying beetles: [Müller & Eggert 1989](#); two species of digger wasps: [Peckham 1977](#); [Hook & Matthews 1980](#); isopods: [Linsenmair 1989](#)).

Several explanations have been offered for high sexual activity in a species. The classic explanation is sperm competition among males ([Parker 1970](#); [Birkhead & Møller 1992](#)). Another possibility is that females may get better genes for their offspring by copulating with several

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males (Trivers 1972; Andersson 1994). Female sexual behaviour may also play an important role in controlling male behaviour and thereby secure more male help in reproduction (see e.g. Dawkins 1976; Alexander & Noonan 1979; Taub 1980; Lumpkin 1983; Hrdy & Whitten 1986; Gowaty 1996; Enquist et al. 1998). In this paper we follow the latter suggestion and look at the possibility that females manipulate males through an increase in their sexual activity. We ask whether female sexual strategies that include an increased and prolonged interest in sexual activities, even outside the fertile period, can evolve and be evolutionarily stable.

The problem of increased female sexuality is interesting from a game theoretical point of view since in some species, including humans, males cannot observe directly whether a female is fertile. In the majority of games where one player has access to more information than the other, hiding of information is achieved by not signalling. However, in the present case nonsignalling is not a viable strategy because females need to copulate when fertile. Thus, for females to conceal whether they are fertile, they must be receptive and sexually active (Alexander & Noonan 1979; Cheng et al. 1981).

In many species females provide males with reliable cues about their fertility. Only fertile females seek contact with males and/or use particular signals to attract males, respond to courtship and take part in copulations (see e.g. Butler 1974; Crews 1975; Thornhill & Alcock 1983; Hrdy & Whitten 1986). After copulation the male usually leaves. This makes sense when copulating again adds little to male fitness and males waste opportunities elsewhere by remaining with the female. In addition, females may not be receptive for a considerable time after copulation. For example, the female of the lizard *Anolis carolinensis* enters a male's territory and signals to the male when she becomes fertile. The male approaches and copulates. Females become completely unreceptive 5–7 min after copulation and will not copulate again for at least 10–14 days (Crews 1975).

In species in which females are more sexually active, males might benefit from behaving differently. If females engage in sexual behaviour independently of whether they are currently fertile, males will have less information about their reproductive state. Can increased female sexuality have evolved because more sexually active females have been more successful in securing male assistance? If males had a tendency to stay with females as long as they were sexually active, females with longer receptivity periods might be favoured: they would receive more male assistance. This possibility has been discussed in the literature (Alexander & Noonan 1979; Cheng et al. 1981; Lumpkin 1983; Hrdy & Whitten 1986; Gowaty 1996), but has not been subjected to game-theoretical analyses (but see Enquist et al. 1998). From the fact that a strategy makes intuitive sense we cannot automatically draw conclusions about evolutionary stability, because a number of factors might contribute to destabilizing increased female sexuality. For instance, males need not benefit from staying with sexually active females. Or, if copulations are costly, both males and females may profit from avoiding the cost of sex as long as the female is not

fertile. An increase in sexual activity, therefore, need not be the outcome of this evolutionary game.

Our aim in this paper is to present the results from a game-theoretical analysis of the problem of increased female sexuality: we want to know under which conditions female sexuality outside the fertile period can evolve because it allows females to secure male assistance in reproduction. We have not included sperm competition or variability in male quality in the model. Thus, if we find that the model leads to increased female sexuality, we can be sure that sperm competition and the 'good genes' hypothesis are not responsible for the result.

In the model, females cannot store sperm and they copulate with only one male per unit time. Indeed, a female can breed at time t only if she has sufficient energy reserves and if she has copulated with a male during that time unit. Sperm received in previous time steps neither contributes to nor interferes with breeding. Furthermore, since a female can encounter only one male per time unit it will never be the case that the sperm from two or more males must compete for fertilization. Similarly, the 'good genes' hypothesis cannot be responsible for any increase in female sexual activity because, in our model, individuals may differ in their breeding strategies, but are otherwise identical. This does not mean that we consider sperm competition and the good genes hypothesis unimportant for the evolution of female sexuality.

THE MODEL

The model combines stochastic dynamic programming with elements from game theory. We start by explaining the general features and work our way through the more technical details. For simplicity of exposition, we describe the model as if we were dealing with birds. Hence, we talk of clutches, incubation, etc. The model, however, is not restricted to birds by its assumptions. The logic and results can be applied to other taxa without modification.

Payoffs

In our model, we consider species with well-defined breeding seasons. The breeding season is divided into discrete time steps, labelled by the index t . In the first time step of the season $t=0$ and in the last time step $t=T_{\max}$. Females breed only once per season. For simplicity, we concentrate on the possibility of male attendance prior to breeding. To make sure that females have no incentive to remain with a male (referred to as 'paired' in what follows) after laying their clutch, we assume that the value of a clutch is a function of the time of breeding, $V(t)$, but is unaffected by the presence of males thereafter. Specifically, we assume that

$$V(t)=1-t/T_{\max},$$

so that females have an incentive to breed as soon as possible. Males may sire the offspring of more than one female. The fitness of a male is given by the sum of the values of the clutches he sires.

Social Structure and Behavioural Dynamics

At any point in time, the breeding population can be divided into a number of groups. There will be groups consisting of one male and two females (trios), pairs of males and females, single males and single females. (The trios must be understood as an abstraction representing the fact that males may have to make choices between females. If a male has no option but to help one particular female, this female will not need to manipulate the male in order to gain his favours: the male has nothing better to do. It is only if a male must choose between helping one female or another that female manipulation makes any sense.) Within each time step, the following sequence of events takes place.

(1) At the beginning of the time step, we have a certain number of single males and females, pairs and trios.

(2) Females in pairs and trios choose between displaying (soliciting copulations) or not. We assume that females do not know whether the male with whom they interact has a second female. (In other words, females ignore whether they are part of a pair or a trio.)

(3) Males observe the number of females and their behaviour. If one or more females are displaying, males can choose whether to copulate with them. Subsequently, males have to decide whether to remain with a female. We assume that males can remain at most with one female, although they may copulate with both. Males in trios who opt to remain will have to decide with which female to remain. For these males, if the two females behave differently, males will be able to choose to remain with the displaying or the nondisplaying one. But if both females behave in the same way, we assume that males will choose one of them at random. This implies that males do not remember which female was with them in the previous time step. We make this 'assumption of male stupidity' to simplify the model.

In what follows, we say that a female is 'paired' if she has found a male and the male has decided to remain with her. All other females are 'unpaired'. (Note that a female's status can change in time from paired to unpaired and from unpaired to paired.)

(4) Females who have copulated and are in breeding condition lay their clutch with a certain probability (see below). After laying, females stop searching for males and are not included in subsequent steps. Females incubate and rear their young on their own.

(5) Those females who have not laid a clutch spend the rest of the time period searching for food. The probabilities of finding food are specified below.

(6) At the end of each time period a proportion q of all unpaired females are distributed randomly over all males. If q is high it is easy for males and females to find each other. If q is small it is difficult. For simplicity, we assume that unpaired females or males cannot simultaneously encounter more than one individual of the opposite sex. If we denote by N_p and N_u the number of paired and unpaired males, respectively, then each individual female has probabilities ρ_e , ρ_p and ρ_u of not meeting a male, meeting a male that already has a female and meeting a single male, respectively, where:

$$\rho_e = 1 - q,$$

$$\rho_p = q \frac{N_p}{N_p + N_u},$$

$$\rho_u = q \frac{N_u}{N_p + N_u}.$$

The Internal State of Females

Before breeding, females must store sufficient energy reserves to produce a clutch. We denote by $x(t)$ the level of energy reserves of a female at the start of time step t . At the beginning of the breeding season, females have no energy stores, so that $x(0)=0$ for all females in the population. From then on, in each time step t two things can happen. A female can find food during this time step, in which case her energy reserves increase by a unit (and $x(t+1)=x(t)+1$), or she may not find food, in which case her reserves remain unaltered (so that $x(t+1)=x(t)$).

For nonfertile females to display, they must gain something from being paired. In our model, this benefit is an increased probability of finding food. Hence, the probability that a paired female finds food, f_p , is greater than the probability that an unpaired female obtains food, f_u : $f_p > f_u$. (This, of course, is not universally true. In many species females do not gain from having a male around and may even be better off on their own: our model does not apply to such species.) Paired females may be more likely to find food than unpaired females if they gain access to the territory of their mate and the food it contains. Females can also increase their intake rates if males watch out for predators, so that females can increase time spent foraging without risking being preyed upon, or if paired females are not sexually harassed by other males.

We assume further that sexual activity, in terms of displays and copulations, is costly. For females, displaying reduces the probability of finding food by a factor $C_d < 1$. Copulating reduces the probability of finding food by a factor C_c . The reason for introducing displaying and copulation costs is that we are interested in understanding why sexual activity is maintained at times when it cannot lead to the production of offspring. In species where sexual activity is not costly, its presence needs no further explanation: there is simply no selective pressure tending to its elimination. Hence, we can increase our understanding of the problem only if we can show that costly sexual activity involving nonfertile females can be stable. Figure 1 represents the probability of finding food for all possible scenarios.

Breeding

To rule out sperm competition as a possible explanation of any increased sexual activity that the model might show, we assume that females cannot store sperm. A female can produce a fertilized clutch during time step t only if she copulates at the beginning of that time period. Similarly, if a female breeds at time t the male who has copulated with her at the beginning of that time

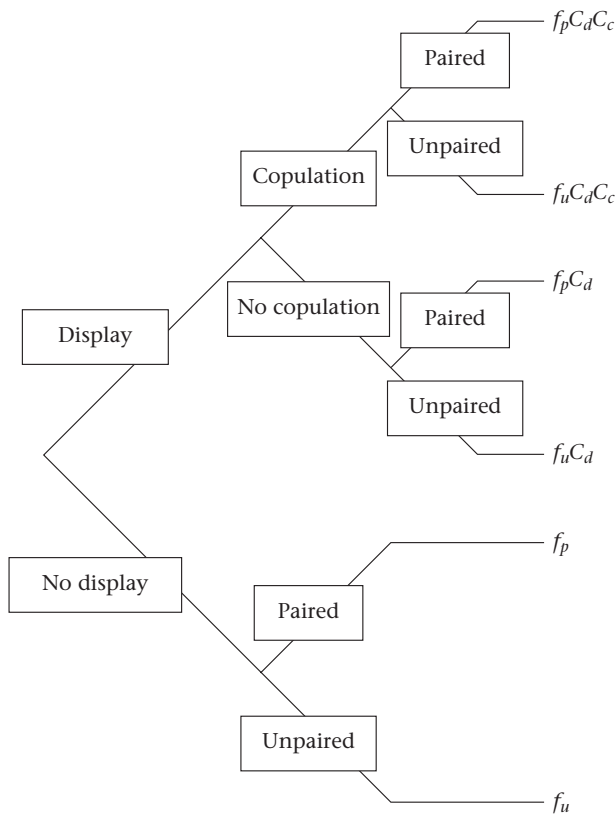


Figure 1. Probability that females find food after the different possible sequences of events. f_u and f_p are the probabilities that an unpaired and paired female, respectively, find food in the absence of displays and copulations. C_c and C_d are the costs incurred by displaying and copulating, respectively.

period sires her offspring, regardless of how often, and with how many males, the female has copulated in the past. Females cannot copulate with more than one male in a time step.

Let us denote by X_{\min} the energetic cost of producing a clutch. Females can breed only if their level of energy reserves is greater than or equal to the cost of producing a clutch, $x \geq X_{\min}$. We say that a female is in breeding condition if $x(t) \geq X_{\min}$.

Females who copulate at the beginning of time period t , and who have $x(t) \geq X_{\min}$, breed with probability p_{fert} . A female in breeding condition who fails to breed despite copulating will have to copulate again, since she cannot store sperm from one time step to the next.

Game Structure

Behavioural strategies are defined as follows. For females, we specify the probability of displaying as a function of time and energy reserves, $Disp(x, t)$. For males, we need to specify the probability of copulating with a female that displays, $Cop(t)$, and the probability of remaining with the displaying female if faced with two females, only one of which displays, $H_d(t)$. (Given the structure of the model, a male with only one female will remain with her with probability 1 and a male with two

females that behave in the same way will remain with one of them, chosen at random.)

To find stable pairs of behavioural strategies, we make a guess concerning the solution of the model and then iterate the following algorithm.

(1) Given that the population behaves according to $Disp(x, t)$, $Cop(t)$ and $H_d(t)$, determine the strategies maximizing the fitness of an individual female, $Disp^*(x, t)$.

(2) Update $Disp(x, t)$ according to:

$$Disp(x, t) \rightarrow (1 - \alpha) \times Disp(x, t) + \alpha \times Disp^*(x, t).$$

(3) Given the new behaviour of the population, determine the strategies maximizing the expected fitness of individual males, $Cop^*(t)$ and $H_d^*(t)$.

(4) Update the male strategies according to:

$$Cop(t) \rightarrow (1 - \alpha) \times Cop(t) + \alpha \times Cop^*(t)$$

and

$$H_d(t) \rightarrow (1 - \alpha) \times H_d(t) + \alpha \times H_d^*(t).$$

Steps 1–4 are repeated until the optimal behaviour of individuals (given what the rest of the population is doing) coincides with the population's behaviour. At that point no mutant can increase its expected fitness by deviating from the population's behaviour, and hence the population strategies cannot be invaded by mutants. The optimal strategies are found using a stochastic dynamic program (Mangel & Clark 1988) as explained in the Appendix.

RESULTS

We used different combinations of parameter values to search for the possible evolutionarily stable strategies (ESSs) of the model. For each set of parameter values, we tried four starting conditions to see whether the simulations converged to different results depending on the initial population strategies. The four initial conditions resulted from combining two possible female strategies with two possible male strategies. The initial female strategies were as follows: (1) only those females who have sufficient energy reserves to breed display to males and (2) all females display when they find a male, regardless of their level of energy reserves. The male strategies explored are described in Table 1.

When the second female strategy and the second male strategy were combined to constitute the initial condition, the end result was that, at the ESS, all females display and males remain with females after copulating. (Males with two displaying females select one of them at random.) This result applies to all combinations of parameter values tested.

In the other three cases, the ESS can be characterized as follows. In the first part of the season, when there are no fertile females in the population, no females display and males remain with the females they encounter. (If faced with two females, males select one at random.) As soon as some females become fertile, all females start displaying

Table 1. Male strategies used as initial conditions

| No. of females | No. of displaying females | Strategy S1 | Strategy S2 |
|----------------|---------------------------|---|---|
| 1 | 0 | Stay | Leave |
| 1 | 1 | Copulate and leave | Copulate and stay |
| 2 | 0 | Select one at random to stay with | Leave |
| 2 | 1 | Copulate with displaying female and stay with nondisplaying one | Copulate and stay with displaying female |
| 2 | 2 | Copulate with both and leave both | Copulate with both and stay with a random one |

(regardless of whether they have sufficient reserves to breed), while males remain with their partners after copulation. (Males with two females select one of them at random.) The duration of this second stage (hereafter referred to as the 'display run') is regulated by the sex ratio at the beginning of the season and the probability of fertilization per copulation. After this phase, the female strategy reverts to displaying only when fertile. In this last stage, males keep copulating with females. Males with a single female stay with her, males with two females that behave in the same way stay with a randomly chosen one, and males paired with two females, only one of whom displays, stay with the nondisplaying female. In this way, males have a certain probability (p_{fert}) of siring the offspring of the female with whom they have copulated (since this female must have had sufficient reserves to breed, otherwise she would not have displayed) and guard the other female, with whom they will mate later in the season, when she accumulates sufficient energy reserves to breed.

Figure 2 shows the quantitative effect of initial sex ratio and probability of fertilization on the duration of the display run, Fig. 3 how the total number of displays (displays by all females throughout the season) changes with initial sex ratio and probability of fertilization, and Fig. 4 the proportion of these displays that involve non-fertile females. These figures show that, for a given probability of fertilization, the display run ends when the operational sex ratio (defined as the number of females attempting to breed at a particular time divided by the number of males searching for females at the same time) decreases below a certain threshold, which is roughly independent of the initial sex ratio.

Figure 5 shows the threshold value of the operational sex ratio as a function of the probability of fertilization per copulation.

To understand better the implications of these results, we ran the simulations again in such a way that female behaviour could not evolve. Specifically, we fixed the female behaviour to the strategy 'display only if in breeding condition' and let the behaviour of the males evolve until their optimal behaviour was found. Comparison of the two sets of simulations showed that allowing female behaviour to evolve leads to a marked increase in the total number of displays (Fig. 6), but that, at evolutionary equilibrium, this increase in sexual activity need not

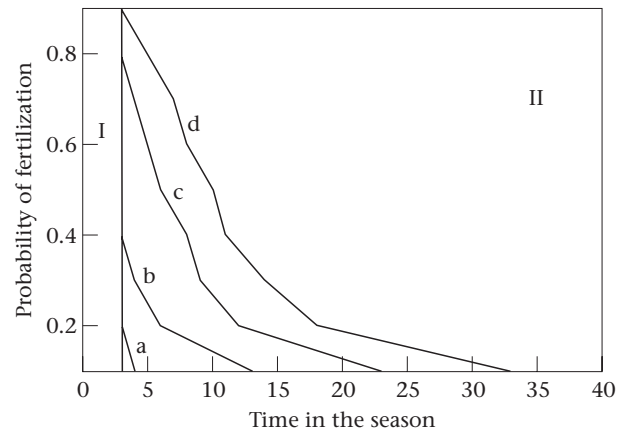


Figure 2. Female strategies at equilibrium. At the beginning of the season (I) females are not fertile and do not display. At the end of the season (II) only those females in breeding condition display. Between regions I and II there is a 'display run', where females display regardless of their breeding condition. Display runs start at the end of period I and their end is determined by the probability of fertilization (p_{fert} , Y axis) and the initial sex ratio (SR, f:m), as shown by lines a–d: (a) SR=0.5, (b) SR=1.0, (c) SR=1.41, (d) SR=2.0. In these simulations, the following parameter values were used. The copulation and displaying costs were $C_c=C_d=0.995$, the probabilities of finding food for unpaired and paired females were $f_u=0.1$, $f_p=0.4$, respectively. There were 100 males in the population and the energetic cost of producing a clutch was $X_{min}=4$.

benefit females (Fig. 7). Indeed, expected female fitness decreases, by $0.014 \pm 0.075\%$ ($\bar{X} \pm SD$). This may be somewhat counterintuitive: if sexual activity increases because females who are sexually active are fitter than those who are less active, how can female fitness at equilibrium be lower when their behaviour is allowed to evolve? This sort of paradox is, however, extremely common in game theory, and the answer to the paradox lies in the fact that payoffs are frequency dependent: the expected payoff of a displaying female is always greater than the payoff of a nondisplaying female, but all payoffs decrease as the proportion of displaying females increases.

DISCUSSION

The most important result of this model is that, in the absence of any sperm competition or variability in male

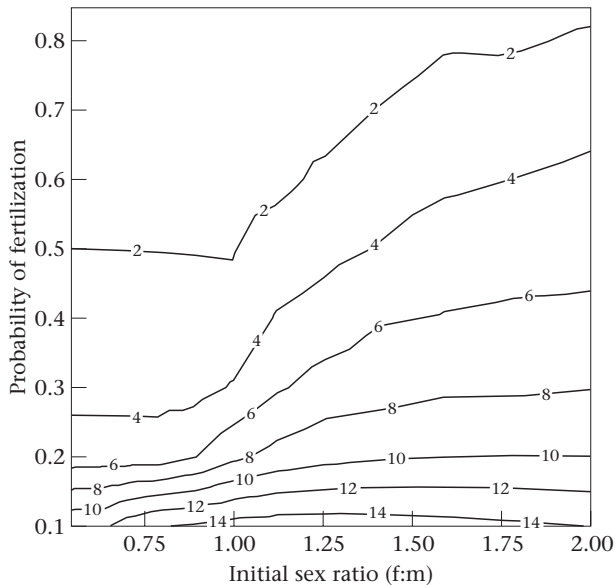


Figure 3. Contour plot of the average number of displays per female, as a function of the probability of fertilization and the initial sex ratio. Parameters as in Fig. 2.

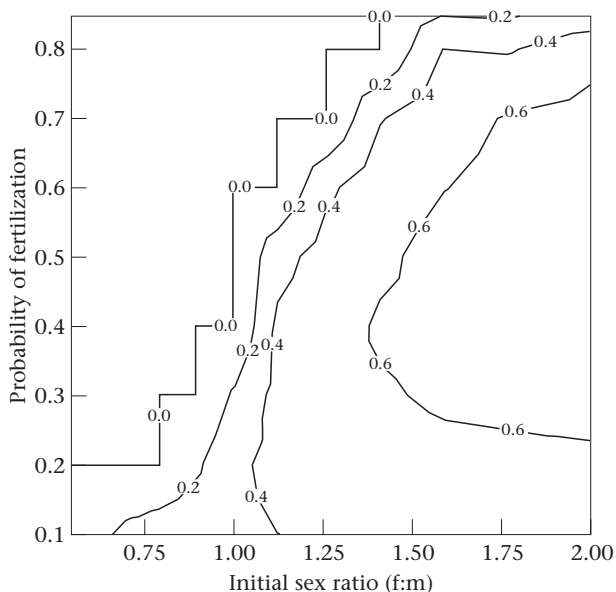


Figure 4. Proportion of displays observed that involve a nonfertile female. Parameters as in Fig. 2.

genetic quality, an evolutionary equilibrium can exist in which females can benefit from copulating even when (1) copulations cannot lead to fertilization of eggs and (2) copulations entail a cost. In general, these 'superfluous' copulations start as soon as some fertile females appear in the population. The duration of the period during which nonfertile females display (the 'display run') is determined by the sex ratio in the population and the probability of fertilization per copulation: low probabilities of fertilization and female-biased sex ratios increase the duration of the display run.

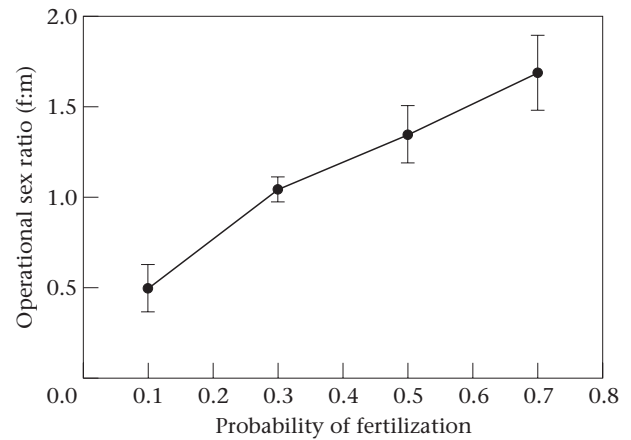


Figure 5. Mean \pm SD operational sex ratio at the end of the display run, plotted as a function of the probability of fertilization per copulation. Parameter values as in Fig. 2.

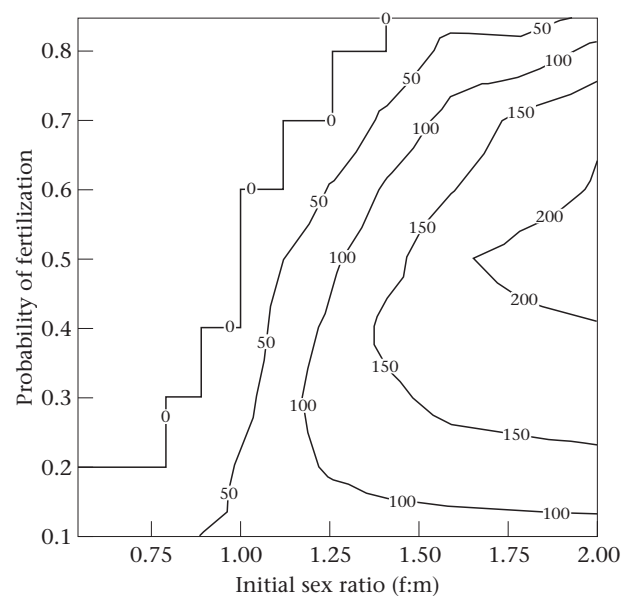


Figure 6. Contour plot of the increase in the total number of displays caused by the evolution of superfluous copulations. The figure plots the percentage increase in number of displays, relative to the number of displays observed in a population where only fertile females display and males behave optimally (i.e. $100 (disp_{ev} - disp_c) / disp_c$, where $disp_{ev}$ is the number of displays per female in a population where female behaviour is allowed to evolve, and $disp_c$ is the number in a population where female behaviour is constrained to the strategy 'display if in breeding condition'). Parameter values as in Fig. 2.

One prediction from the model is that we should observe more female sexual activity when males have more possibilities to meet females. We are not aware of any data addressing this question directly. However, female European starlings, *Sturnus vulgaris*, solicit copulations at an increased rate when they are faced with the risk of polygyny (Eens & Pinxten 1996). Our result also suggests that females should be sexually active rather early, even before they are fertile, provided that some

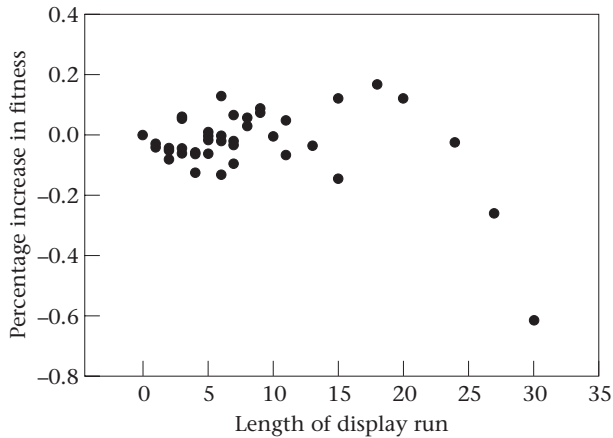


Figure 7. Increase in female fitness (calculated as in Fig. 6). Negative values correspond to those cases where female fitness decreases if the behaviour of the females is allowed to evolve.

females are fertile. Lumpkin (1983) and Birkhead & Møller (1992) reported a number of monogamous bird species in which females are sexually active for prolonged periods. It is also clear that not all females are at their peak of fertility at the same time although the variation between species is considerable (see e.g. Stutchbury & Morton 1995). These observations are consistent with our model but specific studies of the relationship between sexual behaviour and factors such as operational sex ratios would be revealing.

Similar reasoning as in our model might explain sexual receptivity during pregnancy. In birds, completed egg laying provides a reliable cue to males that the female is no longer fertile. In mammals the time between fertilization and unavoidable signs of pregnancy is potentially long and continued receptivity could be maintained for similar reasons as in the model. Our hypothesis, however, cannot explain cases when copulations occur when all females (and males) are not yet fertile. In the mallard, *Anas platyrhynchos*, and common guillemot, *Uria aalge*, copulation starts several months before egg laying and when the males' testes cannot produce sperm (Birkhead & Møller 1992). The same argument applies to sexual activity during late pregnancy or during lactation as in the porcupine, *Hystrix indica* (Sever & Mendelsohn 1988), when reliable cues indicate that the female is not fertile.

We have built the model in such a way that sperm competition and the 'good genes' hypothesis cannot be the forces leading to the appearance of superfluous copulations: there is no sperm storage and all males have identical quality.

Our model assumes that females benefit from males in two ways. (1) Paired females acquire food faster than unpaired females. (2) Females benefit from copulating as soon as they become fertile. When must a female actively do something to secure a mate, and what can she do? The answer to the first question is clear: females need only to persuade males to stay with them if males have more profitable options. At a time when there are no unpaired females in the population, males gain nothing from deserting their partners (because males pay no cost for

being paired) and hence superfluous copulations are not observed (see e.g. Figs 4 and 5).

To find out how a female can secure a mate, a more subtle reasoning is required. The best strategy for a female to follow depends on what everyone else is doing, and on the parameter values. It is easiest to discuss first the optimal behaviour of the males, and, taking this into account, reconsider the female's behaviour.

With the assumptions of the model, a male faced with a single female always benefits from staying with her. Similarly, a male in a trio will never benefit from deserting both females, although he will have to choose which female to stay with. When both females behave in the same way, the male will, in all cases, choose one of them at random. What if only one of the two females displays? Consider first the situation where the probability of fertilization, p_{fert} , is low.

A male who stays with the nondisplaying female will sire the offspring of the other one with some small probability (p_{fert} if the displaying female was fertile, zero otherwise). The male can stay with the nondisplaying female until she becomes ready to reproduce and then mate with her.

On the other hand, if the male stays with the displaying female, she may or may not breed as a result of the copulation. If the female breeds, the male has wasted time by remaining with her: he needs to find a new partner. Alternatively, by staying with the displaying female the male increases his chances of siring her offspring; and, if unpaired females are abundant and there is plenty of time before the end of the season, the male can be almost sure that he will find a new mate once the displaying female breeds.

Hence, if the probability of fertilization is low, the best strategy of the males is as follows: if there are plenty of unpaired females (female-biased sex ratio) and sufficient time left, a male should remain with a displaying female until she breeds. If, on the other hand, there are few unpaired females, the male should stay with the nondisplaying female (gambling on the possibility that the displaying female is fertilized with a single copulation).

If the probability of fertilization is close to one, it will always pay males in trios to stay with the female with whom they have not copulated: if the female with whom they have copulated was fertile, she will most likely breed and hence there is no point in remaining with her. If, on the other hand, she was only 'pretending' to be fertile, her internal condition (e.g. energy reserves) need not be higher than that of the nondisplaying female, and hence males lose nothing by remaining with the latter.

The optimal female strategy can be derived from the male's behaviour. If males that have a displaying and a nondisplaying female stay with the displaying female, females will display regardless of their internal condition (assuming that the benefit from having a male around is greater than the costs of displaying and copulating). But once males desert the displaying female, it pays females to display only when they are fertile.

The importance of female-female competition as a factor driving the appearance of female displays involving nonfertile females results in the disappearance

of these displays once the operational sex ratio decreases below a certain threshold (Fig. 5), and hence once the level of female–female competition becomes sufficiently low. But a more direct evidence of the key role played by female–female competition in our model is given by the results of a slightly modified version of the model. In the model discussed so far, when a female is in the presence of a male, she ignores whether she constitutes part of a pair or a trio, and it is the possibility that the male leaves her for another, more profitable female that induces nonfertile females to display in some circumstances. We have also explored a model in which trios never occur. (In this version of the model, a male can find a female only if he is unpaired, but paired males never encounter new females.) In this model, although there exists an ESS where all females display regardless of their level of reserves, this ESS can be reached only if the population is initialized at the ESS itself: superfluous copulations do not evolve (unpublished data).

It can be argued in our model that males remain with females because they indirectly benefit from helping them: females reach breeding condition sooner in the presence of a male ($f_p > f_u$) and, therefore, a female that has been with a male is (on average) more valuable (i.e. has more energy reserves) than a female that has always been unpaired. Although there is no reason why males should not benefit indirectly from the help they provide to their mates (sexual reproduction need not be a zero-sum game), we have explored the possibility that females benefit from the presence of males in such a way that males get nothing in return. Specifically, we assumed that $f_p = f_u$ (breeding condition is reached at the same rate by paired and unpaired females), but that female fitness increased by 0.01 units every time period that they remained paired. The results of this model are very similar to the original one (compare Fig. 8 with Fig. 3). This ‘direct benefits’ model allows for increased female sexuality to evolve in the absence of direct female–female competition (i.e. when trios are excluded from the model): if $f_p = f_u$, female fitness increases by 0.01 units every time unit that they remain with a male and male fitness decreases by 0.01 every time that they help a female, then superfluous copulations can appear for some parameter values, although in general the convergence of the model is rather poor (unpublished data). The evolution of increased sexual activity therefore appears when there is a conflict of interests between males and females. The conflict may be due to males wanting to be paired with the most profitable females, while females want to be paired with males regardless of whether there are more profitable females around.

The reason why superfluous displays evolve is that, prior to their appearance, displays convey information: originally, displaying and nondisplaying females have different levels of energy reserves. Because males prefer to remain with females having sufficient reserves to breed, and because males can infer the condition of a female only from her behaviour, it becomes advantageous for females to ‘cheat’ and display: this enhances the probability that the male remains with them and, eventually (when all females display, regardless of their internal

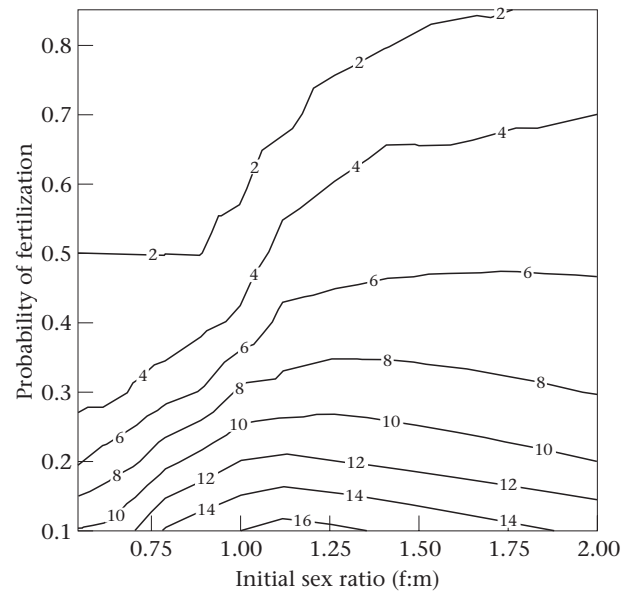


Figure 8. Average number of displays per female with the ‘direct benefits’ model. Parameters are as in Fig. 2, except that $f_u = f_p = 0.3$. Female fitness is increased by 0.01 units each time step that they spend with a male.

condition, e.g. energy reserves), removes the information content from the display.

To conclude, we discuss some of the factors that have been suggested to favour the evolution of increased female sexuality (Table 2). We have completed Table 2 under the assumption that males cannot force females to have sex, and that sex entails some small cost to females. When the only female purpose of sex is fertilization, superfluous copulations do not evolve. If the genetic quality of males varies, evolution may favour females that seek extrapair copulations (see e.g. Birkhead & Møller 1992). This would lead to more sexual activity among females but only while the female is fertile. We have shown that when females can gain assistance from males, superfluous copulations can evolve as females attempt to sequester male assistance if males are deprived of all cues about female fertility. Even though superfluous copulations ultimately lead to a decrease in expected fitness, they are none the less evolutionarily stable. Increases in female sexual activity can also be observed if males copulate with different females and allocate parental care in proportion to the number of copulations with each female (e.g. Davies 1992). Similarly, females could benefit from making surrounding males potential fathers and thereby decrease hostility from these males (Hrdy 1977; Hrdy & Whitten 1986). Finally, Enquist et al. (1998) have hypothesized that sexually active females may draw attention from other males, influencing the male mate to stray less. This would secure more male assistance. It is of course possible that several of the above hypotheses operate together.

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Table 2. Summary of hypotheses proposed to explain increased female sexual activity in monogamous species

| Function of copulations | Prediction | | | |
|--|-------------------------|----------------------|--------------------|-------------------------|
| | Prolonged period of sex | Sex when not fertile | Higher rate of sex | Interest in other males |
| Fertilization only | No | No | No | (Yes) |
| Fertilization+attempt to get high-quality males as fathers (Walker 1980; Birkhead & Møller 1992) | (No) | No | (Yes) | Yes |
| Fertilization+depriving males from information about fertility to secure male assistance in competition with other females (this paper) | Yes | Yes | (Yes) | No |
| Fertilization+persuading the male to assist in parental care. Male will help rear the clutch that contains most of his offspring and uses number of copulations as cue (Davies 1992) | Yes | Yes | Yes | (Yes) |
| Fertilization+trying to monopolize her mate by attracting other males and thereby influencing the mate to stray less (Enquist et al. 1998) | (Yes) | (Yes) | (Yes) | Yes |

It is assumed that males cannot force females to have sex, and that sex entails some small cost to females. Parentheses indicate likely outcomes that can be altered by small modifications in other assumptions.

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References

- Alexander, R. D. & Noonan, K. N. 1979. Concealment of ovulation, parental care and human social evolution. In: *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective* (Ed. by N. A. Chagnon & W. G. Irons), pp. 436–453. Scituate: North Duxbury Press.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Birkhead, T. R. & Lessells, C. M. 1988. Copulation behaviour of the osprey *Pandion haliaetus*. *Animal Behaviour*, **36**, 1672–1682.
- Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds*. London: Academic Press.
- Birkhead, T. R., Atkin, L. & Møller, A. P. 1987. Copulation behaviour in birds. *Behaviour*, **101**, 101–138.
- Butler, H. 1974. Evolutionary trends in primate sex cycles. *Contributions to Primatology*, **3**, 2–35.
- Carter, C. S. & Lowell, L. G. 1993. Monogamy and the prairie vole. *Scientific American*, **368**, 70–76.
- Cheng, M-F., Porter, M. & Ball, G. 1981. Do ring doves copulate more than necessary for fertilization? *Physiology and Behavior*, **27**, 659–662.
- Crews, D. 1975. Psychobiology of reptilian reproduction. *Science*, **189**, 1324–1335.
- Davies, N. B. 1992. *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Dixon, A. F. 1998. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Humans*. Oxford University Press: Oxford.
- Eens, M. & Pinxten, R. 1996. Female European starlings increase their copulation solicitation rate when faced with the risk of polygyny. *Animal Behaviour*, **51**, 1141–1147.
- Enquist, M., Rosenberg, R. & Temrin, H. 1998. The logic of Ménage à trois. *Proceedings of the Royal Society of London, Series B*, **265**, 609–613.
- Gowaty, P. A. 1996. Battles of the sexes and the origins of monogamy. In: *Partnerships in Birds* (Ed. by J. M. Black), pp. 21–52. Oxford: Oxford University Press.
- Gubernick, D. J. & Nordby, J. C. 1993. Mechanisms of sexual fidelity in the monogamous California mouse (*Peromyscus californicus*). *Behavioral Ecology and Sociobiology*, **32**, 211–219.
- Hook, A. W. & Matthews, R. W. 1980. Nesting biology of *Oxybelus sericeus* with a discussion of nest guarding by male sphecoid wasps (Hymenoptera). *Psyche*, **87**, 21–37.
- Hrdy, S. B. 1977. *The Langurs of Abu*. Cambridge, Massachusetts: Harvard University Press.
- Hrdy, S. B. & Whitten, P. L. 1986. Patterning of sexual activity. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 370–384. Chicago: University of Chicago Press.
- Linsenmair, K. E. 1989. Sex-specific reproductive patterns in some terrestrial isopods. In: *The Sociobiology of Sexual and Reproductive Strategies* (Ed. by A. E. Rasa, C. Vogel & E. Voland), pp. 19–47. London: Chapman & Hall.
- Lumpkin, S. 1983. Female manipulation of male avoidance of cuckoldry behavior in the ring dove. In: *Social Behavior of Female Vertebrates* (Ed. by S. K. Wasser), pp. 91–112. New York: Academic Press.
- Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, New Jersey: Princeton University Press.
- Müller, J. K. & Eggert, A-K. 1989. Paternity assurance by 'helpful' males: adaptations to sperm competition in burying beetles. *Behavioral Ecology and Sociobiology*, **24**, 245–249.

- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Review*, **45**, 525–567.
- Peckham, D. J. 1997. Reduction of Miltogrammine cleptoparasitism by male *Oxybelus subulatus* (Hymenoptera: Sphecidae). *Annals of the Entomological Society of America*, **70**, 823–828.
- Ridley, M. 1988. Mating frequency and fecundity in insects. *Biological Reviews*, **63**, 509–549.
- Sever, Z. & Mendelsohn, H. 1988. Copulation as a possible mechanism to maintain monogamy in porcupines (*Hystrix indica*). *Animal Behaviour*, **36**, 1541–1542.
- Stutchbury, B. J. & Morton, E. S. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour*, **132**, 675–690.
- Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Trivers, R. L. 1972. Chapter title? In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 139–179. Chicago: Aldine.
- Taub, D. M. 1980. Female choice and mating strategies among wild barbary macaques (*Macaca sylvanus* L.). In: *The Macaques: Studies in Ecology, Behavior and Evolution* (Ed. by D. G. Lindburg), pp. 287–344. New York: Van Nostrand Reinhold.
- Walker, W. F. 1980. Sperm utilization strategies in nonsocial insects. *American Naturalist*, **115**, 780–799.

Appendix A: Dynamic Program Equations

In this appendix, we assume that the reader is familiar with the principles of stochastic dynamic programming. For details about this technique see Mangel & Clark (1988).

Female's behaviour

Denote by $Fit_f(d | x, st, t)$ the fitness of a female which, at time t , displays ($d=1$) or does not display ($d=0$), given that she has x internal reserves and status st ($st=0, 1$ or 2 for females which are single, members of pair and trios, respectively).

Let $Prob(x', st' | d, x, st, t)$ be the probability that a female (which at time t is in status st , condition x and behaves according to d) is, at time $t + 1$, in status st' and condition x' . (This probability can be calculated from the behaviour of the males and the probability of finding food.) Then, if we denote by $p_{breed}(d, x, st, t)$ the probability that the female lays a clutch between t and $t+1$ and by $d^*(t+1)$ the optimal behaviour of the female at time $t+1$, we have:

$$Fit_f(d | x, st, t) = p_{breed}(d, x, st, t) \times V(t) \\ + (1 - p_{breed}(d, x, st, t)) \times \sum_{x', st'} Prob(x', st' | d, x, st, t) \\ \times Fit_f(d^*(t+1) | x', st', t+1),$$

where the sum is over all possible values of x' and st' .

Because we have assumed that paired females ignore whether they are part of a pair or a trio, in order to determine their expected fitness from producing behaviour d , $Fit_f(d | x, t)$, females must take into account the probabilities of being in a pair or trio, p_{pair} and p_{trio} , respectively. With these probabilities,

$$Fit_f(d | x, t) = p_{pair} \times Fit_f(d | x, 1, t) + p_{trio} \times Fit_f(d | x, 2, t).$$

The optimal behaviour of the female at time t is therefore obtained by comparing her expected fitness if she does, or does not, display.

To complete the description of the female's behaviour, we need to specify their fitness at the end of the season. We simply assume that

$$Fit_f(d | x, st, T_{max}) = 0.0001 \times x,$$

for all values of d and st .

Male's behaviour

Let us assume that we know the expected fitness of a male which, at the beginning of time step $t+1$, has nf ($0 \leq nf \leq 2$) females, of which nd ($0 \leq nd \leq nf$) are displaying and which behaves optimally from $t+1$ onwards. We denote this fitness by $Fit_m(nf, nd, t+1)$.

Let $\rho(x | d, t)$ be the probability that a female which, at time t , produces behavioural response d , is in condition x . Let $p_{brood}(b, t)$ be the probability that the male's behaviour, b , leads to the production of a clutch. And let $p_{nf', nd'}$ (b) be the probability that, at time $t+1$, the male has nf' females, nd' of which are displaying. These probabilities are calculated by forward iteration. The male's expected fitness from behaving according to b , $Fit_m(b | nf, nd, t)$, is:

$$Fit_m(b | nf, nd, t) = p_{brood}(b, t) \times (nd \times V(t) + Fit_m(0, 0, t+1)) \\ + (1 - p_{brood}(b, t)) \times \sum_{nf', nd'} p_{nf', nd'}(b) \times Fit_m(nf', nd', t+1).$$

Comparison of the expected fitness from different behaviours allows us to determine the optimal behaviour of the male at time t , b^* , and the expected fitness of a male that behaves optimally from t onwards. To complete the calculations of male's fitness and behaviour we must specify residual fitness at the end of the season. In our model, we have chosen

$$Fit_m(b | nf, nd, T_{max}) = 0.0,$$

for all values of b , nf and nd .