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Sperm precedence in zebra finches does not require special mechanisms of sperm competition

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SUMMARY

Competition between the spermatozoa of different males to fertilize the eggs of a single female acts as a selection pressure on the behaviour of males and females. However, quantitative predictions about behaviour can only be made if the paternity consequences of different patterns of copulation are known. Because exhaustive empirical measurement of these consequences may be impractical, interest has centred on determining the mechanisms by which sperm competition occurs, knowledge of which may allow consequences to be calculated. One method of elucidating mechanisms of sperm competition is to use mathematical models to determine which mechanisms are necessary or sufficient to account for empirical observations. We use this approach for zebra finches *Taeniopygia guttata* and show that empirically measured rates of disappearance of sperm from the reproductive tract, and differences in the number of sperm in the first and subsequent ejaculates of each male, are sufficient to account for observed levels of sperm precedence. Special mechanisms of sperm competition, such as displacement or stratification of sperm, are therefore unnecessary to explain sperm precedence in this species.

1. INTRODUCTION

The recognition that sperm competition – competition between the spermatozoa from different males to fertilize the eggs of a single female (Parker 1970) – may be frequent even in apparently monogamous species has led to considerable advances in the understanding of male and female behaviour during the female's fertile period (Birkhead & Møller 1992). However, a lack of detailed knowledge of the paternity consequences of different patterns of insemination by pair and extra-pair males, particularly in birds, has hindered the making of precise quantitative predictions about optimal behaviour. This deficit has led to increased interest in mechanisms of sperm competition: knowledge of such mechanisms may provide an alternative to empirical measurements in determining the fitness consequences of different copulation strategies (Lessells & Birkhead 1990).

In birds, one of the most intriguing observations in terms of the mechanism of sperm competition is the apparently disproportionate success of extra-pair copulations (EPCs). For example, in several wild bird populations the proportion of extra-pair young is considerably higher than the observed proportion of EPCs (see, for example, Westneat *et al.* 1990; Dixon *et al.* 1994; Mulder *et al.* 1994). Although such a discrepancy might be accounted for by the discreteness, and hence low observability, of EPCs in the wild, studies of caged birds, where all copulations can be observed, reveal a similar inconsistency between the proportion of EPCs and extra-pair young (the single EPC experiment in Birkhead *et al.* 1988*a*). Such observations encourage the provocative suggestions that either the mechanism

of sperm competition entails an advantage to the last male to copulate, over and above any advantage from minimizing the loss of sperm through constant disappearance between insemination and fertilization (Lessells & Birkhead 1990), or females are in some way able to influence the outcome of sperm competition and select sperm providing a favourable genetic endowment to their offspring (Birkhead *et al.* 1993*a*). However, before pursuing these possibilities, the alternative explanation that the success of EPCs is due to differences in the number of sperm inseminated, and the relative timing of EPCs in conjunction with constant sperm loss rates, should be evaluated. In particular, Birkhead & Fletcher (1992, 1995; T. R. Birkhead & F. Fletcher, unpublished results) have recently demonstrated that the number of sperm transferred in copulations by zebra finches *Taeniopygia guttata* is considerably larger when the male is 'rested' than when he has inseminated a female within the previous calendar day. If EPCs normally occur after the male has ceased copulating with his own mate (Birkhead *et al.* 1988*b*; Morton *et al.* 1990; Birkhead & Møller 1992), larger ejaculate size may account for the disproportionate success of EPCs.

The aim of this paper is, therefore, to investigate whether levels of sperm precedence in the zebra finch measured in captivity can be accounted for by the number of sperm inseminated in conjunction with a constant disappearance rate of sperm between insemination and fertilization. To do this, we use mathematical models together with empirical measurements of: (i) the number and timing of copulations; (ii) the proportion of copulations that result in insemination; (iii) the number of sperm inseminated; and

(iv) the rate of loss of previously inseminated sperm from the reproductive tract, to make predictions of levels of sperm precedence. We then test these predictions by comparing them with levels of precedence in captivity measured by Birkhead *et al.* (1988*a*), (reanalysed by T. R. Birkhead, unpublished results): (i) a single EPC performed after the last of several copulations by the pair male fertilizes 53.7% (95% confidence limits: 41.6–66.1%) of the potentially fertilizable eggs (allowing for the timing of copulation, fertilization and oviposition) ('EPC experiment'); (ii) when males are switched during the female's fertile period, the second male fertilizes 75.3% (65.2–83.2%) of the potentially fertilizable eggs ('mate-switching experiment'). A fit between the predicted and observed levels of extra-pair paternity (EPP) or second-male precedence would imply that no special mechanism is required to explain the level of sperm precedence observed in the zebra finch.

2. METHODS

We modelled the female's reproductive tract as a single 'compartment' (see Lessells & Birkhead 1990). Sperm are deposited into this compartment at insemination, and then disappear at a constant rate. Any remaining sperm are eventually used for fertilization. We assumed that the probability of each male fertilizing an egg depends only on the proportion of sperm in the reproductive tract that is his at the time of fertilization. This model is the simplest possible linear model, i.e. it embodies a situation in which sperm from different ejaculates experience the same rate of loss from the reproductive tract, and are not favoured or disadvantaged by the order in which they are introduced into the tract

Table 1. *The pattern of copulations and number of sperm inseminated by paired male zebra finches*

(The number and timing of copulations is that observed in video trials of ten paired males (Birkhead *et al.* 1988*a* (reanalysed by T. R. Birkhead, unpublished results)). The number of inseminations was estimated by assuming that 67% of copulations transfer sperm (Birkhead *et al.* 1989). The number of sperm inseminated was estimated by assuming that 7.815×10^6 ($\pm 4.035 \times 10^6$ s.d.) sperm are inseminated in the first successful copulation by a male, and 1.699×10^6 ($\pm 1.339 \times 10^6$) in subsequent successful copulations by the same male ($n = 30$ males; Birkhead & Fletcher 1995; T. R. Birkhead, E. J. Pellatt & F. Fletcher, unpublished results).)

day	number of copulations	number of inseminations	number of sperm inseminated $\times 10^6$
-5	2.304	1.544	8.739 ^a
-4	1.836	1.230	2.090
-3	1.584	1.061	1.803
-2	2.448	1.640	2.787
-1	2.088	1.399	2.377
0	1.476	0.989	1.680
1	0.804	0.539	0.915
2	0.612	0.410	0.697
3	0.264	0.177	0.300
4	0.168	0.113	0.191
5	0.192	0.129	0.219

^a $8.739 = 7.815 + 0.544 \times 1.699$.

(Parker's (1990) 'loaded raffle') or through physiological discrimination by the female. Success of sperm is still affected by the timing of insemination but only because, with a constant loss rate, more sperm from earlier ejaculates will have disappeared by the time of fertilization. More complex linear models are possible (Lessells & Birkhead 1990) but first, empirical measurements of the parameters included in such models are lacking, and second in linear models asymptotic levels of sperm precedence are dominated by the loss rate from only one compartment, and that loss rate will be equal to the observed rate of disappearance in all compartments in the system (Lessells & Birkhead 1990).

Within the framework of this model, the pattern of insemination by two (or more) males can be varied in terms of both the timing and size of ejaculates and the probability of fertilization of each egg in the clutch by each of the males predicted. Initially we modelled the paternity of clutches of six eggs (as in domesticated zebra finches) when the pair male made the normal pattern of about 14 copulations between days -5 (relative to the laying of the first egg) and +5 (see table 1), and a different male made a single EPC between days -5 and +3. We then modified the pattern of insemination by each of the two males to predict the expected paternity of chicks in each of Birkhead *et al.*'s experiments (1988*a*).

The first insemination by any male was assumed to transfer about 8 million sperm, subsequent copulations by the same male to transfer about one and a half million sperm (see table 1). When a male was expected to make less than one whole insemination on his first day of copulation, the larger ejaculate size was assumed to apply to the remaining fraction of a 'first insemination' made on subsequent days. The number of sperm inseminated by each male on each day was calculated by summing the amount of sperm transferred in each insemination (see table 1).

Of copulations by zebra finches, 67% result in insemination of the female (Birkhead *et al.* 1989). This creates stochastic variation in the amount of sperm inseminated, which is expected to alter the predicted average paternity. We investigated the magnitude of this effect by carrying out preliminary simulations for single EPC models in which; (i) insemination by both males was deterministic (i.e. each copulation resulted in 0.67 of an insemination); (ii) insemination by the pair male was deterministic, and by the extra-pair male stochastic (i.e. each copulation resulted in insemination with a probability of 0.67; this was determined in the simulations using a random-number generator); and (iii) inseminations by both males were stochastic. These simulations showed that whereas stochasticity in insemination by the extra-pair male had a large effect, stochasticity in insemination by the pair male generally altered the predicted paternity by less than 1%. Similar simulations showed that variation in ejaculate size of first and subsequent ejaculates by either male (ejaculate size chosen from mean-s.d., mean and mean+s.d. with equal probability; see table 1 for means and s.d.s) also had a trivial effect on the predicted paternity. We therefore used models in which insemination by the pair male was deterministic, and by the extra-pair male stochastic. This allowed us to calculate an exact expected mean EPP ($= 0.67 \times \text{EPP}$ when the extra-pair male does inseminate the female), rather than estimating the expected mean from multiple runs of the simulation. The effect of stochasticity in insemination in simulations of the mate-switching experiment was rather more variable, but because the effect was generally small (about 1–2%) and occurred in both directions, and an overall prediction could only be made by summing separate predictions for each trial (see below), we used deterministic models to make predictions for the mate-switching experiment.

In birds, fertilization of an egg occurs about 30 min after it is ovulated, and about 1 day before it is laid (Howarth 1974). In zebra finches, eggs are laid early in the morning, and copulations are concentrated in the same period of the day (Birkhead *et al.* 1989). Because sperm take time to reach the infundibulum (the site of fertilization at the top of the reproductive tract), we have made the simplifying assumption that all the copulations by the pair or first male on any day occur immediately after fertilization of the egg ovulated on that day. To be consistent with Birkhead *et al.*'s (1988*a*) protocol, we have assumed that EPCs, and copulations made by the second male on the day of mate switching, are made 4 h later. Thus the earliest egg that a copulation (pair or extra-pair) on day 0 (the day that the first egg is laid) can fertilize is that ovulated on day 1 and laid on day 2, i.e. the third egg.

While the sperm is in the reproductive tract we assume that it suffers an instantaneous loss rate of 0.026 ± 0.007 (s.e.) h^{-1} , as estimated from the decline in the number of sperm adhering to the vitelline layer of sequentially oviposited eggs (Birkhead *et al.* 1993*b*). The extent to which this loss rate reflects use in fertilization, death or inactivation in the reproductive tract, or evacuation from the reproductive tract is unknown, but is immaterial to the predictions of the model. The finite survival rate of sperm on day d ,

$$D_d = \exp(-t \cdot r), \quad (1)$$

where r is the hourly instantaneous loss rate and t is the number of hours on day d that the sperm was present in the reproductive tract. Thus for the sperm of an extra-pair male, or of the second male on the day of switching, D_d for the day of insemination is 59.5% ($\exp(-20 \times 0.026)$). In all other cases D_d is 53.6% ($\exp(-24 \times 0.026)$). If N_i sperm are inseminated on day i , the number of them surviving to be able to take part in fertilization on day f ,

$$S_{i,f} = N_i \cdot \prod_{a=i}^{f-1} (D_a). \quad (2)$$

Thus, the total number of sperm from a given male, available to take part in fertilization on day f ,

$$S_{\text{tot},f} = \sum_{i=-5}^{f-1} (S_{i,f}). \quad (3)$$

The probability of a given male fertilizing an egg ovulated on day f is then his value of $S_{\text{tot},f}$ divided by the sum of the values of $S_{\text{tot},f}$ for all males who have copulated with the female.

3. RESULTS

We used the model to predict levels of sperm precedence. Figure 1 shows the expected probability of EPP for each egg when a single EPC is made between days -5 and $+3$. The probability of EPP varies through the laying sequence of eggs. Sperm cannot fertilize eggs laid less than 2 days after insemination (see above), so that eggs laid early in the laying sequence may have no EPP. After the last insemination by any male the number of each male's sperm will continue to decrease, but the proportions will not, so that the probability of EPP would then remain constant. Thus when, as in this case, the pair male continues to copulate after the EPC, the predicted EPP drops from an initial peak. In general, the later the EPC, the higher the level of EPP in those eggs that could be fertilized, but the lower the number of eggs that could be fertilized (see figure 1). This is because the amount of the pair male's sperm in the reproductive tract reflects the balance

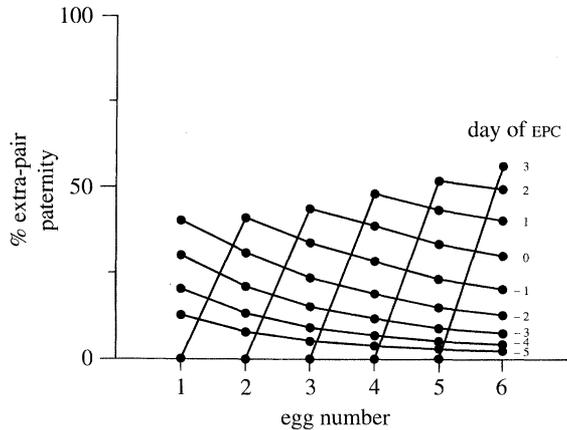


Figure 1. Predicted levels of EPP when pair males make about 14 copulations between days -5 and $+5$ (see table 1), and there is a single successful EPC between days -5 and $+3$. The EPC was assumed to occur 4 h after fertilization of the egg ovulated on that day. All other copulations were assumed to take place immediately after fertilization of the egg ovulated on that day. While in the reproductive tract, sperm are assumed to disappear at an instantaneous rate of 0.026 h^{-1} . The probability of paternity was determined by the proportion of sperm in the reproductive tract at the time of fertilization.

between gains through insemination and losses through constant disappearance. In zebra finches, this balance results in a decline in the amount of pair male's sperm in the reproductive tract over the period when the clutch is being fertilized (although this is not necessarily true for other rates of insemination and disappearance). Thus the later the EPC, the higher the proportion of sperm in the tract that it represents.

Birkhead *et al.*'s (1988*a*) single EPC experiment represents the case where the EPC occurs on day 0, and the pair male achieves the normal pattern of copulations until day -1 (see table 1), and 0.2 copulations on day 0 in the 1 h that he has access to the female (further analysis of video trials (Birkhead *et al.* 1988*a*: T. R. Birkhead, unpublished results)). As a result, the extra-pair male can only fertilize eggs laid on or after day 2, but is then predicted to achieve a constant 49.2% paternity of eggs. This is well within the observed 95% confidence limits of 41.6–66.1% (mean 53.7%).

In Birkhead *et al.*'s (1988*a*; T. R. Birkhead, unpublished results) mate-switching experiment, mate switching in each trial occurred after a variable number of days of copulation by the first male (mean = 3.6; range = 2–5), and a variable number of days before the female began egg laying (2.0; 0–4). We therefore predicted the pattern of copulation by each male from that observed in the separate video trials of mate switching. In these video trials, the number of copulations by the first male did not vary with day number relative either to laying (linear or quadratic terms) or mate switching, nor did it differ between the day of mate switching and other days. We therefore assumed that first males in the paternity trials made the observed mean rate of 1.268 copulations per day. The number of copulations by second males in the video trials varied only relative to the day of laying (number of copulations per day = $0.874 - 0.266$ (day

number); $F_{1,62} = 5.98$, $p = 0.017$). We used this relation to estimate the number of copulations made each day by second males in each of the paternity trials. Because of the variation in the timing of mate switching we predicted paternity separately for each paternity trial, and summed over all trials to obtain an overall prediction of paternity by the second male of 77.9%. This is again well within the observed 95% confidence limits of 65.2–83.2% (mean 75.3%).

4. DISCUSSION

Our model has considerable success in predicting levels of sperm precedence: the predictions for both of Birkhead *et al.*'s (1988a) experiments lie well within the 95% confidence limits for the observed values. We are thus able to conclude that special mechanisms of sperm competition are not necessary to explain measured sperm precedence in zebra finches. This conclusion is not affected by any difference in parameters such as ejaculate size between captive and wild birds: this is because our main aim was not to predict levels of sperm precedence in the wild, but to use comparisons of observed and predicted levels of sperm precedence in captivity to test ideas about the mechanism of sperm competition. However, we have made several simplifying assumptions and made predictions for only a single value for the loss rate of sperm and for the relative numbers of sperm inseminated at first and subsequent inseminations. We therefore carried out further analysis to determine how sensitive our predictions were to these assumptions.

First, the estimate of instantaneous loss rate has a large standard error. The predicted second male precedence when the model was rerun using values one standard error below or above the mean was 43.5–53.3% for the EPC experiment and 71.4–82.7% for the mate-switching experiment. Moreover, the method used to estimate the disappearance of sperm (counting sperm adhering to the vitelline layer) prevents any estimate of disappearance rate being made for the period before the fertilization of the first egg. Loss rates might be much higher once eggs have begun to be fertilized, for instance if loss-free storage is physiologically incompatible with use of sperm for fertilization. We therefore repeated the calculations with a zero loss rate until the time of fertilization of the first egg. This resulted in lower predicted second male precedence of 31.5% for the EPC experiment and 52.4% for the mate-switching experiment, but did not alter the qualitative pattern of EPP through the laying sequence of eggs. A higher loss rate until the fertilization of the first egg would have the opposite effect on EPP, but is not so likely biologically.

Second, the standard errors for the number of sperm inseminated at first and subsequent copulations are also large. Because it is the ratio of sperm from different males that is used in the model to determine the expected EPP, it is only the ratio of the numbers of sperm at first and subsequent copulations which is important. The standard error of this ratio is approximately 1.41 (Armitage & Berry 1987), and when we reran the model using values one standard error below

Table 2. *The effect of disappearance of sperm and ejaculate size on predicted levels of second male sperm precedence for Birkhead et al.'s (1988a) (a) EPC experiment (b) mate-switching experiment*

	sperm disappearance rate/h ⁻¹		
	0	0.026	
(a) EPC experiment			
ratio of sperm in	1	8.4%	26.6%
1st: subsequent ejaculates	4.6	20.3%	49.2%
(b) mate-switching experiment			
ratio of sperm in	1	41.6	69.4
1st: subsequent ejaculates	4.6	46.3	77.9

or above the mean, the predicted second male precedence was 44.5–52.1% for the EPC experiment and 76.1–78.9% for the mate-switching experiment. The general conclusion from these sensitivity analyses is that increased accuracy in the parameter estimates or in the experimentally determined values of second male precedence would increase the power of the model to discriminate between different hypotheses concerning the mechanisms of sperm competition.

Our model also assumes that all inseminated sperm enters the single compartment in the model, which might not be the case if, for example, females expel sperm from the reproductive tract. This would have no effect on the predictions of the model if the same proportion of all ejaculates are expelled by females (because only relative sperm numbers are important), but would alter the expected level of precedence if females expelled a different proportion of ejaculates from different males, or on different days relative to laying. We have no information on these possibilities. In addition, the single compartment of the model implies that there is essentially only one 'route' by which inseminated sperm can reach the infundibulum. Because it is biologically implausible that sperm storage tubules (ssts) do not function in sperm storage, this amounts to assuming that sperm cannot pass directly up the reproductive tract, bypassing the ssts. The ability of sperm to exploit any 'fertilization window' (Cheng *et al.* 1983) by moving directly up the reproductive tract would increase the predicted level of last male sperm precedence (Lessells & Birkhead 1990).

Finally, the controlled circumstances under which the number of sperm inseminated were measured in captivity preclude differences in male quality contributing to differences in ejaculate size between pair and extra-pair males. In the wild, females may choose good quality males with whom to perform EPCs (Kempenaers *et al.* 1992; Møller 1994). These males may also have larger ejaculates (Sheldon 1994), thus exaggerating the disproportionate success of EPCs.

In our model, both constant disappearance of sperm and differential ejaculate size may contribute to the disproportionate success of EPCs. To judge their relative importance we also predicted EPP when no sperm disappeared, or when all ejaculates contained the same number of sperm (see table 2). These calculations

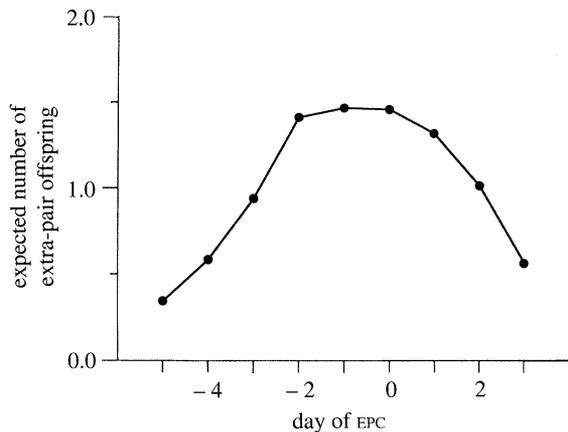


Figure 2. The optimum time for a single EPC. The expected number of extra-pair offspring was determined by summing the expected EPP for each chick in the brood (see figure 1), and reaches a maximum when the single EPC takes place on day -1.

suggest that, in the case of single EPC, both constant disappearance of sperm and differences in ejaculate size have approximately equal effects, and both are needed to achieve high levels of EPP. In the case of mate switching, disappearance of sperm has an important effect relative to that of ejaculate size differences.

Our conclusion that observed levels of sperm precedence in zebra finches do not require any special mechanism of sperm competition contrasts with that of Lessells & Birkhead (1990) for the domestic chicken *Gallus domesticus*. A series of mathematical models similar to that used here suggested that observed levels of sperm precedence measured by Compton *et al.* (1978) could only be explained by a nonlinear model embodying some advantage to the last male, for instance sperm displacement or stratification. Recent failed attempts to replicate the empirically measured value of second-male precedence (T. R. Birkhead & G. J. Wishart, unpublished results) used in these models suggest that unreliability in this value may account for the discrepancy between the conclusions for domestic chickens and zebra finches.

An important motive for studying mechanisms of sperm competition is as a first step in a functional understanding of the copulation behaviour of males and females. Figure 1 suggests that an individual able to achieve a single EPC faces a trade-off, governed by the timing of that EPC, between the number of young that the EPC can potentially father in the brood and the likelihood of paternity of each. By summing the expected EPP over all offspring in the brood (see figure 2), it is possible to predict the optimal timing of an EPC. The model suggests that maximum EPP in the whole brood is achieved when the EPC occurs on day -1, although there is little reduction in EPP if it occurs on day 0 or -2. Mate guarding and extra-pair courtship in the wild and in aviaries do not show a close fit with this prediction of maximum mate guarding and extra-pair courtship on day -1. In the wild, mate guarding (in the form of following) remains at a constant high level throughout the female's fertile period and extra-pair courtship peaks on days 0 and 1 of the female cycle (Birkhead *et al.* 1988*b*). In aviaries, mate guarding (in

the form of frequent copulations) does peak on day -1, but extra-pair mounting peaks earlier, on day -3 of the female's cycle (Birkhead *et al.* 1989). The poor fit is not surprising given that the optimal timing of an EPC is an evolutionary game between the pair male, the extra-pair male and the female, in which males may have less than perfect information about the timing of laying. However, our example illustrates the kinds of functional predictions that can be made given a knowledge of the mechanism of sperm competition.

In conclusion, the simple model presented in this paper makes predictions which are in agreement with the observed levels of precedence in zebra finches in captivity. It suggests, therefore, that the outcome of sperm competition in this species may simply be a consequence of the number of sperm inseminated and the constant disappearance of sperm from the reproductive tract, rather than any specialized mechanism. It therefore serves to caution against invoking mechanisms that entail an advantage to the last male to mate (other than constant disappearance of sperm) or the active physiological intervention of the female in determining the outcome of sperm competition. However, the predictions of our model are sensitive to the parameter estimates, so further empirical work making more accurate estimates will increase the power to discriminate between hypotheses: both theoretical models and empirical studies are needed to make progress in understanding mechanisms of sperm competition.

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