

## Sperm competition in birds

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Sperm competition in birds occurs when a female is inseminated by more than one male during a single breeding cycle. Despite most birds being socially monogamous, sperm competition is widespread and results in frequent extra-pair paternity. Sperm competition is a fundamental part of sexual selection since it results in differential reproductive success among males. Male adaptations to sperm competition include relatively large testes, large sperm stores and long spermatozoa, mate guarding and frequent pair copulations. Females show no obvious morphological adaptations to sperm competition but, by controlling whether copulations are successful, they probably determine its frequency and extent. Despite this, the evolutionary benefits females acquire from extra-pair fertilizations are poorly understood. Experiments in which females are inseminated with equal numbers of spermatozoa from two males usually show last male sperm precedence. Understanding the mechanism of sperm competition requires understanding of why the last male to inseminate a female fertilizes a disproportionate number of eggs. The data from sperm competition studies on the domestic fowl, turkeys and zebra finches are consistent only with a passive sperm loss model of sperm competition. The mechanism is as follows: after insemination, spermatozoa enter the sperm storage tubules located in the oviduct, from which they are lost at a constant rate over days or weeks. All else being equal, the interval between two inseminations determines the probability of fertilization: the second of two inseminations fertilizes most eggs simply because, by the time fertilization occurs, fewer of these spermatozoa have been lost. Other factors also affect the outcome of sperm competition: the timing of insemination relative to oviposition, the differential fertilizing capacity of males and differences in the numbers of spermatozoa inseminated; as a consequence, last male sperm precedence is not automatic. On the basis of the mechanism of sperm competition, the optimal strategy for both males and females to maximize their likelihood of extra-pair fertilization is to copulate with an extra-pair partner as close as possible to the onset of oviposition.

A common assumption about reproduction is that the spermatozoa in the vicinity of ova around the time of fertilization are from a single male. However, for a wide range of organisms, both internal and external fertilizers, this assumption is almost certainly wrong. It is wrong because among internal fertilizers, females typically copulate with more than one male during a single reproductive cycle, and among externally fertilizing animals, often several males simultaneously release spermatozoa near a spawning female. When the ejaculates from two or more males compete to fertilize the ova of a particular female, the process is referred to as sperm competition (Parker, 1970). Sperm competition is virtually ubiquitous and its biological consequences are considerable. The widespread nature of sperm competition means that all reproductive features, including behaviour, anatomy and physiology, have evolved in a context of competitive fertilization.

Sperm competition is a part of sexual selection: the differential reproductive success of individuals. Until the 1970s it was assumed that sexual selection ceased with the acquisition of partners by each sex, either via male–male competition or female choice (Andersson, 1994). However, studying insects in the early 1970s, G. A. Parker realised that sexual selection can continue beyond copulation. Parker (1970) recognized that

any male that could use his own spermatozoa to fertilize ova, in the presence of spermatozoa from other males, would be at a large selective advantage. At the same time, any male that allowed this to happen to a female that he had recently inseminated would be at a selective disadvantage. In other words, sperm competition generates conflicting selection pressures, and as such constitutes a powerful evolutionary force. On the one hand selection favours males possessing those traits that enable them to fertilize already inseminated females, but at the same time it favours males possessing traits that prevent ‘their’ female from being inseminated or fertilized by other males (Parker 1970). It is no coincidence that the birth of sperm competition as a field of study coincided with the birth of behavioural ecology as a discipline: both are concerned with the way natural or sexual selection operates on individuals. In fact there are two levels at which this, and indeed all other fields of biology, can be discussed: proximate (or mechanistic) and ultimate (or evolutionary) (Alcock and Sherman, 1994). Traditionally, most reproductive biologists have focused on mechanistic aspects (for example, the transport of spermatozoa, capacitation and fertilization) whereas behavioural ecologists have been concerned with the adaptive significance of morphology and behaviours associated

with reproduction. The aim in this review is to consider both the evolutionary and mechanistic aspects of sperm competition and, using birds as an example, to show how addressing questions at both levels has been useful in giving comprehensive understanding of this field.

### Evidence for sperm competition in birds

Because most birds are socially monogamous, with a male and a female working together to raise offspring, sexual relationships were assumed to be exclusive and sperm competition unlikely. Once detailed field studies of individually recognizable birds (that is, marked with colour rings) commenced in the 1950s and 1960s, it became apparent that copulations outside the pair bond (extra-pair copulations) were not uncommon. However, before the selfish gene era of biological interpretation, such observations were dismissed as unimportant or aberrant (Birkhead and Møller, 1992). In the 1970s, behavioural ecology provided a framework in which extra-pair copulations took on a new meaning: males that secured extra-pair fertilizations would leave more descendants than males that didn't, and even more than the males that were cuckolded (Trivers, 1972). The adaptive significance of extra-pair copulations, for males at least, was obvious, and it was clear that sperm competition could be an important component of sexual selection. A major breakthrough occurred in the mid-1980s with the discovery of DNA fingerprinting as a way to assign parentage. Before this, some investigators had used allozymes in parental exclusion analyses (Westneat and Webster, 1994) but, because birds were one of the first groups for which this new methodology was developed, DNA fingerprinting revolutionized the study of sperm competition in birds (Burke, 1989).

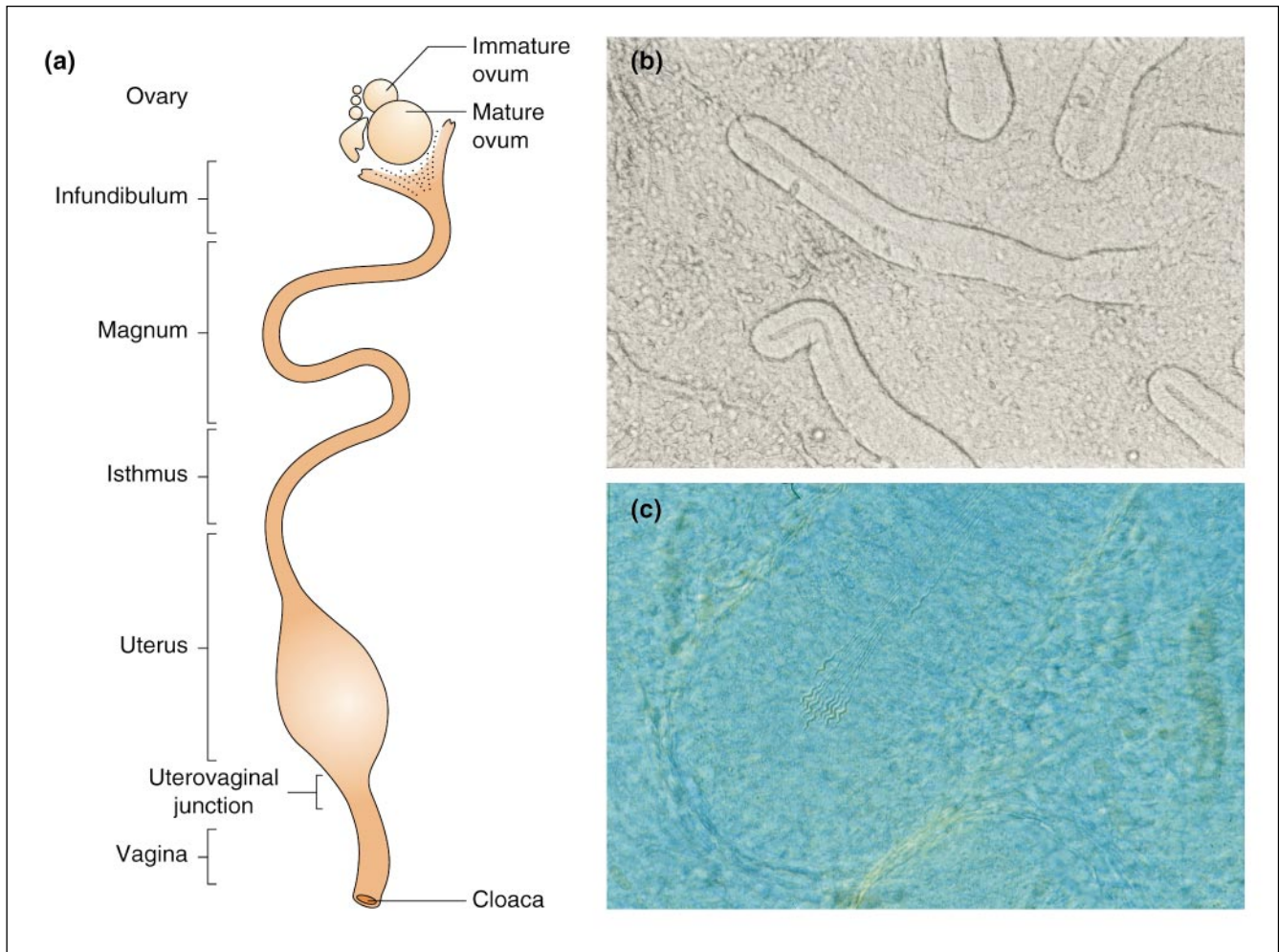
Since the discovery of DNA fingerprinting, parentage studies have been conducted on over 120 species of bird and a number of patterns have emerged. First, the degree of extra-pair paternity varies considerably across different species of socially monogamous birds. In many non-passerines, such as seabirds, herons and birds of prey, the degree of extra-pair paternity is generally low, with 0–5% of all offspring fathered by a male other than the one that helps to rear them. In passerines (song birds, or perching birds), extra-pair paternity is generally more frequent, often with 10–20% and occasionally as many as 70% of all offspring fathered by extra-pair males (Birkhead and Møller, 1992; Westneat and Webster, 1994). Few ecological correlates of the frequency of extra-pair paternity have been found – diet, sociality, and habitat do not appear to have much influence on the degree of extra-pair paternity. However, one pattern that has been detected is the link between extra-pair paternity and plumage dimorphism. Sexually dimorphic species are those in which males are brighter and more ornamented than females – a phenomenon resulting from either male–male competition or female choice for males with elaborate traits. Such dimorphism is not unexpected in polygynous species, such as pheasants and peafowl, where males attract harems of females, but the occurrence of sexual dimorphism among socially monogamous species had always been enigmatic. In a cross-species comparison, Møller and Birkhead (1994) showed that the amount of extra-pair paternity was positively correlated with the extent of sexual dimorphism, indicating that bright plumage in male birds has evolved

because it increases the likelihood of such males obtaining extra-pair copulations.

### Adaptations to sperm competition

Female birds show no gross morphological adaptations to sperm competition but do exhibit sophisticated behaviours enabling them to elude their guarding partner and engage furtively in extra-pair copulations (Kempnaers *et al.*, 1992). Nonetheless, their reproductive anatomy and physiology predisposes female birds, to some extent, to sperm competition. Females have a protracted fertile period during which inseminations may result in fertilized ova. Because they possess several hundred to several thousand sperm storage tubules in the uterovaginal junction (Fig. 1), spermatozoa can be stored for several days or even weeks before fertilization and each ovum is fertilized separately, usually on successive days (Etches, 1996). A copulation, within-pair or extra-pair, at any time during the fertile period has some chance of fertilization. Paired males employ a range of paternity guards to minimize the risk of being cuckolded and having to bear the energetic cost of rearing the offspring of another male. In passerine birds, males typically follow every move of their fertile partner, a behaviour known as mate guarding. Studies in which guarding males have been removed temporarily have shown that extra-pair copulation is more likely without a guarding male (Birkhead and Møller, 1992). For colonial birds and raptors, mate guarding by close following is less feasible because one member of the pair usually remains at the nest to defend it. Instead, these birds use frequent pair copulations to minimize their risk of being cuckolded – simply by inseminating more spermatozoa they increase their likelihood of fertilization (Birkhead and Møller, 1992). If sexual selection favours males that minimize the risks of being cuckolded, it simultaneously favours males that can overcome these paternity guards. One obvious way is by sneaky behaviour, and many studies of extra-pair copulation in birds have reported the remarkable behavioural strategies that males adopt to get close enough to a female to attempt an extra-pair copulation without being detected by her partner.

Perhaps the most ubiquitous male adaptation to sperm competition in birds and other taxa is a morphological one: testis size. In birds, as in most other taxa, testes mass scales allometrically with body mass, with an exponent of 0.67. However, testes are larger, relative to body mass, in those species in which sperm competition is more intense (Møller, 1991). Large testes enable a male to produce large numbers of spermatozoa and, in turn, this has an important effect on his likelihood of fertilization. These spermatozoa can be allocated to either many small or a few large ejaculates. We know very little about the numbers of spermatozoa males transfer to females but, through the judicious use of model females with false cloacas, it has proved possible to collect this type of information (Birkhead *et al.*, 1995a). Sperm morphology (size and structure) also appears to have been shaped by sperm competition. The variation in total sperm length in different passerines is remarkable, ranging from 50 to 300  $\mu\text{m}$ , and a comparative study of passerine birds showed that spermatozoa length is greater in those species in which extra-pair paternity is greatest (Briskie *et al.*, 1997). This implies that longer



**Fig. 1.** (a) Diagram of the female reproductive tract showing the location of the uterovaginal junction where the sperm storage tubules occur (modified from Birkhead, 1996). (b) Photograph of the sperm storage tubules of Japanese quail *Coturnix japonica*. (c) Photograph of a single sperm storage tubule containing spermatozoa from a chaffinch (*Fringilla coelebs*).

spermatozoa confer some advantage, to either the pair male or extra-pair male, when sperm competition is intense. However, the way this advantage operates is presently unclear.

### Levels of analyses and two questions

There are two fundamental questions about sperm competition: why do females engage in extra-pair copulations and when they do, what determines which male fathers most offspring? These are, respectively, evolutionary (functional) and mechanistic questions. Female animals in many taxa copulate routinely with more than a single male during a breeding cycle (Smith, 1984; Birkhead and Møller, 1998). Why they do so remains one of the biggest puzzles in behavioural ecology. It seems particularly bizarre in socially monogamous birds for a female to form a pair-bond with one male but then engage in extra-pair copulations. The adaptive significance of extra-pair copulations for females is a major issue and two categories of benefit have been proposed: (i) direct benefits (those that a female gets for herself) and (ii) indirect (genetic) benefits

(which she acquires for her offspring). The most frequently suggested direct benefit is fertility insurance, but there is very little evidence for this in birds. Genetic benefits include the production of genetically diverse offspring or, more controversially, genes for attractiveness or viability. The last two genetic benefits are problematic because it is generally thought that traits closely linked with fitness have low heritabilities (Andersson, 1994), although this view has recently been challenged (Pomiankowski and Møller, 1995; Rowe and Houle, 1996, but see Alatalo *et al.*, 1997). Since, in some bird species at least, females engage in extra-pair copulations preferentially with males that are either older or more attractive than their social partner, this has been taken as evidence that females are seeking genes for attractiveness or viability. However, few studies have provided convincing evidence that females acquire genes for attractiveness or viability from extra-pair copulation partners (but see Hasselquist *et al.*, 1996).

The second major question is a mechanistic one: if females copulate with more than one male, what determines the outcome of sperm competition? This question is important simply

in terms of understanding the processes of sperm transport and fertilization, but if we understand the rules that determine fertilization success, it provides us with a better opportunity to understand the adaptive significance of male and female physiology, morphology and behaviour.

### The mechanism of sperm competition in birds

The ancient Greeks had some idea about sperm competition mechanisms since they knew from observation that if two cockerels copulated with the same hen, a mixed brood could result. More importantly in the present context, they also knew that the cockerel that copulated last would father most offspring (Peck, 1943). This effect is referred to as last male sperm precedence, and is now known to be widespread in several bird species (Birkhead and Møller, 1992). It also occurs in other taxa, especially insects (Birkhead and Parker, 1997). In some animal groups, first male precedence occurs, but this is relatively rare. In mammals, there is no consistent pattern of precedence because fertilization is determined by the timing of insemination relative to ovulation (Ginsberg and Huck, 1989). The key to understanding the mechanism of sperm competition in birds involved discovering what determines last male precedence.

Because the events after insemination and associated with fertilization take place at a microscopic level, it is extremely difficult to follow the fate of particular spermatozoa. Two alternative approaches have been adopted. Either to: (i) infer mechanisms from the structure of the female tract, particularly the oviductal sperm storage sites, or (ii) to construct mathematical models that assume particular processes and then compare predicted and observed results. The earliest studies of sperm competition in birds were conducted by poultry biologists. It was well known that female domestic fowl *Gallus domesticus* and turkeys *Meleagris gallopavo* could store spermatozoa for protracted periods and these studies were motivated in part by a need to know the minimum interval between inseminations from different males to maintain genetically pure stocks. One of the most influential of these studies was performed by Compton *et al.* (1978). In a reciprocal experimental design involving the sequential artificial insemination of equal numbers of spermatozoa from two male genotypes 4 h apart, these authors found that regardless of which genotype was inseminated first, approximately 77% of offspring were fathered by the second insemination. They attributed this last male precedence to the morphology of the sperm storage tubules. Domestic fowl possess a large number (~ 20 000) of blind-ending sperm storage tubules located at the junction of the uterus and vagina (Fig. 1) and Compton *et al.* (1978) assumed that spermatozoa from the first insemination positioned themselves at the distal end of the tubule with spermatozoa from successive inseminations becoming stratified behind each other so that a 'last in – first out' system operated. However, there was no direct evidence for the stratification of spermatozoa within the sperm storage tubules and subsequently Birkhead *et al.* (1995b) showed that the experiment of Compton *et al.* (1978) was flawed because it confounded the interval between inseminations with the time of insemination relative to oviposition. By making their first insemination soon after oviposition, a time when spermatozoa uptake by the female tract is at its lowest (see Johnston and Parker, 1970), Compton

*et al.* (1978) unwittingly gave the spermatozoa from the second insemination a huge advantage – hence the marked last male precedence.

Lessells and Birkhead (1990) used the second approach and constructed three mathematical models that could potentially provide plausible explanations for last male sperm precedence. Briefly, the three models were: (a) stratification, (b) passive sperm loss, and (c) displacement. Subsequent experimental evidence from a study by Birkhead *et al.* (1995b) was consistent with the passive sperm loss model, which is now discussed in detail.

### The passive sperm loss model

This model proposes that spermatozoa are lost from the female reproductive tract at a constant rate and that the greater the time interval between two inseminations (containing equal numbers of spermatozoa), the larger the last male effect (Lessells and Birkhead, 1990; Birkhead and Biggins, 1998). This is simply because by the time fertilization occurs fewer of the spermatozoa of the second male have been lost (Fig. 2).

In the passive sperm loss model:

$$\ln(p/(1-p)) = d + \mu T \quad (1)$$

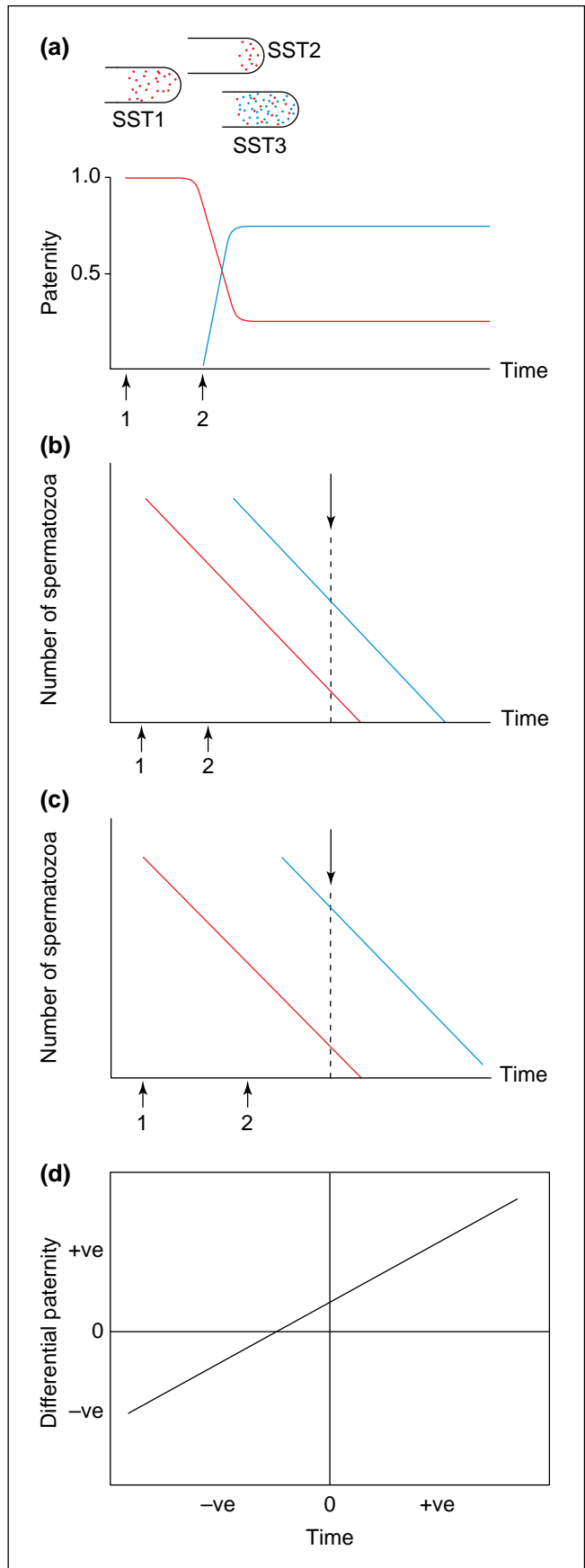
$\ln(p/(1-p))$  is referred to as differential paternity, where  $p$  = the proportion of offspring fathered of one of two males (or one of two genotypes) expressed as the log odds, and where  $\ln$  is the natural logarithm.  $T$  = the time interval between two inseminations,  $d$  = the differential fertilizing capacity, and  $\mu$  = the instantaneous per capita rate of sperm loss (see Birkhead *et al.*, 1995b; Birkhead and Biggins, 1998). Differential fertilizing capacity (DFC) is the difference in the ability of different males to fertilize ova and can be estimated either from differential paternity after a single mixed insemination of equal numbers of spermatozoa from two or more males, or from the outcome of reciprocal sperm competition experiments (Birkhead *et al.*, 1995b). The biological bases for DFC are poorly known, little is known about its occurrence in wild birds and, given that it can provide males with a considerable competitive advantage in sperm competition, it is not clear how variation in DFC is maintained in a population. Moreover, it is not known whether DFC is an entirely male effect: breeders of domestic animals often assume it is (for review see Dziuk, 1996), but the possibility exists that some female factors explain some of the variance in fertilization success (for example, Zeh and Zeh, 1996). The instantaneous per capita rate of sperm loss can be estimated directly: Wishart (1987) showed that the number of spermatozoa trapped on the outer perivitelline layers of successive eggs provides a good measure of the rate of loss of spermatozoa from the sperm storage tubules (for review see Bakst *et al.*, 1994). The instantaneous per capita rate of loss ( $\mu$ ) is the slope of the relationship between the natural log number of spermatozoa on the perivitelline layer of successive eggs and time ( $h$ ) (Lessells and Birkhead, 1990). For domestic fowl,  $\mu = 0.0128h^{-1} \pm 0.0014$  SEM (G. J. Wishart, cited in Lessells and Birkhead, 1990).

With two inseminations containing equal numbers of spermatozoa the model makes four predictions: (i) differential paternity is positively and linearly related to  $T$ , the time between inseminations, (ii) the slope of this relationship is  $\mu$ , the same as the per capita rate of sperm loss from the female tract,

(iii) the intercept of this linear relationship is  $d$ , the differential fertilizing capacity, and (iv) the ratio of offspring from the two inseminations is the same regardless of the time between inseminations.

Birkhead and Biggins (1998) tested the model using data from four studies of sperm competition in poultry (three of domestic fowl and one of turkeys). The protocols of all experiments were similar and comprised two artificial inseminations of equal volumes of semen or equal numbers of spermatozoa from different genotypes made at different intervals. The experimental design was reciprocal: in half the cases, spermatozoa from one genotype was inseminated first and in the other half, the spermatozoa from the other genotype was inseminated first. The results of these studies confirmed that almost all of the predictions of the passive sperm loss model were supported (Birkhead and Biggins, 1998), providing good evidence that passive sperm loss is the most important mechanism creating last male sperm precedence in birds. However, it is

**Fig. 2.** The passive sperm loss model. (a) Temporal pattern of paternity after two inseminations of equal size at some fixed interval. After the first insemination, a typical sperm storage tubule (SST1) contains only spermatozoa from this male. By the time the second insemination occurs, many of the spermatozoa from the storage tubules have been lost (SST2), so once the spermatozoa from second insemination enter the tubules they are numerically dominant (SST3). The lines indicate paternity by each male: the ratio of offspring from the two males after the second insemination remains constant. After the first insemination, only this male fathers offspring, but by the time the second insemination occurs, the number of spermatozoa in the tubules from the first male is relatively low (SST2), and the spermatozoa from the second male fertilizes the majority of eggs. Although the total numbers of spermatozoa in the tubules continues to decline with time (SST4), the ratio of spermatozoa and, hence, the offspring of the two males, remains constant. (b) Schematic representation of the rate of loss of spermatozoa from the female tract after two inseminations of equal size (arrow 1 and arrow 2)  $N$  hours apart: the straight lines represent  $\mu$ , the instantaneous per capita rate of spermatozoa loss from the female tract. The third arrow indicates the time of fertilization: at this point the spermatozoa from the second male outnumber those of the first, hence, second male precedence. (c) When the interval between the two inseminations is increased, a greater proportion of the spermatozoa from the first male has been lost by the time of fertilization, so the degree of precedence by the second male is even greater. (d) Predictions of the passive sperm loss model. The relationship between the interval between inseminations ( $T$ ) and differential paternity ( $\ln(p/(1-p))$ ) (Birkhead and Biggins, 1998) is predicted to be linear, with a slope  $\mu$  and an intercept  $d$ , the differential fertilizing capacity. When no difference exists in  $d$  between the two males, the regression line would fall through the origin. The axes span both positive and negative values to accommodate reciprocal experimental designs: for example, with two genotypes, A and B, in half the experiments spermatozoa from male A is inseminated first and in the other half spermatozoa from male B is inseminated first. Differential paternity is that of just one of the genotypes and, hence, will be higher or lower depending on the insemination order. If  $p$  = the proportion of offspring from genotype B, then when spermatozoa from male A is inseminated first, both differential paternity and  $T$  will be positive, whereas when spermatozoa from male B is inseminated first, both differential paternity and  $T$  will be negative (see Birkhead *et al.*, 1995b).



important to note that several factors other than the interval between inseminations affect the outcome of sperm competition and that last male sperm precedence is not automatic. Additional factors include the timing of inseminations relative to oviposition (Johnston and Parker, 1970; Compton *et al.*, 1978: see above), differential fertilizing capacity of males (above) and numbers of spermatozoa inseminated (see below).

### A test of the passive sperm loss model in a passerine

The passive sperm loss model has also been tested in the zebra finch, *Taeniopygia guttata*, a small (12–15 g), sexually dimorphic, colonial passerine that breeds in Australia and the Lesser Sunda Islands (Zann, 1996). Extra-pair copulations occur in the wild, and males show a range of paternity guards, including mate guarding and frequent copulation (Birkhead *et al.*, 1987; 1988a, 1990). In captivity, two experiments demonstrated the occurrence of last male sperm precedence: when a female switched partners half way through her fertile period, and when a female engaged in a single extra-pair copulation after a succession of nine within-pair copulations, the second male to copulate fertilized most eggs (Birkhead *et al.*, 1988b). Three pieces of information are necessary to test the passive sperm loss model: (i) the timing of inseminations relative to egg-laying, (ii) the rate of sperm loss from the female reproductive tract, and (iii) the numbers of spermatozoa inseminated by each male. The first of these was determined by video analysis of birds. The second was determined from counts of spermatozoa on the perivitelline layers of successive eggs after copulations ceased: the instantaneous per capita rate of loss was  $0.026 \text{ spermatozoa h}^{-1} \pm 0.007 \text{ SEM}$ . The third was more difficult to determine because there were no established methods for determining the number of spermatozoa in avian ejaculates reliably during natural copulations. However, male zebra finches will copulate with a model female and deposit their ejaculate within a false cloaca (Pellatt and Birkhead, 1994). The validity of this method was verified by comparing the number of spermatozoa in the seminal glomera of males before and after a single copulation. When the false cloaca method was used, the number of spermatozoa a male zebra finch ejaculates was shown to be determined by the number of spermatozoa in the seminal glomera which, in turn, is determined by the time since the previous ejaculation (Birkhead *et al.*, 1995a). It was possible to estimate the numbers of spermatozoa transferred in the sperm competition experiments from the relationship between ejaculate size and time since previous ejaculation. Levels of paternity can be predicted by combining these values in the passive sperm loss model and comparing them with the values obtained in the two sperm competition experiments: for both experiments the fit was remarkably good (Colegrave *et al.*, 1995).

### Optimal strategies

By understanding the mechanism by which last male sperm precedence occurs, we can start to predict the optimal behavioural strategies of the participants, thereby linking mechanistic and functional questions. Extra-pair copulations involve three participants, (i) the pair female, (ii) the extra-pair male and (iii) the pair male. Assuming both the pair female and

extra-pair male have a common interest in maximizing the number of eggs fertilized by the extra-pair male, predictions about the optimal timing of extra-pair behaviours for both sexes can be made using knowledge of the rules of sperm competition mechanisms. (i) Females 'should' perform extra-pair copulations close to the start of egg-laying. Extra-pair copulations have a reduced chance of success before egg-laying because they are more likely to compete with pair copulations and, as a consequence of passive sperm loss, early copulations will result in fewer spermatozoa at the time of fertilization. Extra-pair copulations taking place after laying starts have an advantage in that there are fewer pair copulations to compete with. However, this is offset by the reduced number of eggs available for fertilization the later the copulation occurs. Extra-pair copulations are seen relatively infrequently in the wild because they often occur furtively, so there are few data to allow us to determine whether females engage in extra-pair copulations at the optimal time (that is, around the start of laying). In some ways, it would be surprising if the match between observed and predicted timing was particularly close because the behaviour of the guarding male partner almost certainly constrains both the pair female and the extra-pair male (see below). The success of extra-pair copulations will also be affected by the number and timing of previous copulations a female has had with her partner. The longer the interval between her last pair copulation and an extra-pair copulation, the greater the likelihood of extra-pair fertilization. This may explain why, in many bird species, females stop copulating with their partner or reduce the rate at which they copulate soon after laying begins – several days before her fertile period ends. This pattern of pair copulations simultaneously ensures that a female has sufficient spermatozoa to fertilize her entire clutch, and increases the likelihood of extra-pair fertilization if she encounters an appropriate male (Birkhead and Møller, 1993a).

(ii) From the perspective of the extra-pair male, the timing of an extra-pair copulation relative to his own partner's fertile period and his pair copulation period is crucial in determining his spermatozoa supplies, ejaculate size and, hence, his likelihood of fertilization. For example, in zebra finches, there is an eightfold difference in the number of spermatozoa per ejaculate in a regular pair copulation ( $\sim 1 \times 10^6$ ) and after a male has not copulated for 5 days ( $\sim 8 \times 10^6$ ) (Birkhead *et al.*, 1995a). This difference in numbers of spermatozoa could have a marked effect on fertilization success. Therefore, it is not surprising that male zebra finches, and many other passerines, tend not to seek extra-pair copulations during their own copulation period (Birkhead and Møller, 1992); by waiting until their partner is incubating they are able to transfer many more spermatozoa if they get the opportunity to engage in an extra-pair copulation.

(iii) The objective of the pair male is to minimize the risk of being cuckolded and the most effective way of doing this is to guard his partner most intensively in the few days around the onset of laying. By remaining close to his partner at this time, he can constrain her extra-pair activities: in virtually no species do females engage in extra-pair copulations while their partner is present. The observed pattern of mate guarding in many passerines follows this predicted pattern very closely, reaching a peak around the start of egg-laying. The fact that male guarding does not remain high throughout the female's entire fertile period suggests that guarding is energetically costly, and that

males balance the costs and benefits to optimize their guarding behaviour.

### Conclusion

Sperm competition is widespread in socially monogamous birds, especially passerines. The adaptive significance of extra-pair copulations for males is obvious: it increases their reproductive success. The adaptive significance of females copulating with more than one male remains more controversial, with little evidence for direct benefits, and only limited evidence for indirect benefits. The main factors determining the outcome of sperm competition (sperm numbers, differential fertilizing capacity, and timing of inseminations relative to other males and to oviposition) and the basic mechanism, the passive loss of spermatozoa from the female reproductive tract, are now well established. However, there is still much we do not know, including the relative importance of female factors (Birkhead and Møller, 1993b; Eberhard, 1996).

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