

# **The operation of sexual selection in the red junglefowl**

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*A mes parents*



## ABSTRACT

Julie M.M. Collet. The operation of sexual selection in the red junglefowl

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Sexual selection acts on traits that increase the reproductive success of an individual in competition with other individuals of the same sex over reproductive opportunities, through intra-sexual competition and inter-sexual mate choice. Because males benefit more from remating than females, they are subject to more intense sexual selection. Modern genetic tools have shown that females often mate promiscuously, thus prolonging sexual selection after insemination through intra-sexual (sperm competition) and inter-sexual (cryptic female choice) episodes. Despite increasing interest in post-copulatory sexual selection, the implications of sperm competition, cryptic female choice and underpinning mechanisms remain little understood. This thesis adopts an integrated approach to quantify the relative importance of post-copulatory episodes in the operation of sexual selection, elucidate their proximate mechanisms in the red junglefowl *Gallus gallus*. By combining behavioural observations of replicate groups with paternity data, I show that female promiscuity decreased the total opportunity for sexual selection in a group, but accounts for an unexpectedly large proportion of the variance in male reproductive success. By comparing the operation of sexual selection on multiple male traits, I show that post-copulatory sexual selection reinforced pre-copulatory sexual selection for male social dominance and that female preferred to mate with compatible males.

I used experiments to study the mechanisms of post-copulatory sexual selection by studying the effect of seminal fluid in sperm competition and cryptic female choice in relation to male status and relatedness. Following previous work indicating that seminal fluid products influence sperm quality in this species, I tested *in vivo* whether the seminal fluid of an ejaculate acts differentially towards sperm from the same ejaculate and rival sperm, and found no evidence for this idea. Finally, I show that cryptic female choice can drastically bias the outcome of sperm competition, and that female fowl might bias paternity toward unrelated males.



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# CHAPTER 1: INTRODUCTION

## Sexual selection

Darwinian selection favours individuals that produce more offspring in their lifetime than other members of the same population. Natural selection explains the evolution of traits that increase survival (Darwin 1859). However, natural selection fails to explain a common trend, that adult males and females often differ within species, and males sport typically exaggerated phenotypes, which diverge more across related species than the more utilitarian female phenotype. Sexual dimorphism is especially paradoxical relative to natural selection theory in species where traits carried by males are so exaggerated that they compromise male survival. To explain this paradox, Darwin proposed that sexual selection acts on variation in the number and in quality of reproductive partners arising from variation in the ability of individuals to compete with conspecific members of the same sex over access to reproductive opportunities (Darwin 1871). More than a century later, Pitnick *et al.* (2001) confirmed Darwin's intuition that sexual selection is a strong evolutionary force (Darwin 1871) by demonstrating that removal of any opportunity for sexual selection in the fruitfly, *Drosophila melanogaster*, causes drastic phenotypical shifts in population in only a few generations: males become smaller, develop proportionally smaller testes and invest less in sperm production. Darwin (1871) recognized two episodes responsible for intra-sexual variation in reproductive success under competitive conditions: (i) intra-sexual selection: direct competition among members of the same sex for access

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to partners and their gametes, and (ii) inter-sexual selection: discrimination of members of one sex by prospective reproductive partners of the opposite sex.

Males are usually the target of sexual selection and have developed ornaments such as the 'musical instruments of the males' in different classes of insects, the colours of males stickleback during breeding season, the long train of the peacock or the horns of stags (Darwin 1871). Therefore, Darwin recognized that sexual selection acted mainly on males whose measurements 'present a greater range of variation' than females (Darwin 1871). However, he did not fully understand the reason why sexual selection is more intense on males than on females and thought it came from the 'eagerness' of males. Almost a century later, Bateman (1948) conducted an experiment that explored the different selective pressures acting on male and female mating success. By using individual *Drosophila melanogaster* with different dominant marker genes, Bateman was able to assign paternity and maternity in 'free mating' populations. He deduced the number of partners of an individual fly from the number of partners with whom this fly had produced offspring (i.e. genetic partners). Bateman noted that: (i) males had greater variance in their number of offspring than females, (ii) males had a greater variance in their number of mates than females, and (iii) the reproductive success of males increased according to their number of mates (i.e. remating rate), while female reproductive success appeared less sensitive to female remating rates. Bateman's results were later generalised as principles. The first two principles propose that males' genetic contribution to the next generation is more variable than that of females, thus creating a higher opportunity for sexual selection in males than in females. The third principle indicates that remating rates covary with offspring number in males but not in females. Taken together, Bateman's three principles propose that the benefits of remating are greater in males and thus explain why sexual selection is more intense in males than in females.

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The biological basis for the higher opportunity and intensity of sexual selection in males is ultimately caused by anisogamy. Anisogamy is the difference in size between male and female gametes. In 1972, Trivers investigated the differential investment of both parents and proposed a biological explanation for Bateman's results (Trivers 1972). Males produce numerous small sperm; each gamete bearing a small cost for the male. Mating with more females and fertilizing additional eggs therefore requires relatively low investment by the male, resulting in large fitness benefits to males associated with increasing the number of offspring. Investment in individual eggs, on the other hand, is more costly to the female because eggs are larger and contain more nutrients than sperm. Female fecundity is therefore limited by resource availability. Trivers (1972) argued that anisogamy creates an imbalance in the potential reproductive rates between sexes: spermatogenesis being faster than oogenesis. This is expected to bias the operational sex ratio (ratio of males ready to mate to females ready to mate) of a population towards males (Clutton-Brock and Parker 1992). Thus, receptive females are a limiting resource, intense competition occurs among males for accessing females, generating intra-sexual selection. In addition, because females have limited possibilities to increase their reproductive success quantitatively, they are particularly sensitive to qualitative changes in reproductive success, and benefit from improving the quality of their offspring in terms of their increased survival or reproductive potential. To improve the quality of her offspring, a female would benefit from choosing a reproductive mate that can convey the highest benefits to her directly and/or to her offspring, setting the scene for female discrimination of males and thus creating inter-sexual selection. Therefore, according to the Darwin-Bateman paradigm, males compete with each other to access females, whilst females choose the best potential father to fertilise their precious eggs.

## Disentangling the effects of intra- and inter-sexual selection

Often males need to both, compete with other males to access females and induce females to mate with them. Intra-sexual selection selects for male traits such as armaments that convey an advantage in male-male competition, while inter-sexual selection promotes traits such as ornaments, which increase the probability that a female will seek to mate with a male. The distinction between armaments and ornaments is not straightforward. Intra- and inter-sexual selection can both select the same male traits so that the episode of sexual selection operating on any trait may be difficult to identify. For example, the colourful dewlap of lizards is used by males of some species such as *Anolis carolinensis* to attract females (Sigmund 1983), and to signal social status by males of other species such as *Urosaurus ornatus* (Thompson and Moore 1991). In some cases, the same male trait might be selected in divergent directions by different episodes of sexual selection. In the dragonfly *Libellula luctuosa*, bigger males are better competitors but females prefer male with an intermediate value of body size (Moore 1990). In other cases, intra- and inter-sexual selection operate consistently on a trait, reinforcing each other (Hunt *et al.* 2009). Heritable male traits that reliably signal competitiveness can allow females to enhance the competitive ability of their offspring through mate choice, and in this case intra- and inter-sexual selection reinforce each other (Berglund *et al.* 1996). Berglund *et al.* (1996) concluded from their analysis of armaments and ornaments in several taxa that intra-sexual selection is the first mechanism to operate on male traits and female mate choice usually reinforce intra-sexual selection (but see Qvarnström and Forsgren 1998). The distinction between intra- and inter-selection processes is further complicated by the fact that females often use male competitive interactions to select partners (Wiley and Poston 1996). For example females incite dominant males to

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interrupt copulation with subordinates in elephant seal, *Mirounga angustirostris*, (Cox and Boeuf 1977), or in the fowl, *Gallus gallus* (Pizzari 2001). This reveals the importance of studying the effects of both intra- and inter-sexual selection simultaneously, because studying one episode isolated from the other may produce a distorted view or hide part of sexual selection (Hunt *et al.* 2009).

### How do females benefit from choosing mates?

*'I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect'* (Darwin 1859).

Since Darwin's proposal of sexual selection theory, female mate choice has been more debated and challenged than male-male competition (Zeh and Zeh 2003). Eager males competing to conquer the heart of the coy female was more socially acceptable than conceding an active role to females (Cunningham and Birkhead 1997; Dewsbury 2005). Beyond arguments of cultural bias against the idea of female mate choice, the evolution of female preference also presented considerable theoretical challenges (Andersson and Simmons 2006). Experimental demonstrations of female mate choice and its role in the maintenance of male ornaments (Ryan 1980; Andersson 1982; Petrie *et al.* 1991) catalysed interest in inter-sexual selection as a powerful evolutionary agent (Birkhead and Møller 1993a). However, the functional significance of female preference remains controversial and not fully understood (Andersson 1994; Andersson and Simmons 2006).

***Direct selection on female preference***

Female preference can be directly selected according to three distinguishable models. First, preferred males can directly increase female fitness. Females directly enhance their fecundity by choosing a male that provide them with high quality territories, energy and food through nuptial gifts, paternal care or efficient protection against predators. Direct benefits can play a major role in a wide range of taxa, even if they are insufficient to explain from the evolution of female mate choice in most species (Kirkpatrick and Ryan 1991; Møller and Jennions 2001; Barbosa and Magurran 2006). Second, female preference may be non-adaptive and the by-product of a naturally selected sensory bias that helps females survive or forage (Ryan 1998). For example, in frugivorous species, individuals may be naturally selected to be attracted by bright colours, which mean healthy food; this attraction being unlinked to reproduction. If some males tend to display a bright coloured phenotype, it would 'fool' the female natural attraction for bright colours and attract them. This hypothesis received indirect support especially in fish where it could explain female preference for bright colours (Rodd *et al.* 2002; Smith *et al.* 2004) and the evolution of some male ornaments (Basolo 1990). Finally, female preference may have evolved through male-female antagonistic coevolution over mating (Holland and Rice 1998). The chase-away sexual selection hypothesis proposes a cycle of evolution where males develop a trait preferred by females (for example through sensory bias), increasing their control on copulation. Then females evolve to resist the male trait and increase their control over mating. Thus, males would benefit from exaggerating this trait or develop a novel trait and the cycle goes on (Holland and Rice 1998; Parker 2006). While there is theoretical support for the 'chase-away' (Gavrillets 2000; Rowe *et al.* 2005), this hypothesis remains debated (e.g. Getty 1999; Rosenthal and Servedio 1999; Cameron *et al.* 2003; Cordero and Eberhard 2003)

***Indirect benefits: Fisherian runaway, good genes and handicaps***

The first argument that male ornaments evolved in response to indirect selection on female preference was proposed by Fisher (1915; 1958), and was subsequently formally explored by Lande (1981) and Kirkpatrick (1982). In a population where female-specific alleles code for female preference for a male trait, such alleles will indirectly be selected to the extent to which: (i) the male trait is favoured by intersexual selection, (ii) and female preference displays positive genetic covariance with the male trait. Positive genetic covariance between preference and trait is expected to arise through linkage disequilibrium when females carrying preference alleles reproduce preferentially with males carrying alleles for the preferred trait. If the female preference and the male trait are genetically linked, this can lead to a self-reinforcing coevolution (Fisher 1915; 1958; Mead and Arnold 2004; Andersson and Simmons 2006). There is limited evidence consistent with the Fisherian runaway (Kirkpatrick and Ryan 1991). In the three-spined stickleback, *Gasterosteus aculeatus*, females prefer intense red males and male colour is variable within populations. A positive genetic correlation was found between male red intensity and female preference for brighter red (Bakker 1993). Similarly, in the field cricket, *Gryllus bimaculatus*, the mating success of a male is transmitted to his male offspring (Wedell and Tregenza 1999). A variant of Fisherian runaway is the 'sexy son' hypothesis, where the choosy female produces sons with a higher mating success at the cost of her daughters' fitness (Weatherhead and Robertson 1979). In the red flour beetles, daughters pay the costs of the production of good sons (Pai and Yan 2002). Cost for daughters may come from intralocus sexual conflict, because males and females can differ in their optimal value for a trait (Chippindale *et al.* 2001). For example, Pischedda and Chippindale

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(2006) found that in *Drosophila melanogaster* high fitness females produce low fitness sons and high fitness males produce low fitness daughters.

Other mechanisms of indirectly selected female choice, known as the ‘indicators’ or ‘good genes’ models, are based on the genetic covariance between viability and the expression of the male ornament preferred by females. Here, female preference is directed toward traits that reveal heritable male quality (Andersson 1994). Zahavi (1975; 1977) proposed the ‘handicap’ principle which posits that male ornaments are particularly costly and handicap a male’s ability to survive. Ornament expression therefore is condition-dependent and a reliable indicator of a male breeding value for viability (Rowe *et al.* 2005). Despite initial scepticism (Kirkpatrick 1986), the ‘handicap principle’ has been formally demonstrated by some genetic models (Pomiankowski 1987; Iwasa *et al.* 1991) and has received some experimental support (reviewed by Johnstone 1995). Hamilton and Zuk (1982) noticed in North American passerines a correlation across species between parasite load and traits that are susceptible to play a role in mate choice (colour and male song). Thus, they hypothesised that females can use male traits to assess male quality and resistance to parasite, consistent with the ‘good genes’ model. The difference from a simple good genes model is that the rapid parasite evolution does favour different resistant genotypes throughout time (Hamilton and Zuk 1982; Kirkpatrick and Ryan 1991). According to the Hamilton and Zuk hypothesis, females rely on an honest signal such as male display to secure a mate that carries heritable resistance to the most common parasites. A meta-analysis on good genes effects in sexual selection showed a consistent but small trend for offspring survival to be positively correlated with their father traits, so that female choice of viability-based traits would be widespread but weak in explaining the full fitness of offspring (Møller and Alatalo 1999). However, studies rarely investigate offspring survival and reproductive success simultaneously, thus potentially missing

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important indirect benefits of female mate choice. On the other hand, these effects may be caused by differential maternal allocation rather than by paternal genetic quality (Sheldon 2000; 2001).

The distinction between mechanisms of Fisherian runaway and the 'indicator' hypothesis is subtle. These mechanisms are not necessarily mutually exclusive, and it may even be unlikely for one process to lead to a stable female preference without the other one occurring at the same time (Kokko 2001; Mead and Arnold 2004; Kokko *et al.* 2006; but see Cameron *et al.* 2003). When considering long-term evolution, indirect benefits of mate choice including both offspring viability and attractiveness lead to similar predictions (Kokko *et al.* 2006). Direct and indirect selection of female mate choice are not necessarily exclusive either. In the butterfly, *Pieris napi*, females produce more eggs after receiving a bigger nuptial gift. Male donations are heritable so that females benefit both directly, from males donation, and indirectly, by producing sons donating large nuptial gifts (Wedell and Karlsson 2003).

### ***Female choice mate compatibility***

An outstanding challenge in sexual selection theory is to explain the maintenance of individual variation in reproductive success despite consistent sexual selection. While we expect the mechanisms of sexual selection outlined above to erode the variability in sexually-selected traits, genetic variation in sexually selected traits persists and is often even larger than in non-sexually selected traits (Borgia 1982; Taylor and Williams 1982; Pomiankowski and Møller 1995). The persistence of genetic variation in sexually selected traits is often referred to as the 'lek paradox'. A lek is a mating system where males display in groups so that females assess male relative quality before making their choice (Campanella and Wolf 1974), typically

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characterised by an intense mate choice and a strong mating skew among males. A potential resolution of the lek paradox is that female preference varies between females. It has been suggested that genetic compatibility among prospective partners might on its own represent a sufficiently strong force to result in balancing selection on males (Zeh and Zeh 1996; Yasui 1998; Tregenza and Wedell 2000; Roberts and Gosling 2003; Griffith and Immler 2009). For example, mating with related individuals can lead to inbreeding depression (Charlesworth and Charlesworth 1987; Pusey and Wolf 1996; but see Kokko and Ots 2006). Females, which typically invest more per offspring than males, are particularly likely to show a preference for unrelated males. For example in the highly inbred, eusocial, naked-mole rat, *Heterocephalus glaber*, reproductively active females show a clear preference for unfamiliar males (Clarke and Faulkes 1999). Because of the social system of the naked-mole rat, unfamiliar males are unlikely to be closely related. More generally, in insects (Bretman *et al.* 2004; Simmons *et al.* 2006), amphibians (Garner and Schmidt 2003), reptiles (Olsson *et al.* 1996) and birds (Thuman and Griffith 2005), unrelated males have a higher fertilising success than males more closely related to their partner, thus showing potential for inbreeding avoidance to drive female mate choice.

An indicator females could use to assess male relatedness is the Major Histocompatibility Complex (MHC). The MHC is the most polymorphic region in vertebrate genomes and can be positively selected for its diversity (Klein 1986; Piertney and Oliver 2006; Worley *et al.* 2008). Because of its extreme polymorphism, two individuals with similar MHC have high chance to be genetically related. Thus, MHC-based mate choice may be a mechanism to avoid inbreeding depression (Potts and Wakeland 1993; Grob *et al.* 1998). In addition to mediating kin discrimination, MHC dissimilarity might also be selected *per se*. The MHC is expressed in membrane proteins that present foreign peptides to immunological cells in order to initiate

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specialized response (Janeway and Travers 1994). Some MHC types are associated with susceptibility or resistance to pathogens (Briles *et al.* 1977; Bacon 1987; Bonneaud *et al.* 2009). More generally, it was demonstrated that MHC diversity is an advantage during co-infections of several parasites in mice (Penn *et al.* 2002; McClelland *et al.* 2003), in the three-spined stickleback, *Gasterosteus aculeatus* (Wegner *et al.* 2003) or in humans (Penn 2002). Because of its key role in defence against parasites and pathogens, females may benefit from choosing partners according to male MHC in order to increase offspring survival (Penn and Potts 1999; Ziegler *et al.* 2005b). Indeed, a growing number of studies showed female mate choice based on MHC compatibility in several taxa of vertebrates (Wedekind *et al.* 1995; Roberts and Gosling 2003; Ekblom *et al.* 2004; Milinski *et al.* 2005). However, it is often difficult to disentangle the dynamics of this female choice (Penn and Potts 1999):

(i) *Frequency-dependent choice*. The red queen hypothesis proposed that there is an antagonistic co-evolution between pathogens and hosts resistance to these pathogens (Ladle 1992). Necessity for hosts to adapt themselves to rapidly evolving parasites would be so strong that it could explain maintenance of sex in most of living beings (Hamilton *et al.* 1990; Ladle 1992). According to this principle, individuals with an MHC type resisting to a pathogen will gain in fitness and spread this MHC type. Then, pathogens would become adapted and resist to this MHC type. So another rare MHC type would positively select and so on... In this case, the value in fitness for a MHC type depends on its frequency.

(ii) *Choice for MHC-diversity per se*. Choosing a MHC-dissimilar mate promotes offspring immunocompetence, thus females would benefit from mating preferentially with MHC-heterozygous males (Ziegler *et al.* 2005b).

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(iii) *Optimal number of alleles*. Too high MHC diversity may carry costs including higher chance of auto-immune diseases (Nowak *et al.* 1992; Milinski 2006). Mate choice on MHC compatibility can be used in order to produce offspring with an optimally intermediate number of MHC alleles that would guaranty the resistance against certain pathogens while avoiding the risk auto-immune diseases (Reusch *et al.* 2001).

The combination of additive and non-additive genetic variation in fitness represents the total 'genetic quality' of a prospective mate (Neff and Pitcher 2005). Such measure of genetic quality is relative to the individuals considered and the current environmental conditions (Hunt *et al.* 2004).

## **Female promiscuity**

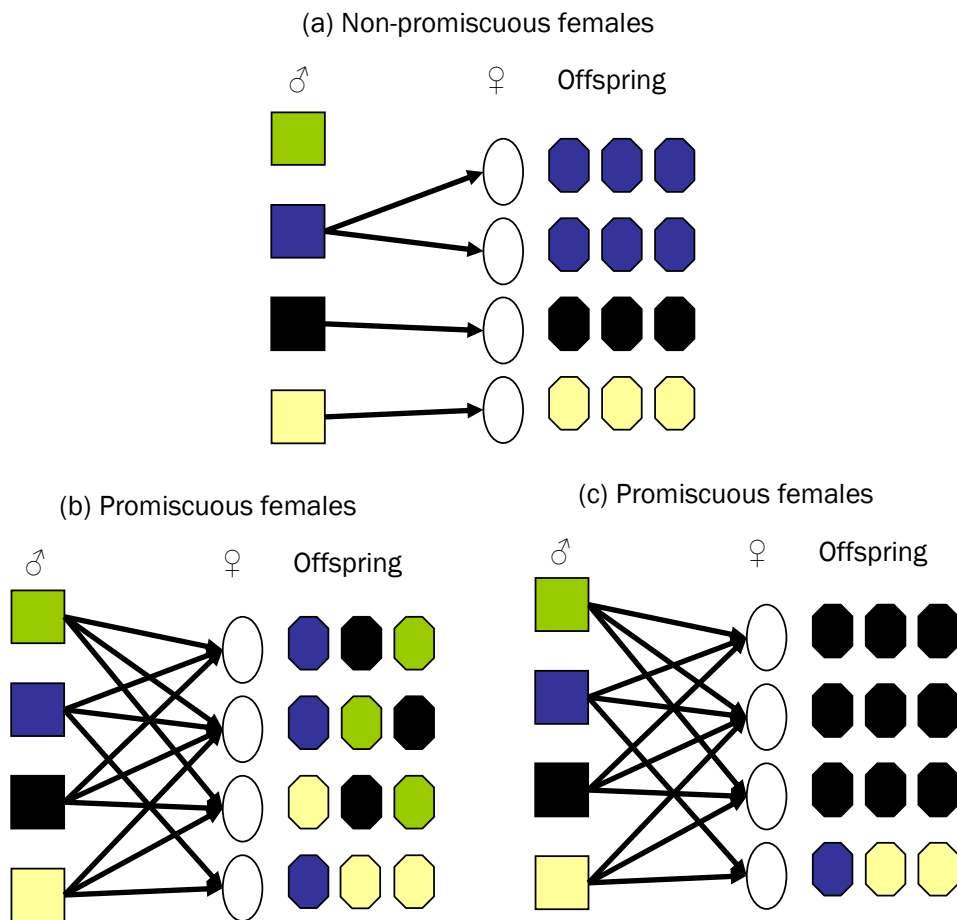
Recent studies have drastically changed the view on the operation of sexual selection. Mounting evidence shows that in many species the ejaculates of multiple males can fertilise the same set of eggs because females are polyandrous (i.e. sexually promiscuous (Milkman and Zeitler 1974; reviewed by Jennions and Petrie 2000; Tang-Martinez and Ryder 2005). The most striking example of the change of perception on female remating due to paternity analyses comes from birds. Lack (1968) assumed that most species were monogamous. It is now appreciated that females are often promiscuous including in species which display socially monogamous pair bonds (Birkhead and Møller 1992b). Female promiscuity changes the way we understand sexual selection because it prolongs its operation after copulation. This post-copulatory sexual selection can also be distinguished between intra- and inter-sexual selection. Indeed, male-male competition continues after insemination through competition between ejaculates of different males called sperm

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competition (Parker 1970a). Females can also consistently bias the outcome of sperm competition in favour of the ejaculates of certain males, this is cryptic female choice (Thornhill 1983; Pitnick and Brown 2000). Thus, intra- and inter-sexual selection can operate on male traits during pre- or post-copulatory episodes.

In addition to sexual selection for male remating with multiple females (Bateman 1948) and mating with fecund females (Darwin 1871), post-copulatory sexual selection favours males that are able to fertilise a high proportion of eggs of each female they inseminate. Theoretically, female promiscuity could either increase or decrease the intensity of sexual selection on males. In the absence of female promiscuity male mating success translates directly in reproductive success and reproductive skew is proportional to the skew in mating success (fig.1.01a). When females are promiscuous, on the other hand, the effective population size of females available for copulation to each male is potentially higher (Sugg and Chesser 1994; Parker and Waite 1997). If all males mating with a female sire a similar portion of eggs ('all fertilize some'), female promiscuity can reduce variance in paternity and thus reduce the intensity of sexual selection (Jones *et al.* 2001; Andersson and Simmons 2006), by reducing the overall opportunity for sexual selection (fig. 1.01b, Shuster and Wade 2003). Conversely, if some males have a higher post-copulatory success than others ('winner fertilize all'), female promiscuity can increase opportunities for male sexual selection (fig. 1.01c, Shuster and Wade 2003). In this situation, increasing the number of mates does not necessarily increase the number of offspring fathered by a male, and male reproductive success is limited by the promiscuity of his partners.

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**Figure 1.01:** Hypothetical scenarios of a population of four males and four females having each four offspring. The colour of the offspring corresponds to their paternity. (a) females do not remate and the number of offspring for each male depends on his number of mates. In cases (b) and (c), females are promiscuous and all males have the same mating success. (b) female promiscuity decreases male variation in reproductive success. (c) female promiscuity increases variation in reproductive success.

Direct tests of the effect of female promiscuity on the opportunity for sexual selection in males are scarce. Jones *et al.* (2001) showed a potential for female promiscuity to decrease the opportunity for sexual selection. Some studies investigated the relative importance of post-copulatory sexual selection in socially monogamous birds performing extra-pair copulations. Results are contradictory with some studies showing that sperm competition was explaining an important part of the variance in male reproductive success (Weatherhead and Boag 1997; Webster *et al.* 2007), whilst other results show that variation in male reproductive success is mainly

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due to male mating success (Westneat 1993; Whittingham and Dunn 2005). Clearly, the contribution of post-copulatory sexual selection to the total sexual selection in males remains little understood.

### Male post-copulatory strategies

Males have evolved a number of traits in response to post-copulatory sexual selection. Male investment in reproductive behaviours can vary according to female promiscuity. For example, males from the Grevy's zebra, *Equus grevyi*, where females remate with several males, invest more in reproductive behaviour (calling, mounting, ejaculations) than the closely related plains zebra, *Equus burchelli*, in which females stay closely to only one male (Ginsberg and Rubenstein 1990). Males can modify their behaviour and guard their mate in order to diminish the risk for her to be mounted by another male. In the goshawk, *Acciper gentilis*, males spend more time near their mate when females are the most likely to copulate in terms of the time of the day and of the breeding season (Møller 1987). The efficiency of mate guarding strategies was shown in the Seychelles warbler *Acrocephalus sechellensis* where close guarding males are less likely to have offspring sired by an extra-pair males in their nest (Komdeur *et al.* 2007). Moreover, when males were induced to limit mate-guarding (by mimicking the end of female fertile period), levels of extra-pair paternity were increased in the same species (Komdeur *et al.* 2007). Some studies have also speculated that mate guarding strategies might occur in humans (Shackelford 2006). Men are more likely to use mate retention strategies when they perceive a high risk of sperm competition: either because they rate their partner as highly attractive (Goetz *et al.* 2005), because their partner is fertile (Gangestad *et al.* 2002), or according to the perceived probability of partner's infidelity (Buss and Shackelford 1997).

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A potential benefit of mate guarding is also that it enables a male to mate repeatedly with the same female, thus potentially outcompeting the ejaculates of other males. After copulation, male hide beetles, *Dermestes maculatus*, stay on the back of females (Archer and Elgar 1999). This male behaviour may at the same time be used as a mate-guarding strategy and enable the male to remate with the same female and increase fertilisation success. Remating with the same partner proved to increase reproductive success in the dragonfly *Nannophya pygmaea* (Tsubaki *et al.* 1994).

Sperm competition promotes traits that confer a fertility advantage in a competitive environment. In response to sperm competition, males can develop strategies to outcompete rival ejaculates such as increasing the number of sperm inseminated in order to statistically increase their chances of fertilisation (Martin *et al.* 1974; Birkhead and Møller 1998). In many taxa, inter-species comparison reveal that species where females are promiscuous have males with larger testes for their body size (Harcourt *et al.* 1981; Møller 1988; Gage 1994; Birkhead and Møller 1998), which indicates higher rates of spermatogenesis. Experimental modification of the mating system of the mouse *Mus musculus* also showed that sperm competition promotes sperm production (Firman and Simmons 2009). Gage and Morrow (2003) used another approach by artificially selecting male crickets, *Gryllus bimaculatus*, according to the sperm amount they produced and to sperm length. They showed that males selected for producing more sperm and shorter sperm had a greater success in sperm competition (Gage and Morrow 2003).

Sperm quality can also vary according to sperm competition risk. Comparative studies in species of insects (Hunter and Birkhead 2002) passerines (Kleven *et al.* 2009 Immler and Birkhead 2007) and in cichlid fishes (Fitzpatrick *et al.* 2009) revealed the increase of sperm quality with the risk of sperm competition. Sperm competition can also promote plasticity in sperm quality with males adjusting the

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quality of their ejaculates according to the risk of sperm competition in their mate. For example the male cricket, *Teleogryllus oceanicus*, adapt the quality of their ejaculates (measured by the percentage of live sperm) according to their perception of sperm competition risk (Simmons *et al.* 2007). Sperm competition can also be source of selection on sperm morphology. Sperm size varies according to the rate of sperm competition in species of nematodes (LaMunyon and Ward 1999) and butterflies (Gage 1994). The midpiece of spermatozoa is rich in mitochondria furnishing the energy for sperm motility. Lüpold *et al.* (2009) found a positive correlation between midpiece size and sperm swimming velocity in New World blackbirds. In primates, the midpiece of species where females are promiscuous is more voluminous than in monoandrous species (Anderson and Dixson 2002).

Competing ejaculates are composed by spermatozoa and seminal fluid, so both components are likely to determine sperm fertilising efficiency. The size of the accessory organs producing the seminal fluid varies with the degree of female promiscuity across rodents (Ramm *et al.* 2005) and gobies species (Mazzoldi *et al.* 2005). In the black goby, *Gobius niger*, accesosory gland size also varies according to male strategy. Sneaker males, that systematically experience more sperm competition than parental males as they spawn in the nest of a parental male, had bigger accessory glands than parental males (Rasotto and Mazzoldi 2002).

Female promiscuity also influences the evolution of seminal fluid products. Numerous studies show a high rate of evolution due to an intense Darwinian selection by genes coding for reproductive proteins, in particular components of seminal fluid consistent with strong sexual selection (Swanson *et al.* 2001; Clark and Swanson 2005; Panhuis *et al.* 2006). A comparison between *D. melanogaster*, *D. simulans*, *D. yakuba* and *D. pseudoobscura* accessory gland proteins (Acps) also showed dissimilar evolutionary dynamics consistent with adaptive selection (Mueller *et al.* 2005). By

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comparing Expressed Sequence Tags between *D. simulans* and *D. melanogaster*, Swanson *et al.* (2001) showed a rapid divergence of many of the male accessory gland genes, typical of a positive Darwinian selection. This rapid evolution of Acps genes has also been demonstrated in all *D. melanogaster* subgroup and is consistent with a rapid evolution of seminal fluid function (Begun and Lindfors 2005). The high divergence of seminal fluid peptides is accompanied by an elevated within species polymorphism (Begun *et al.* 2000). Computation analysis compared Acps genes to the entire *Drosophila melanogaster* genome and strengthen the conclusion that Acps may often be under directional selection (Holloway and Begun 2004). These high rate of evolutionary change in seminal fluid proteins is thus found within and between species (Chapman 2001).

Seminal fluid components can manipulate female behaviour or physiology by decreasing her receptivity or reducing her attractiveness. Craig (1967) showed that implantation of males accessory gland in mosquito females of different species, including *Aedes spp.*, *Anopheles spp.* and *Culex spp.* prevented them from being inseminated by any male. In *Culex quinquefasciatus*, the injection of some Accessory Gland secretions extract switches female behaviour from mate- to host-seeking (Jones and Gubbins 1979). By this manipulation of female behaviour, males both avoid competition and increase female's energy income that can improve maternal effects on their offspring. In *Drosophila melanogaster*, both reduction of attractiveness and decrease of receptivity are observed (Tram and Wolfner 1998). The drop of female receptivity is mainly due to a 36 amino acids peptide found in male seminal fluid called the Sex Peptide (SP) or Accessory gland Protein 70A (Acp 70A, Chen *et al.* 1988; Aigaki *et al.* 1991). SP is carried by spermatozoa (Liu and Kubli 2003) and gradually released after mating (Peng *et al.* 2005). After its release, SP travels through the vagina wall to bind to the nervous system where it can modify female behaviour (Ding

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et al. 2003). Finally, males can produce a physical plug in the female reproductive tract that would prevent further insemination. In Primates, a protein of the seminal fluid forms a semen coagulum after mating and is thought to prevent fertilization by rival males (Dixson and Anderson 2002). Dorus et al. (2004) showed that the evolution of the protein forming the mating plug is accelerated in primates that experience sperm competition compared to monoandrous. In *Drosophila melanogaster*, a mating plug is detectable few minutes after the beginning of the mating, before any sperm transfer (Bairati and Perotti 1970). The major protein present in the plug is similar to those in homopolymer-forming proteins found in spider silk (Lung and Wolfner 2001). Females may also benefit from male mating plugs as they can cooperate in the formation of the plug as in spider *Leucauge mariana* (Aisenberg and Eberhard 2009). In the ground beetle *Leptocarabus procerulus*, a unique seminal fluid substance is responsible for the induction of female refractory behaviour and the mating plug (Takami et al. 2008), thus showing again that male strategies to decrease sperm competition are not exclusive.

Thus, female promiscuity can potentially drive the evolution of numerous male behaviours and sperm traits.

## The evolution of female promiscuity

Female promiscuity was initially considered to be due to male sexual harassment of females or a genetic by-product of selection on male remating. However, evidence is accumulating that females can benefit from mating with several males. In the adder, *Vipera berus*, females that mate several times with different partners had higher offspring viability (Madsen et al. 1992). In the blue tit, *Cyanistes caeruleus*, extra-pair young were more likely to survive than within-pair ones (Kempnaers et al. 1992).

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Moreover, artificial evolution of house mice showed that lines in which females evolved under a regime of female promiscuity produced significantly bigger litters (Firman and Simmons 2009). These results challenge Bateman's results that females do not benefit from having more than one mate (Bateman 1948). Mating with several partners has costs such as time and energy due to courtship and copulation, increased risk of predation, increased risk of sexually transmitted pathogens (Sheldon 1993) and potential harm from male seminal fluid content (Chapman *et al.* 1995). Most of the hypotheses that explain female promiscuity are derived from hypotheses on female mate choice (Zeh and Zeh 2003), and here again we can separate direct benefits that increase the fitness of promiscuous females and indirect benefits that enhance female offspring fitness.

### ***Direct benefits of female promiscuity***

Remating can increase female fitness directly. A reanalysis of Bateman's data showed that contrary to Bateman's original conclusions, females that mated with more than one male had a higher reproductive success than monoandrous females (Snyder and Gowaty 2007). The difference between male and female correlation between mating success and reproductive success is also weaker than originally inferred by Bateman (Snyder and Gowaty 2007). Direct benefits of female promiscuity are particularly evident in some arthropods, particularly in species where males provide some form of nuptial gifts to the female. For example in the pseudoscorpion, *Cordylochernes scorpioides*, females mated twice to different males had 32% more offspring than females mated twice to the same male (Newcomer *et al.* 1999), or in the field cricket, *Teleogryllus oceanicus*, monoandrous females had a lower hatching success than promiscuous females with the same number of matings (Simmons

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2001a). These examples are representative of a more common trend that female insects benefit directly from remating with different males (Arnqvist and Nilsson 2000).

Direct benefits for promiscuous females have also been investigated in other taxa, but here evidence is more ambiguous (Barbosa and Magurran 2006), the acceptance of new mates in order to avoid male harassment being one of the most common explanation (Lee *et al.* 2004).

### ***Indirect benefits of female promiscuity***

Female promiscuity may also be selected indirectly, through the benefits that it conveys to the offspring of promiscuous mothers. For example, promiscuous females have larger offspring in the spider *Neriene litigiosa* (Watson 1998). Female promiscuity can enable females to bias paternity after insemination to improve offspring quality through cryptic female choice (Thornhill 1983; Eberhard 1996). Cryptic female choice is the ability of a female to control paternity by biasing the outcome of sperm competition in favour of the ejaculates of certain males (Eberhard 1996), or more generally a female effect that biases male paternity after copulation (Pitnick and Brown 2000). In species with internal fertilisation, females have multiple mechanisms to exert cryptic female choice, including differential sperm ejection, transport and storage before fertilisation; and differential maternal allocation and abortion after fertilisation (Eberhard 1996).

Females benefit from cryptic female choice for essentially the same reasons as they benefit from choosing a mate; the choice is simply delayed after copulation. If females are at risk of not meeting a potential partner at all (for instance in a low-density population), they would benefit from mating with a low quality male to ensure

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fertilisation. Then, if they meet a better quality male, they could favour fertilisation by the sperm of the second, better male (Jennions and Petrie 2000). Cryptic female choice is in this case a way to 'trade-up' partners, and P2 (paternity of the second male in the case of a female inseminated by two males) is expected to be high. The 'trade-up' hypothesis received support from several studies in avian models. Collared flycatcher *Ficedula albicollis* females engage extra-pair copulations with males that have a wider white forehead patch than their social partners (Michl *et al.* 2002). If their partner is attractive according to this signal, females are less likely to engage extra-pair copulations (Michl *et al.* 2002). The mechanism of female cryptic choice is likely to be due to timing decision, with females mating with an extra-pair male when their fertility is higher (Michl *et al.* 2002). So paired males have to keep good quality signals even after the bonding to increase their paternity ratio. In barn swallows, males that were experimentally brighter received greater paternity from their mate (Safran *et al.* 2005). The strategy of female side-blotched lizards, *Uta stansburiana* is even more sophisticated (Calsbeek and Sinervo 2004). In this species, large males have higher viability, and females are positively selected when small. To increase the fitness of both sons and daughters, remating females use preferentially Y-bearing sperm from big males to produce sons and X-bearing sperm from small males to produce daughters, suggesting cryptic female choice at the level of sperm haplotype (Calsbeek and Sinervo 2004).

Post-copulatory choice can also select for sperm quality itself, if additive covariance occurs between ejaculate fertilising efficiency and viability ('good sperm' hypothesis Yasui 1997). By mating with several males, a female would ensure that her eggs are fertilised by the best sperm competitor, and thus that her offspring inherit paternal genes associated with high viability. In this model, females benefit passively from remating, without any choice involved. This hypothesis has received limited

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empirical support (Hosken *et al.* 2003; Eizaguirre *et al.* 2007), but this may reflect the lack of rigorous tests (Simmons 2005). The 'sexually-selected sperm' or 'sexy sperm' hypothesis presents female promiscuity as a particular case of Fisherian runaway process, i.e. promiscuous females are inseminated by several males whose ejaculates compete for fertilisation. A male might win by transferring more and/or faster swimming sperm, by displacing the previously stored sperm from other males, or by preventing the female to mate again. If any of these traits are heritable, sons of promiscuous females will inherit a fertilising advantage in sperm competition and daughters, their mother's tendency to remate (Keller *et al.* 1995). While plausible, the sexually-selected sperm hypothesis has received little support (Simmons and Kotiaho 2007).

Females may also benefit from a non-additive effects of choice, favouring paternity of more genetically compatible mates after copulation. Genetic incompatibility is deleterious to offspring (Zeh and Zeh 1997), females may benefit from mating with several males for the most genetically dissimilar male to father their offspring. However, tests of the effect and the potential causes of genetic incompatibility are scarce (Simmons 2005). Here, I consider mate compatibility as a general term to include both genome-wide genetic similarity and relatedness, and diversity at specific loci, controlling for genome-wide similarity. There is increasing molecular evidence for differential paternity according to relatedness or genetic similarity (e.g. Olsson *et al.* 1996; Bretman *et al.* 2004; Thuman and Griffith 2005).

In addition, it may benefit females to produce genetically diverse progeny (Jennions and Petrie 2000). Multiple paternity will allow some offspring to disperse in new environments and decrease siblings competition (Jennions and Petrie 2000). In species where dissemination is low, multiple paternity decreases the relatedness rate between siblings so that we can observe a higher heterozygosity than the mating

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pattern would suggest (Winters and Waser 2003). Offspring diversity can also directly increase female fitness. In spotted hyenas, male infanticide is common as a mean to reduce the reproductive success of male competitors. It is thought that females benefit from multiple matings for males not to be sure of their paternity, thus they do not take the risk of killing youngsters that may be theirs (East *et al.* 2003).

## **Sexual conflict**

The traditional view that males and females cooperate to reproduce has been challenged by theoretical and experimental work indicating that males and females have divergent fitness optima that cannot be reached at the same time (Arnqvist and Rowe 2005; Parker 2006). A critical repercussion of promiscuity is that it exacerbates sexual conflict because reproductive investment is costly and individuals must partition out their investment across multiple reproductive events with different partners. If one sex evolves adaptations to reach its own optimum at the cost of the other sex, the latter will be selected to counteract such antagonistic adaptations. Sexual conflict mediated by different sex-specific loci (inter-locus) can therefore lead to rapid antagonistic coevolution or evolutionary arms race between the sexes (Parker 1979), which can act as a 'fuel for evolution' (Chapman and Partridge 1996), and which could eventually lead to reproductive isolation (Martin and Hosken 2003) and speciation (Hayashi *et al.* 2007).

In *Drosophila melanogaster*, lines of males and females were randomly monogamously mated, thus removing any opportunity for sexual conflict. When these artificially selected lines mated with control stocks of free-mating population, the lines with no sexual conflict showed a greater net reproductive rate in both sexes, males were less harmful to their mates and invested less in spermatogenesis than the

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control line (Holland and Rice 1999). However, when females only were randomly monogamously mated to a control male, thus preventing only females from coevolving with males, their survivorship was significantly reduced at the same time as their remating rate was increased (Rice 1996).

Conflict can arise over different reproductive decisions, including mating (chase-away sexual selection) and fertilisation. The most documented examples of post-copulatory sexual conflict are mediated by seminal fluid substances. Patterns of seminal fluid proteins evolution are consistent with expected patterns of rapid evolution driven by sexual conflict in both Abalone, *Haliothis*, and *Drosophila* (Panhuis *et al.* 2006). In *Drosophila melanogaster*, several proteases inhibitors are transferred by the seminal fluid to females during mating including Acp62F (Lung and Wolfner 1999) and Acp76A (Coleman *et al.* 1995). Acp62F is a trypsin inhibitor. 90% of the Acp62F transferred by an ejaculate remains in the reproductive tract where it protects sperm or other seminal fluid proteins from proteases attacks (Lung *et al.* 2002). Acp62F is toxic upon ectopic expression in both males and females (Lung *et al.* 2002). After mating, 10% of Acp62F go through the vaginal wall to join the haemolymph circulation where it is toxic (Lung and Wolfner 1999). Thus multiple exposures to seminal fluid is toxic for the female and decreases her lifespan with a dose-effect: the more the female is exposed to seminal fluid, the more female lifespan decreases (Chapman *et al.* 1995). It is still discussed if the increase of female death rate is a by-product of seminal fluid components (Chapman *et al.* 1995) or if Acps have been selected to harm the female (Johnstone and Keller 2000). Seminal fluid harms could benefit males because females would lower their remating propensity in order to protect from other seminal fluid inseminations, or because she dies before remating. This male strategy of harming female to limit competition would be stable over a broad range of conditions (Johnstone and Keller 2000). However, growing evidence tend to

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show that females may indirectly benefit from male harms through their offspring fitness (Priest *et al.* 2008). Experimental manipulations of the intensity of sexual conflict over many generations confirm the central importance of seminal fluid sexually antagonistic properties. Wigby and Chapman (2004) created lines with various sexual conflict intensities. They found that females from high sexual conflict lines lived significantly longer in the presence of males than did females from low conflict lines (Wigby and Chapman 2004).

### **The red junglefowl as a model species of sexual selection**

The red junglefowl, *Gallus gallus sp.*, originates from South-Eastern Asia and natural populations have been studied in Indonesia (Nishida *et al.* 1985), Thailand, Laos, Vietnam (Nishida *et al.* 2000) and up to Nepal (Collias and Collias 1967; Nishida *et al.* 1992). The red junglefowl is the ancestor of the domestic chicken, *Gallus gallus domesticus* (Darwin and Murray 1868; Fumihito *et al.* 1994; 1996).

Red junglefowl flocks are small and characterised by a tight social structure through sex-specific social hierarchies which mediates social interactions between same sex birds (Banks 1956; McBride *et al.* 1969; Wood-Gush 1971). Hierarchies are stable (Banks 1956), but not always linear (Banks 1956; Guhl 1964). A newly introduced bird is generally subordinate, potentially explaining the stability of flock composition (Banks 1956). Social status is established through competitive contests and fights, however aggressiveness decreases as the hierarchy is stabilised (Guhl 1969). Natural flocks are typically composed of one dominant male, several (two to twelve) females and several (up to seven) subordinates males (Johnson 1963; Collias *et al.* 1966; Collias and Saichuae 1967; Collias and Collias 1967; Sullivan 1991). Flock cohesion relies especially on female-female interactions (Sullivan 1991), and

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flock structure is stable as juveniles usually stay in their flock of origin (Collias *et al.* 1966; Collias and Collias 1996). Dominant males enjoy privileged access to females, perform more copulations, and copulate when females are more receptive (Cheng and Burns 1988; Pizzari 2001). Dominant males are also able to interrupt their competitor's copulations (Pizzari 2001). As a result, male reproductive success is typically skewed, with a small proportion of dominant birds accounting for most reproductive success (Jones and Mench 1991; Collias *et al.* 1994; Collias and Collias 1996), indicating high opportunity for intra-sexual selection. Parental investment is almost entirely restricted to females, as females incubate and provide maternal care for three months on average (Collias *et al.* 1966), suggesting potential for inter-sexual selection (Clutton-Brock and Scott 1991; Clutton-Brock and Parker 1992). Consistent with this expectation, studies have shown a marked female preference for dominant males (Graves *et al.* 1985). Females can also indirectly favour fertilisation by dominant males, as they are more likely to resist a mating with a subordinate male, or can perform an indirect mate choice through male behaviour manipulation, favouring copulations with dominant males (Pizzari 2001). Females can directly benefit from choosing a dominant male that is more vigilant against predators (Pizzari 2003). Female choice and its direct benefits could thus explain that males performing more alarm calls have a higher reproductive success (Wilson *et al.* 2008). Female may also indirectly benefit from mating with a dominant male by producing socially dominant males as dominance is heritable (Craig *et al.* 1965; Guhl 1969). Separately from studies testing female mate choice according to male social status, females have been shown to prefer males with larger and brighter combs (Zuk *et al.* 1990a; Zuk *et al.* 1990b; Parker and Ligon 2003). However, female choice is hardly repeatable as may depend on the female social status (von Schantz *et al.* 1995), and conclusions of different studies can be contradictory (Johnsen and Zuk 1996). Moreover, male traits

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are often intercorrelated. Dominant males are usually more ornamented with larger comb and variation of social status has a rapid effect on the expression of some testosterone-mediated male traits, such as the comb, and status-related behaviours (Graves *et al.* 1985; Ligon *et al.* 1990; Zuk and Johnsen 2000). Because the effects of male social status and male ornaments such as comb have seldom been tested concomitantly, the relative importance of these two male traits remains unknown and untested.

Female preference can also be based on male courtship behaviours. Males perform several courtship behaviours. Waltzing consists of a male stepping around a female with one wing dropped (Davis and Domm 1943; Wood-Gush 1954; 1956). This behaviour is also used for agonistic interactions between males so it is difficult to know the real function of this behaviour (dominance or courtship) and its effect on mating success (Wood-Gush 1954; 1956). Food call is a male behaviour directed towards females potentially used as courtship. Food calls are normally performed by a hen for her chicks as a way to show them sources of food (Moffatt and Hogan 1992). The exact same call is performed by males (Stokes 1971) and attract females to approach the signal sender (Stokes and Williams 1971). The motivation for females to approach a food-calling male could be to get fed (Marler *et al.* 1986; Evans and Evans 1999), but it seems that the main function of male food calls result from reproductive behaviour (Van Kampen 1994; 1997; Van Kampen and Hogan 2000) .

Females could also choose mates that increase their fitness by non-additive effects, in particular according to their MHC. MHC-dissassortative mate choice was already shown in certain conditions in males (Gillingham *et al.* 2009). The chicken MHC is called 'minimal essential' (Kaufman *et al.* 1995). 'Minimal' because it is composed of only four loci, two for each class of MHC, physically close from each other so that recombinations occur rarely, if ever (Kaufman *et al.* 1999; Jacob *et al.* 2000).

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In each MHC class, one gene is expressed at a higher level (major locus) than the second (minor locus, Kaufman *et al.* 1995; Kaufman *et al.* 1999; Jacob *et al.* 2000; Wallny *et al.* 2006). Patterns of evolution in each MHC locus show that minor loci seem to be evolving according to neutral selection whilst major loci reflects diversifying selection (Shaw *et al.* 2007; Worley *et al.* 2008). The chicken MHC is 'essential' because it carries certain alleles directly correlated with resistance to Marek's disease (Briles *et al.* 1977; Briles *et al.* 1983; Bacon 1987; Schat *et al.* 1994) Rous sarcoma virus (Bacon *et al.* 1981; Wallny *et al.* 2006) and *Salmonella* (Joiner *et al.* 2005). Overall, MHC heterozygosity appears to be an advantage in terms of survival, and early death was observed to be linked with particular MHC alleles (Worley *et al.*, *subm.*). Therefore, the MHC-genotype of an individual is particularly correlated with its survival and female mate choice based on the male MHC could indirectly increase female fitness.

Female red junglefowl are sexually promiscuous (Cheng and Burns 1988; Collias and Collias 1996), and can store viable sperm for a median period of 14 days (Etches 1996). During that time, females can be inseminated by several males, setting the scene for sperm competition to occur. Males that transfer more sperm are more likely to fertilise female eggs (Martin *et al.* 1974; Pizzari *et al.* 2008; but see Bilcik *et al.* 2005). Interestingly, male copulation order does not seem to play a role in paternity (Birkhead *et al.* 1995). Sperm quality is also an important predictor for male fertilising efficiency promoting faster sperm (Froman and Feltmann 1998; Birkhead *et al.* 1999; Froman 2003). Thus, sperm quantity and quality are both predicting male fertilisation success (Bilcik and Estevez 2005), but have temporal different effects (Pizzari *et al.* 2008). In general, the non-spermatozoa part of semen or seminal fluid and its influence on sperm quality and fertilisation success have little been studied in birds. Male fowl lack the accessory reproductive organs typical of males of some mammalian

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species (Lake 1971), but Sertoli cells in seminiferous tubules and vasa efferentia, epididymis, ductus deferens and the ejaculatory groove can act such as and produce semen plasma and transparent fluid whose functions remain unclear (Fujihara 1992).

Female ability to control paternity is limited by coerced copulations (Lovlie and Pizzari 2007), thus female could benefit from being promiscuous by performing a post-copulatory choice. Females can eject sperm from males and are more likely to perform sperm ejection when inseminated by a subordinate male (Pizzari and Birkhead 2000). However, the mechanism for sperm ejection, the possible criteria for female decision to eject and the efficiency in terms of decreasing of male fertilisation success remain unclear. Selective transport of sperm in the vagina has been observed to vary according to the species of the sperm donor (Steele and Wishart 1992). Moreover, paternity varies across females after artificial inseminations controlling for male effect, thus showing that cryptic female choice could occur through another mechanism than sperm ejection (Birkhead *et al.* 2004). Cryptic female choice can select for unrelated males. For example, females retain fewer sperm from their siblings (Pizzari *et al.* 2004). Females could use the male MHC to select for unrelated males, or they could specifically prefer males with certain MHC genotypes, but these hypotheses have been seldom tested (Gillingham 2008). Cryptic female choice for non-additive effects may occur through sperm storage mechanisms. The utero-vaginal junction of the female oviduct has (around 25,000) sperm storage tubules (SST, Birkhead and Møller 1992a; Bakst 1993; Etches 1996; King *et al.* 2002) that might be used to discriminate sperm from different males (Eberhard 1996; Hellriegel and Ward 1998; Ward 2000; King *et al.* 2002; Snow and Andrade 2005), since sperm from different males can be kept from mixing with each other (King *et al.* 2002).

## **Objectives of my PhD**

The objectives of this thesis are to:

1. Quantify the opportunity and strength of male and female sexual selection, integrating pre- and post-copulatory episodes, and investigate the influence of female promiscuity on the operation of sexual selection on males.
2. Identify male traits targeted by sexual selection and measure the way different selective episodes operate on such traits.
3. Investigate the role of seminal fluid effects on the outcome of sperm competition.
4. Test mechanisms of cryptic female choice based on male social status, and the MHC similarity with-, and relatedness, to the female.

### ***Study population***

These studies were carried out at the John Krebs field station of the University of Oxford, Wytham (UK). The population of red junglefowl *Gallus gallus* was established in 2006 from a random-bred stock of two populations originating from Skara (Sweden) and Copenhagen (Denmark). The Copenhagen population was founded in the 1950's and kept in a zoo since (Håkansson and Jensen 2005). The Skara population originated from Thailand and was kept in captivity for less than 10 years (Schütz *et al.* 2001). Most of the birds that were used here hatched in 2006. The population size varied between around 70 and 100 birds over the three years of experiments.



## CHAPTER 2: OPPORTUNITY AND STRENGTH OF SEXUAL SELECTION IN PROMISCUOUS POPULATIONS

### Introduction

Darwin (1871) proposed sexual selection theory to explain phenotypic differences between adult males and females of the same species (sexual dimorphism) and thus the evolution and maintenance of exaggerated secondary sexual characters that do not increase survival. Sexual selection acts on traits that increase the reproductive success of an individual in competition with other individuals of the same sex over reproductive opportunities. As reproductive success is an essential component of fitness, sexual selection can potentially have a crucial role in the evolution of phenotypes. Darwin (1871) identified two episodes of sexual selection: intra- and inter-sexual selection. Intra-sexual selection accounts for the evolution of armaments such as horns through which individuals outcompete rival members of the same sex over access to mates. Inter-sexual selection promotes traits such as ornaments and courtship displays through which individuals attract mating partners. However, Darwin did not fully understand the reason why sexual selection was often more intense in males more than in females.

Bateman (1948) conducted the first study that compared sexual selection in males and in females. Bateman used strains of *Drosophila melanogaster* with different dominant marker genes that allowed him to assign paternity and maternity in “free mating” populations. He thus knew the number of offspring produced by each individual and used the number of genetic parents of one sex as a proxy for the mating

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success of an individual of the opposite sex. Bateman's study generated three main conclusions. First, the number of offspring is more variable in males than in females. Second, the number of mates is more variable in males than in females. Third, some replicates showed that the number of offspring of a male 'increased steadily' with his number of mates, whilst females reach their maximum number of offspring with only one mate. The first two results indicate that sexual selection is potentially more intense in males than in females because male contribution to the next generation is more variable than female. Bateman's third result indicates that the relationship between remating rates (i.e. number of mates) and reproductive success (i.e. number of offspring) is sex-specific. Because males gain more than females from remating, competition over access to reproductive opportunities is stronger in males.

### The influence of Bateman's experiment: the appreciation of sex roles and the definition of sexual selection

Bateman's results have been later generalised as principles. Bateman's three principles formed the cornerstone of sexual selection theory, introducing the concept of distinct 'sex roles'. The first biological interpretation of Bateman's experiment came from Trivers (1972), who investigated sex-specific differences in cost of reproduction through parental care. Parental care is any investment made by the parents to their offspring, including gamete production, incubation or gestation and post-hatching care (Clutton-Brock and Scott 1991). Generally, females produce a rather small amount of large eggs compared to males that produce a colossal amount of smaller sperm, so that a female's investment per zygote produced is much greater than a male's. Because of this first differential gametic investment, females usually carry on giving the most parental care in order not to lose their former investment (Trivers 1972; but

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see Kokko and Jennions 2003; and 2008 for alternative explanation of widespread maternal care). Moreover, because sperm production is typically faster than eggs, more males are ready to mate at a given time than females. Therefore, the operational sex ratio (OSR) is biased towards males, thus increasing male-male competition (Clutton-Brock and Parker 1992). And indeed, remating is often more beneficial to males than to females in terms of offspring production (Bateman 1948; Andrade and Kasumovic 2005; Krakauer 2008). In addition, because females are limited in the number of eggs they produce, they are particularly sensitive to qualitative changes in reproductive success and are selected to mate preferentially with males that convey the highest benefits to the female directly, through reproductive resources and paternal care, or to the offspring in terms of viability and reproductive success (Andersson 1994; Jennions and Petrie 2000). Female choice creates an inter-sexual selection on males as the males that are chosen by females have a higher reproductive success.

In some species, sex roles are reversed and males invest more in offspring than females (Vincent *et al.* 1992). Trivers' theory states that sexual selection should be stronger in the sex that invests less in reproduction. It is thus expected to see a stronger sexual selection in females in sex-role reversed species. And indeed, females of sex-role reversed species show more variance in their mating and reproductive success and a tighter relationship between mating and reproductive success than males (Jones 2000; Lorch 2002).

Bateman's experiment (1948) also enabled to understand of how sexual selection was operating in males and Bateman three principles are the basis for defining and measuring sexual selection. To explain the potential evolution and maintenance of sexual phenotypes, it is important to be able to quantify how much sexual selection can operate on each sex as Bateman did. The more variable

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reproductive success is within a sex, the more variable is the contribution of each individual to the next generation, and the more potential there is for sexual selection to operate in a population (Bateman 1948). The same applies for traits causing variation in reproductive success: for a trait to be selected, it needs to vary in the population. Thus, Bateman's first two principles measuring the variability of male and female mating and reproductive success measure the opportunity of sexual selection.

Numerous attempts have been made to measure intra-sexual variation in mating and reproductive success in order to measure the opportunity of sexual selection (Box 1, reviewed by Kokko *et al.* 1999). The indices listed in box 1 represent the most commonly used measures of opportunity of sexual selection and show that there is no consensus on how to estimate variability of reproductive and mating success. These indices are often inter-correlated (Kokko *et al.* 1999; Mills *et al.* 2007); but have different properties that capture different aspects of sexual selection. Thus, it is recommended to use multiple indices quantifying the potential of sexual selection and carefully analyse their difference (Kokko *et al.* 1999). Indices of sexual selection based on the estimation of the variance in mating and reproductive success cannot be used to assess the actual operation of sexual selection as has often been done, in particular with *Is* (Klug *et al.* 2010), as they tell us nothing about the relationship between mating success and reproductive success. A further limitation shared by all the indices outlined in box 1 is that they tell us nothing about the strength of sexual selection without assuming a correlation between mating success and reproductive success (Lorch 2005).

For a trait to be actually selected, it has to be correlated with some component of reproductive success. Thus, the strength of sexual selection on a trait is the correlation between the trait and reproductive success (Arnold and Duvall 1994). The strength of sexual selection on remating is a function of the number of additional offspring

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obtained by an individual by mating with an additional mate (Bateman 1948; Arnold and Duvall 1994). Therefore, in contrast with the numerous indices quantifying the opportunity of sexual selection (box 2.01), the Bateman gradient is generally accepted to well describe the strength of sexual selection. The Bateman gradient, first proposed by Arnold and Duvall (1994) is the least square regression line between number of offspring and number of mates. That is to say that the Bateman gradient is the number of additional progeny brought by additional mates such as it shows how mating success translates in the production of offspring and it measures selection on remating (Lorch 2005). In terms of path analysis, the Bateman gradient has been identified as the final path to fitness for all traits selected by sexual selection on remating (Arnold and Duvall 1994, but see below). Consistent with theory, the Bateman gradient varies with the manipulation of the operational sex ratio (OSR) and is steeper in the most competing sex (Jones 2000; 2002; Jones *et al.* 2004; Jones *et al.* 2005; Bjork and Pitnick 2006; Mills *et al.* 2007).

For sexual selection on remating to operate on males, the three following conditions are necessary: (1) variance in the number of offspring, (2) variance in number of mates and (3) positive correlation between number of mates and number of offspring (Bateman 1948; Arnold and Duvall 1994; Jones 2009). It is thus crucial to quantify these three conditions to evaluate to strength of sexual selection and how male and female phenotypes can be affected by it. In addition, quantifying the heritability of a trait is also necessary to study the evolutionary response to selection. In this chapter, I will focus on the operation of sexual selection on phenotypes of one generation that does not require principles of heredity (Lande and Arnold 1983).

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**Box 2.01:** Some of the most commonly used indices for the opportunity for sexual selection: their definition, main properties, limitations and some precautions needed when using them

	Opportunity for sexual selection ( <i>I</i> )	Opportunity for selection ( <i>I<sub>s</sub></i> )	$I = \frac{\sigma^2}{\bar{X}^2}$	Upper limit of Bateman gradient
<b>Definition</b>	These indices created by Crow (1958) have been applied to sexual selection theory by Wade and Arnold (Wade 1979; Wade and Arnold 1980). If all variance in fitness is due to additive genetic effects, <i>I</i> would measure the single-generation increase in absolute fitness in the population divided by the mean fitness in the original population (Crow 1958; Jones 2009).			The upper limit of Bateman gradient is the number of additional zygotes produced after a second mating with an 'ideal' (=virgin) mate (Lorch 2005). For example, if virgin females can produce on average 100 eggs and each mating with a female allows a male to fertilise all of her eggs, the upper limit of Bateman gradient is 100.
<b>Min/ max values</b>	Even distribution: <i>I</i> =0/ Poisson distribution: <i>I</i> =1 / different maximum value according to population size (Krebs 1989)			If the upper limit of Bateman gradient is null, there is no opportunity for sexual selection on remating to operate on an individual's reproductive success
<b>Pros</b>	<i>I</i> is the closest index to Darwin's definition of potential for sexual selection as it quantifies the upper boundaries of fitness on which selection can act (Arnold 1986, Jones et al. 2004, but see Koenig and Albano 1986). Because <i>I</i> is expressed in variance units, it is easily decomposable in several factors corresponding to different episodes of selection (Bohrnstedt and Goldberger 1969; Wade and Arnold 1980; Arnold 1983; Arnold and Wade 1984b; Webster et al. 1995; Kokko et al. 1999). <i>I</i> and <i>I<sub>s</sub></i> are the most used indices (reviewed by Shuster and Wade, 2003). Shuster and Wade (2003) predicted that, when OSR (Operational Sex Ratio) would be modified, <i>I</i> would be higher for the sex towards which the OSR is biased. This relationship between OSR and <i>I</i> was proven by several studies (Jones et al. 2004; Jones et al. 2005; Mills et al. 2007) and showed the link between <i>I</i> and Darwin-Bateman sexual selection theory. Moreover, <i>I</i> and <i>I<sub>s</sub></i> are concordant with measures of selection on phenotypical traits (Jones 2002).			The upper limit of Bateman gradient measures the potential benefit given by each mating, so it is a direct measure of the opportunity of sexual selection on remating. Variance of mating and reproductive success is not only due to sexual selection and natural selection can also act on mating and reproductive success. An attractive male would have a low reproductive success if he was unable to feed and produce viable sperm. Thus variance-based indices such as the ones seen before can vary not only because of sexual selection. The upper limit of Bateman gradient is the only index of opportunity for sexual selection that only takes into account sexual selection.
<b>Cons</b>	<i>I</i> and <i>I<sub>s</sub></i> values depend on sample sizes and mean fitness value. Thus, <i>I</i> and <i>I<sub>s</sub></i> cannot be simply compared across populations, or even in the same population across different duration of study (Downhower et al. 1987; Brodie and Janzen 1996; Ruzzante et al. 1996; Fairbairn and Wilby 2001). It is difficult to conclude how "high" the opportunity for sexual selection is in a population with no reference to compare it to. In addition, <i>I<sub>s</sub></i> is relevant to sexual selection only if there is a positive correlation between the number of mates and the number of offspring fathered (Lorch 2005).			The upper limit of Bateman gradient is hardly usable in females of many species. For example, it would be difficult to measure it in females that delay remating due to male manipulation (Chen et al. 1988) or in females that store sperm, where remating benefits may vary with the delay between the first and the second mating. Upper limit of Bateman gradient may produce some results suggesting a different mating system than the one observed (Lorch et al. 2008).
<b>!</b>	<i>I</i> and <i>I<sub>s</sub></i> cannot be used when the mean success is less than one or it would be artificially increased as the square of the mean is less than the mean (Downhower et al. 1987). Observation duration must be the same across groups. Results may be slightly biased and hardly comparable across sexes when sex ratio is uneven (Downhower et al. 1987). <i>I</i> and <i>I<sub>s</sub></i> do not tell us if sexual selection actually does occur, and are in no case a predictor for phenotypic selection (Clutton-Brock 1983; Fairbairn and Wilby 2001; Lorch 2005)			The upper limit of Bateman gradient has to be measured in experimental conditions, which raises problems such as insuring that sperm transfer accompanies each mating.

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Box 1 (following)

**Morisita index ( $l\delta$ )**

$$I_{\delta} = n \left[ \frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \right]$$

$\sum x$  = sum of mating/ reproductive success in a group,

n=number of individuals of the same sex

**Definition**

Variance of mating or reproductive success corrected by the variance when acquisition is equal. First proposed to measure dispersion (Morisita 1962), this index was later applied to sexual selection theory (Tsuji and Tsuji 1998).

**Min/ max values**

$l\delta=1$  when resources are randomly distributed,  $l\delta<1$  when resources are more evenly distributed,  $l\delta$ =population size when resources are monopolized (Morisita 1962; Tsuji and Tsuji 1998, Kokko 1999).

**Pros**

Contrarily to  $l_s$  where the null model is an even distribution of resources, the null model for the Morisita index is a random distribution of the resource (Poisson distribution, Morisita 1962). So  $l\delta$  is independent of the population size and the average resource acquisition as long as resource acquisition is not even (Morisita 1962; Tsuji and Tsuji 1998; Kokko *et al.* 1999).  $l\delta$  has a consistent behaviour across groups of different sex ratios (Fairbairn and Wilby 2001; Mills *et al.* 2007), so that the Morisita index was selected as the most accurate measure of the potential for sexual selection by Fairbairn & Wilby (2001).

**Cons**

When resources distributions are even,  $l\delta$  is dependent of population size and mean resource acquired (Kokko *et al.* 1999; Fairbairn and Wilby 2001). This reflects the fact that monopolization of resources in a big population is more difficult than in a small population but it can make the comparison between species difficult (Tsuji and Tsuji 1998). Because of the stability of Morisita index, detection of a treatment effect, when the operational sex ratio is manipulated, is more difficult than with the other indices (Fairbairn and Wilby 2001).

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The use of Morisita index is justified as long as the distribution of the resources is not even (Kokko *et al.* 1999; Fairbairn and Wilby 2001).

**Index of resource monopolization (Q)**

$$Q = \frac{(\sigma^2 - \overline{X})}{(n \overline{X^2} - \overline{X})}$$

$\sigma^2$  = variance of mating/ reproductive success,  
 $\overline{X}$  average success

As  $l\delta$ , Q uses a random (Poisson) distribution of resources as null model, however Q is expressed as a fraction of the maximum possible variance (Fairbairn and Wilby 2001). Q has been proposed by Ruzzante (1996) as a standardized index of the opportunity for sexual selection.

$Q<0$  when the distribution of resources is more even than expected at random,  $Q=0$  when resources are randomly distributed,  $Q=1$  when all resources are monopolized by one individual (Ruzzante *et al.* 1996).

Because Q is standardized to the maximum value, it is easier to compare values across populations with different resource abundance than  $l\delta$ . Q is independent of the mean resource abundance and the population size as long as resources are not shared in a more even way than expected by a Poisson distribution (Ruzzante *et al.* 1996). Q is sensitive to differences in monopolization of resource (Blanckenhorn *et al.* 1998).

Properties of Q, especially independence of the sample size, only apply in cases where one individual is potentially able to monopolize all resources (Ruzzante *et al.* 1996). Q may be misleading if there is no sexual selection and resources are more even than expected at random (Ruzzante *et al.* 1996). When the number of competitors is small, Q may overestimate the opportunity for sexual selection as complete monopolization is easier to obtain than when competition is high, but the value of Q is constantly 1 (Fairbairn and Wilby 2001).

The use of Q is justified when one male can potentially monopolized all females of a group. Additionally, care should be taken if distribution of resources are more even than expected at random. When the number of competitors is small, opportunity for sexual selection may be underestimated by this index (Fairbairn and Wilby 2001)

## Female promiscuity and the limits of the Darwin-Bateman paradigm

The Bateman's principles have been increasingly challenged. Bateman's results have been reanalysed with modern statistical tools. Sutherland (1985) found that chance alone could explain the variance in number of mates and number of offspring. Snyder and Gowaty (2007) found that females in Bateman's study were actually gaining from remating, and the correlation between number of mates and number of offspring was not significantly different from the male correlation. It is possible that gender stereotypes in human societies contributed to initial biased interpretations of Bateman's results, leading to partly erroneous conclusions (Dewsbury 2005). Bateman like Darwin lived in a society where women were expected to be coy, and by extension female animals were not expected to benefit from, and actively seek remating opportunities.

Recent appreciation of female remating identified considerable limitations in Bateman's study which, once taken into account may change the conclusions of the study. First, Bateman used the genetic number of offspring as a proxy for number of mates. However, when females mate with multiple males, mating does not necessarily translate into fertilisation (see below). Considering only males that fertilised some eggs can underestimate variation in male mating success and overestimate the relationship between mating rates and reproductive success. Second, variation in the number of mates is only a component of variation in number of offspring. Males can be sexually selected to increase their number of mates, but they can increase their number of offspring by mating with more fecund females and by increasing their fertilisation success. Thus, studies focusing on male traits that can increase male number of mates may partially miss the whole picture of sexual selection in males.

***The effect of female promiscuity on sexual selection***

Darwin already noticed that males of some monogamous species developed sexually selected traits such as bright plumage (Darwin 1871). If sexual selection acted only on male remating rate, there would be no sexual selection on strictly monogamous populations with an even sex ratio as there is no variance in number of mates. Darwin explained this paradox with difference in female's fecundity or an unequal sex ratio that would create a competition between males.

However, an additional explanation for the evolution of sexually-selected traits in socially monogamous species emerged from the development of molecular biology. For the last 20 years, genetic tools have revealed that female sexual promiscuity is widespread (reviewed by Birkhead and Møller 1998; Simmons 2001a; Tang-Martinez and Ryder 2005). Female promiscuity prolongs the operation of sexual selection after mating, by setting the scene for post-copulatory intra- and intersexual episodes (Dunn *et al.* 2001). First, male-male competition continues after insemination through the competition of their ejaculates for the fertilisation of a set of eggs, a process known as sperm competition (Parker 1970a), and males will be selected for their ability to fertilise a greater proportion of the eggs of a female. Second, as sperm competition occurs in the female reproductive tract, females can also play a role and bias paternity through multiple mechanisms collectively referred to as cryptic female choice (Eberhard 1996). Therefore, selection on male remating is not the only final path acting on male reproductive success as stated Arnold and Duvall (1994). Instead, variation in male reproductive success has three different sources: number of mates (i.e. remating rate), female fecundity, and –under female promiscuity- the proportion of eggs fertilised for each female clutch.

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The influence of female promiscuity on sexual selection in males is not fully understood (Webster *et al.* 1995; Møller and Ninni 1998; Sheldon and Ellegren 1999; Webster *et al.* 2007; Krakauer 2008), and few studies have directly tested this (but see Jones *et al.* 2001). If females remate with several males, more matings are available per female, thus increasing female effective population size (that is to say females available for breeding, Sugg and Chesser 1994). If more females are available per male, competition is relaxed and sexual selection should decrease. However, female promiscuity does not guarantee that all mating result in similar fertilisation success and some males may gain more paternity than other males mating with the same female, through sperm competition and cryptic female choice. Female remating may thus also increase the variance of male reproductive success and the opportunity of sexual selection.

The extent to which variation in reproductive success arising from post-copulatory episodes associated with female promiscuity account for overall paternity skew in a population has been especially studied in birds, with ambiguous results. In socially monogamous birds, the variation of reproductive success due to extra-pair fertilisation had little impact on the variance of male number of offspring in the eastern red-winged blackbirds *Agelaius phoeniceus* (Westneat 1993), scarlet rosefinch *Carpodacus erythrinus* (Albrecht *et al.* 2007), common yellowthroat *Geothlypis trichas* and house wren *Troglodytes aedon* (Whittingham and Dunn 2005). However, in the fairy-wren *Malurus splendens* (Webster *et al.* 2007) and in another study of the red-winged blackbirds (Weatherhead and Boag 1997) extra-pair fertilisations had a strong effect on male fitness variance. Sperm competition is also mainly explaining variance in number of offspring in the collared flycatcher *Ficedula albicollis* (Sheldon and Ellegren 1999) and in the promiscuous wild turkey *Meleagris*

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*gallopavo* (Krakauer 2008). Overall, a meta-analysis of studies using paternity analyses across different species of birds revealed that post-cop sexual selection is an important component of sexual selection in this group (Møller and Ninni 1998).

### ***Female promiscuity and the measure of sexual selection***

Because of female promiscuity, mating is not synonymous to fertilisation and this raises the problem of how to measure mating success in the field. Following Bateman (1948) most studies have used the number of genetic mates inferred from paternity analysis as a proxy of male mating success (Jones 2000; 2002; Jones *et al.* 2004; Jones *et al.* 2005; Mills *et al.* 2007; Krakauer 2008). This approach creates an obvious bias as it does not take into account all matings that did not result in fertilisation (Parker and Tang-Martinez 2005; Uller and Olsson 2008). For example, using the genetic number of mates to calculate Bateman gradient underestimates the role of sperm competition as a female that is laying only one egg would be treated as monogamous when she may have had several mates. An alternative to genetic number of mates is to directly observe mating behaviour and record mating rates of each individual (Bjork and Pitnick 2006). The problem with this measure of mating success is that it assumes that a male that mates several times with the same female will have the same mating success as a male that mates once with several females. Therefore, the number of matings cannot disentangle the effect of mating multiply with the same female and mating with multiple females. A more satisfactory approach is to measure the actual number of mates for each individual. This requires intensive observations of individually tagged males and females.

Another problem, which arises from measuring mating success, is the duration of the record of mating success. Mating success should be recorded in a relatively long interval of time such as a season of reproduction and when records only last for a

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short period of time, it should be called “instantaneous mating success” (Clutton-Brock 1983). However, long-term studies would take into account long-term trade-offs between investment in reproduction and survival and thus underestimate variance in mating and reproductive success (Clutton-Brock 1983). If a male has more success because he is displaying a costly signal, he may pay for this cost by having a lower mating success later in life or in season, so his total number of offspring would be affected by both natural and sexual selection at the same time. By removing long-term trade-offs and limiting the effect of natural selection, instantaneous mating success only captures the effect of sexual selection on reproductive success (Koenig and Albano 1986). Moreover, the record of mating success is different if two males mate with a female such as she could store the sperm from the two males at the same time or if they mate such a long time apart so that sperm competition cannot occur. Therefore, the ideal observation duration to capture both, pre- and post-copulatory episodes varies according to female sperm storage duration, and a *priori* biological understanding of the study system is therefore fundamental.

### ***Are promiscuous females sexually selected to remate?***

The reanalysis of Bateman results (Sutherland 1985; Snyder and Gowaty 2007) showed that females could potentially benefit from remating in terms of number of offspring. A potential way to explore sexual selection in females is to look at female traits that may have evolved from sexual selection on remating. Females are ornamented in many species (Clutton-Brock 2007; Clutton-Brock 2009). It has long been considered that female ornamentation was a genetic bi-product of male ornamentation, but growing evidence shows that female ornamentation may have evolved independently in males and females (Amundsen 2000; Clutton-Brock 2009;

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Wright *et al.* 2009). The cause of female ornamentation seems to be found in another competitive process: social competition or competition for resources not directly related to males (West-Eberhard 1983; LeBas 2006). For instance, in the parrot *Electus roratus*, females are brightly coloured and males are camouflaged. Female competition in order to access rare nest hollows seems to be the origin of this extreme female ornamentation (Heinsohn *et al.* 2005).

However, under sperm competition female might also compete with each other over another scarce resource: ejaculates. Even if each sperm production is not costly compared to egg production, the insemination of large ejaculates promoted by sperm competition might make sperm a limiting resource (Wedell *et al.* 2002). Because of this limitation, males can benefit from being choosy and invest more resources in highly fecund females, thus creating inter-sexual selection in females. In the empidid dance flies, *Rhamphomyia tarsata*, females have ornaments that honestly reflect their fecundity. Males empidid dance flies provide more nuptial gifts to ornamented females and this alone could explain the maintenance of female ornamentation (LeBas *et al.* 2003). In the feral fowl, *Gallus gallus*, female fecundity is honestly signalled by female comb size and males invest more in high quality females (Cornwallis and Birkhead 2007).

Strategic male sperm allocation may result in some females facing a risk of infertility associated with sperm depletion (Wedell *et al.* 2002). In other cases, seminal fluid products or other male traits associated with mating can directly stimulate female fecundity (e.g. Wedell and Karlsson 2003), thus qualitatively changing the relationship between remating and reproductive success in females. In such species, positive Bateman gradients in females may occur (Arnold 1994; Ketterson *et al.* 1998; Worden and Parker 2001; Snyder and Gowaty 2007).

***The red junglefowl as a model species for the operation of sexual selection***

Red junglefowl, *Gallus gallus*, males and females are ornamented with a comb that is bigger in males; males also have a brighter plumage and are bigger than females (Darwin and Murray 1868). Number of mates in males is uneven with a small proportion of birds getting most of the matings (Collias *et al.* 1994; Collias and Collias 1996). Male-male competition is expressed through a stable social status in the flock that is the basis of all interactions between same sex birds (Guhl 1958; 1964). Predictors for male reproductive success are at the same time: social with dominant birds getting most of the matings, phenotypical with larger male, and males with a larger comb performing better, and behavioural with the most vigilant males having a higher number of offspring (Johnsen *et al.* 2001; Wilson *et al.* 2008). Female choice can also be an important driving force for sexual selection on males (Wood-Gush 1954; Zuk *et al.* 1990a; Zuk *et al.* 1990b; Pizzari 2001; Parker and Ligon 2003).

The red junglefowl is a promiscuous species (Cheng and Burns 1988; Collias and Collias 1996), where sperm competition has been intensely studied (Pizzari *et al.* 2002). Males who transfer more sperm (Martin *et al.* 1974) and sperm of better motile quality (Froman and Feltmann 1998; Birkhead *et al.* 1999; Froman 2003) have a fertilising advantage in sperm competition. The number of sperm a male transfers varies according to sperm competition risk, social status, previous mating history, female fecundity and more generally to the female likelihood to produce eggs fertilised by his sperm (Pizzari 2002; Pizzari *et al.* 2003; Cornwallis and Birkhead 2006; Cornwallis and Birkhead 2007). Male sperm quality can also vary rapidly within a male, in particular with his social status (Pizzari *et al.* 2007).

## **Aims**

The objective of this chapter is to measure sexual selection under female promiscuity in red junglefowl. Specifically, I will address the following aims:

(1) Quantify the opportunity and strength of pre- and post-copulatory sexual selection arising from three components of reproductive success: mating success, mate fecundity and fertilisation success within mates

(2) Investigate the opportunity and the intensity of sexual selection in females and compare it to the sexual selection operating on males

(3) Quantify the effect of female promiscuity on the total sexual selection operating on males

## **Material and methods**

### Observations in semi-natural conditions

This study was conducted on a population of red junglefowl, between May and September 2007 and between August and September 2008. All males and females hatched in March 2006, but for one female hatched in October 2007 and used in summer 2008. I observed groups composed of three males and four females, which represents a group size and sex ratio within the range observed in natural populations (Collias *et al.* 1966). Groups were kept in outdoor pens of at least 50m<sup>2</sup>. Birds were sexually rested for at least 10 days for females and two days for males (Etches 1996). Observations started 12 hours to four days after birds were put together. Some birds were used in several groups (one bird was used in four groups), within or across years. Observations were recorded 5 hours a day at peak mating activity (Løvlie and Pizzari 2007 for daily mating pattern): two hours in the early morning starting when the first

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female got off the perch, and three hours in the afternoon finishing when all females were roosting. As all data are standardized per group, departures from these hours of observations (one to two days during the observation period, observations lasted only four hours) were taken into account. Observations consisted of recording behaviours of individual birds, including interactions within or across sexes. Mating was recorded when a male mounted a female and dipped his train. From the second day of observation (*i.e.* from day 2 to day 11 inclusive), eggs were collected. One group departed from this pattern as observations and egg collection only overlapped during the last four days of observation. Analyses were carried out with or without this group and no significant difference was observed so only results with this group are presented. A female died during observations and was removed from all analysis, but the interactions of other birds towards her were kept in the analysis.

### Paternity and maternity assignment

Eggs were kept in a fridge during zero to seven days before being put in an incubator at 37°C and 41% humidity. After seven days of incubation, eggs were opened and embryos were collected and put in 1,000 µL of pure ethanol. Unfertilised eggs were recorded in 2008.

Paternity and maternity were assigned for each egg laid during the observations by a microsatellites analysis performed by Dr Kirsty Worley in University of East Anglia.

‘Genomic DNA was extracted using a standard salt extraction method (Sunnucks and Hales 1996). Extractions were normalised to concentrations of 10 ng/µl and stored at -20° C. All samples were genotyped at seven variable microsatellite loci; ADL0299 (Cheng and Crittenden 1994), LEI0078 (Gibbs *et al.* 1997), LEI0196

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(Dawson *et al.* 1998), LEI0246 (McConnell *et al.* 1999), MCW0123 (Crooijmans *et al.* 1996), MCW0183 (Crooijmans *et al.* 1997) and ROS0081. Microsatellite loci were amplified in 10  $\mu$ l reactions containing 1.5  $\mu$ l DNA, 0.5  $\mu$ M of each primer and 5  $\mu$ l PCR Reddymix (Abgene) containing 1.5 mM MgCl<sub>2</sub>, 0.8 mM dNTPS and 0.625 U *Taq* polymerase. PCR profiles consisted of 5 mins at 94 °C followed by 35 cycles of 30 s each at 94 °C, variable annealing temperature of between 52–58 °C and 72 °C. Reactions were terminated with an additional 5 min at 72 °C. Amplified products were genotyped using an ABI 3730 sequencer and analysed using GENEMARKER software (Softgenetics)' (Worley *et al.* *subm.*).

All parental assignments were done in cervus (Marshall *et al.* 1998), after saving the microsatellite data as a genepop file and then converting this to cervus file format in cervus (as described in the cervus manual). Maternity was assigned first and then the male assigned with cervus adding female as the known parent. All mismatches between embryo and putative parents were checked again by re-genotyping the embryo at any suspect loci and re-running assignments. If there was then still a mismatch the parent was accepted (providing this was the only mismatch) as mutations can occur frequently in microsatellite loci or null alleles could theoretically be present in small frequency.

Both parents were assigned for 164 embryos in 2007 and 90 embryos in 2008. Between 6 and 28 eggs were laid per group. 89% of the eggs were fertilised in 2008. No group had more than 22% of eggs unfertilised, 67% of which were laid for the first two days of egg collection. Unfertilised eggs could not be assigned a mother so female number of offspring only included fertilized eggs.

## Statistical analyses

### ***Indices to compare male and female mating success, reproductive success and their relationships***

Observed number of mates is the number of individuals with which the focal bird has been observed mating during the 10 days of observations. The observed number of mates takes into account promiscuity in females that just lay one egg. Genetic number of mates is the number of mates given by paternity and maternity analyses. Some matings were not observed (either because they occurred before the onset of monitoring or outside of the daily pattern of observations), so that some matings were revealed by genetic analysis. Total number of mates is the observed number of mates corrected by the genetic number of mates. Number of offspring corresponds to the number of embryos collected that was sired by an individual.

I quantified opportunity and strength of sexual selection using multiple indices, as recommended by Kokko *et al.* (1999). Using the same individuals in different groups creates pseudo-replication. In order to know the bias due to pseudo replication I calculated repeatability scores (Lessells and Boag 1987). Repeatability scores were low for male number of offspring ( $r = 0.11$ ), number of mates ( $r = -0.04$ ), male mate fertility ( $r = -0.19$ ), the proportion of offspring sired within mates' clutch ( $r = 0.16$ ) and female number of mates ( $r = 0.09$ ) so that same individuals in different groups can be considered as independent samples. However, female number of offspring was highly repeatable ( $r = 0.42$ ) so variability in number of offspring may be underestimated.

The different indices of opportunity for sexual selection calculated are:  $I$ ,  $I_s$ , the Morisita index ( $I_\delta$ ) for number of mates and offspring and the index of monopolisation ( $Q$ ) for number of mates and offspring (Box 2.01). Precautions linked to each index (!

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in Box 2.01) were taken in consideration. Each index was calculated for each group, and the values given are the average across groups. Each index was calculated with total, observed and genetic number of mates and indices were then compared by a Kruskal-Wallis test. Indices were compared between males and females by a paired t-test. To know the distribution of number of mates and number of offspring, indices were compared to the value expected from an even/ random or monopolized distribution (Box 2.01, Kokko *et al.* 1999) by a one sample t-test. An even distribution corresponds to an equal access to resource (mates or offspring) across individuals, a random distribution means that each resource unit is consistent with a random assignment across individuals according to a Poisson distribution. It does not necessarily mean that distribution is actually random as the most successful males may consistently perform better for a reason not taken into account in the study, only that variability in success across males follows a Poisson distribution. Finally, a monopolized distribution would be found if one individual gets all resources.

The Bateman gradient ( $\beta$ ) is given by the least square regression line between number of offspring and number of mates. The Bateman gradient was calculated in two ways. First, the Bateman gradient was calculated for each group and then averaged. A problem in this calculation was that, for one group all males had the same number of mates and for two groups all females had the same number of mates, and thus no Bateman gradient existed. Therefore, the groups without variability in number of mates were not taken into account in this analysis. Second, to remove the effects of the different groups and the fact that some individuals have been used several times, an overall Bateman gradient including all groups was calculated with a mixed model (function `lme` in library `nlme` in R 2.6.1, Crawley 2007). To test if male and female Bateman gradient was significantly greater than zero (meaning that supplementary

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mates gives supplementary offspring), a t-test was performed. To compare male and female Bateman gradients a t-test with independent samples was performed to use all information available even if males or females of the group did not have a Bateman gradient. I could not investigate if the shape of the relationship between number of mates and number of offspring was different between males and females as females did not have the possibility to mate with more than three males and males with more than four females. For the indices that were not normally distributed (p value < 0.05 in a Ryan-Joiner/ Shapiro-Wilk test), values were transformed using a Johnson transformation according to table 2.01.

**Table 2.01:** Normalisation of the indices of mating and reproductive success for t-tests. The transformation used is the best-fitted Johnson's transformation given by Minitab 15.0.

	Number of mates	Number of offspring
$\beta$	None	
$I/ I_s$	$-1.115 + 0.5113 * \text{Asinh}((x - 0.02507) / 0.01409)$	$0.7380 + 0.6402 * \text{Ln}((X + 0.01968) / (3.236 - X))$
$I_o$	$-0.3708 + 0.5297 * \text{Asinh}((x - 0.7227) / 0.0498)$	$0.9498 + 0.7662 * \text{Ln}((X - 0.7808) / (3.623 - X))$
Q	$-0.3696 + 0.4614 * \text{Asinh}((X + 0.1040) / 0.01373)$	$1.700 + 1.426 * \text{Ln}(X + 0.1379)$

### ***Decomposition of male reproductive success due to pre- and post-insemination sexual selection***

As the index of opportunity for selection  $I$  is based on variance, it can be decomposed in several episodes of selection that are multiplicative components (Arnold and Wade 1984b). The total number of offspring a male has is equal to the number of his female mates times the number of offspring each mate produced times the proportion of offspring he sired with each of his mates. The decomposition of multiplicative factors is given by Webster *et al.* (1995):

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$$\text{Var}(M * N * P) = \bar{N}^2 \bar{P}^2 \text{Var}(M) + \bar{M}^2 \bar{N}^2 \text{Var}(P) + \bar{M}^2 \bar{P}^2 \text{Var}(N) + \text{Cov}(M, N) + \text{Cov}(M, P) + \text{Cov}(N, P) + Dt$$

$M$  is the number of mates. It has been calculated with total number of mates, observed number of mates and genetic number of mates and results will be compared across the different methods. If the variance in number of offspring is mainly explained by  $M$ , the opportunity for sexual selection in males is mainly due to mating opportunities and sexual selection is mainly pre-copulatory.  $N$  is the average number of offspring sired by a male's mate or mate fecundity.  $N$  was calculated with observed, genetic and total number of male's mates. If  $N$  mainly explains the variance in number of offspring, male mate choice mainly explains the opportunity for selection.  $P$  is the average proportion of offspring fathered by a male in females he mated with. Here again, several  $P$  were calculated according to data given by total, observed and genetic number of mates. If  $P$  mainly explains the variance in number of offspring, post-copulatory sexual selection mainly explains the opportunity for selection.  $Dt$  is an error term. All variances and covariances were calculated in each group and then averaged across groups. Variance are always presented both standardized (divided by the squared total mean number of offspring per male) and not.

### ***Selection gradients of the different episodes of sexual selection***

I performed a mixed model (lmer in R 2.6.1, library lme4, Crawley 2007) of the number of offspring according to number of mates, mate fecundity and proportion of offspring sired in mates. For this mixed model, the random effects were bird identity and group. When a male did not have any mates, mate fecundity and proportion of offspring were not taken into account (NA in R). This model has been performed with and without the year fixed effect. As no difference was observed according to an

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ANOVA table, the results presented are those without the year as a fixed effect. p-values were calculated from a linear model (glm) and do not include random effects, so they are just presented as a reference to see the difference between models taking into account observed, genetic or total number of mates. For these models, data were standardized such that the response had a mean of 1 (each individual value was divided by the group mean) and the predictors had a mean of zero and a standard deviation of one per group (each individual value was subtracted by the mean of the group and then divided by the standard deviation of the predictor for the group, Lande and Arnold). No value was entered (NA in R) when the standard deviation was null in a group (all males from a group had the same value for the predictor), or for mate fecundity and proportion of offspring in mates when a male did not mate with any female.

### ***Relationship between the opportunity for selection and female promiscuity***

$I$  (the opportunity for selection) and mean female promiscuity (average total number of mates for females of each group) were correlated with a simple regression (lm in R.2.9.1, Crawley 2007). Normality of residuals was checked with a Shapiro-Wilk test.

## Results

### Comparison between genetic vs observed measures of mating success

The different mating success measures (total, genetic, observed number of mates or number of matings) gave significantly different results for all indices (table 2.02).

**Table 2.02:** Comparison between indices calculated in males with total, observed and genetic number of mates ( $M$ ) or number of matings and results of Kruskal-Wallis test. All these indices are averaged across the 13 groups except for the Bateman gradient that are averaged over the 13 groups for the number of matings and across 12 groups for total number of mates, observed number of mates and genetic number of mates.

	M total	M observed	M genetic	number of matings	H	df	p
mean	2.82 ± 0.22	2.62 ± 0.24	1.97 ± 0.20	15.49 ± 2.45			
var	1.90 ± 0.54	2.49 ± 0.60	1.64 ± 0.29	247.46 ± 50.72			
$I/I_s$	0.50 ± 0.23	0.74 ± 0.29	0.71 ± 0.23	1.36 ± 0.27	8.5	3	0.037
$I_b$	1.12 ± 0.17	1.28 ± 0.22	1.16 ± 0.17	1.88 ± 0.18	13.31	3	0.004
Q	0.06 ± 0.09	0.14 ± 0.11	0.08 ± 0.09	0.44 ± 0.09	13.31	3	0.004
$\beta$	5.11 ± 0.99	4.04 ± 1.10	4.84 ± 0.59	0.41 ± 0.10	24.74	3	<0.0001

The decomposition of the variance of male number of offspring between number of mates ( $M$ ), mate fecundity ( $N$ ) and proportion of offspring sired within each mate ( $P$ ) gave different results according to the measure of mating success. The term  $P$  is much more important when the observed number of mates is used than when the genetic number of mate is used (table 2.03).

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**Table 2.03:** Comparison of the decomposition of variance of the total number of offspring ( $T$ ) between number of mates ( $M$ ), mate fecundity ( $N$ ) and proportion of offspring sired in mates ( $P$ ) if the number of mates is the observed number of mates (left) or the genetic number of mates (right). Values are presented absolute, standardized and as a percentage of the total variance.

Term	Interpretation	Observed number of mates			Genetic number of mates		
		Absolute value	Standardized value	% total variance	Absolute value	Standardized value	% total variance
$Var(T)$	Variance in number of offspring	47.85	1.13	100.00	47.85	1.13	100.00
$\overline{N^2 P^2} Var(M)$	Variance in number of mates	11.65	0.27	24.34	14.56	0.34	30.43
$\overline{M^2 P^2} Var(N)$	Variance in number of offspring per mate	1.83	0.04	3.82	0.97	0.02	2.04
$\overline{M^2 N^2} Var(P)$	Variance in proportion of offspring sired per mate	16.09	0.38	33.62	9.13	0.22	19.07
$\overline{2MNP} Cov(M, N)$	Covariance between number and fecundity of mates	1.88	0.04	3.92	1.46	0.03	3.06
$\overline{2MPN^2} Cov(M, P)$	Covariance between number of mates and proportion of offspring sired in them	4.57	0.11	9.56	9.00	0.21	18.82
$\overline{2NPM^2} Cov(N, P)$	Covariance between mate fecundity and proportion of offspring sired in them	0.44	0.01	0.91	-0.01	0.00	-0.02
Error		11.40	0.27	23.83	12.73	0.30	26.61

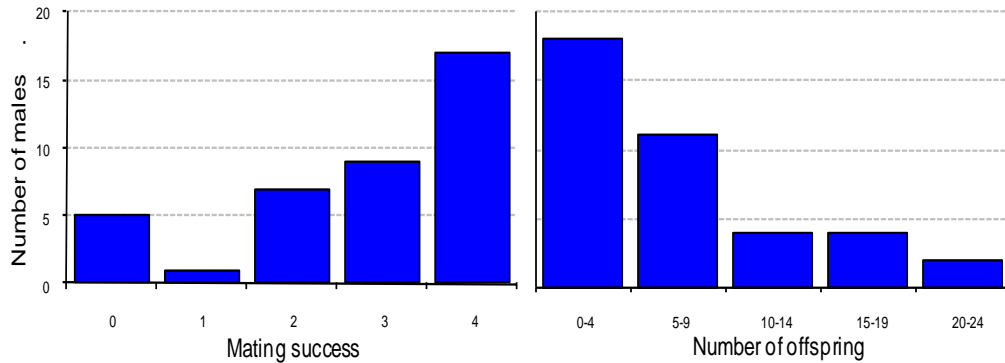
Number of mates was more correlated with number of offspring when using the genetic number of mates (coef =  $0.48 \pm 0.14$ ,  $p=0.002$ ) than with the observed number of mates (coef =  $0.26 \pm 0.15$ ,  $p=0.0961$ ). The proportion of offspring was more correlated with number of offspring when it was evaluated by observed number of mates (coef =  $0.67 \pm 0.13$ ,  $p=0.00002$ ) than by the genetic number of mates (coef =  $0.47 \pm 0.13$ ,  $p=0.002$ ). Thus, the genetic number of mates overestimated the role of the variation in mating success and the observed number of mates showed a higher importance of the post-copulatory episode of sexual selection.

### Opportunity and strength of the different episodes of sexual selection in males

Males had between zero and four mates and sired between zero and 23 offspring (fig. 2.01). 23 males out of 24 fathered at least one embryo in 2007 and 10

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males out of 15 fathered at least one embryo in 2008. All indices of variance of number of mates and offspring were higher in 2008 than in 2007 as all indices were higher in 2008 (table 2.04).



**Figure 2.01:** Distribution of mating (left) and reproductive (right) success in males.

**Table 2.04:** Average and variance of number of offspring (T) and number of mates (M) in males in 2007, 2008 and in both years together. All results included eight groups in 2007 and five groups in 2008, except for the Bateman gradient that only included seven groups in 2007 that is to say 12 groups all together.

	both years		2007		2008	
	T	M	T	M	T	M
mean	6.51 ± 0.99	2.82 ± 0.22	6.83 ± 1.14	3.13 ± 0.23	6.00 ± 1.86	2.33 ± 0.42
var	47.85 ± 12.28	1.90 ± 0.54	38.04 ± 13.63	1.29 ± 0.51	63.53 ± 23.60	2.87 ± 1.06
<i>I</i> / <i>I</i> <sub>s</sub>	1.17 ± 0.26	0.50 ± 0.23	0.74 ± 0.24	0.21 ± 0.12	1.85 ± 0.41	0.98 ± 0.54
<i>I</i> <sub>δ</sub>	1.71 ± 0.18	1.12 ± 0.17	1.41 ± 0.17	0.91 ± 0.07	2.20 ± 0.29	1.44 ± 0.41
<i>Q</i>	0.36 ± 0.09	0.06 ± 0.09	0.20 ± 0.09	-0.04 ± 0.04	0.60 ± 0.14	0.22 ± 0.21

Number of mates was never significantly even across males or monopolized by a male (table 2.05). *I*<sub>δ</sub> and *Q* agreed with a random distribution of mates across males and *I* seemed to show that the distribution of the number of mates was between even and random (table 2.05). Number of offspring was neither significantly even across males nor monopolized by a single male (table 2.05). *I* was consistent with a random distribution of offspring across males whilst the other indices show a distribution of the number of offspring per male that would be more variable than expected at random, thus showing the opportunity for sexual selection to operate in males (table 2.05).

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**Table 2.05:** Tests of deviation from distribution of number of mates and number of offspring in males.  $\mu$  values are the constant to which data are compared from Kokko *et al.* (1999) and are transformed by the Johnson's transformation (table 2.01).

		Number of mates			Number of offspring		
		Even	Random	Monopolized	Even	Random	Monopolized
I/ Is	$\mu$	-1.8	1.41	2.5	-2.53	0.24	
	t	5.81	-3.9	-7.21	8.77	-0.04	
	df	12	12	12	12	12	
	p	<0.0001	0.002	<0.0001	<0.0001	0.97	
I <sub>5</sub>	$\mu$	-0.33	0.91	2.02	-1.53	-0.95	1.92
	t	5.34	-1.2	-7.08	6.42	4.3	-6.21
	df	12	12	12	12	12	12
	p	0.0002	0.25	<0.0001	<0.0001	0.001	<0.0001
Q	$\mu$	-1.11	0.89	1.97	-1.86	-1.12	1.88
	t	5.81	-1.86	-6.04	7.16	4.77	-4.97
	df	12	12	12	12	12	12
	p	<0.0001	0.087	<0.0001	<0.0001	0.0005	0.0003

Males had on average 2.82 mates and 6.51 offspring in 10 days (table 2.04). Each additional mate gave on average 5.11 more offspring for a male (fig. 2.02) over the two years. For the seven groups that had a Bateman gradient in 2007, the Bateman gradient was  $4.61 \pm 1.19$  in 2007 and  $5.81 \pm 1.83$  for the five groups recorded in 2008. The maximum standardized differential due to sexual selection on rematings in males was  $2.13 \pm 0.37$  across years,  $1.48 \pm 0.31$  in 2007 and  $3.04 \pm 0.62$  in 2008.

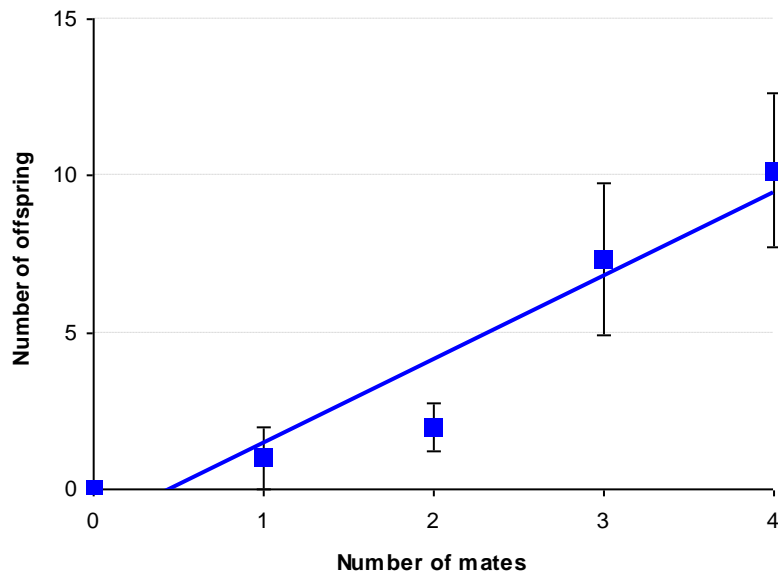


Figure 2.02: Number of offspring versus number of mates in males.

Bateman gradient was significantly greater than zero ( $t = 4.98$ ,  $df = 1, 11$ ,  $p = 0.0004$ , fig. 2.02). The mixed model that took into account random effects such as group and bird identity showed the same pattern ( $\beta = 2.82 \pm 0.57$ ,  $df = 1, 25$ ,  $t = 4.92$ ,  $p < 0.0001$ ).

$P$ , the variation in the proportion of offspring that a male sired within each of his mates arising from female promiscuity, explained almost half of variation in male number of offspring (table 2.06).  $M$ , the number of mates, explained almost 20% of variance and the positive covariance between  $M$  and  $P$  explained more than 15% of the variance of male number of offspring (table 2.06).

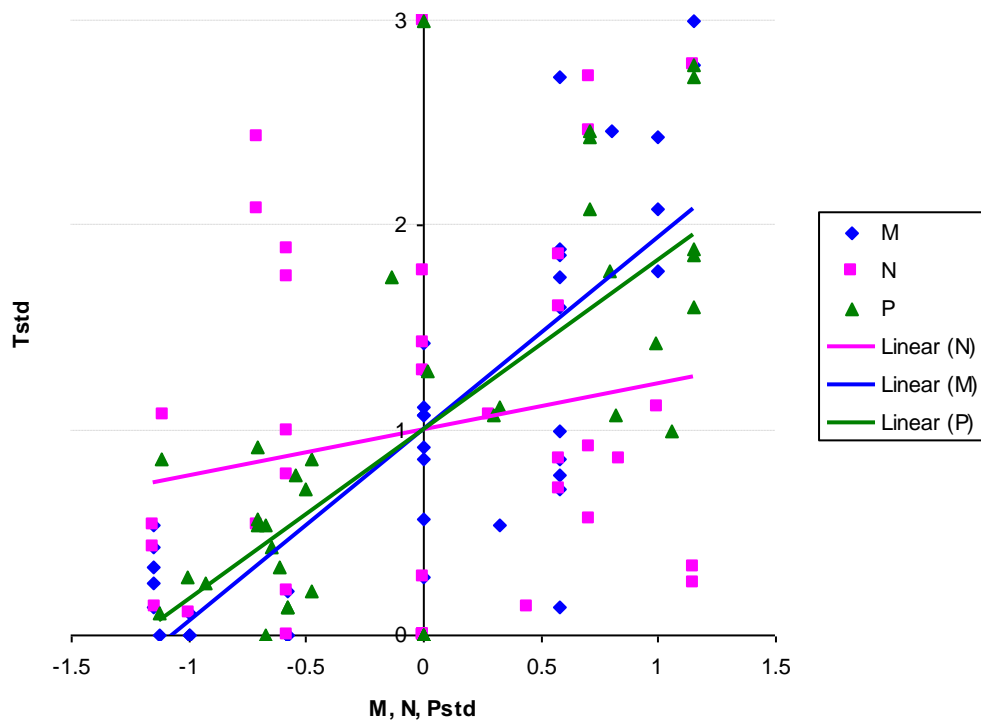
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**Table 2.06:** Decomposition of variance of the total number of offspring ( $T$ ) between number of mates ( $M$ ), mate fecundity ( $N$ ) and proportion of offspring sired in mates ( $P$ ). Values are presented absolute, standardized and as a percentage of the total variance.

Term	Absolute value	Standardized value	% total variance
Var ( $T$ )	47.85	1.13	100.00
Var ( $M$ )	1.90		
Var ( $N$ )	0.51		
Var ( $P$ )	0.09		
$\overline{N^2 P^2} \text{Var} (M)$	9.39	0.22	19.62
$\overline{M^2 P^2} \text{Var} (N)$	0.68	0.02	1.41
$\overline{M^2 N^2} \text{Var} (P)$	20.47	0.48	42.79
$2 \overline{M N P^2} \text{Cov} (M, N)$	-1.15	-0.03	-2.40
$2 \overline{M P N^2} \text{Cov} (M, P)$	7.29	0.17	15.23
$2 \overline{N P M^2} \text{Cov} (N, P)$	-0.21	0.00	-0.44
Error	11.38	0.27	23.79

$P$ , the proportion of offspring sired within each mate and  $M$ , number of mates were positively selected (respectively, coefficient =  $0.59 \pm 0.13$ ,  $p = 0.00008$ , coefficient =  $0.41 \pm 0.14$ ,  $p = 0.0063$ , fig. 2.03), however, mate fecundity was not significantly selected (coefficient =  $0.15 \pm 0.10$ ,  $p = 0.12$ , fig. 2.03).

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**Figure 2.03:** Standardized  $T$  (total number of offspring) according to standardized  $M$  (number of mates),  $N$  (fecundity of mates) and  $P$  (proportion of offspring fathered in mates).

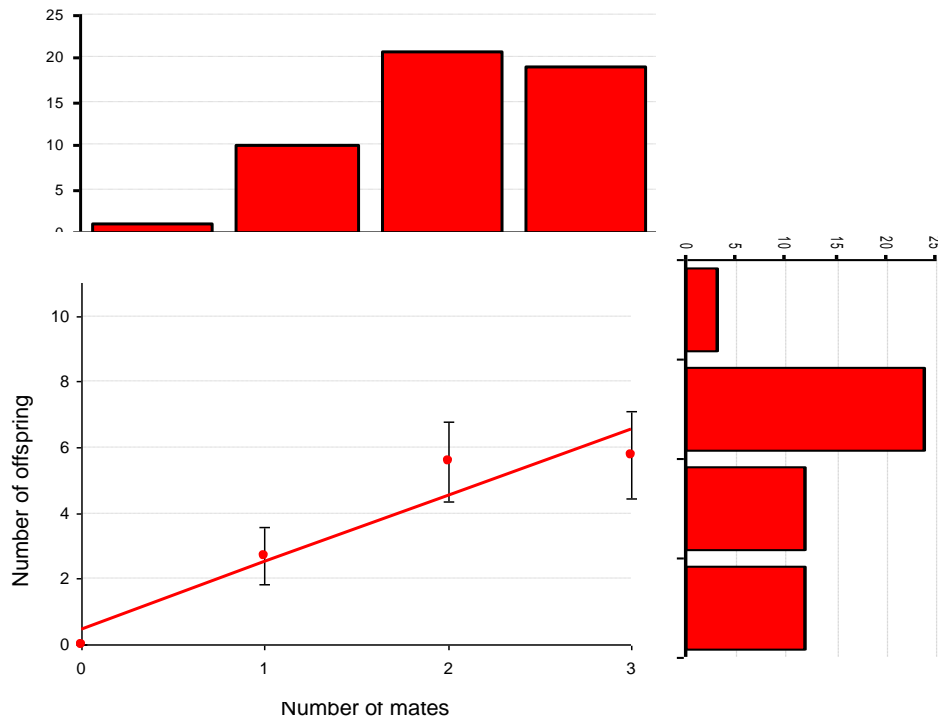
### Sexual selection in females compared to the sexual selection in males

Females had on average 2.14 mates and laid 4.98 fertile eggs in 10 days (table 2.07, fig. 2.04). Four females out of 32 in 2007 and four females out of 20 in 2008 did not produce any fertile egg. The number of offspring was more variable in 2008 than in 2007 (table 2.07).

**Table 2.07:** Total number of mates ( $M$ ) and number of offspring ( $T$ ) in females in 2007, 2008 and in both years together. All results include eight groups in 2007 and five groups in 2008, except for the Bateman gradient that only include seven groups in 2007 and four in 2008 that is to say 11 groups altogether.

	both years		2007		2008	
	$T$	$M$	$T$	$M$	$T$	$M$
mean	$4.98 \pm 0.42$	$2.14 \pm 0.11$	$5.29 \pm 0.54$	$2.39 \pm 0.11$	$4.50 \pm 0.69$	$1.75 \pm 0.20$
var	$8.58 \pm 1.68$	$0.42 \pm 0.16$	$9.39 \pm 2.56$	$0.30 \pm 0.06$	$7.30 \pm 1.76$	$0.62 \pm 0.41$
$l/s$	$0.63 \pm 0.20$	$0.12 \pm 0.05$	$0.55 \pm 0.19$	$0.07 \pm 0.02$	$0.76 \pm 0.45$	$0.20 \pm 0.14$
$l_0$	$1.37 \pm 0.15$	$0.67 \pm 0.07$	$1.34 \pm 0.17$	$0.72 \pm 0.01$	$1.41 \pm 0.32$	$0.59 \pm 0.18$
$Q$	$0.11 \pm 0.05$	$-0.12 \pm 0.02$	$0.09 \pm 0.05$	$-0.10 \pm 0.01$	$0.14 \pm 0.11$	$-0.14 \pm 0.06$

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**Figure 2.04:** Number of offspring according to number of mates in females. On the top of the graphic: distribution of the number of mates and on the side: distribution of the number of offspring.

For number of mates and number of offspring, none of the indices agreed with the distributions tested (even, random or monopolized, table 2.08). However, by estimating where the  $t$  value would equal zero, it is possible to see that the true distribution of female number of mates was more even than expected at random (table 2.08).  $I$  values suggest a distribution of number of offspring that was more even than a random distribution while  $Q$  and  $I_5$  suggest that the number of offspring of females was more monopolized by certain females than the Poisson distribution predicts.

The Bateman gradient showed a non-significant tendency to be greater than zero ( $t = 2.16$ ,  $df = 10$ ,  $p = 0.056$ , fig. 2.04). A mixed model that took into account random effects showed a positive correlation between the number of mates and the number of

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offspring in females ( $\beta = 1.52 \pm 0.51$ ,  $df = 1, 37$ ,  $t = 2.98$ ,  $p = 0.005$ ). Consistent with this trend, Figure 2.04 shows a higher number of offspring for females remating than for females mating with one male, but this was not tested.

**Table 2.08:** Tests of distribution of number of mates and number of offspring in females.  $\mu$ -values are the constants to which data were compared (Kokko *et al.* 1999) and were transformed by the Johnson transformation (see table 2.01). Monopolized values could not be tested for number of offspring for  $I$  and  $I_b$  because the expected values of  $\mu$  could not be transformed by the Johnson transformation

		Number of mates			Number of offspring		
		Even	Random	Monopolized	Even	Random	Monopolized
$I/Is$	$\mu$	-1.8	1.41	2.51	-2.53	0.24	
	t	6.07	-7.48	-12.12	6.52	-2.59	
	df	12	12	12	12	12	
	p	<0.0001	<0.0001	<0.0001	<0.0001	0.024	
$I_b$	$\mu$	-1.26	0.91	2.21	-2.05	-0.95	
	t	2.96	-6.69	-12.49	6.49	2.26	
	df	12	12	12	12	12	
	p	0.012	<0.0001	<0.0001	<0.0001	0.04	
Q	$\mu$	-1.09	0.89	1.97	-1.84	-1.12	1.88
	t	2.85	-6.18	-11.15	5.46	2.44	-10.2
	df	12	12	12	12	12	12
	p	0.015	<0.0001	<0.0001	0.0001	0.031	<0.0001

The number of offspring and number of mates were on average higher in males than in females due to the biased sex ratio, so only the indices of variance and the Bateman gradient were compared between sexes (table 2.09).

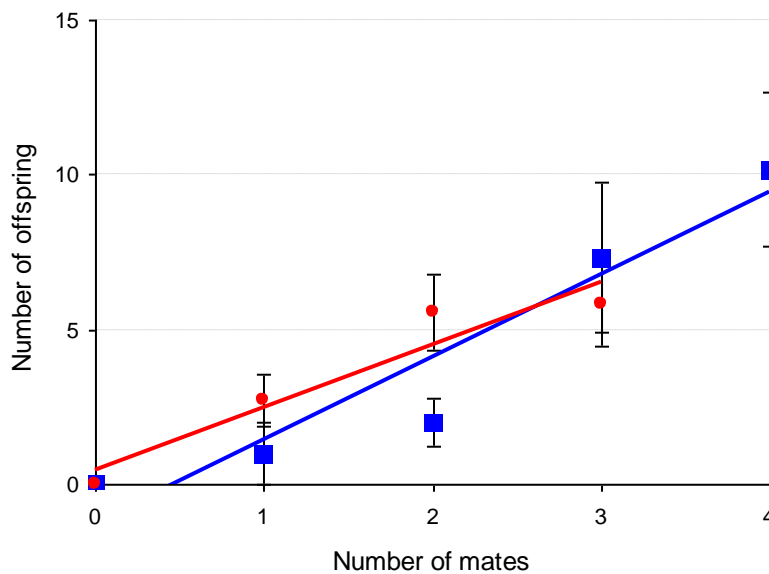
**Table 2.09:** Mean and indices of variance for number of mates and number of offspring in males and females and comparison between males and females with a t-test. All indices are calculated across the 13 groups except for the Bateman gradient in males (12 groups) and in females (11 groups).

	Number of mates					Number of offspring				
	Male	Female	t	df	p	Male	Female	t	df	p
mean	2.82 ± 0.22	2.14 ± 0.11				6.51 ± 0.99	4.98 ± 0.42			
var	1.9 ± 0.54	0.42 ± 0.16				47.9 ± 12.28	8.58 ± 1.68			
$I/Is$	0.5 ± 0.23	0.12 ± 0.05	1.3	12	0.22	1.17 ± 0.26	0.63 ± 0.2	2.1	12	0.057
$I_b$	1.12 ± 0.17	0.67 ± 0.07	3.3	12	0.006	1.71 ± 0.18	1.37 ± 0.15	1.77	12	0.1
Q	0.06 ± 0.09	-0.12 ± 0.02	1.85	12	0.09	0.36 ± 0.09	0.11 ± 0.05	2.41	12	0.03
$\beta$						5.11 ± 0.99	1.8 ± 0.77	2.5	20	0.021

Indices of variability in number of mates and number of offspring were not significantly different between males and females except  $I_b$  for number of mates, Q for

## Chapter 2: The measure of sexual selection

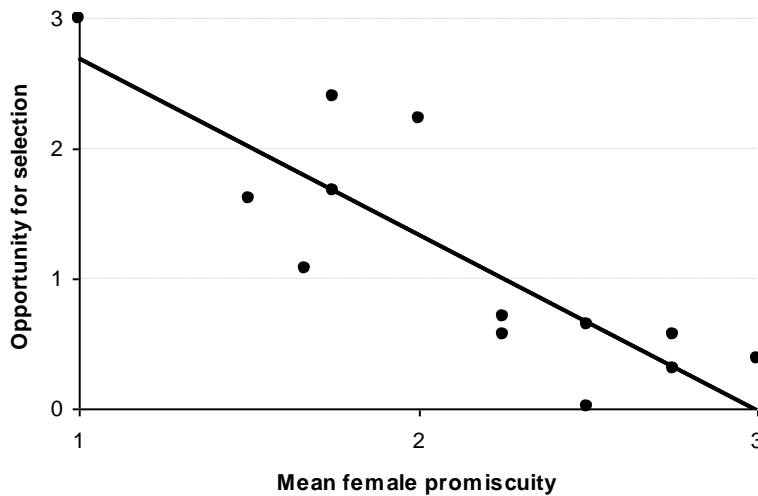
number of offspring and a strong tendency with  $I$  for number of offspring (table 2.09). However, sexual selection on remating was more intense in males than in females as the Bateman gradient was 2.84 times steeper in males than in females (table 2.09, fig. 2.05). Therefore, males experienced at least nearly three times more selection on remating than females (table 2.09, but see discussion for the meaning of this value in females).



**Figure 2.05:** Number of offspring according to number of mates in males (blue) and females (red).

### Female promiscuity decreases the opportunity for selection on male reproductive success

The opportunity of sexual selection in males decreased with the mean female promiscuity across groups (adjusted  $R^2 = 0.68$ ,  $p = 0.000299$ , fig 2.06).



**Figure 2.06:** Opportunity for selection according to mean female promiscuity across the 13 groups.

## Discussion

This chapter quantified variation in different components of reproductive success and measured the opportunity and strength of pre- and post-copulatory sexual selection in replicate red junglefowl groups. I found that:

(1) The use of genetic measures of mating success leads to severe underestimation of post-copulatory sexual selection.

(2) Indices measuring variability in male reproductive success were generally consistent in showing opportunity for sexual selection in males. Males are sexually selected to remate but even more strongly selected at a post-copulatory stage.

(3) Bateman's results were partly confirmed; variance in reproductive success was higher in males than in females and benefits of remating were stronger in males than in females. However, the Bateman gradient in females suggests that females too might be selected to remate to some degree.

## Chapter 2: The measure of sexual selection

(4) With increasing levels of female promiscuity in a group, the intensity of post-copulatory sexual selection increases, but the overall opportunity for sexual selection is reduced.

### Mating system of the red junglefowl

Indices of variability in number of mates were not significantly higher in males than in females, except the Morisita index. The variability in number of offspring was significantly higher in males than in females. However, variability in female reproductive success was underestimated due to pseudo-replication, so no definitive conclusion can be drawn from these results. All indices showed that the variability in number of offspring was higher or equal to a random distribution in males. This variance creates an opportunity for sexual selection. The opportunity for sexual selection due to the variance of number of mates was much lower than the opportunity for selection due to variance in number of offspring in males and in females. Both male and female distributions of number of mates fitted an even to random distribution. Sexual selection may thus operate through different ways than remating as all males and females of the same group had similar mating success.

As both males and females showed a positive Bateman gradient, males and females could benefit from remating and we expect a polygynandrous mating system, which is the one observed. There was a low repeatability of number of mates and number of offspring in males and number of mates in females, which means that mating and reproductive success for males and number of mates for females depends on the social environment and is especially dependant on the success of the other birds from the same group.

## Chapter 2: The measure of sexual selection

A strong difference in indices describing the mating system was visible between 2007 and 2008 with all indices being higher in 2008 than in 2007 for males and the Bateman gradient being steeper in females in 2008. Several factors that can account for this tendency changed between the 2 years of observations. First, intrinsic factors such as age of the fowls. Birds were 1.5 years old the first year and 2.5 the second year. Being 2.5 years old, it is possible that some males may see their fertilisation efficiency decreasing due to senescence more than other, thus increasing variance in reproductive success. Moreover, the difference in male social status (one of the best predictor of reproductive success, see Chapter 3), could be stronger after birds spent one more winter together before observations in 2008. Second, environmental factors such as seasonality could be responsible for this change. In 2008, observations were carried later in the season. Unfortunately, too few birds were used across years to discriminate between these hypotheses. In the future, it would be interesting to further investigate the reasons for the increase in the variability in male reproductive success and female Bateman gradient across years.

### Female promiscuity drastically modifies the operation of sexual selection in males

This study largely confirmed Bateman's results that males were under more intense sexual selection than females in the fowl: males showed a higher variability than females in their number of offspring according to  $I$  and  $Q$  indices and a higher variability in their number of mates according to  $I_{\delta}$  and males also had a stronger Bateman gradient than females. Female promiscuity decreased the variance in male reproductive success (number of offspring), as predicted by Sugg and Chester (1994).

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The present study also revealed the importance of the post-copulatory component of reproductive success. Insuring paternity within a mate clutch was positively selected in our male population. Krakauer (2008) demonstrated the importance of the proportion of offspring sired by a male in wild Turkey, as it explained a large proportion of the variance in male reproductive success as mating success. It is thus crucial to consider the Bateman gradient as a source among others of sexual selection.

Total variance in the reproductive success is also explained by a term of positive covariance between the number of mates ( $M$ ) and the proportion of offspring fathered by a male in females he mated with ( $P$ ) which means that males that had more mates were also better competitors after mating. A negative covariance would have explained a trade-off between the two aspects of sexual selection and showed the potential for two male alternative strategies. However, results showed directional selection towards males that were better competitors before and after mating at the same time. In the junglefowl, dominant males can potentially mate with more females and mate more often with the same female to increase fertilisation success (Johnsen *et al.* 2001). Mating opportunities according to social status could then explain the positive covariance between  $M$  and  $P$  (this hypothesis will be tested in chapter 3).

Mate fecundity did not significantly predict male reproductive success. Models predicted that mate choosiness is linked to variation in mate fecundity (Owens and Thompson 1994). In our system, mate fecundity is variable for males as variation in female number of offspring, even if underestimated by pseudo-replication, was equal or higher than expected in a random model. However, it seems that males did not benefit from mating with more fecund females, so would not benefit from being choosy. This result is puzzling as it is known that males invest more sperm in more fecund females (Pizzari *et al.* 2003).

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As a general remark, my results also showed a need to be careful in the use of the vocabulary related to sexual selection. Sexual selection is often used to describe pre-copulatory sexual selection only. The Bateman gradient only refers to the pre-copulatory sexual selection undergone by the subset of males achieving fertilisation as mating success generally only includes genetic paternity. The overall use of *Is* and the Bateman gradient to quantify sexual selection does not take into account a significant part of sexual selection due to the variation in male post-copulatory success. Total sexual selection and pre-copulatory sexual selection would only be the same in truly monogamous species. The present results clearly show that post-copulatory sexual selection plays a far from negligible role.

### Decomposition of the variance in male reproductive success based on genetic number of mates underestimates sperm competition

Indices of variance of mating success across males varied according to the measures of mating success considered. Number of matings is obviously more variable across males than number of mates. In the fowl, mating does not always end up with sperm transfer, especially if the male had recently mated with the same female (Pizzari *et al.* 2003). Moreover, a high number of matings could be either due to a male mating numerous times with the same female (selection due to post-copulatory episodes) or to a male copulating with numerous mates, thus increasing the maximum number of offspring he can sire (selection for remating due to pre-copulatory episodes). Using the number of matings as an indicator of mating success does not enable one to make this difference (Arnold and Wade 1984a). For these

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reasons, the number of matings is not a reliable method for measuring sexual selection on remating in this species.

When decomposing sexual selection between pre and post-copulatory components, the way to measure mating success had a crucial importance. When using the genetic number of mates, as it is usually done, the post-copulatory sexual selection is highly underestimated. The reason is that genetic number of mates does not take into account males that did not fertilise any egg as it assumes that a pair that did not produce offspring did not mate. Therefore, all the males taken into account in the genetic number of mates fertilised at least one egg. Thus, the correlation between mating and reproductive success is overestimated as each genetic mate always gives a certain number of offspring. I would thus strongly recommend not using genetic number of mates to measure the importance of pre and post-copulatory sexual selection on phenotypes.

The observed number of mates does take into account unsuccessful matings, but does not take into account sneaky males that mate out of observation periods. These matings have a lower chance of ending up with fertilisations as they occur when females are less receptive (Cheng and Burns 1988). Thus, there is a potential for unsuccessful matings not to be recorded and the observed number of mates may also underestimate post-copulatory sexual selection, but less than the genetic number of mates. The observed number of mates, when observation time covers most of the potential mating time, is a reliable approximation for mating success.

### Comparison of different indices for sexual selection

$l_\delta$  and  $Q$  gave the same distribution of male and female number of mates and of offspring.  $I$  had the tendency to predict a distribution more even than the two other indices (for female and male number of mates and number of offspring). As  $l_\delta$  and  $Q$  use the Poisson distribution as a null model, they may be more reliable indices to categorize the distribution of resource across individuals than  $I$ .

The tested indices gave different results when comparing variance of number of mates and number of offspring between males and females.  $I$  and  $Q$  showed a difference in the variation of number of offspring between males and females and failed to show one in their number of mates whilst  $l_\delta$  showed a significant difference between male and female variance in number of mates, but no difference in their variance in number of offspring.  $l_\delta$  measuring variance in number of mates may be biased in our experiment as, in a group where all males would have mated with all females (four mates per males and three mates per female); the Morisita index would be higher in males (0.83) than in females (0.73).  $l_\delta$  is expressed as a proportion of the variance when acquisition is equal, so it is hardly usable to compare males and females when the sex ratio is uneven as an equal acquisition of resource by males would give a different value than an equal acquisition of resources by females. I thus disagree with some previous results that found a consistent behaviour of  $l_\delta$  in groups of uneven sex ratios (Fairbairn and Wilby 2001; Mills *et al.* 2007). Comparison of indices in an uneven sex ratio should then be limited to the use of  $I$  and  $Q$ .  $I$  and  $Q$  both give almost the same minimum and maximum values for males and females.  $Q$  can be considered more reliable as it is expressed as a fraction of a maximum possible variance so would completely take into account an uneven sex ratio. For example,  $Q$  would give the exact same value to variation in male and female number of

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mates in a group where all possible pairs are done but one. In the same situation, the value of  $I_s$  would be superior in females than in males.

The Bateman gradient is generally acknowledged as the best index to quantify sexual selection (Jones *et al.* 2004; Mills *et al.* 2007). However, the present results reveal that care must be used to interpret the Bateman gradient. Indeed, the Bateman gradient was high for males (on average  $5.11 \pm 0.99$  more offspring per new mate), so it appears that increasing the number of mates would be highly selected for males. However, this benefit of remating was less important than expected by the mere calculation of the Bateman gradient and less important than the benefits due to increasing the proportion of offspring sired in each mate, because the Bateman gradient calculated on its own also accounts for the covariance between number of mates and proportion of offspring sired in mates. Here, the steep Bateman gradient is due to both, the positive covariance between number of mates and proportion of offspring sired in mates than directly to the benefit of remating. Thus, the Bateman gradient would only be informative when all other source of change in the number of offspring (mate fecundity or proportion of offspring sired in mates) are kept constant, or at least it should be checked before any analysis that number of mates is not correlated to these other source of variation of the reproductive success. Otherwise, the Bateman gradient alone may be misleading and there is a risk of concluding that males are positively selected to increase the number of mates when the correlation between number of offspring and number of mates is hiding another correlation of greater importance.

Bateman gradient is not informative for sexual selection in females

Even if significantly lower than the male Bateman gradient, female Bateman gradient was almost significantly positive, especially when considering female that mated with one or two males. The conclusion is that, as in the bank voles (Mills *et al.* 2007), in *Drosophila* (Snyder and Gowaty 2007) or in some case the wild turkey (Krakauer 2008) (see review Clutton-Brock 2007 and 2009), females may be experiencing sexual selection for remating, even if at a lower rate than males. However, in a bird system, what does the Bateman gradient really represent? How can sexual selection for remating really occur in females?

The Bateman gradient is by definition the number of additional offspring given by additional mates (Arnold and Duvall 1994). In some systems, especially in Insects, remating can directly benefit the female in terms of offspring production through nuptial gifts or stimulation of egg-laying (e.g. Wedell and Karlsson 2003, reviewed by Arnqvist and Nilsson 2000). The meaning of Bateman's gradient in females has already been questioned by Parker and Tang-Martinez (2005) in studies that use genetic markers. Larger clutches are more likely to contain multiple paternities by the simple mathematical fact that a clutch of two eggs cannot show more than two fathers when a clutch of ten eggs can potentially show ten different fathers. Therefore, the Bateman gradient has to be used with caution in small clutches size. A positive Bateman gradient would mean that females are sexually selected to remate to increase their brood size. Females can directly benefit from mating with several mates through paternal care (e.g. Davies 1983) which is limited in the fowl, male vigilance which could increase female survival but not instantaneously female reproductive success, and courtship feeding. However males feeding more do not obtain more matings (Pizzari 2003; Wilson *et al.* 2008), so it is unlikely that females would remate

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to increase their food resource. Finally females may benefit by securing sufficient supplies of sperm. In the fowl, large ejaculates can be stored for a median period of 14 days (Etches 1996), that is more than the duration of our observations (10 days). Most of the collected eggs were fertilised, especially when just taking into account eggs laid after three days of observation so it does not seem like sperm is a resource rare enough to be able to create sexual selection in hens in our experimental conditions. Moreover, recent work has indicated that infertility is a rare cause of hatching failure in wild birds (Hemmings 2009). Therefore, it seems that the number of offspring a female would have is more dependent on the rate of egg laying than on fertilisation success.

A positive correlation between female remating rates and number of offspring probably does not reflect sexual selection for remating. Inverting the causality may reveal the real significance of the positive female Bateman gradient: the correlation between the number of mates and the number of offspring may show that more fecund females get more mates, not that females with more mates get more offspring (Parker 1992).

Number of offspring varied across females as the distribution of number of offspring is less even than a random distribution, so that some females produced more eggs than others. This variation could simply be due to natural selection with some females producing more eggs than others do or long-time trade-offs between investments in reproduction and survival. A positive Bateman gradient would simply show that females that produced more eggs, so females that were more fecund, would attract more males. Thus, Bateman gradient in females is actually not showing the operation of sexual selection in females but it is a component of sexual selection in males!

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Several studies showed a positive Bateman gradient in females and concluded that sexual selection was acting in females (Mills *et al.* 2007; Snyder and Gowaty 2007). In some cases like sex-role reversal (Vincent *et al.* 1992) or female parasitic brood (Woolfenden 2002), maternal investment is limited so females can lay more eggs and competition could arise to get sperm and a positive Bateman gradient may reflect sexual selection in females. In other cases like in our experiment, a positive Bateman gradient may only be due to male preference for more fertile females.

The simplest way to test the meaning of Bateman gradient in females is to experimentally manipulate the number of males a female mate with and see the effect on her number of offspring (Lorch 2005; Lorch *et al.* 2008). To test the meaning of Bateman gradient in a non experimental study, I would propose to test two potential consequences of sexual selection in females. First, does mating success correlate with a female phenotype trait that correlates with female fecundity (body size, comb size...)? If there is a correlation between mating success and visible female traits, the Bateman gradient is likely to reflect male preference for more fecund females. If there is not such a correlation, sexual selection for female remating is more likely to occur (Woolfenden 2002). In the fowl, females with longer comb lay more eggs and males invest more sperm in those females (Cornwallis and Birkhead 2007). It is thus likely that males also attempt to mate more with highly fecund females. Second, is the Bateman gradient steeper when the population is female-biased (more female competition)? If so, the Bateman gradient is likely to reflect sexual selection in females. However at present, it is difficult to establish the functional significance of positive Bateman gradients in females.

Chapters 3, 4 & 5 are not currently  
available in ORA

## **CHAPTER 3: THE OPERATION OF SEXUAL SELECTION ON MALE TRAITS**

This chapter investigates the way different episodes of sexual selection operate on multiple male traits, behaviours and interactions with females.

## **CHAPTER 4: SPERM COMPETITION AND SEMINAL FLUID**

### **EFFECTS**

## **CHAPTER 5: CRYPTIC FEMALE CHOICE**

## CHAPTER 6: DISCUSSION

### Thesis aims

My doctoral work focuses on the operation of sexual selection in populations where females are sexually promiscuous. I first adopted a quantitative approach to measure sexual selection arising under promiscuity and identify its targets. Second, I investigated through experiments the proximate mechanisms mediating post-copulatory sexual selection caused by female promiscuity, sperm competition and cryptic female choice.

The operation of sexual selection on male and female traits remains a source of numerous challenges for evolutionary biologists. The first building blocks of sexual selection theory were developed by Darwin more than 150 years ago (Darwin 1859). Darwin disentangled the operation of two selective episodes of sexual selection in the competition within individuals of the same sex to access mates and fertilisations (intra-sexual selection) and choice of the partner (inter-sexual selection, Darwin 1871). However, Darwin's theory of sexual selection failed to explain why sexual selection is often more intense in one sex (typically males). Analysing the results of his experiments on *Drosophila melanogaster*, Bateman (1948) subsequently identified the reasons why males are subject to more intense sexual selection than females: (i) variance in reproductive success (i.e. number of offspring) is higher in males than in females, (ii) variance in mating success is higher in males than in females, and (iii) male reproductive success increases with remating more than female reproductive

## Chapter 6: Discussion

success. The importance of Bateman's intuition was only fully appreciated more than twenty years later (and more than a century after Darwin's 'Descent of man and selection in relation to sex' (1871)). Bateman's work was a fundamental contribution to understand how sexual selection might operate on traits, and enabled theoreticians to develop quantitative tools to measure sexual selection (Arnold 1994; Arnold and Duvall 1994). Bateman's results also explained the differences between sex roles; as males benefit from remating, they compete with each other to access more females (Bateman 1948; Trivers 1972). Females, that are less sexually selected to remate would then benefit from choosing a good quality male (Bateman 1948; Trivers 1972).

However, the Darwin-Bateman paradigm is proving insufficient in the light of recent developments in sexual selection. Paternity analyses have revealed the widespread occurrence of female promiscuity (Birkhead and Møller 1998). Because of female promiscuity, intra- and inter-sexual selection can continue after insemination through respectively sperm competition (Parker 1970b), and cryptic female choice (Thornhill 1983). Despite extensive experimental studies on sperm competition and cryptic female choice (reviewed respectively in Birkhead and Møller 1998, Eberhard 1996), the field continues to suffer from a lack of integrative studies quantifying the relative importance of these episodes and their impact on the overall operation of sexual selection. In chapter 2, I studied the relative importance of pre- and post-copulatory sexual selection in males, and investigated the effect of female promiscuity itself on the total opportunity for sexual selection in males.

Previous studies have investigated the role of individual traits in sexual selection mostly by experimentally manipulating such trait and measuring its consequences under controlled conditions. This approach is invaluable to establish the proximate mechanisms which might mediate reproductive skew and their causal effects (e.g.

## Chapter 6: Discussion

Andersson 1982; Birkhead *et al.* 1999). However, it tells us little about how sex selection actually operates in a population. In chapter 3, I adopted a path analysis approach to measure the way different episodes of sexual selection target multiple morphological, genetic, physiological and behavioural traits, both before and after copulation.

Ever since the theory of sexual selection was revolutionised by the intuition that female promiscuity can continue after copulation, an increasing amount of work has focused on post-copulatory episodes, sperm competition and cryptic female choice. Sperm competition and the importance of ejaculate traits in sperm competition have been extensively documented (Birkhead and Møller 1998). Seminal fluid, the non-sperm physiological constituents of the ejaculate, can also determine sperm fertilisation efficiency (Chapman and Davies 2004; Poiani 2006; Chapman 2008). Seminal fluid can increase the reproductive success of a male by modifying the female behaviour and physiology (Craig 1967; Borovsky 1985; Chen *et al.* 1988; Lung and Wolfner 2001; Liu and Kubli 2003) and by increasing the rate of fertilisation within females (Arienti *et al.* 1999; Neubaum and Wolfner 1999; Alavi and Cosson 2006; den Boer *et al.* 2008). Novel scenarios have recently emerged regarding the potential for the seminal fluid effects of one ejaculate to influence the fitness of competing ejaculates inseminated in the same female, and thus the potential for rival ejaculates to exploit the seminal fluid effects of each other (Hodgson and Hosken 2006; Garcia-Gonzalez and Simmons 2007; Alonzo and Pizzari 2010). One possibility to avoid these effects is self-recognition so that seminal fluid would only improve fertilisation efficiency of the sperm produced by the same male. Therefore, in chapter 4, I experimentally tested the hypothesis that seminal fluid preferentially increases the fertilisation success of sperm of the same male (self).

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Cryptic female choice is the inter-sexual episode of post-copulatory sexual selection and refers to female traits that bias paternity towards certain males (Thornhill 1983; Eberhard 1996). Cryptic female choice is particularly difficult to study in internal fertilisers as the understanding of sperm storage and fertilisation mechanisms lacks in many species. However, genetic paternity analysis enabled the demonstration of cryptic female choice in several species even if the mechanism used by the female to bias paternity was unknown (Clark *et al.* 1999; Ward 2000; Birkhead *et al.* 2004). However, the debate remains on how to demonstrate cryptic female choice (Birkhead 1998; Telford 1998; Birkhead 2000; Eberhard 2000; Kempnaers *et al.* 2000; Pitnick and Brown 2000). It is thus crucial to test both whether females can bias paternity towards preferred males and the behavioural or physiological mechanisms used to selectively use sperm of certain males. In chapter 5, I investigated multiple mechanisms of cryptic female choice in relation to male phenotype and male-female genetic similarity.

## **Outcomes**

### ***Importance of post-copulatory sexual selection***

I compared the relative importance of the three sources of variance in male reproductive success: (i) remating, (ii) mate fecundity, and (iii) the proportion of eggs fertilised within a single clutch. While (i) represents the Bateman principle, (iii) captures the opportunity of post-copulatory sexual selection. My study confirmed Bateman principles, by showing that males are strongly sexually selected to remate. However, the variance in mating success, considered by Bateman (1948) as the only source of sexual selection, was only responsible for around 20% of the total variation

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of male reproductive success. Variance in post-copulatory success and covariances between post-copulatory success and the other episodes of sexual selection explained more than half of the variance in male reproductive success. The correlation between reproductive success and post-copulatory success was also stronger than sexual selection on remating. Thus, the results of my study indicate that the most important source of sexual selection in male red junglefowl is due to female promiscuity.

My study also pointed out some critical points that are relevant to future empirical work. Caution must be used when inferring the operation of sexual selection from paternity data, which identify genetic mates but do not detect mates that did not fertilise eggs. The quantification of the sexual selection is not straightforward and cannot be only reduced to selection on remating. The use of *Is* (opportunity for sexual selection) to characterize mating systems has already been criticised (Klug *et al.* 2010) and the results of my work support previous criticism. *Is* is the standardised variance of mating success, so *Is* does not, in any account, show the whole picture of what is the opportunity for sexual selection on reproductive success *I*. The Bateman gradient, which by definition considers only genetic mates (Arnold and Duvall 1994) overestimates the selection on remating as it does not take into account mating that do not translate into fertilisations. The Bateman gradient thus quantifies selection on fertilisation and includes part of the post-copulatory sexual selection. Total sexual selection and sexual selection on remating would only be the same for males, in genetic monoandrous species, which strongly limits the potential use of the Bateman gradient and *Is*. In chapter 2, I used a methodology that clearly separates different episodes of selection and their relative importance on the total variance of male fitness. With methodology comes semantics. There is a strong tendency to call sexual selection what is in fact only sexual selection on remating as it is quantified with *Is* and

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the Bateman gradient. By mathematically separating different episodes of sexual selection, the use of terms should also change and pre-copulatory sexual selection should not be confused with total sexual selection.

Despite strong sexual selection acting on male post-copulatory success, I found little evidence for selection on ejaculate traits. When comparing all the potential predictors of male reproductive success, sperm quantity and sperm quality were not selected (chapter 3). Moreover, I tested in chapter 4 the hypothesis that males could defend against ejaculate exploitation by producing seminal fluid that would differentially benefit to the male donor. This hypothesis was strongly refuted, thus, showing that the investment in seminal fluid traits could potentially promote the fertilisation efficiency of self and of competitors. If the effect of sperm quality on fertilisation success was highly important, the transitive effect of seminal fluid would hardly be viable. Numerous studies experimentally tested for the effect of sperm quantity and sperm quality on fertilisation success, controlling for other traits such as male social status (Birkhead *et al.* 1999; Donoghue *et al.* 1999; Gage and Morrow 2003; Gage *et al.* 2004; Denk *et al.* 2005; Garcia-Gonzalez and Simmons 2005). This approach may over-estimate the importance of ejaculate traits and underestimate that of male behaviours (chapter 3).

My results also indicate that post-copulatory sexual selection may also be due to female cryptic choice. I showed in chapter 5 that females could bias paternity through at least two mechanisms: (i) female could bias paternity toward genetically dissimilar males (MHC and overall genetic similarity between males and females) after artificial inseminations, and (ii) sperm ejection reduced the fertilisation efficiency of a male. Despite having a fertilising advantage (chapter 5), genetically dissimilar males did not produced more offspring in the semi-natural experiment (chapter 3), thus it may be

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only play a weak role in total sexual selection undergone by males. Unfortunately, quantification of the sexual selection on males due to female sperm ejection was not possible in the semi-natural experiment (chapter 2 and 3) as few sperm ejections were observed during the semi-natural experiment.

### ***Intra- inter-sexual selection***

The study of sexual selection in semi-natural conditions revealed that female preferred mating with dominant males (chapter 3). Surprisingly however, this strong female preference did not influence male reproductive success. Many studies investigated the effect of specific male traits on female preference for male traits in the fowl, often leading to contradictory results (Wood-Gush 1954; Zuk *et al.* 1990a; Zuk *et al.* 1990b; Johnsen and Zuk 1996; Zuk *et al.* 1998; Pizzari 2001; Parker and Ligon 2003). Female mate choice may be inconsistent across population of fowl for the only reason that it is a weak driving force of selection. Thus, investigating female mate choice may not necessarily reveal any potential sexually selected trait in males. Therefore, my study showed how crucial it is to complement experimental studies with works considering sexual selection as a whole, including all episodes and different traits, to avoid spurious conclusions.

Despite the little effect of female mate choice before copulation, females can select for dominant males through other mechanisms than solicitation. As female preferred dominant males, which are by definition selected by intra-sexual competition, females can use male-male interaction to preferentially mate with dominant males (Pizzari 2001). Thus, intra- and inter-sexual selection can reinforce each other to favour dominant males. However, I did not find any evidence that sperm from dominant males were preferentially retained by females, contrarily to previous

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results (Pizzari and Birkhead 2000). It would be interesting to investigate what differed between the two experiments testing for the rate of sperm ejection according to male social status, namely: the degree of sexual harassment on the female and the male group size. On an evolutionary point of view, social status is an interesting trait to study. Some evidence tend to show that social status is heritable (Craig *et al.* 1965; Guhl 1969) with very probably a polygenic mode of inheritance (Craig *et al.* 1965). However, the social status of a male necessarily depends on his social environment. The variance in social status only varies with population size. Thus, the problem of the lek paradox (expected decrease in trait variance due to directional selection) is not directly relevant for social status, even if status is subjected to strong directional sexual selection. However, social status was correlated with other traits and the causes of social status remain unclear. Directional sexual selection could thus decrease the variance on the traits causing social status, but not directly the variance of social status.

I showed in chapter 3 that female solicitation increased with male genetic dissimilarity. Moreover, I showed in chapter 5 that females could bias fertilisation towards sperm from unrelated males in a competitive situation controlling for male effects. However, genetic compatibility was not predicting male reproductive success (chapter 3). Because female choice for unrelated males is both pre- and post-copulatory, one would expect that it influences male reproductive success. Female preference may be counteracted by male effects. Pizzari *et al.* (2004) showed that male invested larger ejaculates in unrelated females. This male adaptation to female strategy may thus be buffering female preference and female preference for unrelated males is in conflict with male interests, potentially leading to antagonistic evolution.

***Evolution of female promiscuity***

I quantified the effect of female promiscuity on the overall opportunity for sexual selection to operate in males. I showed that the more females remate, the less opportunity there is for male to be sexually selected, as variance in reproductive success decreased. The influence of female promiscuity has rarely been tested previously. Jones *et al.* (2001) studied the genetic mating system of the sand goby, *Pomastochistus minutus*, and showed that female promiscuity could decrease the opportunity for male sexual selection. However, thus this test is restricted to a model quantifying the effect of sneaker males on the variance of reproductive success of all males. My experimental results showed that, consistent with Jones' model (2001), female promiscuity also decreased the opportunity for male sexual selection in a system where all males had the same strategy.

From the male perspective, female promiscuity increases access to mating opportunity and thus decreases variance in paternity; this could have lead to different male strategies with some male investing in mating success and other 'sneaker' males investing in fertilisation success despite low remating, as in the sand goby (Jones *et al.* 2001). Previous studies revealed that dominant males may have a lower sperm quality than subordinates in the fowl (Froman *et al.* 2002; Pizzari *et al.* 2007). Thus, female promiscuity may enable subordinates to access matings and give them the opportunity to fertilise some eggs, thus decreasing the gap between subordinate and dominant male reproductive success. Even if I did not find any evidence for sperm quality to be a sexually selected male trait, it was clear from my results that female promiscuity enabled subordinate males to access reproductive success, even if it is still lower than the reproductive success of the dominant male.

## Chapter 6: Discussion

From the female perspective, I pointed out that despite finding an almost significant Bateman gradient in females, the actual sexual selection on remating in females is difficult to obtain and requires experimental work. It is thus not possible to reach conclusions on the effect of female promiscuity on female selection to remate. However, my results show that females could in principle benefit from remating by being able to bias paternity toward certain males, in particular unrelated males.

I hope that my work, by revealing mechanisms through which sexual selection can operate on male traits, would unravelled part of the complexity of sexual selection.

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