Chapter 7
Sexual Selection: The Logical Imperative

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Abstract Modern sexual selection theory, developed from Darwin's original intuition, is a cornerstone of evolutionary theory and represents the most parsimonious and robust explanation for a bewildering array of evolutionary patterns and diversity. Here we first outline the principles of modern sexual selection theory and discuss their heuristic value. Second, we review empirical demonstrations of the operation of sexual selection through the case study of the yellow dung fly. Finally, we propose that a sequence of evolutionary events flows inevitably from the early evolution of sexual recombination and gametes, to anisogamy and in dioecious organisms, to the unity sex ratio via Fisher's principle. As Darwin and Bateman predicted, it was the primary sexual difference—anisogamy—that became an almost obligatory, irreversible transition favouring socio-ecological conditions that ultimately generated secondary differentiation of sexual strategies between the sexes, and typically plays a strong part in their maintenance (though sex roles can, rather rarely, be reversed). When considered within the broader context, sexual selection emerges deductively as the logical consequence of this evolutionary succession. We conclude by highlighting aspects integral to sexual selection theory that are currently the focus of on-going discussion.

Keywords Anisogamy · Sex roles · Sperm competition · Sexual conflict · Yellow dung fly

7.1 Introduction

Darwin (1874) defined sexual selection as competition between individuals of one sex (usually males) to gain matings with the limiting sex (usually females), and interpreted male and female sex roles and much behaviour and morphology in terms of

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what is now termed pre-copulatory sexual selection. Bateman (1948) in a classic paper elucidated the mechanism behind this form of selection, and explained Darwin's claim that sexual selection is typically stronger in males in light of factors arising ultimately from the primary sexual difference between the sexes due to anisogamy.

We argue here that there is a remarkable logical beauty in the sequence of events (the 'sexual cascade'; Parker 2014) that flows inevitably from the early evolution of sexual recombination and gamete formation, to result in sexual selection and ultimately the differentiation of sexual strategies in males and females. The evolution of sexual recombination and gametes led (in multicellular organisms and some unicells) directly to the evolution of anisogamy, the primary sexual differentiation underlying the two sexes, males and females—which in turn typically generated the unity sex ratio via Fisher's sex ratio principle in organisms with separate sexes. Ancestrally, sexual selection would have operated entirely by sperm competition, until enhanced mobility allowed higher fertilisation gains via female-targeted sperm release and pre-mating competition, leading (as an economic consequence) to testes reduction, the rise of precopulatory sexual selection and enhanced sexual conflict, and to high degrees of secondary sexual differentiation as Darwin (1874) and later Bateman (1948) predicted.

Despite the power of the logic supporting these sequential evolutionary steps and their consequence, the Darwin-Bateman Paradigm (DBP; Dewsbury 2005) of typical male and female sex roles, sexual selection has been controversial. The first critique came from Alfred Russell Wallace (see e.g. Prum 2012), followed by a period where even male-male competition was doubted, ignored, or at best grudgingly accepted (e.g. Huxley in the 1930s). In spite of one or two notable exceptions (e.g. Bateman 1948; Jacobs 1955) these doldrums persisted until the behavioural ecology revolution of the 1970s, after which sexual selection experienced an explosion of interest and accumulation of theory and supporting evidence. In the past few years, however, Darwinian sexual selection has been attacked as a flawed and unsubstantiated concept, and the DBP characterised as a misinterpretation due to gender bias (see Sect. 7.5). We argue that both these attacks are misguided, since the evidence for sexual selection is overwhelming, and its conceptual basis (and that of the DBP) logically sound (see also Parker and Birkhead 2013).

We first introduce the fundamentals of sexual selection theory and argue that this theory represents a powerful heuristic tool and the most parsimonious explanation for a very wide range of biological patterns. Next, we illustrate how the Darwinian concept of sexual selection is the logical consequence of evolutionary transitions originating from the evolution of sex and recombination. Finally, we focus our discussion on some issues that have contributed to ignite recent debate over sexual selection theory.

7.2 Sexual Selection Theory is a Powerful Heuristic Tool

Darwin (1874) viewed sexual selection as a process targeting variation in reproductive success among individuals of the same sex and species solely due to intrasexual competition over access to reproductive opportunities. This definition was later formalized in the concept of the opportunity of sexual selection, I_T, which is the standardized variance in intra-sexual reproductive success

$$I_T = \frac{\sigma^2}{\overline{T}^2},$$

where $\overline{T}$ is the average total reproductive success for an individual and σ^2 is the variance in T across individuals of the same sex (Arnold and Wade 1984; Shuster and Wade 2003; Jones 2009). I_T represents a useful empirical measure of the potential of sexual selection that can operate in a given population (but see Sect. 7.5.3). A trait explains a significant portion of I_T when a standardised increment in the trait causes a standardised change in individual reproductive success, and the strength of sexual selection on the trait is measured by the slope of the regression of individual reproductive success against standardised trait expression (the sexual selection gradient, β, Arnold and Wade 1984). There is an elegant simplicity in this view, which makes it broadly relevant (i.e. applicable to all sexually-selected organisms, from unicellular to human) because it does not depend on assumptions about the proximate (i.e. cognitive, physiological or morphological) mechanisms underpinning variance in T.

Crucially although Darwin developed sexual selection theory to explain sexual dimorphism, he was aware that intra-sexual competition occurred in both males and females, and his framework is equally applicable to both sexes, making no *a priori* assumptions about sex-specific patterns of sexual selection. Instead, sexual dimorphism and 'sex roles' emerge as properties of sex differences in the opportunity of sexual selection. Darwin recognised that intra-sexual variance in T depends on the number and 'quality' of reproductive mates secured. The number of partners corresponds to individual mating success (M). Mate 'quality' (Q) captures a number of ways through which the contribution of an individual to a reproductive event affects the fitness of its mate, so that the total reproductive success of an individual can be expressed as:

$$T = (M \cdot Q) + \varepsilon$$

where ε is an error term with zero mean. Female quality for example, would include clutch size, or the number of eggs produced by a female in a given event, but clearly maternal investment in the eggs and zygotes, as well the expression of maternal genes in the descendants would also play an important role in quality. Similarly, male quality would include paternal investment and the genetic contribution to the offspring.

7.2.1 Sex Roles and the Darwin-Bateman Paradigm

In a series of experiments on *Drosophila melanogaster* published in 1948, Bateman presented empirical evidence suggesting that the regression of T on M was steeper in male rather than female flies, suggesting that sexual selection is more intense in males than in females. Bateman (1948) generalised these results and proposed that the sex experiencing more intense sexual selection has higher standardised variance in both T and M (i.e. I_T and I_M respectively) and a steeper slope β of the regression of T on M:

$$T = (\beta \cdot M) + \varepsilon.$$

Therefore, β measures the gradient of sexual selection on mating success and is often referred to as the Bateman gradient. Bateman (1948) argued that because of anisogamy (see below) males typically produce orders of magnitude more sperm than there are eggs available for fertilisation; their reproductive success is essentially limited by their ability to access mating opportunities, resulting in higher male I_T and I_M, and a steeper Bateman gradient than females. The larger investment in individual gametes would constrain (but not necessarily eliminate) the Bateman gradient on females. For $M \geq 1$, lower (or zero, or even negative) Bateman gradients in females are therefore expected, though positive female gradients can arise for many reasons, including increased fertility, male nuptial gifts, or may partly reflect the proportion of female I_T that is explained by variation in male Q. Anisogamy therefore creates a fundamental difference in the way Darwinian selection operates on adult males and females: sexual selection pushing primarily males to compete with each other over access to mating opportunities, and females to compete more strongly for resources to produce young and to discriminate amongst prospective mates.

Bateman's intuition therefore provided a conceptual framework for Darwin's original prediction that sexual selection favours the exaggeration of male traits that result in higher M and/or Q by conveying a competitive advantage in intra-sexual selection and/or by matching more closely female mating preferences (inter-sexual selection). Darwin gave much evidence for patterns of male-male competition for females, which have subsequently been amplified considerably. A sex role pattern of high observable male-male competition when male parental investment (PI; Trivers 1972) is zero or very low is undeniable, this is correlational only but fits explanations based on the primary sex role divergence due to anisogamy (e.g. see Kokko et al. 2013; Schärer et al. 2012)—as we later discuss. This view, the Darwin-Bateman paradigm (DBP), was further developed and nuanced to become the backbone of modern sexual selection theory (Trivers 1972; Arnold and Duvall 1994).

7.2.2 Sperm Competition

A significant advance in the DBP and developments in modern sexual selection theory has been the realisation of an additional source of variance in T giving rise to episodes of sexual selection unexplored by Darwin. Parker (1970a) reviewed female mating behaviour in insects and proposed that whenever a female mates with more than one male in a way that their sperm co-occur at the time of fertilisation of a set of eggs, these ejaculates compete for fertilisation opportunities, a process that became known as sperm competition. Sperm competition therefore represents a form of intra-sexual selection, which occurs under some degree of female polyandry, and can account for many sexual adaptations (Parker 1970a). Despite scientific history, in evolutionary terms sperm competition long predates Darwinian pre-copulatory sexual selection, as we later argue.

The possibility that a male might not fertilise the entire clutch of his mate(s) introduces variability in the proportion of the eggs fertilised by each of the males that mated with the same female within the relevant time window (i.e. in time for their sperm to have a non-zero probability of fertilisation). Under sperm competition the reproductive success of a male therefore becomes:

$$T = (M \cdot Q \cdot P) + \varepsilon,$$

where P represents the paternity share within a clutch across M females (Webster et al. 1995; Collet et al. 2012).

It has been proposed that polyandry can also create potential for females (and/or their ova) to exert a systematic bias of the outcome of sperm competition in favour of the ejaculates of certain male phenotypes or genotypes, a process known as cryptic female choice (Eberhard 1996). Mechanisms of cryptic female choice represent an episode of inter-sexual selection generated by polyandry. In internally fertilising organisms sperm competition and cryptic female choice follow necessarily episodes of male competition and mate choice (pre-copulatory sexual selection). In some external fertilisers (e.g. corals, echinoderms) however, sperm competition and cryptic female choice might to a large extent replace pre-copulatory sexual selection.

As for pre-copulatory episodes of sexual selection, episodes of post-copulatory sexual selection are not necessarily restricted to males. Under some extreme conditions of male sperm limitation or sex-role reversal, the ova of different females can compete for access to sufficient sperm supplies to guarantee fertilisation. Similarly, like females, males can also perform ‘cryptic’ mechanisms of mate choice, by strategically adjusting their ejaculate expenditure based on the phenotype or genotype of their mates (see below).

7.2.3 Evidence of Sexual Selection

Over the last 40 years the study of sexual selection has exploded and represents one of the most dynamic and topical areas of evolutionary biology. Reviewing such vast empirical effort is well beyond the scope of this chapter, and rather than give a long list of the successes, in Sect. 7.3 we showcase detailed studies carried out on one species as an example of how sexual selection theory can explain adaptation. The reader is encouraged to refer to a number of excellent reviews on this subject (e.g. Andersson 1994; Andersson and Simmons 2006; Kokko et al. 2006; Jones and Ratterman 2009). Suffice it to note here that overwhelming empirical evidence has accumulated that exaggerated traits, which convey no viability benefits (i.e. the traits that inspired Darwin to think about sexual selection theory in the first place), can deliver significant advantages in intra-sexual competition by increasing M and Q, as hypothesised by Darwin (1874). In most cases, sexual selection remains the only parsimonious explanation to account for the evolution and maintenance of such traits. There is also robust evidence that sexual selection is determined by direct intra-sexual competition and by differential patterns of mating responses and mate discrimination in the opposite sex, consistent with mate choice. While sexually-selected male traits to increase M are intuitive, the adaptive nature and functional significance of mate choice (in other words, the mechanisms through which females evolved preference for certain mate types) is less clear, as one would expect given the following elements: (a) the multidimensional and context-dependent nature of Q, (b) the different inter-sexual co-evolutionary trajectories that mould preference, and (c) the often weaker (compared to M) effect of Q on T. It is important to note here that sexual selection theory predicts some degree of inter-sexual selection through forms of mating preferences or discrimination, but does not require specific assumptions about the evolutionary mechanisms underpinning such preferences.

In conclusion, sexual selection theory typically provides the only parsimonious and robust explanation for variation in sexual dimorphism and the evolution of a class of traits, exaggerated ornaments and armaments. One could argue that this is reassuring but hardly surprising considering that exaggerated male ornaments and armaments are the traits that originally inspired Darwin's theory of sexual selection. Crucially however, the heuristic power of sexual selection theory transcends the explanation of such traits, and has been successfully applied to explain biological patterns that were unknown to Darwin. Below, we consider two such triumphs of sexual selection theory.

7.2.4 De Novo Evolution of Sexually-Selected Traits

The yeast, *Saccharomyces cerevisiae*, reproduces sexually through disassortative fusion between sex cells of two types, MATa and MATα, which attract each other through the production of, and attraction to, a-pheromone and α-pheromone. Normally, the diploid organism undergoes meiosis and produces a tetrad of four haploid sex cells (two of each type) and self-fertilization occurs within the tetrad between MATa and MATα cells. This reproductive mode prevents sexual selection by removing sexual competition between individuals. If however, haploid sex cells from different individuals are mixed, potential for competition arises between individuals to attract and fuse with cells of the opposite type. Rogers and Greig (2009) have used this experimental construct to artificially create sexual selection in this system. The authors created six replicate (isogenic) populations in which the ratio of mating types was experimentally biased in favour of MATα. The artificial excess of MATα creates opportunity for sexual selection by forcing competition within this cell type to attract MATa cells. In each of the populations, the authors introduced a rare allele coding for an increased production of α-pheromone in MATα. The study monitored the spread of this strong signalling allele in the replicates evolving under sexual selection and six additional control populations evolving in the absence of sexual selection (i.e. equal ratio of MATa and MATα) for 13 generations. In all sexually-selected populations the strong signalling allele increased rapidly in frequency and had approached fixation in five out of six by the 13th generation. In stark contrast, in five out of the six the control populations there was no appreciable increment in frequency and only a modest increase in the sixth. The study provides an elegant experimental demonstration of the central axiom of sexual selection theory, intra-sexual competition can favour the spread of a trait that confers a competitive advantage.

This is but one example of many 'experimental evolution' studies in which the predictions of sexual selection theory have been validated. Many such investigations have compared populations after several generations of breeding under 'enforced monogamy' (in which sexual selection is absent) with those breeding under increased male-male competition or 'enforced polyandry' (e.g. see Sect. 7.3.2(iv)).

7.2.5 Sperm Competition and Ejaculate Expenditure

As noted above, Darwin's original theory of sexual selection was largely limited to pre-mating events. The intuition of sperm competition and post-copulatory sexual selection came about a century later (Parker 1970a), and led to the discovery of a remarkable diversity of traits and mechanisms—largely unsuspected by Darwin—mediating the outcome of sperm competition. Yet, the application of the general principles of sexual selection theory has enabled evolutionary biologists to understand the operation of post-copulatory events just as successfully as we can predict the operation of pre-copulatory episodes. A large body of theoretical work, ejaculate economic theory, has been developed to predict the way sperm competition drives the evolution of male ejaculate expenditure (Parker and Pizzari 2010). Qualitative and sometimes quantitative support for many of these predictions has been accumulated by a plethora of empirical studies investigating patterns of male ejaculate expenditure in terms of the percentage of body mass devoted to gonads (i.e. the gonadosomatic index or $GSI = 100[\text{gonad mass}/\text{total mass}]$), and in terms of number of sperm allocated to individual copulations (Parker and Pizzari 2010; Kelly and Jennions 2011), demonstrating that ejaculate economic theory can be a powerful heuristic to explain variation in ejaculate expenditure across species, across males within species and even plastic changes within individual males (Parker and Pizzari 2010). More recently, ejaculate economic theory has been extended to consider widespread cases where non-sperm ejaculate compounds have gonadotropic effects on females boosting their clutch size or oviposition rate (Alonzo and Pizzari 2010). These models predict that males evolve dynamically strategies of differential ejaculate allocation by preferentially investing in sperm and less in gonadotrophic compounds when they mate with a female after another male. This strategy would enable the second male to invest in sperm competition while simultaneously exploiting the fecundity investment made by the first male in a female. Patterns of strategic ejaculate exploitation consistent with these theoretical expectations have been experimentally demonstrated in *D. melanogaster*, where males preferentially reduce their investment in the gonadotropic accessory gland compound ovulin when they mate second with a female (Sirot et al. 2011).

7.3 The Yellow Dung Fly as a Case Study

Research on the common yellow dung fly, *Scatophaga* (=*Scathophaga*) *stercoraria* L., carried out over many years, has resulted in probably the most extensive data available on sexual selection in a given species. Studies published in the 1970s (reviewed by Parker 1978a) began in 1965 specifically for the purpose of testing Darwin's theory of sexual selection at a time when it was largely ignored, using a hypothetico-deductive approach of testing observations against predictions generated by optimality modelling. This has the aim, not to show that animals behave optimally, but to provide evidence that the selection pressures used in the model are those that have moulded the adaptations under consideration (Parker and Maynard Smith 1990). The early models for the dung fly mating system were constructed on the assumption that sexual selection acts to maximise a male's overall fertilisation rate in competition with other males. An evolutionarily stable strategy (ESS) approach was used to determine the male competitive optima for several traits. Studies of sexual selection in this species continue to present day, and by now have covered a wide range of sexually-selected adaptations (both pre-and post-copulatory). From the outset they have shown that sexual selection can generate very fine-grained adaptive optima (Parker 1978b).

The mating system of dung flies was described by Hammer (1941) and Parker (1978b). Males arrive swiftly around fresh cattle droppings to await the arrival of gravid females, who typically lay all their mature eggs as a batch in a single dropping. Although generally already containing sperm from previous matings, a gravid female copulates at each visit to the dung to oviposit. Struggles between males for the possession of females are common. After copulation the male does not dismount but releases genital contact and then guards the female from other males until she has finished laying her mature eggs, which she signals by side-to-side movements. The male then dismounts and the female flies away immediately, returning only when her next egg batch is mature, when she mates again before laying the next batch, and so on.

This pattern poses the question of why females are polyandrous (the average number of ejaculates stored is around 3 per female; Demont et al. 2011). Tregenza et al. (2003) found no simple benefits or costs of double versus single mating for females, but Hosken et al. (2002) found that females mated once survived longer than those mated three times, suggesting that longevity costs are associated with multiple mating. There are physical costs of mating to females (Hammer 1941; Parker 1978a; Demont et al. 2011). There are also obvious time costs of supernumerary matings (Parker 1970b). All this suggests that significant female benefits must accrue to polyandry to offset its costs. A number of possible advantages have been found or proposed. Polyandrous mating at each return to the dropping for oviposition can result a large saving in time at the dropping to a female, which arises from the benefits of gaining a guarding male for oviposition (Parker 1970b). Also, males that were more successful in sperm competition sired offspring that developed faster (Hosken et al. 2003). Another possible benefit relates to cryptic female choice (see also Sect. 7.3.2(v)). For example, elegant field experiments, in which all reproducing parents and progeny arising from artificial droppings were genotyped, showed that for females the total number of offspring and proportion of offspring emerging increased with the degree of polyandry (Demont et al. 2012).

The maximisation criterion used in optimality models of male-male competition in dung flies is eggs fertilised per minute of reproductive activity. The expected value of time at the dropping to a male (0.23 eggs/min; the mean for over a hundred droppings) was calculated as: total eggs oviposited into the dropping by all females divided by total time spent by all males at that dropping (Parker 1970c).

7.3.1 Pre-Copulatory Adaptations

7.3.1.1 Competitive Mate Searching by Males Matches Ideal Free Predictions

The numbers of each sex at a dropping shows a rise to a peak, then a gradual decay as the dropping ages; the male peak is much earlier than the female peak (Parker 1970c). From the average time each female spends at the dropping, the rate of arrival of females was calculated to be a decay curve, with the highest female arrival rate, $F(t)$, immediately after dropping deposition at time $t=0$. Knowing the number of males present through time t, males present at the earliest times could be shown to experience highest fertilisation rates. Thus males arriving instantly and remaining for a very short "stay time" would appear to be at an advantage. However, such males would experience high fertilisation losses due to excessive times spent searching for new droppings (the average time taken to find a new dropping is c. 4 min). The ESS consists of a distribution of stay times such that all males achieve equal fitness in terms of probability rates of capture of females ($=c$ per min). When travel time between droppings was included, all males were shown to experience similar gain rates, whatever their stay time at the dropping (Parker 1970c). Their behaviour matched the ESS, which is defined by all males arriving as quickly as possible to a given new dropping, then showing a phased departure so that the number of males present at time t, $m(t)$, balances the rate of arrival of new females: $m(t) = c^{-1} \cdot F(t)$, i.e. they should obey 'input matching' (Parker 1978a), a temporal version of the ideal free theory distribution (Fretwell 1972). Later, the claim of equal male gain rates was criticised by Curtsinger (1986) on various grounds, including the fact that differences in stay time had not been tested statistically. However, when examined, no statistical difference from the input matching prediction could be found, and other criticisms were also refuted (Parker and Maynard Smith 1987). The evidence that male dung flies show input matching during mate searching, as predicted by sexual selection, remains strong.

In addition to this temporal ideal free evidence, there is also good evidence that males obey ideal free searching in space around the dropping (Parker 1974b). There are three sources of gain for a male: newly-arriving, gravid females, take-overs of females from copulating pairs, and take-overs of females from guarding males while the female is laying her eggs (after a take-over, the successful male immediately mates with the female and then fertilises over 80 % of the subsequent egg batch). During the first 20 min after deposition, male search strategy is geared towards newly-arriving females (often encountered in the grass round the dropping); the proportions of males searching in each of a series of concentric zones on and around the dropping matched ideal free expectation (Parker 1974b, 1978b). But later, gains from take-overs (especially of ovipositing females) become significant, drawing more males to the dropping surface rather than the surrounding grass. Parker (1974a) predicted y = the ESS proportion of the total searching males expected on the dropping surface in relation to two variables: x = time after dropping deposition, and z = the total number of searching males. This predicted three-dimensional profile of $y(x,z)$ showed a good fit to the observed profile, suggesting that males respond to both (i) time after dropping deposition and (ii) number of competitors in determining where to search for females (surrounding grass versus dropping surface).

7.3.1.2 Males Show Intense Struggles for the Possession of Females

Dung fly males show specialised guarding behaviour and extreme contest behaviour; both are directed exclusively to gaining or retaining females (Parker 1970d)—there can be no doubt that they have evolved through Darwinian intra-sexual selection. The male mounts as soon as a gravid female is encountered, copulates, and then guards the female during oviposition. However, especially when a female flies directly to the dropping with a high density of searching males, two or more males may contact the female simultaneously and a protracted struggle then develops between males for possession of the female. If a searching male approaches a copulating or ovipositing pair, the paired male shows specialised behaviours that deflect the attacker away from the female. But should a second attacker approach while the paired male is deflecting the first attacker, the second attacker may manage to grasp the female and insert himself between the paired male and the female, resulting in a struggle. The probability of take-over is higher during oviposition than during copulation (Parker 1970d), but irrespective of when it occurs, after a take-over the new male copulates and guards the female while she lays her remaining eggs.

Parker and Thompson (1980) examined the time distribution of dung fly struggles, again taking male fitness as expected number of eggs fertilised per min, but modifying the struggle time to take account of the energetic costs of struggling relative to searching for an alternative female. One second spent struggling was assumed to cost k seconds searching; likely values for k were deduced from published data on insects. Superficially, struggles between males could plausibly match the predictions of the symmetric war of attrition with linear costs (Maynard Smith and Price 1973) since struggle durations showed a negative exponential distribution with a mean in the expected range. However, this concordance was lost when the data were examined in categories; for example, there was a much higher probability that the holder will win than the attacker.

Dung fly struggles are asymmetric contests, and males with larger body size have a greater probability of winning (Sigurjónsdóttir and Parker 1981). Struggles are probably settled by assessment as information is acquired during the contest about the relative 'resource holding power' (RHP; Parker 1974b) of the two males. The attacking male is typically larger than the guarding male, and as the relative size of the guarding male increases, the persistence duration of the attacker decreases. The RHP of the guarder appears to be influenced by his size relative to both (i) the attacker and (ii) the female he guards. Interestingly, the duration of struggles in which there was no take over (i.e. when the attacker gave up) increased with the number of eggs remaining to be laid by the female, suggesting that the paired male's choice of persistence time increased with the value of the female, as may be expected from contest theory if the paired male 'knows' how many eggs have been laid. However, this was not so when a struggle resulted in a take over (i.e. when the paired male gave up), suggesting that the attacker had no information about the eggs remaining to be laid, which again seems plausible. Sigurjónsdóttir and Snorrason (1995) examined the body size of flies in relation to their spatial distribution around droppings, and found that males guarding ovipositing females were on average similar in size to those copulating on the dung, but larger than males copulating in the grass, which they interpreted as being due to various effects, including the advantage of male size in take-overs. In flies reared under high and low density conditions, Stockley and Seal (2001) found that the propensity to begin struggles increased in relation to body size among males reared at high density, though the opposite trend was found in those reared at low density.

Sexual selection intensity (male mating success) was measured directly in the field by Jan et al. (2000), and conformed to the behavioural observations. As expected, selection intensity increased with male competitor density at a dropping. Though there was some evidence that small males had higher mating success at very low densities, overall, large males had higher mating success. Jan et al. found higher selection intensity for large size in males than females (see also Blanckenhorn 2007), a result consistent with the observed sexual size dimorphism in yellow dung flies, where males are typically considerably larger than females.

7.3.1.3 Pre-Copulatory Female Choice

Though generally agreed to be a predominantly male-controlled mating system, there is some evidence that at low male densities—when females are potentially able to choose between males—they show preference for pairing with larger males; this was argued to relate to the benefits of having a large male guarding during oviposition, and so avoiding struggles, which can be costly and damaging to females (Borgia 1981).

7.3.2 Post-Copulatory Adaptations

7.3.2.1 Emigration from the Dropping at High Male Density Matches Intra-Sexual Selection Predictions

Though many pairs begin mating in the grass surrounding the dropping, some begin mating on the dropping surface; the paired male often then flies the female to the downwind surrounding grass some distance from the dropping, returning some minutes before the end of copulation. Parker (1971) proposed that such behaviour related to a male guarding his paternity, and analysed the relative benefits to males of mating on the dropping versus mating in the grass. Since the temperature of the dropping surface during copulation is typically considerably higher than that of the surrounding grass, copulations in the grass are typically 30–35 % longer than those in the grass, costing the male approximately 8 min (= 1.8 eggs) at 20°C. However, a 'risk map' of the dropping areas showed that the risk of a take-over by another male (with consequent loss of most of the egg batch) is much higher on the dropping than in the down-wind surrounding grass (most males search on the dropping or in the upwind surrounding grass, where most incoming females are found). Take-over risk increases with the density of males searching on the dropping. Comparison of the fertilisation gain rates of the two strategies, emigrate or stay on the dropping, showed that below density of 5 searching males on the dropping, it is favourable to stay on the dropping for mating. Above 5 searching males, it pays to fly to the downwind surrounding grass. The observed emigration behaviour was found to increase steeply with male density, and the density at which 50 % of pairs emigrated was 5 searching males, fitting the expectation from the model. Parker (1971) also calculated the threshold at which it would be in female interests to emigrate, based on minimising the time spent around the dropping. Countering the benefit of the shorter copulation time is the risk of time spent on an extra mating after a take-over. The threshold at which emigration is favourable for the female is around a searching male density of 28, much higher than the 50 % emigration value (and well beyond the density at which the 90 % emigration asymptote has been approached), suggesting as expected that it is sexual selection on males that has shaped the emigration behaviour.

Emigration from the dropping may depend on male body size. Sigurjónsdóttir and Snorrason (1995) found that the mean body size of males copulating in the grass was smaller than single searching males or paired males on the dung surface. This may arise either from a lower emigration threshold for small males due to their increased risk of take-over, or to the fact that they tend to search in the grass, or to a combination of both effects.

7.3.2.2 The Guarding Phase Confers a High Sexual Selection Advantage to Males

A similar cost-benefit analysis suggests that the male's guarding behaviour is maintained by intra-sexual selection, as a paternity guarding mechanism (Parker 1970e).

Guarding the female greatly increases the probability that the paired male will retain paternity of most of the egg batch, but costs the male mating opportunities through the time spent guarding. Taking both effects into account, calculation of fertilisation rates showed that a mutant male lacking guarding would sustain a high intra-sexual selective disadvantage at all densities of searching males common during reproductive activity. This explains why guarding is maintained in the present population, but not how it evolved initially—in an ancestral population in which females are totally unreceptive after mating, guarding could not evolve since male paternity is already protected by female unreceptivity. Many female Diptera become unreceptive at least for some time after an initial mating, though unreceptivity is rarely fully effective in preventing mating against male persistence.

Calculations showed that guarding behaviour would spread provided that more than 10 % of mated females in the ancestral population would have been willing (or could have been coerced) to remate. This is only slightly higher than the level observed in dipterans classified as 'unreceptive', so that given the very high densities of males around the oviposition site in this species, it is not difficult to envisage the origin of guarding. The behaviour of guarding females during oviposition had previously been interpreted as male co-operation with females to increase the efficiency of oviposition by deflecting the attacks of searching males (Foster 1967). While this is an unlikely explanation of the male behaviour, it does appear likely that females gain by allowing copulation to gain a guarding male. With the present rather poor ability of females to reject males, copulating (even in the absence of any other positive benefit) results in an overall time benefit of some 50 min for the female (Parker 1970b).

7.3.2.3 Copula Duration (i.e. sperm allocation) Fits Predictions for Male Optima

The most extensive quantitative investigations of dung flies involve studies of copula duration in relation to sperm competition and the economics of sperm allocation. Gravid females arriving at droppings usually contain sperm from previous matings; copulating males therefore generally compete against previously-stored sperm, which are gradually displaced from the female's sperm stores during copula (Parker 1970f). New sperm are input by a copulating male at a constant rate (Simmons et al. 1999), and the plot of fertilisation gains with time copulating shows diminishing returns (Parker 1970f). There is a trade-off between fertilisation gains from the present mating and gains from future matings. Early analyses showed that the average copula duration of males (resulting in around 85 % paternity) was around the optimum predicted by models that maximise male fertilisation rate during reproductive activity (i.e. time spent mate-searching and mating). This result is obtained from either competitive optimisation procedures (Parker 1970f), or (since payoffs are only very weakly frequency dependent) from marginal value theorem (Parker and Stuart 1976). However, with virgin females, fertility rises very steeply with time after the start of mating, and the male's optimal copula duration is just 11 min (Parker et al. 1993). The observed copula duration is nevertheless the same for virgins and mated females, suggesting that males cannot discriminate.

These studies on the average copula duration with gravid females show a small discrepancy between the observed (36 min; Parker 1970f) and the predicted optima (42 min, including meetings with undetected virgins, Parker et al. 1993). More recent studies have sought to evaluate dung fly copula duration in greater detail by examining optima in terms of phenotypic size variation of males and fecundity variation in females. The evidence suggests that copula duration is optimised across all male size phenotypes (i.e. the observed regression of copula duration against male body size matches the optimal regression, holding female size constant at the species average). Further, holding male size constant at the average, the observed regression varying female size also appears to be around the optimum predicted for the male.

Two factors influence the optimum in relation to male size: (i) sperm displacement rate increases with male size, and (ii) time to find and guard a new female decreases with male size, due to a size advantage in gaining take-overs in struggles for females (Parker and Simmons 1994). Charnov and Parker (1995) showed that these two effects interact so that optimal total sperm allocation should remain approximately constant with male size. Hence small males, with lower displacement rates, should copulate for longer time than large males to achieve equal input. As expected, observed copula duration decreases with male size (Ward and Simmons 1991; Parker and Simmons 1994; Simmons et al. 1999). The first calculation of the predicted relationship between copula duration and male size assumed that males displace sperm directly from the female sperm stores (Parker and Simmons 1994). This gave a good fit with the observed relationship, except for small males, where longer copula durations were predicted than were observed. Later, it was found that sperm displacement is indirect; sperm flow from the male aedeagus into the female's bursa, and is then transferred by movements of the female tract to the spermathecae (Hosken 1999; Hosken and Ward 2000; Simmons et al. 1999). When the predicted relationship was remodelled for this indirect transfer method the poor fit for small males disappeared, generating a very good fit between predicted and observed copula durations across all natural male sizes (Parker and Simmons 2000). Thus size-dependent optimal sperm displacement in dung flies can thus be explained by fertilisation rate maximisation in relation to the factors (i) and (ii) above.

Male dung flies vary their sperm allocation in relation to female fecundity: copula duration increases with female egg content (Parker et al. 1999). This observation matches predictions, and the match is again quantitative both for matings with new, fully gravid females arriving at the dropping, and also for matings with females taken over by a new male part way through oviposition. In addition to egg content, a second factor that must be taken into account in optimality models is the fact that a female's reproductive tract dimensions (notably her spermathecal volumes) increase with her size, decreasing the sperm displacement rate (Parker et al. 1999). Fertilisations in future clutches exert only a small effect on predicted copula duration for matings with fully gravid females, but exert an increasing effect as oviposition proceeds. For gravid, newly-arriving females, the number of mature eggs increases linearly with female size (Parker 1970f). The observed copula duration was found to increase with female size in a close quantitative fit with the predicted relation, and males probably assess female size rather than egg content directly

(Parker et al. 1999). For females taken over during oviposition, the eggs remaining to be laid depends on the timing of the takeover, and the observed copula duration decreases as eggs decrease, again fitting the prediction qualitatively except that the latter is slightly steeper than the observed relation. Males successful at take over may assess female egg content by how her much abdomen is distended; distension decreases notably throughout oviposition.

7.3.2.4 Experimental Evolution Produces Changes Predicted by Sexual Selection

Studies of experimental evolution in dung flies have generated the evolutionary responses predicted by sexual selection (Hosken and Ward 2001; Hosken et al. 2001; Martin et al. 2004). These experiments involved lines selected under either enforced polyandry (each female mated with 3 different males before oviposition, enabling post-copulatory sexual selection), or monogamy (each female mated only once, precluding sexual selection). Theory predicts that relative testis size should increase with the mean level of sperm competition in a population (reviewed in Parker and Pizzari 2010), and matches to this prediction have been found in so many comparative studies that relative testis size is now used ubiquitously as an indicator of sperm competition level. Monitored after only 10 generations, a strong divergence in testis size was found between monandrous and polyandrous dung fly lines, with much larger testes in polyandrous lines, where sperm competition was present (Hosken and Ward 2001; Hosken et al. 2001). Females in polyandrous lines evolved larger accessory sex glands, which are argued to increase female ability to influence paternity: males' success as second mates was lower in females in polyandrous lines (Hosken et al. 2001). However, males from polyandrous lines achieved higher paternity under sperm competition, supporting the prediction of increased testis size. A trade off may apply here: increased investment in testis mass appears to correlate with decreased immune function (Hosken 2001). By rearing larvae under high and low density conditions, Stockley and Seal (2001) found that males reared at high density with larger testes were less active in mate-searching, suggesting a trade off between testis investment and mate searching activity; however, the same trend was not found in males reared at low density.

Martin et al. (2004) compared fitness traits (lifetime reproductive success and longevity) of females evolved under enforced monogamy with those evolved under polyandry after each female had a single mating with a male from one of the two selection regimes. Females from polyandrous lines had lower fitness; they died earlier and produced significantly fewer progeny. Martin et al. plausibly argue that these results arise from sexual conflict inherent with the polyandrous selection regime.

7.3.2.5 Studies on Sperm Selection by Females

There have been several attempts to demonstrate female choice aspects of sexual selection in dung flies in terms of cryptic female choice, i.e. post-copulatory sexual selection in which the female selects sperm from alternative ejaculates (Eberhard 1996). Ward (1993) was first to propose that female dung flies bias paternity, and that this may account for some of the (typically high) variation in the proportion of last-male fertilisations (P_2) typically seen in paternity studies (Ward 2000). Hellriegel and Ward (1998) investigated theoretically plausible mechanisms enabling sperm preference with single or multiple sperm stores. For example, females having one store could apply different storage rates for different ejaculates; those with two or more stores could also separate ejaculates across stores. Ability to choose sperm from a given store enables far more effective paternity control, and offers a plausible hypothesis for why females often have more than one sperm store (e.g. Matsuda 1976; Ward 1993; Eberhard 1996; Hellriegel and Ward 1998). Dung fly females typically have three spermathecae and infrequently four.

The success of dung fly eggs depends on the topography and microclimate of the place of oviposition on the dropping; choice of a suitable oviposition site increases female reproductive success (Ward et al. 1999). Ward (1998) raised larvae of different phosphoglucomutase (*pgm*) genotypes in two different dung conditions with the same means for humidity and temperature, but in one set the temperature remained constant and in the other set it was variable. He found that the most successful genotype differed between the two sets. In an experiment in which females were constrained to lay in simulated 'sun' or 'shade' conditions, one of two *pgm* alleles was relatively commoner in eggs laid in 'sun' the other relatively more common 'shade'; differences in hatching or mortality could be discounted from this effect. He suggested that females use sperm selection to lay eggs of different genotypes under different sun/shade conditions, increasing offspring fitness by matching their genotypes to the larval growth conditions. Ward (1993, 1998) also found that in fixed length copulations, females stored more sperm from larger males, though whether this is due to cryptic female choice (Ward 1998) or to the fact that larger males have higher sperm input (and hence displacement) rates (Simmons et al.1996) remains controversial. Ward (2000) also found higher last male paternity if the second of two males to mate was genetically similar to the female at the *pgm* locus, and suggested that this involved cryptic female choice. In the field, *pgm* alleles from eggs were found to be non-randomly distributed between both (i) north and south slopes and (ii) shaded and sunny areas of artificial cow pats (Ward et al. 2002), but whether this effect arose from sperm selection by females or from different behaviour of females of different genotypes could not be determined.

However, two more recent studies generate pessimistic conclusions about the hypothesis of cryptic female choice of *pgm* alleles. Blanckenhorn et al. (2012) performed extensive lab and field investigations on the activity of *pgm* alleles and their effects on larval development times at different temperatures, and on the distribution of alleles in eggs deposited on the warmer southern slopes of droppings compared to those on the north slopes. They concluded that although *pgm* activity differences were apparent, and that *pgm* genotype did differentially affect development time, eggs laid on the north versus south slopes showed no biases in *pgm* composition as indicated from the previous work, removing the basis for cryptic female choice of sperm with different *pgm* genotypes. Further, Demont et al. (2012) performed field experiments in which females could choose to lay eggs in three different dropping microenvironments (south slope, ridge, and north slope), and genotyped both (i) the resulting offspring, and (ii) the sperm remaining in the female sperm stores after oviposition. Although (as expected) females showed a greater preference to oviposit on north slopes as ambient temperature increased, they found no evidence that females biased paternity towards certain male genotypes depending on the offspring's microclimate.

Bussière et al. (2010) used molecular techniques to demonstrate that although the mean proportion of sperm stored in the spermathecae match the published mean average paternity for the last male (the P_2 value), sperm from different males are not stored randomly across the female's sperm stores (see also Otronen et al. 1997; Hellriegel and Bernasconi 2000). The mean number of ejaculates stored also differs across spermathecae (Demont et al. 2011, 2012). Thus while hints are present, and the capacity for it certainly exists, clear evidence for cryptic female choice in dung flies has so far proven elusive.

7.3.3 General Comments on the Dung Fly Sexual Selection Studies

We have reviewed the dung fly studies at length because they represent perhaps the most detailed investigations of a wide range of aspects of sexual selection in a single species. The male-male competition studies have shown many *quantitative* fits between field and lab observations and model predictions across a wide range of male pre- and post-copulatory reproductive activities, providing very strong evidence that this component of sexual selection has indeed been a prime selective force moulding male behaviour in this species. This evidence clearly runs quite counter to the claim that "….There are fundamental problems that universally undercut all applications of sexual selection theory to any species…." (Roughgarden et al. 2006).

However, while the potential for females to exercise cryptic post-copulatory choice has been well established, and fertilisation biases detected, attempts to demonstrate that females select sperm in a manner that yields clear adaptive benefits have not yet been successful.

Thus the large amount of empirical work and modelling on sexual selection in the yellow dung fly reveals a trend that appears to be rehearsed in general for sexual selection studies: while evidence for male-male competition as a major selective force in evolution is widespread and highly supportive, evidence for female choice is less advanced and often controversial.

7.4 The Logical Imperative: Evolutionary Steps in Sexual Strategy

The logical imperative for Darwinian sexual selection is founded upon a predictable sequence of evolutionary events beginning with the evolution of recombination and sexual reproduction. The inevitability of this sequence is remarkable, since each step drives the next in an evolutionary cascade (the ‘sexual cascade’; Parker 2014) leading to males and females that coexist commonly as two highly differentiated sexual morphs with internal fertilisation. We outline these events as a series of separate steps; although in general the evolution of one step precedes and creates the selective pressure for the next, some degree of synchronicity in adaptation is likely. A further perspective on the sexual cascade is given in Parker (2014).

We argue that the transitions in sexual strategy are driven initially by gamete competition, and after the evolution of anisogamy, by sperm competition in association with changes in mobility and mode of fertilisation, eventually enabling pre- as well as post-copulatory sexual selection to operate. Figure 7.1 gives a summary to accompany the text.

7.4.1 *The Evolution of Sex: Sexual Recombination and Isogamous Gamete Production*

Sexual reproduction is a composite phenomenon that can be subdivided into a number of components—fusion, recombination, fission, and the male-female phenomenon—each component being subject to selection (Baker and Parker 1973). Genetic recombination is ubiquitous in living organisms from the simplest to the most complex, and may have evolved in the earliest organisms. Gametic fusion

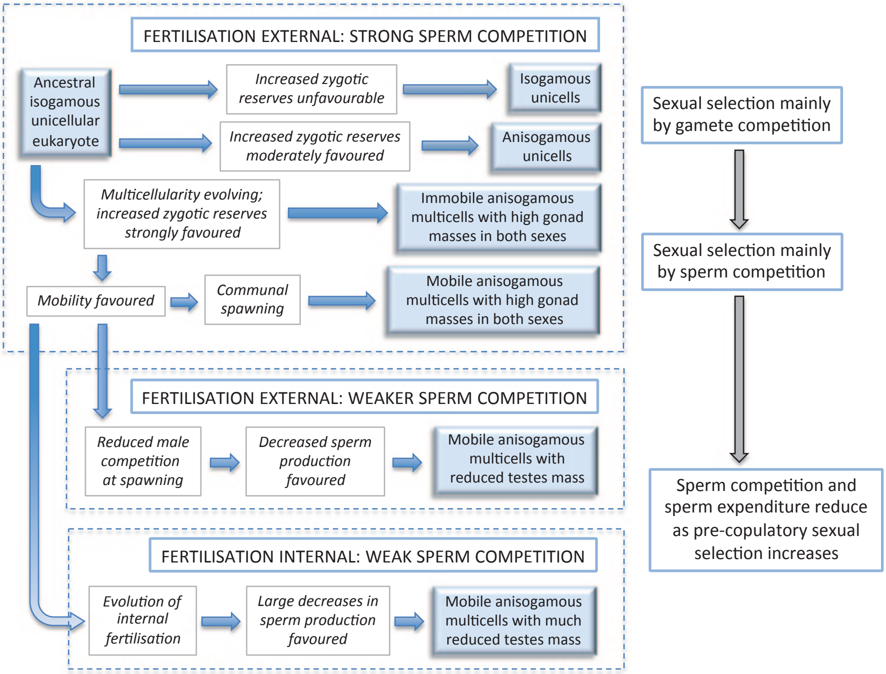

Fig. 7.1 Summary of the influence of sperm competition and mode of fertilisation on the evolution of sexual strategies and sexual selection

(syngamy) and recombination in eukaryotes involve the evolution of meiosis and the haploid-diploid cycle (e.g. see Maynard Smith and Szathmáry 1995). The selective advantage of sexuality over asexuality has been one of the longest and most enduring puzzles for evolutionary biologists. For example, in the nineteenth century, Weismann (1889) proposed that sex functioned to generate genetic variation, while Darwin (1889) favoured an explanation in terms of hybrid vigour. Later, Fisher (1930) proposed that a sexual population could evolve (and hence adapt) faster than an asexual population, and explicitly envisaged that sexual recombination was one of the very few adaptations that relied upon group selection. Muller (1932) noted that individuals in an asexual population irreversibly accumulate deleterious mutations (termed 'Muller's rachet' by Felsenstein 1974), and explained the success of sexual reproduction over asexual reproduction as a means of overcoming this costly accumulation. This benefit may not apply in asexual organisms that have asexual forms of recombination. The start of an avalanche of theoretical research of the past 40 years on the evolution of sexual recombination appears to have begun with Maynard Smith's (1971) classic paper "What use is sex?".

Maynard Smith (1978) noted that the advantage of sex must be sufficiently large to overcome the 'two-fold cost of sex' which arises as the cost of anisogamy (i.e. mainly a cost of producing males, but see Lehtonen et al. 2012): a mutant female able to reproduce parthenogenetically by producing similar females would replicate at twice the rate as a sexual female. Note that this is a requirement for the maintenance of sex in a sexual population rather than a requirement for its origin. Sex is likely to have occurred in an isogamous population (in which parents share the investment in the zygote, allowing each parent to produce twice as many offspring as a female in a sexual population), in which the evolution of sex would be much less costly (e.g. Lehtonen et al. 2012). However, the 'two-fold cost of sex' suggests that the overall advantage of sexual reproduction must be high in order that it is maintained against invasion by asexual mutants.

By now, many different theories have been proposed for the widespread maintenance of sex (see recent review of Hartfield and Keightley 2012), generating a vast literature (including several books). Later in his life, Maynard Smith (pers. comm.) became convinced that no single theory offers a general explanation for sex, but that the many mechanisms taken together may offer a sufficient account. West et al. (1999) have extended this pluralist view, stressing the advantages gained from considering that multiple mechanisms and their interactions operate to maintain the ubiquity of sex.

Whatever the advantage of genetic recombination, sexual fusion (syngamy), with its merging of the cellular investment of one gamete with that of another gamete of different genetic constitution, can set the scene for conflict or cooperation over the investment from each partner, and the evolution of anisogamy.

7.4.2 The Evolution of Two Sexes: Anisogamy

The ancestral state in eukaryotes is likely to have been a unicellular organism with isogamy, i.e. where the fusing gametes are of similar size, and hence contribute equally to the zygote (Fig. 7.1). However, it is clear that under many conditions isogamy is unstable, and in such cases soon after the evolution of gametes and sexual re-combination, selection is likely to have favoured a drive for anisogamy from the ancestral isogamy.

It is convenient to define sexes in terms of the gamete size-morph that an individual produces (Parker 2011). Thus an isogamous population consists of individuals of just one sex; and an anisogamous population consists of two sexes—males (microgamete producers) and females (macrogamete produces). This definition of sexes differs from one defining sexes in terms of mating types, in which one gametic mating type fuses with a dissimilar gametic mating type, which may or may not be the same size. Much less confusion is caused by defining sexes in terms of the gamete size a phenotype transmits (i.e. males convey small gametes, females large gametes, and hermaphrodites, which are male and female in one soma), and by defining mating types in terms of gamete types that can or cannot fuse together. Hermaphroditism (where two sexes coexist in one phenotype) is probably a derived state arising from special conditions (e.g. see Charnov et al. 1976); the initial mutations are likely to have been those affecting the size of gametes produced by given parents, leading to gamete dimorphism with two separate sexes.

There are several theories for the evolution of two sexes, most of which assume an origin from pre-exisiting gametic mating types (e.g. see review of Lessells et al. 2009). Two leading proposals—'gamete limitation' and 'gamete competition'—both focus on: (i) fusions gained, and (ii) zygote survival prospects. The initial theory, gamete limitation, dates back to Kalmus (1932; see also Kalmus and Smith 1960; Scudo 1967; Dusenbery 2000), who showed that when the probability of fusion is limited, a population with anisogamy and union between many micro- and few macro-gametes could achieve more surviving zygotes than an isogamous population with intermediate numbers of gametes. This theory was revitalised in an individual selection context by Cox and Sethian (1984, 1985), and Levitan (e.g. 1996, 1998) who explicitly considered the effect of how gamete size affects collision probability through its effects on 'target' size. More recent demonstrations that the Kalmus effect alone can generate anisogamy under individual selection (e.g. Iyer and Roughgarden 2008) appear marred by bias to demonstrate that cooperation rather than sexual conflict shapes sexual strategies, in line with Roughgarden's 'social selection' hypothesis (see Parker 2011). However, the most advanced recent analysis (Lehtonen and Kokko 2011) clearly and elegantly confirms that Kalmus' gamete limitation hypothesis can account for the evolution of anisogamy by individual selection provided that gamete competition is low or absent. It appears that Darwin had achieved some intuition about this effect, when he wrote: "With lowly-organised aquatic animals, permanently affixed to the same spot and having their sexes separate, the male element is invariably brought to the female; and of this we can see the reason, for even if the ova were detached before fertilisation, and did not require subsequent nourishment or protection, there would yet be greater difficulty in transporting them than the male element, because, being larger than the latter, they are produced in far smaller numbers." (Darwin 1874, p. 222).

The gamete competition theory of Parker et al. (1972) envisaged a large population of ancestral marine unicells with essentially isogamous gametes. Unlike the gamete limitation models, their model (analysed by computer simulation) does not assume that gamete size is linked to mating types; selective fusion is envisaged to evolve later (Parker 1978c). Parents release gametes varying somewhat in size, m, fusion is random and most or all gametes fuse, so that the set of gametes produced by each parent compete in the same 'pool' for fusions. The ESS is isogamy or anisogamy, depending on how the viability or success, f, of the zygote increases with its size $S = m_i + m_j$, i.e. on the zygote-size fitness function, $f(S)$. Many, but not all, of the subsequent developments of this model start with the assumption of mating types, as does that of Bulmer and Parker (2002) who include both a zygote-size fitness function and a gamete-size fitness function, $g(m)$, to show how these interact to determine which ESS is achieved, anisogamy or isogamy. As the zygote-size fitness function moves further away from the gamete-size fitness function, requiring a larger size before fitness begins to increase steeply, the ESS changes from isogamy to anisogamy. Bulmer and Parker (2002) argued that this change would reflect the transition from uni- to multi-cellularity, as originally proposed by Parker et al. (1972).

Which effect, gamete limitation or gamete competition, has been more important in the origin and evolution of anisogamy? Lehtonen and Kokko (2011) have generated important new insights by showing that both gamete competition and gamete limitation can lead to anisogamy, depending on the conditions. Using a development of Bulmer and Parker's (2002) model in which they included 'consistency' (i.e. average fitness of male and female must be equal if the sex ratio is unity), Lehtonen and Kokko modelled the situation where the number of parents in the local mating group could vary. Thus there is no gamete competition when just two parents of different mating type occur, and gamete competition increases with the number of parents in the group. Their analysis shows that anisogamy could indeed originate through either gamete limitation and gamete competition mechanisms. Even low levels of gamete competition generate anisogamy when gametes can fuse fairly readily, but conditions of gamete limitation and low gamete competition can also generate anisogamy. The isogamy ESS disappears relatively quickly (but not immediately) with the numbers of parents in the mating group.

Given that both gamete limitation and gamete competition can lead to anisogamy (and hence the two sexes), which condition has had the bigger influence on its origin depends on conditions in the ancestral isogamous unicells from which anisogamy evolved. Though some gamete limitation in these organisms seems quite plausible, so does fairly intense gamete competition due to gametes being released into the sea. The latter effect (and recent theory; Parker and Lehtonen 2014) would certainly favour gamete competition as the more potent selective pressure, and reflects our own view (see also Lessells et al. 2009), but we suspect that this question may never yield a definitive answer. Gamete (sperm) competition certainly offers a plausible solution for the maintenance of anisogamy in most current populations (Parker 1982).

Theory suggests strongly that increasing organismal complexity during the evolution of multi-cellularity favours anisogamy because of the need for larger zygotes (Parker et al. 1972; Bulmer and Parker 2002; Lehtonen and Kokko 2011), for which there is also empirical evidence (see review of Parker 2011). Thus, once sexual reproduction and sygamy have evolved, we can readily explain the evolution of two sexes due to increased importance of zygotic reserves associated with the evolution of increased organismal complexity in multi-cellularity. Starting from an ancestral isogamous (probably marine) unicellular eukaryote, if increased zygotic reserves are not favoured by selection, the ancestral isogamous state is retained, but if increased reserves are favoured, anisogamy will develop (Fig. 7.1). The most likely candidate driver of this event, in our view gamete competition, is a primitive form of fertilisation competition analogous to sperm competition under sexual selection.

7.4.3 The Evolution of the Sex Ratio

Darwin (1874) struggled with the problem of the evolution of the sex ratio, which was later solved by Fisher (1930; 'Fisher's principle') in a cryptic verbal argument, first made formal by Shaw and Mohler (1953). Envisage a large, random-mating population, in which anisogamy and selective sperm-egg fusions are established, most eggs are fertilised, and the cost of each male or female offspring is equal. Since each offspring has a mother and a father, the summed fitness of all male individuals must equal the summed fitness of all females (a requirement termed 'Fisher consistent' by Lehtonen and Kokko 2011). Thus in a population with unequal numbers of males and females, individuals of the rarer sex will have higher mean fitness, and genes for production of the rarer sex will increase until the sex ratio at the end of parental care becomes unity. This is an equilibrium, at which (deterministically) the mean fitness of each male equals the mean fitness of each female, and selection on sex ratio genes becomes neutral. Differential mortality of males and females after the end of parental investment does not affect the unity sex ratio, since if one sex suffers greater juvenile mortality it becomes the rarer sex, which compensates for its higher mortality. When selection has produced the unity sex ratio in a population, the expected gain from producing a male or a female offspring becomes equal for the parent. Hamilton's (1967) classic paper established a theoretical basis for 'extraordinary' sex ratios, and sex allocation theory has by now become a large research field (Charnov 1982; West 2009).

Lehtonen and Kokko (2011) note that analyses of the evolution of anisogamy that start by assuming the existence of mating types are not strictly 'Fisher consistent'. However, the analysis of the evolution of anisogamy by Parker et al. (1972) involved a genetics-based computer simulation in which gametes fused randomly (i.e. no mating types). Gamete size was determined by alleles at a 'gamete-size locus'. When anisogamy evolved by disruptive selection against alleles for intermediate gamete sizes, the result was a polymorphic equilibrium in which large and small gamete-size alleles coexist. In conditions generating high degrees of anisogamy, most fusions occurred among the vast numbers of microgametes, which died because they lacked enough reserves to survive as zygotes. What remained was a population consisting of equal numbers of proto-males and proto-females. Thus if J is a dominant allele for micro-gamete producing, and A its recessive allele for macro-gamete producing, the surviving genotypes were JA males and AA females, resembling the XY, XX sex-determining system. Reversing the dominance gave JJ males and JA females, resembling the ZZ female, ZW male system. Had the simulations started from mating types, or had they allowed selective fusion to evolve during the evolution of anisogamy, the unity sex ratio would also have been generated but without wastage of huge numbers of micro- x micro-gamete fusions. Parker et al. (1972) interpreted this unity sex ratio result as being due essentially to Fisher's principle operating in their simulations.

Thus unless special conditions apply (Hamilton 1967), anisogamy typically generates an equal sex ratio, essentially by Fisher's principle. With the drive to multicellularity and increasing complexity, anisogamy can readily be explained and will typically generate equal numbers of males and females.

7.4.4 The Evolution of Copulation and Internal Fertilisation

Primitively, fertilisation is likely to have been external. While the ancestral unicells may have been motile, e.g. through the action of cilia and flagella, in plants multicellular forms are usually sessile, as are many primitive multicellular invertebrate animals. Primitive sessile invertebrates such as sponges, certain coelenterates and echinoderms typically broadcast sperm into the sea, and fertilisation may be either external or occur after contact with ova held within the female (or hermaphrodite) soma. Such marine systems may involve intense sperm competition in which ejaculates from large numbers of different males (or hermaphrodites) compete for ova. Theory predicts that intense sperm competition is likely to result in high male gametic expenditure (Parker and Pizzari 2010), and since females should also maximise gamete production, this should result in similar high gonad expenditures in the two sexes in sessile or weakly mobile forms (Fig. 7.1). In conformity with this prediction, equal male and female body size and similar, high gonad masses are indeed characteristic of broadcast spawning marine invertebrates such as relatively immobile sea urchins, where sexual dimorphisms in body and gonad size are rare and related to special biological circumstances (see Levitan 2005). Gonad expenditures remain high and are often similar for the two sexes (or occasionally higher for males than females), resembling what would probably have been the ancestral state (Table 7.1). Sperm limitation has also been argued to maintain high male gametic expenditure in broadcast spawners (Levitan and Petersen 1995). It is important to remember, however, that sperm competition can apply even when there is sperm limitation—the sperm competition level increases with the number of different ejaculates competing for a given set of ova rather than with decreasing sperm limitation, though there will often be a negative correlation between sperm competition level and increasing sperm limitation.

High male gametic expenditure is also retained in many mobile vertebrates with external fertilisation when spawning is communal, so that high levels of sperm competition are retained, and can be even higher than in relatively immobile broadcast spawning invertebrates (Table 7.1), though in such cases males typically use their mobility to release sperm as close to a spawning female as possible (e.g. many communal spawning fish; Breder and Rosen 1966).

Table 7.1 Examples of gonadosomatic index (GSI) in relation to mode of reproduction across the animal kingdom, in taxa with separate sexes

Taxon	Species	Male GSI (%)	Authority	GSI dimorphism	Authority	Comment	Mode of reproduction
Invertebrates							
Cnidaria							
Anthozoa							
	Paramuricea clavata			Male > female	Gori et al. (2007); Coma et al. (1995)	No GSI value available but gonad volume values per polyp given in Gori et al. (2007) and calculated from data in Coma et al. (1995, Table 7.1), both at reproductive peaks	Sessile marine broadcast spawner, zygotes brooded on surface of female colonies (Coma et al. 1995, Gori et al. 2007)
	Eunicella singularis			Male > female	Gori et al. (2007)	No GSI value available but gonad volume values per polyp given in Gori et al. (2007) at reproductive peaks	Sessile marine broadcast spawner, zygotes brooded inside female polyps (Gori et al. 2007)
Scyphozoa	*Aurelia aurita*	6–9 (dry weight) 9–17 (ash free dry weight)	Lucas and Lawes (1998)	Roughly equal	C. H. Lucas, pers. comm	Male GSI values are deduced from female GSI taken from dry weight at peaks of maturity	Sperm shed externally in proximity to females (Lucas 2001) in spawning aggregations (Hamner et al. 1994); fertilisation internal
	Periphylla periphylla	2.8	C. H. Lucas, unpublished data	Male > female; 2.8/1.4	C. H. Lucas, unpublished data	GSI values from wet weights; significant difference between GSI means ($P<0.003$, df=19) but not bell diameters (C. H. Lucas, unpublished data)	Marine non-synchronous broadcast spawner
Echinoderms				Usually equal	Levitan (2005)	Usually high degree of multiple paternity (Levitan 2005)	Usually marine broadcast spawners

Table 7.1 (continued)

Taxon	Species	Male GSI (%)	Authority	GSI dimorphism	Authority	Comment	Mode of reproduction
Asteroidea	*Odontaster validus*	5.5–11.7	Grange et al. (2007)	Roughly equal	Grange et al. (2007)	Female GSI varied between 4.6-10.4 %; SD overlapping with male GSI (Grange et al. 2007)	Marine broadcast spawner
Ophiuroidea	*Ophiocoma alexandri*	28–43	Benítez-Villalobos et al. (2012)	Male > female	Benítez-Villalobos et al. (2012)	From June, September, October and April values; can be lower at other times of year	Marine broadcast spawner
	Ophiocoma aethiops	17–30	Benítez-Villalobos et al. (2012)	Equal	Benítez-Villalobos et al. (2012)	From June, September, October and April values; can be lower at other times of year	Marine broadcast spawner
	Ophionotus victoriae	0.5–2	Grange et al. (2004)	Equal	Grange et al. (2004)	GSI values are at peak maturity	Marine broadcast spawner
Echinoidea	*Sphaerechinus granularis*	2–8	Martínez-Pita et al. (2008)	Equal	Martínez-Pita et al. (2008)	Much variation between localities	Marine broadcast spawner
Molluscs							
Bivalvia	*Adamussium colbecki*	35	Tyler et al. (2003)	Male > female; 35/24.8	Tyler et al. (2003)	GSI values are at peak maturity; Chiantore et al. (2002) give lower values for female GSI of 7-10 %	Marine broadcast spawner
Gastropoda	*Fissurella maxima*	13	Bretos et al. (1983)	Appear roughly equal	Bretos et al.(1983)	GSI for November peak	Marine broadcast spawner
	Helcion pruinosus	25–34	Henniger (1998)	Male > female;	Henniger (1998)	Peak value; two localities	Marine broadcast spawner

Table 7.1 (continued)

Taxon	Species	Male GSI (%)	Authority	GSI dimorphism	Authority	Comment	Mode of reproduction
Cephalopoda	*Illex coindetii*	4.9	(Rosa et al. 2005)	Male < female; 4.9/11.4	(Rosa et al. 2005)	GSI values are at maturity	Internal fertiliser: male places spermatophore inside the female's mantle during mating. High levels of sperm competition reported in cephalopods (Marian 2012)
	Todaropsis eblanae	5.5	(Rosa et al. 2005)	Appear equal; 5.5/5.7	(Rosa et al. 2005)	GSI values are at maturity	Internal fertiliser: male places spermatophore inside the female's mantle during mating. High levels of sperm competition reported in cephalopods (Marian 2012)
Insects						Male GSI positively correlated with level of sperm competition all 5 groups studied (reviewed by Simmons and Fitzpatrick 2012)	Internal fertilisation, usually with copulation
Drosophilidae		2–11	Pitnick (1996)	Male < female?		Male GSI increased with body mass and with sperm length; high GSI associated with production of few remarkably long sperm (Pitnick 1996)	Internal fertilisation with copulation
Tettigoniidae		1–14	Vahed et al. (2011)	Male < female?		High male GSI associated with high polyandry and low nuptial gift investment (Vahed et al. 2011)	Internal fertilisation with copulation

Table 7.1 (continued)

Taxon	Species	Male GSI (%)	Authority	GSI dimorphism	Authority	Comment	Mode of reproduction
Onthophagus species		1.6–3.6	Simmons et al. (2007)	Male < female?		High male GSI ssociated with high frequency of minor males (Simmons et al. 2007)	Internal fertilisation with copulation
Photinus species		0.6–3.2	Demary and Lewis (2007)	Male < female?		Male GSI positively correlated with level of sperm competition which can be high (Demary and Lewis 2007); GSI value is dry weights of testes and seminal vesicles, increases to 0.7–14 if accessory glands added	Internal fertilisation with copulation
Vertebrates							
Fish		0–12	Stockley et al. (1997)	Usually male < female?		Male GSI positively correlated with level of sperm competition (Stockley et al. 1997), highest in communal spawners, lowest in species with internal fertilisation (see also Simmons and Fitzpatrick 2012)	Mostly external fertilisers, range from communal spawning to pair spawning, occasionally internal fertilisation
Amphibia							
Anura		0–8	Jennions and Passmore (1993)			Male GSI positively correlated with level of sperm competition (reviewed by Simmons and Fitzpatrick 2012) and other factors (Emerson 1997)	Mostly external fertilisation with amplexus, sometimes in aggregations
Anura	*Fejervarya limnocharis*	0.3	Othman et al. (2011)	Male < female; 3/12.4	Othman et al. (2011)	GSI for March—April peaks	External fertilisation with amplexus

Table 7.1 (continued)

Taxon	Species	Male GSI (%)	Authority	GSI dimorphism	Authority	Comment	Mode of reproduction
	Rana leptoglossa	0.5	Saha and Gupta (2011)	Male < female; 0.5/6.4	Saha and Gupta (2011)	GSI peak values	Males hold territories; courtship followed by amplexus with external fertilisation (Saha and Gupta 2011)
Reptiles							
Birds		0–10 mean = 1	Pitcher et al. (2005)	Parental care, often by both sexes		Reviewed by Simmons and Fitzpatrick (2012)	Internal fertilisation
Mammals		0–7 64% < 1 6% > 3	Kenagy and Trombulak (1986)	Parental care, usually by female only		Male GSI positively correlated with level of sperm competition in most groups (reviewed in Dixson 2009; Simmons and Fitzpatrick 2012)	Internal fertilisation

The evolution of mobility, involving various advanced modes of locomotion, has had important consequences: it has enabled release of sperm close to spawning females. Thus in many invertebrates and most vertebrates, higher fertilisation benefits have become available through mate searching and female-targeted sperm release than through sheer expenditure on sperm production. Enhanced mobility and female-targeted sperm release, coupled with the fact that Fisher's principle maintains the sex ratio at unity, favoured dramatic reductions in testes mass, associated with the trend towards either pair spawings with external fertilisation or, eventually, to copulation and internal fertilisation (Parker 1970a, 1984 2014; Levitan 1998). Targeted forms of sperm release yield both increased fertility benefits and immediate sperm competition benefits compared to untargeted broadcast spawning, and once expenditure on mate searching and female-targeted sperm release yields higher marginal fertilisation gains than numerical sperm production, reduction in sperm expenditure is predicted (Parker 2014). The ultimate extrapolation of this trend in sexual selection ends in copulation with internal fertilisation, and then the evolution of specialised male intromittent organs, driven perhaps predominantly by the benefits of reduced sperm competition (Parker 1970a). The reduction in testis expenditure creates the 'resource space' for the expansion in pre-copulatory male-male competition (Fig. 7.1)—it 'enables' Darwinian pre-copulatory sexual selection. Thus pre-copulatory sexual selection must be regarded as evolving secondarily to gamete and sperm competition.

The view that internal fertilisation has evolved primarily by sexual selection contrasts with classical views of its evolution solely by natural selection to increase fertilisation efficiency and gamete and zygote survival. While the latter benefits are highly likely to have played a significant part in reinforcing the drive towards internal fertilisation, we see them as being secondary to sexual selection as the main motive force. Copulation, followed by the evolution of specialised male intromittent organs, probably represents the final stages of sexual selection and reduced sperm competition. An alternative scenario could be that they were driven predominantly by female choice (Eberhard 1996), though we envisage that where it occurs, this has evolved later.

There is little doubt that internal fertilisation typically (but need not necessarily) results in much lower sperm competition than external fertilisation with communal spawning. Polyandry, and the evolution of female sperm stores, however, can maintain sperm competition as a powerful selective force. The range of sperm competition levels seen even in one taxon is often so great as to favour a vast array of relative testes sizes, from tiny to huge (e.g. fish; see Stockley et al. 1997).

While anisogamy, with tiny sperm and large ova, is clearly favoured under conditions of high sperm competition, the question remains as to why so many tiny sperm are still produced in internal fertilising species when sperm competition has reached very low levels (Parker 1982). One may imagine intuitively that with low sperm competition, it would pay males to provision sperm so that they could then contribute to the reserves of the zygote, which would challenge the stability of anisogamy. Provided that sperm competition risk is not trivially small, there is a very good reason why anisogamy is not lost due to sperm contributing to zygotic investment (Parker 1982, 2011; Lehtonen and Kokko 2011). This is because extra provisioning would need to be provided to each and every sperm, which would generally have large costs (e.g. under sperm competition) that outweigh the marginal benefits. For instance, it will not pay to add extra provisioning to each sperm to aid with zygote provisioning if the probability that a female will mate twice (generating sperm competition) rather than once (i.e. no sperm competition) is greater than $2/A$, where $A =$ ovum size/sperm size (Parker 1982, 2011). This is an extremely robust condition, since A is usually likely to be a very large number, and for species with maternal care A should include the parental investment as well as the ovum costs, making the condition even more robust. Therefore, anisogamy appears to represent an irreversible evolutionary transition in most multicells. Typically, only when the probability of sperm competition falls towards zero can anisogamy be threatened, and in such circumstances males appear to increase parental care rather than sperm contribution to the zygote (e.g. sea horses, see Parker 2011 p. 49).

In summary, the evolution of enhanced mobility allows a trend towards female-targetted sperm release through higher fertilisation gains with increased proximity of sperm to the ova (for further details, see Parker 2014). Under communal spawning, male gametic investment remains high (often equalling that of females) since sperm competition remains high, but less communal spawning favours reduced sperm expenditure and an increase in expenditure on pre-copulatory male-male competition. Gains from female-targeted sperm release may account for the evolution of internal fertilisation and the evolution of male intromittent organs.

7.4.5 The Consequences: Pre-Copulatory Sexual Selection and High Secondary Sexual Differentiation

Sperm allocation theory predicts ESS expenditure on testes to increase with mean sperm competition level across populations (Parker and Pizzari 2010), and a comprehensive recent review (Simmons and Fitzpatrick 2012) of the many studies available have shown that this expectation is generally met: relative testes size usually (but not always) increases with sperm competition level across many animal taxa, and is now commonly used as an index of sperm competition level in comparative studies. A complication is that sperm competition level is associated with polyandry level (and hence the mating rate of both sexes), which affects sperm demand, though mating rate is more likely to affect the investment per ejaculate than testes investment (Parker and Ball 2005; Vahed and Parker 2012).

Theoretical models assume a fixed resource budget for reproduction, so that pre-copulatory expenditure on gaining matings trades off against post-copulatory expenditure on ejaculates, resulting in a negative relation between pre- and post-copulatory expenditures. While most theory assumes pre-copulatory male-male competition to be some form of scramble competition in which the number of matings increases linearly with pre-mating expenditure (e.g. competitive mate-searching), Parker et al. (2013) have outlined how different forms of male-male pre-copulatory competition can affect the ESS balance between pre- and post-copulatory expenditures, depending on the mean level of sperm competition experienced by the population. This does not appear to affect the general prediction that post-copulatory expenditure (i.e. on testes and ejaculate production) increases with sperm competition level.

Table 7.1 shows some examples of how GSI varies in relation to the mode of reproduction and expected sperm competition level across the animal kingdom, for taxa with separate sexes, in reproductive condition. We stress that (i) GSI is typically allometric, particularly in males, so the ranges shown must bear this in mind, and (ii) the maximum GSI level possible will vary considerably in taxa depending on somatic requirements, so that it is often more informative to consider how male GSI relates to female GSI in discussing the trends in Fig. 7.1. We anticipate that selection will generally push females towards maximum expenditure on GSI, while this will not be so for males when sperm competition is relaxed and pre-mating competition possible.

Marine broadcast spawning invertebrates show much variation in GSI just before spawning, depending on locality (and presumably feeding resources). They typically show (i) no obvious sexual size dimorphism, (ii) either similar GSI in males and females (published measures are often not separated for males and females) or higher male GSI, and (iii) much more male-biased GSI dimorphism than internal fertilising taxa (though exceptions can occur, e.g. the ophiuroid, *Ophionotus victoria*). Thus for cnidarians and echinoderms, selection typically maintains body size at similar levels in the sexes, and we anticipate that in both sexes virtually all reproductive investment is directed towards gametes. In Scyphozoa, the best index of GSI is probably ash free dry weight (see *Aurelia aurita*, Table 7.1). GSI values for *Periphylla periphylla* are expressed in wet weight; converting to dry weight would increase GSI because the percent dry weight of gonads, which are fairly organic-rich, is much higher than whole tissue which is predominantly watery (>95%) mesoglea (Dr. C. H. Lucas, pers. comm.).

The same trends appear to apply for broadcast spawning marine molluscs, with a reduction GSI coinciding with internal fertilisation in cephalopods. Though they have specialised sperm stores and are therefore candidates for raised sperm competition, insects typically show fairly low male GSI (e.g. *Onthophagus* beetles, Table 7.1) unless special features intervene (e.g. *Drosophila*, Tettigonids, Table 7.1). They appear to show associations between sperm competition level and male GSI.

For vertebrates, there is evidence for many of the major taxa that relative testes size correlates positively with sperm competition level. Marine communal spawning fish retain high GSI, and have similar characteristics to marine broadcast spawning invertebrates (see above), despite their high mobility and the fact that males are often competitive in their attempts to ejaculate close to spawning females. Their high GSI and low sexual dimorphism is probably maintained by the high sperm demand due to the high sperm competition prevalent in communal spawns. In amphibians, though anurans usually have external fertilisation this is achieved in pair spawnings in amplexus (mating embrace), which results in reduced male GSI (Table 7.1) and also reduced male body size (Arak 1988). For land animals, internal fertilisation is almost obligatory (though not copulation; e.g. male thysanurans and collembolans deposit spermatophores on the substrate, which are picked up by females). It is quite possible that internal fertilisation first arose in aquatic ancestors to increase fertility and to reduce sperm competition, and served as a preadaptation to land colonisation. Thus birds and mammals have male GSI typically below 1 %, though it can rise to 7–10 %, and there is much evidence that relative testes size increases with sperm competition in these groups. Female GSI is not included in Table 7.1 since birds and mammals typically show high levels of parental care, which forms the large part of the female budget for reproduction.

Also in line with expectations, there is empirical evidence that reductions in relative testis size through reduced sperm competition are associated with increased expenditure on adaptations to pre-copulatory sexual selection, such as male armament, mate-searching and mate-guarding, etc. (e.g. see Poulin and Morand 2000; Parker et al. 2013). As expected, this can generate high levels of secondary sexual dimorphism.

Sexual size dimorphism is usually explained in terms of a different balance for the two sexes between the benefits of larger size through enhanced reproduction and the increased costs of juvenile mortality risk through delaying sexual maturation (e.g. see review of Blanckenhorn 2000). For females, fecundity typically increases with size, while pre-copulatory male-male competition is usually seen as the major selective pressure favouring increased male body size. Male-biased sexual size dimorphism is characteristic of species with high male-male contests for females (see chapters in Fairbairn et al. 2007). When males compete by sperm production alone rather than contests, selection on male size can occur in order to maintain large testes (Parker 1992). While high levels of sperm competition under communal spawning can prevent male size dropping below female size, sperm competition alone (without contest competition) cannot easily push male size above female size, and if sperm competition is very low, small or dwarf males are predicted (Parker 1992).

The notion of gradual evolutionary transition from sexual selection mainly by sperm competition, to a mixture of both pre- and post-copulatory sexual selection with the evolution of mobility and copulation as sperm competition reduces (Fig. 7.1) was, in fact, foreshadowed rather cryptically in Darwin's original treatise. Darwin (1874, pp. 260–265) dismissed sexual selection (i.e. pre-copulatory sexual selection) in "the lower classes of the animal kingdom" on the grounds that they are sometimes hermaphrodite, or sessile (precluding male-male competition: "the one cannot search or struggle for the other"), or because they "have too imperfect senses and much too low mental powers to appreciate each other's beauty or other attractions, or to feel rivalry"). The number of pages he devotes on evidence for (pre-copulatory) sexual selection increases roughly in inverse proportion to relative testis size of the taxa, with most pages devoted to insects, birds and mammals. That pre-copulatory sexual selection (i.e. as envisaged by Darwin) is essentially the province of species with relatively low testis expenditure (viewed across the entire animal kingdom) is hard to dispute.

Thus anisogamy, mobility and internal fertilisation resulted in reduced sperm expenditure and allowed higher male pre-copulatory competition (Fig. 7.1). Coupled with the constraint of the unity sex ratio, the scene was set for the ecological asymmetry between the two sexes leading to the consequences of pre-copulatory sexual selection in terms of stereotypical sex roles, i.e. the Darwin-Bateman Paradigm (DBP). Thus DBP relies on (i) the unity sex ratio, and (ii) ejaculates being cheap and male parental care negligible relative to the cost of ova and any female parental care, i.e. on the rise of pre-copulatory male-male competition at the expense of expenditure on sperm, as outlined above (see Fig. 7.1). DBP, and its many causal interpretations, i.e. in terms of relative parental investment (PI; Trivers 1972), operational sex ratio (OSR; Emlen and Oring 1977), potential reproductive rate (PRR; Clutton-Brock and Vincent 1991), or the relative 'time in' and 'time out' of each sex's availability for mating during adulthood (Clutton-Brock and Parker 1992) all rely on this asymmetry, and are extensions of Darwin's original insight. These three measures of 'sexual selection intensity' are all closely related mathematically (Parker and Birkhead 2013). As such, DBP serves as a null model for mobile species with reduced relative expenditure on testes, and negligible or low male parental care. Of course, there are exceptions to such a proviso, but DBP nevertheless covers most animal species.

Our evolutionary arguments have so far not included the origin of parental care, or parental investment other than that in the gametes. It is too seldom stressed that across the animal kingdom as a whole, parental care by either sex is relatively rare in invertebrates, and the rule only in two taxa, mammals and birds. Parental care has evolved later, and is a complex problem that should not be (but often is) confused with the events described in Fig. 7.1 leading initially to the generality of the DBP. Paradoxically, the male-biased OSR predicted under DBP generates frequency-dependent selection, analogous to Fisherian sex ratio selection, that favours increased parental investment by males (Kokko and Jennions 2008). Undoubtedly, the primary asymmetry of anisogamy and the mode of fertilisation have influenced the subsequent evolution of parental care (Maynard Smith 1977), which is highly biased towards females. Kokko and Jennions (2008) suggest that the predominance in conventional sex roles in species with parental care are maintained by sexual selection on males, reduced paternity through female multiple mating or group spawning, and higher male mortality generating female-biased adult sex ratios.

However, cases of bi-parental care and male-only care have evolved in some taxa (notably fishes and birds). In a few species (notably birds), male-only care can lead to sex role reversal. Though counter to sex roles predicted initially by DBP, such cases can sometimes be explained by a reversal in the ecological asymmetry from that predicted simply by anisogamy and reduced sperm expenditure (e.g. Simmons 1992). Note that when ecological conditions promote higher male PI, this will typically lead to the evolution of different forms of paternal investment, but for the reasons outlined above anisogamy will remain.

As a final evolutionary consequence, sexual selection almost inevitably generates sexual conflict, i.e. an evolutionary conflict of interest between some males and females (Parker 1979; Arnqvist and Rowe 2005), though this is the subject of recent controversy (see Sect. 7.5.2).

7.5 Some Current Controversies

7.5.1 Criticisms of the Darwin-Bateman Paradigm (DBP)

In view of the logical imperative for sexual selection, DBP remains a satisfactory first expectation for species with zero male care and internal fertilisation (i.e. the vast majority of species). As such, it fulfils a similar heuristic purpose as does, say, the Hardy-Weinberg equilibrium for neutral selection on two alleles—i.e. when we find deviations from it, we need to examine why these occur. They are likely to be due to special biological features, which, however interesting, do not negate the validity of DBP as a general rule for the majority of cases (Parker and Birkhead 2013). The current criticisms of DBP relate partly to the fact that deviations from DBP in species with relatively high male parental care are (unsurprisingly) not that uncommon; moreover, there are various other reasons why DBP expectations may not be met (see e.g. Klug et al. 2010).

Attacks on sexual selection and/or DBP have recently arisen from two related but rather different sources. First, Roughgarden et al. (2006) have claimed that the entire concept is flawed and that solutions to male and female sexual adaptation should be sought in terms of 'social selection'—the principle that mating and associated reproductive activities between the sexes will be cooperative. This critique is based on erroneous claims relating to the quality of the evidence for Darwinian sexual selection and has attracted much criticism (see the multiple responses in *Science*, 2006, vol. 312, 689–694). Further, while the notion that reproduction can involve cooperation is certainly not novel (e.g. we have long known that sexual cooperation can occur, for instance in animals such as birds with biparental care), this itself involves sexual conflict, which must be fully considered in understanding its evolution and stability. Further, while mutual benefits to each sex may arise from a given reproductive adaptation, these may offer a weak or negligible selective force compared to those arising directly through sexual selection. For example, the guarding phase of male dung flies was originally (Foster 1967) seen as co-operation with the female to ensure more efficient oviposition, but there is strong evidence to suggest that it has arisen through sexual selection for paternity guarding (Parker 1970e).

A second recent critique is the attack on the DBP paradigm, resulting in a 'gender role' controversy, i.e. whether DBP—and ultimately the primary sexual difference of anisogamy—does offer an explanation of male and female sex roles and behaviour (see review of Parker and Birkhead 2013). This has also been strongly argued to be misguided (Schärer et al. 2012; Kokko et al. 2013; Parker and Birkhead 2013). However, aspects of this critique are possibly not entirely unrelated to what must be regarded as an excellent and growing development in sexual selection studies, namely an increasing focus on the female perspective, and on female interests in multiple mating, i.e. polyandry (e.g. see the recent theme issue in *Phil. Trans. R. Soc. Lond. B* 2013, vol. 368 on polyandry).

7.5.2 Conflict and Co-operation in Sexual Dynamics

One of the areas of current debate is the extent to which sexual selection generates an evolutionary conflict of fitness interests between individual males and females. The debate has been strongly polarised: while some biologists have proposed that sexual selection necessarily coincides with sexual conflict (e.g. Arnqvist and Rowe 2005), others have called for sexual interactions can only be understood in the light of social cooperation (Roughgarden 2006). The biological reality is likely to be more complex.

First, it is undeniable that sexual selection implies a tension between the evolutionary interests of some males and females. Sexual conflict can occur over a number of reproductive events, from mating to parental allocation, and through different mechanisms (Parker 1979). The primordial sexual conflict probably began during the evolution of anisogamy and sperm-ovum fusions (Parker 1978c, 2011), but as divergence in the two sexual phenotypes becomes more exaggerated through the evolution of enhanced mobility, reduced sperm expenditure, and increased male-male mating competition, so does the potential for sexual conflict. For example, the very concept of mate choice necessarily creates a conflict of interests between the chooser and those members of the opposite sex that are less preferred. More generally, conflict will occur whenever an individual gains by differentially allocating reproductive resources to reproduction with individual partners. In the blue head wrasse, *Thalassoma bifasciatus*, the most successful males invest their reproductive resources to attract and mate guard a large number of females. This investment however limits the number of sperm that a male is able to allocate to the eggs spawned by each female, leaving about 7 % of their eggs not fertilised (Warner et al. 1995). Therefore, while this strategy yields a larger number of eggs fertilised by a male across all the females attracted, it imposes fertility costs on individual females (see Ball and Parker 1996 for other predictions on 'adaptive infertility' in external fertilisers). Sexual selection can also promote traits that convey an advantage in intra-sexual competition while imposing a fitness cost on mating partners. These costs are likely to represent collateral side-effects in the majority of cases (e.g. Siva-Jothy 2006), however, in principle it is also possible that sexual selection might favour a male trait precisely for the costs that it imposes on females (e.g. Johnstone and Keller 2000; Lessells 2005). A wide range of such traits has been documented mostly in males. Therefore an element of conflict is unavoidable whenever alternative reproductive opportunities are available to an interacting male and female.

Second, despite the near-ubiquitous potential for sexual conflict, sexual selection does not eliminate potential for inter-sexual cooperation over a number of reproductive decisions. One such example is conflict over female re-mating decisions. Clearly, by mating with a second male a female can reduce the reproductive success of the first male, which may lose paternity through sperm competition. Therefore, whenever females benefit by re-mating (e.g. Arnqvist and Nilsson 2000), sexual conflict is expected between the female and the first male. However, in many species males can stimulate female fecundity, for example through the gonadotropic effect of ejaculate compounds (see above). Alonzo and Pizzari (2010) have shown that when a mating more than doubles female fecundity, as has been documented in a number of taxa, two males actually gain by mating with the same female as double mating yields a higher number of eggs available for fertilisation than would be available to either male mating exclusively with a female. This generates a scenario of inter- and intra-sexual cooperation over female re-mating decisions. A similar example, analysed long ago by Maynard Smith and Ridpath (1972), is that of wife sharing in the Tasmanian Native Hen, *Tribonyx* (= *Gallinula*) *mortierii.* When two males share a female, the number of progeny that can be produced is increased. Conditions favouring wife sharing are more permissive, requiring (in the simplest case) only an increase in progeny of 67% since the two males are brothers. Note that clearly in both cases, conflict remains over who gets to fertilise the eggs.

Finally, much of the current debate over conflict and cooperation in sexual dynamics is narrowly focused on direct consequences that a certain sexual trait or behaviour has on the fitness of the actor and recipient. However, sexual interactions like many other social traits, may also influence the fitness of third parties, creating potential for indirect effects to contribute to the evolution of sexually-selected traits. Indirect effects are the relatedness-weighted effects on the inclusive fitness of social partners (Hamilton 1964; Pizzari and Gardner 2012). Inclusive fitness effects expand the diversity of evolutionary outcomes of sexual interactions by adding the possibility of altruism and spite to conflict and mutualism driven by selfishness and direct effects. Pizzari and Gardner (2012) identify two conditions under which indirect benefits can arise: "(i) the recipient is related to the actor; or (ii) the actor is related to a third party, who will at some point also interact with the recipient." The former condition (i) represents the case of inbreeding. Because of anisogamy and sex differences in parental investment we expect males to gain from inbreeding in situations in which females would lose from inbreeding, and we expect this potential for conflict to expand as opportunity costs associated with mating are progressively reduced (Parker 1979, 2006). Parker (1979, 2006) had already demonstrated how indirect effects –through kin selection—can modulate sexual conflict over inbreeding (see also Kokko and Ots 2006). The latter condition is more broadly relevant but so far has received little consideration. However, recently it has been shown that when male competition occurs locally amongst rivals that are more related to each other than the population average, indirect effects are likely to buffer sexual selection for male traits that harm females (Rankin 2011; Wild et al. 2011), thus reducing the intensity of sexual conflict ('virulence' *sensu* Pizzari and Gardner 2012).

An alternative mechanism through which indirect effects might modulate sexual dynamics is through potential 'greenbeard' effects (Pizzari and Gardner 2012). 'Greenbeards' are genes that allow their carriers to increase each other's fitness through mutual recognition and differential interactions (West and Gardner 2010). The preference and ornament genes in sexual signalling can be thought of as an inter-sexual green beard, and the rapid coevolution of exaggerated ornament and preferences envisaged by Fisher is clearly modulated by green beard indirect effects (Pizzari and Gardner 2012).

These considerations illustrate that potential for sexual conflict should not be assumed but carefully measured for individual reproductive decisions including both direct and indirect fitness effects. It is important to note however, that current debate on conflict and cooperation reflects a development rather than a limitation of sexual selection theory.

7.5.3 Intensity of Sexual Selection

OSR and I_T (and related indices) have long been proposed and used as measures of the intensity of sexual selection. Recently, Klug et al. (2010) have strongly criticised their use on the grounds that they only accurately predict sexual selection under a limited set of circumstances, and more specifically, only when mate monopolization is extremely strong. However, their analysis has been seen as pessimistic by Parker and Birkhead (2013), mainly because it ignored the direct effect of the likely relation between OSR and male time out of the mating pool, which when included, shows that OSR and I_T can indeed be reasonable measures of sexual selection intensity. Independently, a detailed study of how and when male time out and its relation to OSR can allow OSR and I_T to give fair measures of the intensity of sexual selection has been given by Kokko et al. (2012). While measures of the intensity of sexual selection are sometimes useful (e.g. particularly for comparative analyses) many would agree with Klug et al. (2010) that ideally—and provided that one knows *a priori* what traits are currently targeted by sexual selection in a given species—one would measure selection directly on the phenotypic trait of interest, a point originally stressed by Grafen (1987).

7.6 Concluding Comments

We conclude that sexual selection theory is a powerful heuristic tool providing the most parsimonious explanation for a vast diversity of traits, across sexually-reproducing organisms, from unicellular taxa to primates. Overwhelmingly strong qualitative and quantitative evidence has accumulated over the last decades vindicating Darwin's original insight. Crucially, sexual selection theory has also been successfully applied as predictive tool to explain biological phenomena that were unknown to—or not considered by—Darwin. Sexual selection has a strong underlying deductively logical imperative that follows from the predictable sequence of evolutionary events arising after the evolution of sexual recombination and fusion.

It is fallacious to argue that because (actually rather low frequency) differences from DBP occur that DBP does not offer a general explanation. For the vast majority of species where there is no male parental care, it tells us what to expect when special features of biology do not act to change that expectation.

Sexual selection theory certainly does not need to replaced as has been advocated recently (Roughgarden et al. 2006); rather, it represents one of the major triumphs of adaptive explanation. However, we argue that current debates may be more effectively resolved by bringing sexual selection theory more firmly within the framework of social evolution (e.g. Rankin 2011; Pizzari and Gardner 2012) and by a more dynamic integration of theory with the ecological and physiological details of sexual interactions.

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The notion of sexual selection as a logical imperative arising through the sequence of evolutionary events leading to highly differentiated males and females was to have been the central theme of a book entitled *The Evolution of Sexual Strategy* by GAP during the 1970s. This project was 70 % accomplished, mostly during a year (1978–79) in the Research Centre of King's College, Cambridge, but was never completed after his return to Liverpool University in September 1979. GAP has often regretted this failure, but wishes to thank King's College, Cambridge for the opportunity to work in the Research Centre, which nevertheless proved most stimulating.

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