Do popular males always lose out in sperm competition?

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Abstract

The process of sexual selection has been a fascinating topic for scientist for a long time and still is intensively studied. Darwin already suggested two pathways for evolution of traits under sexual selection: male-male competition and female choice. Parker realized that sexual selection can continue after copulation: sperm competition and cryptic female choice were found as potential pathways as well. These processes are not mutually exclusive, and can oppose or reinforce each other. Total male reproductive success is determined by a male's ability to acquire matings (precopulatory processes) and his share in fertilized ova (postcopulatory processes). From a life history point of view, as resources are limited, one would expect a trade-off between investing in precopulatory and postcopulatory success. However, do popular males that have invested in secondary sexual characteristics, always lose out in sperm competition? The phenotype-linked fertility hypothesis states that females should prefer fertile males and that fertility is in some way linked to exaggerated secondary sexual traits. In this review I look at the relation between pre- and postcopulatory success. Do popular males always lose out in sperm competition? Or are they not only more successful in acquiring matings, but also more fertile? For this comparison I compiled the results of studies done on this relation and look for support for the alternative scenarios. For both hypotheses we can find species where such a system appears to be present. No clear condition determining the relation between pre- and postcopulatory success has been found. However, there does seem to be a trend for cryptic female choice to favor males that were also successful before copulation.

Introduction

Darwin was one of the first to recognize the selective power of sexual selection. It starts with an inequality between the sexes, for example anisogamy: the difference in size and number of eggs and sperm. Darwin suggested male-male competition for mating opportunities and female choice as two pathways for evolution of traits under this selection [1]. For a long time after Darwin, scientists focused on male-male competition as the primary means of sexual selection. At present day however it has been well established that both male-male competition and female choice are important mechanisms that can lead to the evolution of exaggerated secondary sexual traits. These processes happen before copulation occurs and are referred to as precopulatory processes. Parker suggested in 1970 [2] that sexual selection can continue after copulation as well: sperm competition and cryptic female choice [3], which are referred to as postcopulatory.

Total male reproductive success is determined by both these properties: a male's ability to acquire matings (the precopulatory processes) and his share in fertilized ova (the postcopulatory processes).

Currently two major movements that describe the potential relation between pre- and postcopulatory success can be distinguished in scientific literature: Sperm competition theory suggests that males successful in acquiring matings will lose out in sperm competition, as they have to trade-off investment in secondary sexual characteristics to investment in sperm [4]. The phenotype linked fertility hypothesis on the other hand suggests that females should prefer fertile males, and that secondary ornaments signal fertility. In this scenario males with attractive ornaments should also produce higher quality sperm.[5]. Evidence has been found for both theories.

In this review I try to compile the current knowledge on the relation between pre- and postcopulatory sexual selection. Do popular males always lose out in sperm competition? If not, when do we expect them to win? When we find a relation between both stages of sexual selection, can we indicate what process causes the relation?

In the next section I will outline the different 'forms' of sexual selection and how they affect trade-offs for males. All in all there are four processes that can result in sexual selection: male-male competition and classic female mate choice are pre-copulatory, whereas sperm competition and cryptic female choice are the postcopulatory counterparts. After the different 'forms' I detail research where the relation between pre- and postcopulatory success has been studied and what results come from them.

Male-male competition and overt female choice

Male-male competition arises from anisogamy. Abundant sperm have to compete for a small number of eggs. Males therefore have to compete to acquire matings and fertilize the eggs. This competition triggers an arms race to develop weapons and strategies to maximize competitive potential. Well known examples are beetle horns and deer antlers (e.g. [6]and [7]). Next to that (overt) female choice is an important factor for male mating success. For instance, the male firefly (*Photinus greeni)* able to elicit the highest female flash response has the highest probability of mating [8]. Another classic example is female choice for the exaggerated plumage of male peacocks. At a first glance, one might expect the most dominant or popular males to win most mating opportunities and therefore most fertilizations. Selection would be based on pre-copulatory sexual selection. However, dominant males can get sperm depleted [9].

Cost of sperm

Bateman argued that since males invest so much less in each fertilization, they should be able to produce much more offspring [10]. Females are limited by the number of eggs they can produce, whereas males are only limited by the number of matings they can get. However, Nakatsuru and Kramer [11] showed that sperm is far from cheap. Males have a limit to the amount of sperm they can produce. Nakatsuru and Kramer showed the effect of sperm depletion on number of developing eggs. When the number of spawning acts increases, males can no longer fertilize all eggs, leading to a strong reduction in developing eggs.

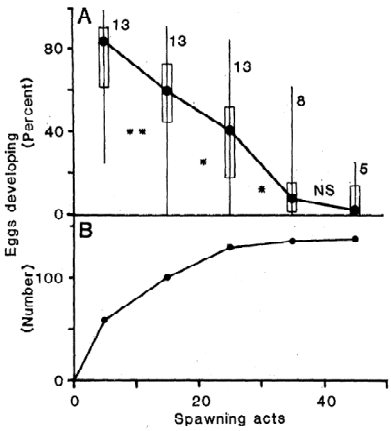

Fig. 1. The relation between total daily spawning acts and fertility (A) or estimated total number of offspring (B) in male lemon tetras. From: Nakatsuru & Kramer, 1982 [6]

Gage & Cook [12] for instance showed that when moths are limited in protein intake, they produce less sperm. Males successful in precopulatory competition can have higher costs of sperm production. In this situation, where popular males can expect to have multiple successive matings and fertilizations are expensive, males can get sperm limited and suffer lower fertilization success. Mating with a sperm limited male incurs fitness losses for the females, when not all eggs are fertilized. In many species we therefore see females mate multiply. When this happens males not only have to compete for matings with rival males, but also with rival sperm after copulation.

Sperm competition

Parker [2] was one of the first to realize that sexual selection can continue after copulation. When females mate with multiple mates (a polyandrous system), males face sperm competition. It is a widespread phenomenon across many species and it happens when sperm has to compete with sperm of rival males in the reproductive tract of the female.

There can be a trade-off between current and future matings, a crucial aspect of male strategic mating effort. Popular males that mate often have to distribute a limited amount of sperm over multiple copulations. Sperm competition game theory therefore suggests that males should invest strategically in matings [13]. Engqvist and Sauer (2002) for example, show this for scorpionflies [14]. As seen in figure 2, males offer a smaller amount of (expensive) salivary mass to low quality females in the beginning of the season, but get less discriminatory as the season progresses. This shows how males trade-off invest less in low quality matings when they expect higher quality matings to happen later in the season. When the mating season progresses, the chance of acquiring better quality matings decreases and males invest equally in high and low quality matings.

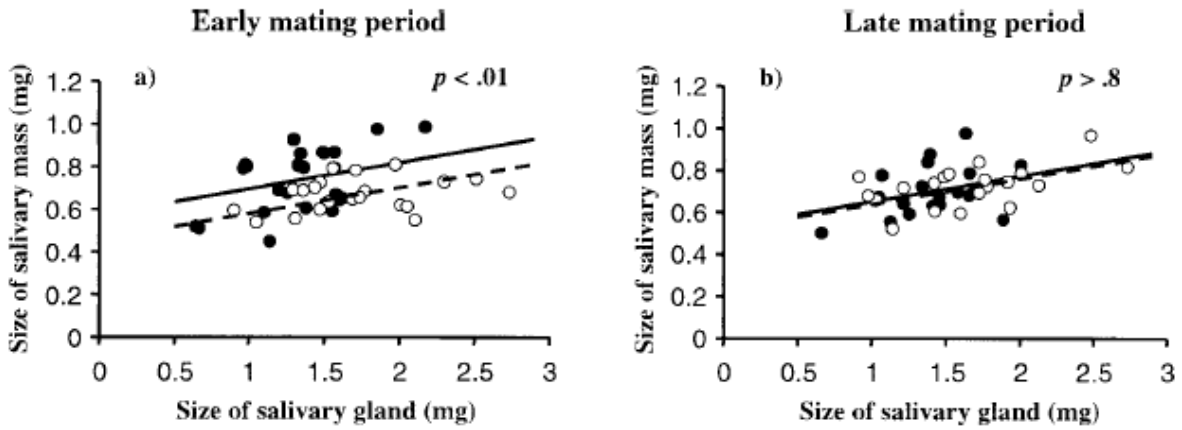

Fig.2. Comparison of relative male mating effort in matings with high- and low-quality females (a) early and (b) late in the breeding season. Solid symbols and lines depict matings with high-quality females, and open symbols and dashed lines depict matings with low-quality females. Relative size of the salivary mass is a measure for investment in a mating (From Engqvist & Sauer (2002) [13].

Sperm competition in its simplest form is usually treated as a fair raffle: the more tickets (in this case sperm) you buy, the higher your chance of winning (fertilizing the egg). In some cases the raffle is loaded, e.g. specific males' sperm has an advantage over that of other males. Since sperm is expensive, males should invest the minimal amount of sperm required to fertilize all eggs, but only if there is no sperm competition. When competing with a rival male, it pays to invest more sperm [15].

According to Parker, the amount of sperm invested should therefore depend on the (perceived) level of sperm competition but also on the information available to that male. Bluegill sunfish for instance have alternative mating tactics. Dominant males (guarders) are permanently mated with their females, whereas subordinate males (sneakers) attempt to steal fertilizations. The sneaker males usually face sperm competition, but guarders don't. Sneaker males should therefore invest more sperm to win extra fertilizations. Relative to their body weight, sneakers have the largest testes, indicating larger sperm stores [16].

Parker also models male strategies when competing with more than one male. Due to diminishing returns, males should not invest more sperm when multiple rivals are present.

Information available to a male can also change sperm investment. Female mated status increased ejaculation investment in butterflies [17]. Virgin females, with low sperm competition risk received less sperm then their mated counterparts.

Cryptic female choice

Apart from precopulatory female choice, females can influence sexual selection after the copulation: cryptic female choice. In the feral fowl, a highly promiscuous species, a large portion of copulation is coerced by the physically stronger males. When coerced by a sub-dominant male female fowl can actively eject the unwanted sperm, see Fig. 3. [18].

Similarly, female red flour beetles display cryptic choice by aiding the transport in the reproductive tract of sperm of the preferred male [19]. Males stimulate the females during copulation and fertilization success was higher for those males that displayed a higher rate of stimulation.

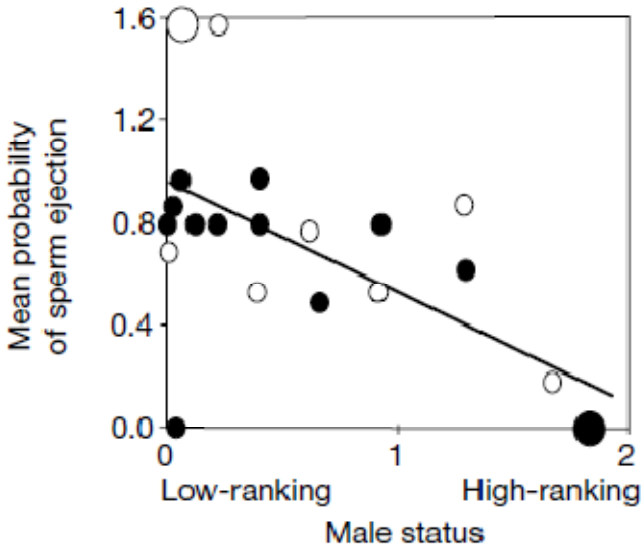

Fig.3. Relationship between mean probability of sperm ejection and male social status in the domestic fowl. From: Pizarri & Birkhead, 2000 [15]

Eberhard lists over 20 ways for a female to influence the chance for a given male to sire her offspring [20]. These strategies range from the examples given previously (sperm discarding, active sperm transport) to aiding the males in displacing sperm from previous males and even abortion of previously formed zygotes.

Trade-off between investments

As stated before there are four mechanisms that can result in sexual selection. Hunt et al. [21] argue that, even though most empirical studies have focused on only one mechanism, the combined effect can be very different. For example body size can be a trait selected for by both male-male competition and female choice, thus reinforcing sexual selection. However, in water striders, body size benefits males in competition with other males, while smaller males are more succesful in sperm competition, because they copulate longer [22]. In Hunt's diagrams the two opposing forces result in no net selection if both are equal.

Because of the potential for both pre- and postcopulatory selection, one would expect relations between investing in secondary sexual traits (pre-copulatory) and investment in sperm competition or other post-copulatory strategies. In many species this relation has been found. Preston [9] for example states that 'constraints on sperm production mean that those males that are most successful in overt contests can become ineffectual in covert sperm competition'. Gasparini et al. [23] show similar results in the green swordtail, where sperm swimming velocity determines fertilization success instead of male secondary sexual characteristics. The opposite has also been found, for instance in *Drosophila simulans* [24], where attractive males also had higher paternity success in sperm competition. Head et al. showed that female house crickets invest more in offspring sired by popular males, thereby increasing the total reproductive result as attractive male house crickets also sire attractive sons [25].

Type of trade-offs

Clearly, there is no clear cut relation between pre- and postcopulatory male reproductive success. Instead there appear to be at least three mechanisms that make up the sum of the relation. Most studies done on this subject, focus on only one of these mechanisms.

First, as stated before, it is likely that there is a trade-off between investing in pre- and postcopulatory traits, as a male's resources are limited and sperm is expensive. This can lead to a negative relation between male mating and fertilization success, when males investing more in an attractive (secondary sex) trait are forced to invest less in fertilizations. Male horned beetles of the genus *Onthophagus* for example have to trade-off investing in large horns, to win in direct competition between males, against investing in larger testes to have higher fertilization success [6]. Simmons et al. showed a similar relation for field crickets [26]. Males win matings by producing energetically expensive courtship songs. They trade investing in courtship songs for other important life-history traits such as sperm quality or immunity and vice versa.

Even though the trade-off is likely, variation in investing in pre- or postcopulatory traits may be small compared to variation in resource acquisition. In this case, dominant males have access to more resources, allowing them to invest in both pre- and postcopulatory traits.

Secondly, there is the trade-off between current and future matings as shown by Preston et al. [9] Male Soay sheep copulate very often and are well adapted to sperm competition. A larger body size leads to more copulations, but as the rutting season progresses, dominant males sire less lambs: dominant males lose out by sperm depletion. Svensson et al. show similar results for turnip moths, where males deposit a smaller ejaculate as the number of matings increases, resulting in a reduction

of fertilized eggs [27]. Male scorpionflies offer an expensive salivary secretion to a female to increase copulation duration and sperm transfer. Engqvist showed a negative correlation between male investment and female quality and suggests it is advantageous for male scorpion flies to reduce their nuptial gift size as they expect to encounter more receptive females [28].

Finally, of course, female cryptic choice plays a large role when she biases postcopulatory fertilization success based on precopulatory attractiveness. This has been shown in guppies by Evans et al. [29] and Pilastro et al. [30]. Females prefer the more colorful (orange) males that display higher rates of courtship. The amount of sperm inseminated following a solicited copulation depends largely on female perception of male quality. Eberhard lists the surprisingly long list of processes controlled by the female that must be executed if copulation is to result in fertilization success for a particular male. Other things being equal, any male better able to induce the female to carry out one of these processes more completely than she does when mating with other males stands to produce more offspring [20]. In more and more species, cryptic female choice is proven to be an important factor determining fertilizations outcome [31].

Literature review of past and current research

Although sexual selection studies have traditionally focused on variation in precopulatory sexual selection, it is now clear that variation in reproductive success can also occur after mating has begun: post-copulatory sexual selection. Our understanding of variation in male post-copulatory reproductive success still lags behind our understanding of variation in male pre-copulatory reproductive success. Without an understanding of the relation between both pre- and post-copulatory influences on male reproductive success, we cannot fully evaluate the role of sexual selection in the evolution of phenotypic traits.

As stated earlier, sperm competition theory predicts that there should be a trade-off between investment in ejaculate quality and investment in mate attraction [4], while the phenotype-linked fertility hypothesis predicts males with exaggerated secondary sexual traits should produce higher-quality ejaculates [5]. Studies supporting sperm competition theory should have a negative relation between the studies parameters, while those supporting the phenotype-linked fertility hypothesis should have a positive relation.

For this review I started with articles by Evans et al. [29], Hosken et al. [24] where males with a higher mating success also enjoy a higher fertilization success per mating. From these I studied articles cited and articles citing them, arriving at an article by Merilä & Sheldon on the phenotype-linked fertility hypothesis [32] . For the negative relations I started with articles by Engqvist [28], Danielson [22] and Preston et al. [9] as examples for the sperm competition theory. From there I assembled 25 studies where the relation between pre- and postcopulatory success was studied. Among these are studies done on insects, a spider, birds, mammals and fish.

As shown in table 1, the relations between precopulatory and fertilization success vary greatly, not only between different taxa, but also between closely related species. Soay sheep and red deer are both mammals and for red deer the size of the antlers is both an indicator of strong fighting abilities and of high quality sperm [7]. For the soay sheep however, large size wins a male more copulations, but by the end of the rutting season popular males get sperm depleted, strongly reducing their potential in sperm competition [9]. As shown in table 1, popular males do not always lose out in sperm competition as predicted by sperm competition theory, but they certainly don't always win either. There are several cases that support the phenotype-linked fertilization hypothesis. From the 25 studies, eight showed a negative relation between pre- and post copulatory processes and are considered in support of sperm competition theory. Fourteen studies showed a positive relation. These studies can be further subdivided in seven studies that support the phenotype-linked fertility hypothesis (PLF) and six that are thought to be caused by cryptic female choice (CFC)

Table 1: Studies that have investigated the relationship between pre- and postcopulatory success. The pre- and postcopulatory trait columns indicate what trait was measured as representative of success. A + in the relation column indicates a positive relation, a – indicates a negative relation. An O indicates no relation was found. CFC in the relation column indicates a positive relation caused by cryptic female choice. PLF indicates that this is considered support for the phenotype-linked fertility hypothesis. The focal trait column indicates what trait net selection is thought to work upon.

Species	Precopulatory trait	Postcopulatory trait	Relation	Focal trait	Reference
Insects					
Drosophila simulans	Copulation latency	fertilization success	**+**	Body size	[24]
Teleopsis dalmanni	Eyespan	No. of Fertile eggs	**+** PLF	Eyespan	[33]
Teleogryllus commodus	Copulation latency	Spermatophore removal time	**+**CFC	Mate guarding	[34]
Acheta domesticus	Copulation latency	Sperm quality	**-/o**	Body size	[35]
Requina verticalis	[1]	Ampulla weight		Spermatophore size	[36]
Oecanthus nigricornis	Body size	Gift size[2]	**+**	Body size/song	[37]
Gerris lacustris	Body size	Viable egg	**-**	Body size	[22]
Tribolium castaneum	Olfactory attractiveness	No. of progeny	**+** CFC	Pheromone	[18]
Onthophagus nigriventris	[3]	Testes weight	**-**	Horn size	[6]
Panorpa cognata	Copulation latency	Gift size	**-**	Nuptial gift	[28]
Utetheisa ornatrix	Body mass	No. of progeny	**+** CFC	Body size	[38]
Spiders					
Nephila edulis	Body size	Copulation duration	**+**	Body size (negative)	[39]
Birds					
Taeniopygia guttata	Song rate	Sperm chartacteristics[4]	**o**	Song/coloration	[40]
Malurus melanocephalus	Coloration brightness	Testis size	**+/-**[5] PLF	Plumage brightness	[41]
Carduelis chloris	Plumage brightness	Testis size	**+** PLF	Plumage brightness	[32]
Gallus gallus domesticus	Social dominance	Sperm number & mobility	**-**	Social dominance/ sperm mobility	[42]
Gallus gallus domesticus	Social dominance	Sperm ejections	**+**[6] CFC	Body size (social dominance)	[43]
Anas platyrhynchos	Bill color	Sperm mobility	**+** PLF	Bill color	[44]

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Mammals					
Cervus elaphus	Antler size	Sperm velocity & testis size	**+** PLF	Antlers (Body size)	[7]
Ovis aries	Body /horn size	Lambs sired	**-**	(Body) size	[9]
Fish					
Poecilia reticulata	Coloration (orange)	Paternity share	**+** CFC	Coloration	[29]
Poecilia reticulata	Coloration (orange)	Sperm velocity	**-**	Coloration	[45]
Xiphophorus helleri	Sword length	Sperm velocity & length	**o**	(Body) size	[23]
Lepomis macrochiru	[7]	Sperm number & density	**-**	Body size	[46]
Ophthalmotilapia ventralis	Pelvic fin length	Paternity share	**+** CFC	Pelvic fin length	[47]

[1]: In this research no precopulatory trait was measured. Instead, male matings success was manipulated. Simmons uses ampulla weight as an indicator for sperm volume.

[2]: Males attach the spermatophore shortly after the onset of courtship feeding. During feeding sperm is transferred to the female. Nuptial gift size is therefore and indicator of sperm transferred.

[3]: In this research no precopulatory trait was measured. Males were manipulated to not grow a horn. The resulting growth of the testes was used as a measure for postcopulatory success.

[4]: Specifically, number of sperm, percentage of live sperm, absolute number of sperm, sperm length or sperm swimming velocity.

[5]: A positive relation was found between the pre- and postcopulatory trait when comparing the different types of males (black-red/brown/brown auxiliaries). Within breeding back-red males there was a slightly negative relation between red intensity and sperm characteristics.

[6]: This study by Pizarri & Birkhead shows an opposite trend for the relation, but this is thought to be caused by female sperm ejection (CFC), biasing the outcome of fertility success towards the attractive male.

[7]:No specific precopulatory trait was measured, but the difference between several alternative mating strategies is well known for *Lepomis macrochiru.* Guarding and sneaking males were compared .

Case studies

In the following I will describe some of the studies that have been done on the relation between pre- and postcopulatory success.

Feral fowl

Feral fowl are highly promiscuous birds with a strong social hierarchy. Sperm competition is typically intense and dominant males inject more sperm per individual female. They actively disrupt matings initiated by their subordinates. However, sperm mobility, which plays an important role in sperm competition, is lower for dominant males. Froman et al. showed for domestic fowl (*Gallus gallus domesticus*) that there is a negative relation between mating success and sperm mobility [42], indicating the kind of relation sperm competition theory would predict, however, Pizarri et al. showed that the females actively eject the sperm of subdominant males [43]. They strongly bias fertility towards the dominant males. Without looking at sperm characteristics, one would deduce a positive relation between pre- and postcopulatory success. Here, cryptic female choice masks the underlying mechanisms of sperm competition for the feral fowl. If a female is content with the social status of the fertilizing male, she may not eject and sperm characteristics will play a large part in determining fertility outcome. When she is not, she will eject the subordinate male's sperm even though the sperm itself may be of higher quality than that of the dominant male.

Flour beetles

Beetles from the *Tribolium* genus are major pests around the world. Males attract females with a pheromone. There is no precopulatory courtship before mating and neither males nor females are aggressive to their own or the opposite sex. Males do stimulate the female during copulation by rubbing the lateral edges of the females' elytra with their tarsi during copulation [19]. Lewis & Austad [18] showed that there is a positive relation between sperm precedence and male olfactory attractiveness. They were not able to determine what the underlying process was that resulted in the relation between male attractiveness and sperm precedence. They suggest that attractive males may have higher copulation rates, higher sperm transfer or better displacement of previously stored sperm. Later research by Edvardsson & Arnqvist presents evidence of cryptic female choice [19], where females influence fertility success on their perception of male stimuli, rather than the actual male performance.

Water striders

Water striders from the genus *Gerris* are often mentioned as a classic example of an antagonistic relation between pre- and postcopulatory success. Larger *Gerris lacustris* males have an advantage in male-male competition and win most copulations. However, copulation duration is significantly longer for smaller males and they have a higher fertilization success [22]. In a previous article Arnqvist & Danielson already showed that copulation duration was correlated with ejaculation size and fertilization success [48]. The total affect was that there seemed to be no relation between body size and fertilizations.

Guppies

Evans et al. state that guppies (*Poecilia reticulata*) with a higher amount of orange coloration are preferred by females and also have a higher quality ejaculate [29]. Table 1 shows a positive relation between pre- and postcopulatory success. However, in a more recent article Evans shows for guppies that ”Males that predominantly performed sneak matings were less ornamented but had faster swimming sperm than those that predominantly used courtship” [45], which shows that within one species, both positive and negative relations can be found. Evans indicates that cryptic female choice may have a strong influence on the relation as was shown by Pilastro et al. [30]. They found that more colorful males transfer more sperm to the female than the less attractive male. This only occurs when the copulation is female-solicited but does not in forced copulations. This strongly suggests that females play a role in accepting more sperm from preferred males. Female choice appears to play a major part in the relation between pre- and postcopulatory sexual selection. Evans also suggests that the reason for varying results may have to do with the conditions at catch locations.

Conclusions

None of the parameters studied seems to be a determining factor in the relation between pre- and postcopulatory success, as for almost every relation an example can be found. Support for both the phenotype-linked fertility hypothesis and for sperm competition theory is present in these studies, as we see both positive and negative relations between pre- and postcopulatory success.

However, many species where cryptic female choice strongly influences outcome of fertilization success, show a positive relation with mating success. Unfortunately, cryptic female choice is still hard to detect, and it may be missed completely when not specifically incorporated in the experimental design. Still, in six studies out of the 25 used, cryptic female choice is thought to be the cause of the positive relation between pre– and postcopulatory success. Seven studies support the phenotype-linked fertility hypothesis. Clearly popular males do not always lose out in sperm competition.

According to sperm competition theory subordinate males should invest more in sperm characteristics. However, when females actively select the dominant male’s sperm, better sperm characteristics will no longer gain many fertilizations and investing in sperm may pay off less expected. In this way, cryptic female choice also masks the (potential) outcome of sperm competition. Even though cryptic female choice may masks sperm competition, I still found eight studies that support sperm competition theory.

As seen in several of the presented case studies, cryptic female choice can be a determining factor for fertilization outcome. In some cases however, e.g. guppies and flour beetles, cryptic female choice was only later found to be an important factor, raising the question in how many other species it plays a far greater role then first assumed.

Future research

Many of the studies done on the relation between pre- and postcopulatory success in the past have been based on phenotypic relations. However, conclusions drawn from genotypic or experimental studies such as those by Evans [45][29] respectively, tend to be more substantiated. Most studies also do not measure actual pre- or postcopulatory success, but traits as a proxy for it.

In the recent study on guppies by Evans [45], a striking genetic covariation was found between two traits characterizing distinctive mating tactics (sneaking and guarding). Underlying the differences between the two mating tactics is an opposing genetic correlation between mating tactic and sperm swimming velocity. This suggests that sneaker males may compensate heavily in this part of sperm quality, which could be adaptive as sneaker males face sperm competition more often than their guarding counterparts.

Since no clear condition determining the direction of the relation between pre- and postcopulatory success has been found, future research should try to determine what systems of pre- and postcopulatory selection are actually present for a given species and then determine the direction of the individual effects. This review has only been a preliminary study and perhaps a meta-analysis study would provide more insight and a stronger statistical background for future studies. As indicated previously, these should also incorporate male reproductive qualities such as sperm quality and viability, rather than 'just' testis size.

Since most studies have been performed under laboratory conditions, the question also remains how mating and fertilization success are affected under natural conditions.

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