Male–Male Strategies

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Synonyms

Male intra-sexual competition; Male–male contest

Definition

Direct or indirect competitive interactions over access to females, their gametes or resources to attract females.

Introduction

Male–male competition is, along with female choice, one of two main mechanisms of sexual selection (Darwin 1871; Andersson 1994). However, male–male competition has received much less theoretical end empirical interest than female mate choice, perhaps because it is conceptually more straightforward and easier to comprehend (Parker 2014). Competition among males that increases their fitness (reproductive success) is performed to increase an individual's access to females or their eggs. It is manifested before copulation (precopulatory male–male competition), between copulation and fertilization (postcopulatory male–male competition), or after fertilization. While it has long been believed that male–male competition and female choice are mutually reinforcing, research in recent decades suggests that it is often not the case.

Forms of Male-Male Competition

Traits that undergo sexual selection are sometimes divided between armaments (weapons used in male–male contests and signals of male fighting ability – status badges) and ornaments (signaling traits used by females in mate choice decisions). However, many sexually selected traits have a dual function and are clearly affected by both forms of sexual selection (Andersson 1994). It appears that many sexually selected traits may have initially undergone selection in the context of male–male contests and then have subsequently been adopted by females as a signal of male quality. This is because male weapons are honest "signals" of male fighting ability since they are routinely put to trial during male contests. Such traits can then be reinforced through female choice, with both intra- and intersexual selection driving the evolution of the trait. The reverse process can also be true. Thus, traits traditionally viewed as ornaments that have been selected through female choice may be used by males in aggressive displays, including such traits as bright

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coloration and elaborated body appendages (Berglund et al. 1996).

The two mechanisms of sexual selection need not always be mutually reinforcing. Recent research documented that male–male competition and female choice can act in concert, independent of each other or in opposition. A common illustration of concerted evolution is male coloration. For example, red nuptial coloration in the male three-spined stickleback fish (*Gasterosteus aculeatus*) appears to be selected through male–male competition and female choice. Red coloration is a characteristic of dominant individuals that win fights, and females prefer to mate with redder males. Additionally, variation in redness increases under male–male competition and this may facilitate female choice (Candolin 2000). In contrast, conflicting selection pressures are involved in the production of social pheromones by males of the speckled cockroach (*Nauphoeta cinerea*), with differences in male–male competition and female attraction signaling optima. Hence, male cockroaches with a pheromone level that enables them to gain a dominant position are not preferred by females (Moore and Moore 1999).

The form of male–male competition varies widely among taxa and mating system. The most obvious is male–male interference competition. It is manifested as a physical contest (direct fight), signaling contest (ritualized fight in which an individual matches themselves against an opponent via the expression or display of signal traits), or a combination of both. Most direct fights ensue when a signaling contest does not lead to a clear winner. For example, male African annual fishes (genus *Nothobranchius*) compete for access to females by rapidly approaching an opponent and performing lateral displays that involves spreading the unpaired fins. Males are brightly colored and coloration and body size usually determine the winner of the contest at the signaling stage. Lateral displays expose bright coloration and include tail beating, which directs a stream of water toward the opponent, and mutual threats performed with prominently displayed branchiostegal membranes (Passos et al. 2015). When the difference between males is small and the contest is not resolved with these displays, the contest escalates, with attempts to bite the opponent's fins and flanks. If the contest is still not resolved, males may lock jaws, sometimes remaining in this position for several minutes (Polačik and Reichard 2009) and with potentially fatal consequences for one of the combatants.

Larger body size or body mass is perhaps the most obvious and probably most common trait that is selected through male–male interference competition. Body size is a good predictor of overall physical strength and performance (McCullough and Simmons 2016). In staged contests, larger males enjoy a substantial advantage, and body size/mass is often the clearest predictor of the outcome of a contest, though it is often correlated with other traits that may contribute to success.

Many direct male–male contests rely on the use of weaponry. Weapons such as horns, antlers, spurs, enlarged jaws and teeth, and other body structures and appendages are used to directly outcompete an opponent. At the same time, weapons often serve as a signal of fighting ability (badge of status) and are used during the signaling stage of a contest. Only when any of the rivals retreats from the signaling contest, a physical interference follows. For example, male red deer fight over possession of females with rivals wrestling with their antlers and attempting to push each other away. Fights in other species may involve pushing, pulling, or dislodging an opponent. The size of weaponry is often associated with body size and both may be indicators of overall male condition (Andersson 1994). Fighting is costly and potentially lethal, and many contests are resolved at the signaling stage despite males possessing formidable weapons. In the case of red deer, rival males walk in parallel and assess the opponent's antlers and body size. It is only when neither male backs down from a contest that a fight with antlers occurs, potentially with serious injuries.

Other traits selected through male–male competition have a primarily signaling function. While they vary more widely than traits used in direct contests, they supposedly also indicate overall individual performance. Acoustic and visual displays are the best researched signaling traits, though chemical traits appear more common that generally assumed, and other modalities, such as electrical discharges in electric knife fishes (Gymnotiformes), are known to serve for signaling individual characteristics. The function of most signals in the context of male–male competition is intimidation. Hence, many such traits tend to be exaggerated. Yet, for a signal to be evolutionary stable, it must carry honest information about the status of the signaler: his physical strength, body size, condition or prior residence, and ownership of a breeding resource. For example, some aspects of the vocal signals of male red deer (minimum formant frequencies) are constrained by individual anatomical features, directly associated with male body size. Hence, it provides receivers with accurate information by which they can measure a rival's competitive ability (Reby and McComb 2003). Signaling male fighting ability, however, may also include subtler signals. Cuticles of most terrestrial arthropods contain cuticular hydrocarbons, semiochemicals with extensive within-species variation (Ingleby 2015). Cuticular hydrocarbons convey complex information about an individual, including information on male competitive ability. Indeed the composition of these chemical signals can have a profound influence on the outcome of male–male competition (Lane et al. 2016).

The expression of weapons and signal traits may be constrained by direct and indirect costs. First, direct costs arise from increased risk of damage or mortality. In the Asian rhinoceros beetle (*Trypoxylus dichotomus*), the risk of breakage is highest for the longest horns, and overly large horns may, therefore, constrain selection on the continued exaggeration of horn length driven by male–male competition by setting a mechanical limit on maximum horn size (McCullough 2014). Second, exaggerated signals of male–male competition ability may incur a cost of increased predation by reducing escape ability or increasing detectability by predators. In *T. dichotomus*, males with larger horns suffer significantly higher predation rates from avian and mammalian predators (Kojima et al. 2014). Likewise, many conspicuous signals of different modalities carry considerable survival costs by attracting enemies exploiting signal transmission such predators or parasitoids (Zuk and Kolluru 1998). Third, there are indirect costs that include energy depletion (allocation of resources to the trait expression traded off against its use in somatic maintenance, immunocompetence, or sperm production). Fourth, increased expression of factors within particular hormonal pathways that are functionally essential for the expression of the trait or signal can be costly for other phenotypic functions (Blagosklonny 2008). Hence, optimal trait expression to maximize lifetime fitness (reproductive success and survival) is often much lower than the maximum potential expression of the trait.

Lekking males compete for access to females via displays, aggregating in large numbers in specific spots visited by females. Lekking is relatively widespread among insect, fish, and bird species, but also recorded in other taxa such as mammals. Male–male competition on leks is severe, leading to high variance of male mating success. It is generally assumed that reproductive success of males in leks depends on female choice, but competition to obtain a display site on the lek and for the best positions within the lek also contributes to male success (DuVal and Kempenaers 2008). For example, in black grouse (*Lyrurus tetrix*), lekking males fight frequently and successful males experience high success (Hämäläinen et al. 2012).

Endurance is an important, but often overlooked, aspect of male–male competition and describes the temporal component of male–male competition. To be successful, dominant males must maintain their high rank across a time span of days, weeks, months, or even years. The length of the breeding season varies widely among taxa, environments, and geographic regions. Highly seasonal environments often have a breeding season confined to a relatively short period when most fertilizations occur. In other taxa and less seasonal regions and environments, fertilizations may occur throughout the year. Male–male interference competition is typically highest when female receptivity is temporally clustered within a short period, and the most successful male may secure a large number of fertilizations. However, this scenario is also prone to the evolution of alternative mating behaviors when some males circumvent direct competition with the highest-ranked males and undermine their ability to control access to females. Dominant males typically cannot monopolize all females when they are unable to control their spatial distribution (Reichard et al. 2005).

Harems are examples of mating systems with low temporal clustering of female receptivity combined with an elevated importance of male–male competition for reproductive success. Possession of a harem is physiologically demanding and potentially costly to the territory holder through frequent contests with rival males. Harem holders (and alpha males in social groups with subordinate males) stage many contests from rivals for their position, and there may be substantial turnover of individual males in the possession of the top rank. Defense of harems increases immediate reproductive success (the number of progeny) but has longer-term consequences for survival and may lead to rapid reproductive senescence (Lemaître et al. 2014).

Mate guarding is another mechanism of male–male competition. In some taxa, males restrain female association with other males to ensure paternity of their offspring is not compromised. Males may simply remain in close proximity to a female and attempt to repel any rivals. Sometimes, mate guarding involves prolonged or repeated mounting of a female, despite no further sperm transfer (Baxter et al. 2015). For example, in the bug *Lygaeus equestris*, pairs can remain in copula for over 15 h and regularly move and feed in this position, with males walking backward or being dragged along. Still, only a period of 1–2 h is needed for successful insemination (Alcock 1994), and the remaining time spent on copulation is probably a form of mate guarding that reduces the likelihood of female remating.

Scramble competition for access to females is a frequent, though relatively rarely examined, form of male–male competition. Successful searches for available females may considerably increase male fitness and imposes selection on superior sensory ability and locomotor organs. Hence, the most mobile males in a population can mate with more females, outcompeting less mobile males. In red-spotted newts (*Notophthalmus viridescens*), tail size is associated with locomotory capacity, and males with the largest tails have the greatest mating success, possibly due to higher ability to capture females (Able 1999). In many arthropods, males have larger eyes, antennae, and other sensory organs than females which have presumably evolved as an adaptation to locate mates, indirectly pointing toward the importance of scramble male–male competition. A temporal component is intrinsically important in scramble competition, and in many anurans (toads and frogs), males intercept females already on their way to a breeding pond and clasp them in amplexus to secure early access to females.

Male–male competition for reproductive success goes beyond direct interference, even at the premating stage. In many mating systems, some males can circumvent direct male–male competition by alternative mating behaviors (AMB). AMB are behavioral adaptations that enable males to compete with their rivals (and sometimes outcompete them) through the use of behavior that is different from the “typical” male–male interference competition. The most common examples are sneak copulations (in internally fertilizing species) or sneak fertilizations (in species with external fertilization). When sneaking, a male deceives his rival and his access to a female is typically cryptic, at least until copulation/gamete release. Sneak male deception takes the form of camouflage of their external appearance (female-like appearance), hiding in a structured environment, or their combination. For example, in bluegill sunfish (*Lepomis macrochirus*), males may develop either into a territorial male that sexually matures at the age of 7 years and invests in territory defense, nest construction, female courtship, and parental care. Alternatively, males may mature when only 2 years old as a sneaker and compete with parental males (and other sneakers) for fertilization. Young sneaker males “streak” into the nest of a territorial male during female egg laying and may fertilize a subset of eggs before being chased away by the territorial male. Older sneaker males mimic female behavior and coloration and deceive territorial males into identifying them as a second female in the nest (Neff and Gross 2001).

A traditional view of male–male competition considers sneakers to be of low quality, incapable of winning contests and therefore making “the best of a bad job” to gain any reproductive success. However, there is now good evidence from several mating systems to suggest that females sometimes prefer to mate with sneaker males. By preferring sneaker males, females avoid limitation of the expression of their mating preferences by resource monopolization by males wining contests over breeding resources. This leads to an incongruence between male–male competition and female choice where female choice is affecting the final outcome of male–male competition (Reichard et al. 2007). In European bitterling fish (*Rhodeus amarus*), males defend territories with living freshwater mussels into which females deposit their eggs. A limited number of dominant males may control most oviposition sites, forcing females to lay the eggs in their territories, despite a mate choice preference for other males who have not acquired their own territory. Bitterling females sometimes actively engage in a conspicuous behavior that attracts sneaking males and increase the time window for the eggs to be fertilized (Smith and Reichard 2005), modifying the outcome of male–male competition when males are of unequal competitive ability but when resource defense is crucial for breeding.

Alternative mating behavior may have a genetic basis, depending on the developmental stage or age, or may be entirely flexible and context dependent. In ruff (*Philomachus pugnax*), satellite males tend to steal copulations from dominant males and “faeder” males mimic females. Both alternative male forms differ conspicuously in behavior and coloration from dominant males and the forms are genetically determined. Each alternative male morph possesses a unique, non-recombining chromosomal inversion (Küpper et al. 2016). In many fish (and other) mating systems with breeding resource defense (i.e., nesting sites), males compete with other males by sneaking fertilizations when young and start to compete for breeding resources when they grow older and larger (Wootton and Smith 2015). Yet, in some of these cases, especially in short-living species, differences in body size among males are relatively small, and each male is capable of playing the role of territorial and sneak male, with switches between the tactics within seconds. In the European bitterling, individual males frequently switch between territorial and sneaking behavior, often in a time span of minutes. They attract females to their own breeding territory and, at the same time, attempt to sneak-fertilize the eggs of females laid in the territories of neighboring males (Reichard et al. 2004). In general, the success of alternative mating behavior is dependent on demography (ratio between males and females, population density, male morphs density), environmental conditions (habitat complexity and ability to hide), and the female response to alternative mating behavior (Reichard et al. 2007).

Finally, male–male competition may extend beyond fertilization. In the bluegill sunfish, territorial males care for the offspring for several days. Parental males in this species are often cuckolded by sneakers. However, they have the capacity to assess their paternity level using the visual presence of parasitic sneaker males during spawning and, in addition, using olfactory cues released from the offspring after the eggs hatched. Parental males dynamically adjust their parental care and cannibalize those clutches for which their paternity share is low (Neff 2003). Another example of male–male competition after fertilization can be found in the three-spined stickleback. Male stickleback signaling effort (red body coloration) actually increases during the post-mating period when males fully engage in parental care and no new partners or fertilizations can be obtained. Parental care is exclusively paternal in this species, and male bright coloration may indicate his ability and motivation to defend the nest and offspring against competing intruders that might steal or cannibalize the nest (Candolin and Tukiainen 2015).

The relative importance of male–male competition for reproductive success arises from variation in resource investment, parental care, fertilization mode, and other parameters. In mating systems with no male contribution to postfertilization reproductive effort, the largest or strongest males secure access to a large number of females in harems. In contrast, when high parental effort is needed for raising the offspring successfully, stable pairs are formed, and the importance of male–male competition for fertilization is low or restricted to postcopulatory processes. In mating systems with pair bonds, males may compete for the access to females with the highest reproductive value (i.e., fertility), though pairing in such systems is generally relatively unrestricted by mate coercion and dominated by female or mutual mate choice rather than direct male–male competition.

Conclusion

Male–male competition is a powerful mechanism of sexual selection that takes many different forms but is selected to secure access either directly to females (or their gametes) or to breeding resources critical for reproduction. It may be independent of female choice and postcopulatory processes, but often acts either in concert or in opposition to female choice. Interference competition involves direct physical or signaling contests between males, with development of weapons and expression of signals being constrained by direct and indirect costs associated with their possession. Other forms of male–male competition include scramble competition for access to females, lekking, mate guarding, and alternative mating behaviors (e.g., sneak copulations or mimicking females) that circumvent direct contest with stronger males. Endurance is an important, but frequently neglected, aspect of male–male competition and recognizes that male success integrates over his lifetime. Male–male competition can extend beyond fertilization, and males may adjust the level of their parental care to perceived paternity.

Cross-References

- ▶ Copulatory Intrasexual Competition
- ▶ Direct Male to Male Battles for Females
- ▶ Lekking
- ▶ Multiple Matings
- ▶ Precopulatory Intrasexual Competition
- ▶ Sneak Copulation
- ▶ Sperm Competition
- ▶ Vocal Competition

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