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Male reproductive suppression: not a social affair

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Abstract

In the animal kingdom there are countless strategies via which males optimize their reproductive success when faced with male–male competition. These male strategies typically fall into two main categories: pre- and post-copulatory competition. Within these 2 categories, a set of behaviors, referred to as reproductive suppression, is known to cause inhibition of reproductive physiology and/or reproductive behavior in an otherwise fertile individual. What becomes evident when considering examples of reproductive suppression is that these strategies conventionally encompass reproductive interference strategies that occur between members of a hierarchical social group. However, mechanisms aimed at impairing a competitor's reproductive output are also present in non-social animals. Yet, current thinking emphasizes the importance of sociality as the primary driving force of reproductive suppression. Therefore, the question arises as to whether there is an actual difference between reproductive suppression strategies in social animals and equivalent pre-copulatory competition strategies in non-social animals. In this perspective paper we explore a broad taxonomic range of species whose individuals do not repeatedly interact with the same individuals in networks and yet, depress the fitness of rivals. Examples like alteration of male reproductive physiology, female mimicry, rival spermatophore destruction, and cementing the rival's genital region in non-social animals, highlight that male pre-copulatory reproductive suppression and male pre-copulatory competition overlap. Finally, we highlight that a distinction between male reproductive interference in animals with and without a social hierarchy might obscure important similarities and does not help to elucidate why different proximate mechanisms evolved. We therefore emphasize that male reproductive suppression need not be restricted to social animals.

Key words: indirect sperm transfer, offensive strategies, male pre-copulatory competition, male reproductive suppression, reproductive strategies.

Intrasexual Competition

Within the animal kingdom there are countless ways in which individuals can compete for access to potential mates (Andersson 1994; Eens and Pinxten 2000; Arnqvist and Rowe 2005). These pre-copulatory strategies evolved to maximize the reproductive fitness of an individual. Pre-copulatory competition traditionally encompasses display via ornaments, acoustic stimuli, mate guarding, and contests over mates (Andersson 1994; Andersson and Iwasa 1996). Sexual competition can continue in several forms after mating (i.e.,

post-copulatory). One well-known form is sperm competition, which takes place after fertilization and refers to the competition between male ejaculates to fertilize the ova of a particular female (Birkhead and Møller 1998; Pizzari and Parker 2009). In order to prevent sperm competition, males can, for instance, guard females after mating (Birkhead and Møller 1998; Simmons 2001). In some species, such post-copulatory competition can continue well beyond fertilization through infanticide, that is the killing of conspecific young/eggs (Andersson and Iwasa 1996).

Interestingly, within both pre- and post-copulatory competition mechanisms, a set of behaviors, referred to as reproductive suppression is known to intensify competition for reproduction between same-sex individuals (Clutton-Brock and Huchard 2013). Pre-copulatory reproductive suppression is the ability of an individual to enhance its own reproductive success by winning physical contests, evicting rivals, or suppressing their reproductive function, often achieved via physiological stress (Eens and Pinxten 2000; Young 2009; Clutton-Brock and Huchard 2013). While in species with conventional sex roles this form of competition is greater among males than among females, in sex-role reversed species the opposite is true (Eens and Pinxten 2000). Yet, selection on competitive displays (i.e., colors, ornaments, weapons) due to intrasexual competition is usually stronger on males than on females (Bateman 1948; Dewsbury 2005; Parker and Birkhead 2013).

The focus of this perspective paper lies on competitive strategies of males. Specifically, in the following, we first orient the reader toward a better understanding of the proximate mechanisms of male pre-copulatory reproductive suppression and end by suggesting a broadening of the current view of reproductive suppression.

Male Reproductive Suppression and Levels of Sociality

Pre-copulatory reproductive suppression involving interactions between same-sex adults has been documented in a broad range of taxa. For males living in multi-male social groups, a dominance hierarchy often regulates access to mates. Several winner–loser studies indicate that such dominance-related interactions are mediated by endocrine responses. Males of high rank usually achieve the highest mating success by inducing low testosterone levels in subordinate individuals, as found in several taxa (see e.g., rats: Monder et al. 1994; jays: Vleck and Brown 1999; bonobos: Marshall and Hohmann 2005; cichlid fishes: Maruska and Fernald 2010). Such a reversible, induced infertility is often settled by aggressive interactions that might suppress the gametic development of the subordinates (Maswanganye et al. 1999). As a result some males, although able to reproduce, remain in an adolescent-like state, as shown in male orangutans (Emery Thompson et al. 2012). Another way in which reproductive suppression can take place is through resource monopolization. In some cichlid fishes, for example, dominant males suppress the reproductive success of subordinates by denying them access to females, thus monopolizing females (Ochi 1993). Similarly, monopolization of a critical resource for females (e.g., food or brooding site) by dominants can determine a temporary suppression of reproduction, as demonstrated in the burying beetle (Eggert et al. 2008).

What becomes immediately evident when considering these examples is that reproductive suppression strategies conventionally encompass reproductive interference strategies that occur between members of a complex social system (Young 2009; Clutton-Brock and Huchard 2013). Interestingly, reproductive suppression strategies in simple social systems are never explicitly defined as such in behavioral papers. Yet, mechanisms aimed at impairing a competitor's reproductive output are not exclusive to complex social systems. Therefore, with a selection of taxa displaying a very high diversity of male interference strategies, we here point out that also animals with simple social systems display an arsenal of tactics aimed at suppressing the reproductive fitness of rivals. However, these are generally not referred as reproductive suppression strategies, but rather as pre-copulatory competition strategies. So the legitimate question to be asked is whether there is an actual difference

between such strategies in complex and simple social systems, or whether these different labels are simply accepted by convention.

At this point we feel some definition regarding interactions among conspecifics is needed. Following Freeberg et al. (2012), a complex social system refers to a group of individuals with different social roles, interacting frequently and in many different contexts. There are several levels of social complexity, spanning from subsocial, with no reproductive division of labor to advanced eusocial, involving distinct reproductive and non-reproductive castes (Rehan and Toth 2015). Simple social systems are those in which animals rarely interact, and when they do, interactions tend to be for mating and are almost never repeated with the same individual (Freeberg et al. 2012).

Although we are fully aware that there is often graded variation in the way in which groups of individuals interact, for the purpose of our paper it is necessary (and sufficient) to simplify the categorization of social interactions considerably. Therefore, from this point on, we adopt *social animals* and *non-social animals* to indicate, respectively, complex and simple social systems.

In this perspective paper, we explore a broad range of taxa without pronounced social systems, and illustrate that males of these taxa depress the fitness of rivals. We finally emphasize that evolutionary explanations for understanding variation across species of male reproductive suppression require an integrated approach that considers social and non-social animals within the same framework.

Mechanisms of Male Reproductive Suppression

Conventionally, pre-copulatory mechanisms of male reproductive suppression, defined as inhibition or impairment of reproduction in an otherwise fertile individual, can take place via social interactions (e.g., competitive displays, aggression, social control) and resource monopolization (e.g., monopolization of females, food, or territories). Based on the actual loss of reproductive fitness in the competitors, these proximate mechanisms can be defined as defensive and offensive mechanisms. After briefly defining defensive mechanisms we will subsequently focus on offensive mechanisms as these are the reproductive suppression strategies that we want to draw attention to.

Defensive mechanisms

Defensive mechanisms make a male unable to reproduce as a result of a lack of opportunity. Resource monopolization, such as pre-copulatory mate guarding (Stockley 1997; Jormalainen 1998), implies a contact with at least 1 female but it does not necessarily involve direct interaction with a rival male. For instance, males of several crustacean species maximize their reproductive fitness by ensuring their presence during female receptivity (Jormalainen 1998). Although in some insect and crustacean species, males fight over burrows and branches (Shuker and Simmons 2014), males who lack the resources to engage in battles may adopt alternative strategies to get access to females (Shuker and Simmons 2014). Therefore, a male's loss of reproductive fitness that derives from defendable resources (i.e., females, nest, food) should be seen as lack of opportunity, rather than intentional obstruction. What also goes beyond the focus of our paper are the many examples of post-copulatory monopolization of females through male mating plugs, extra claspers, and forced copulations (see e.g., Contreras-Garduño et al. 2006: scorpions; Uhl et al. 2010: spiders; Friesen et al. 2015: snakes). Similarly to what was explained above for the pre-copulatory mate guarding, these post-copulatory paternity assurance strategies determine a lack of opportunity for the subsequent male, rather than an impairment of the reproductive ability of the competitor. Moreover, copulatory plugs can entail

significant energy costs for mating males, as shown in red-sided garter snakes, where a single copulatory plug constitutes 5–18% of daily energy expenditure (Friesen et al. 2015). This situation is even more extreme in some spider species, where males effectively plug the female genitalia with broken male palps, leading to male sterility in some cases (Li et al. 2012). What is evident from these examples is that post-copulatory female monopolization by a male may trade-off against a subsequent mate acquisition by that male.

Offensive mechanism

Unlike defensive mechanisms, offensive mechanisms make the rival incapable of reproducing (even when females are available) or impair the rival's capacity to compete for females. This distinction highlights that, when examining the way a male depresses the fitness of a rival, the offensive and defensive mechanisms should be weighed differently. Therefore, although we do not wish to downplay the importance of

the very diversity of mechanisms of male reproductive interference, for this perspective paper we will focus on mechanisms that impair the reproductive ability of the competitor via offensive mechanisms only.

Animals that depress the fitness of a rival through more or less harmful behaviors, without compromising their own mate acquisition, belong to this category. We found a wide range of examples of offensive strategies through which male reproductive suppression occurs in non-social organisms. As explained in the following, we can divide these examples into 2 major camps, based on whether they involve a close interaction between the males or not: same-sex conspecific interaction and sperm removal (Table 1).

Same-sex conspecific interaction

We classify same-sex conspecific interaction as interactions between members of the same sex in which one male induces the suppression of the reproductive function of the other. Reproductive suppression

Table 1. Variety of mechanisms through which male reproduction suppression occurs in non-social organisms. The mechanisms are divided up into two main categories: same-sex conspecific interaction and sperm removal. For each mechanism the taxonomic unit and the reference are reported

Category	Mechanisms	Taxonomic unit	References
Same-sex conspecific interaction	Kill-off rival males	*Steinernema* sp. (Rhabditida)	Zenner et al. 2014
	Possible alteration of male ejaculate by homosexual traumatic insemination	*Xylocoris maculipennis* (Hemiptera) *Tribolium castaneum* (Coleoptera)	Carayon 1974 Levan et al. 2009
	Alteration of male reproductive physiology of the recipient by SFPs received from male-acting individual (sperm donor)	*Lymnaea stagnalis* (Gastropoda)	Nakadera et al. 2014
	Homosexual mating resulting in cementing the victim's male genital	*Moniliformis dubius* (Moniliformida)	Abele and Gilchrist 1977
	"Pinching" of the tail region of other males and occasionally inserting spicules into the anus or through the body wall	*Oncholaimus oxyuris* (Enoplida)	Coomans et al. 1988
	Attempted mating via the excretory pore, with certain strains leaving a copulatory plug there	*Caenorhabditis elegans* (Rhabditida)	Gems and Riddle 2000
	Males mount other males to deny them the opportunity to mate	*Hydromyza livens* (Diptera)	Preston-Mafham 2006
	Net spermatophore production lower in competitive scenario (possible inhibition of reproduction)	*Orchesella cincta* (Collembola)	Zizzari et al. 2013
Sperm removal[a]	Deposition of own spermatophores upon rival spermatophores, making the latter inaccessible to the female	*Ambystoma maculatum* (Urodela)	Arnold 1976
	Homosexual courtship (female mimicry), consisting in a male inducing spermatophore deposition of the rival male	*Plethodon jordani, P. ouachitae, P. yonahlossee, Ensatina* sp. (Urodela)	Arnold 1976
	Eating the spermatophores of other males and subsequently depositing fresh spermatophores on that site	*Polyxenus lagurus* (Diplopoda)	Schaller 1971
	Active destruction of spermatophores and funnel spun by another male	*Serianus* sp. (Pseudoscorpionida)	Schaller 1971
	Destruction of a rival spermatophores by eating them	*Orchesella cincta* (Collembola)	Stam et al. 2002
	Destruction of rival spermatophores by pushing them into the substratum	*Bdella longicornis, B. Iconica* (Prostigmata)	Alberti 1974

[a]This category only includes sperm removal from the environment. It does not include sperm removal from the storage organs of mated females, as the latter implies a close interaction with the mating partner.

through same-sex conspecific interaction shows interesting parallels between non-social and social animals. In sequential hermaphrodites males may actively try to prevent the females from changing sex (e.g., Robertson 1972; Collin et al. 2005; Munday et al. 2006). In several fish species this social control of sex change (Warner and Swearer 1991) is indeed a form of male–male competition that results in the depression of fitness of the male function.

That the male function can be the target of an offensive mechanism performed by the sperm donor (male-acting individual) has also been shown in the great pond snail *Lymnaea stagnalis*, a simultaneous hermaphrodite (i.e., not a sequential sex changer). A recent study has revealed that receipt of seminal fluid proteins (SFPs) affects the male function of the recipient, as 2 identified SFPs cause a snail to transfer half the amount of sperm to its next partner. Thus, these hermaphrodites directly influence their partner's male investment, reducing the individual's male reproductive success (Nakadera et al. 2014). Strikingly, unlike sequential hermaphrodites, *L. stagnalis* is a non-social hermaphrodite, which may explain why this species uses a biochemical route to suppress the male function rather than the aggression used in the fish example.

A male might also be induced to temporarily suppress its reproduction based on environmental cues (i.e., the presence of a rival). Examples of such suppression in social animals are represented by the cichlid fishes *Neolamprologus pulcher* and *Astatotilapia burtoni*. In *N. pulcher* a conflict with a dominant male causes subordinate males to increase their submissive behavior as a mechanism to relieve stress from aggressive interactions with the dominant one. As a consequence the subordinate's sexual maturation is delayed (Fitzpatrick et al. 2006). Similarly, male *A. burtoni* avoid aggressive contests by inferring their own relative dominance rank and those of others (Grosenick et al. 2007; Maruska and Fernald 2010). Thus, the reproduction of subordinates in this species is suppressed as a consequence of their social status, although their reproductive plasticity enables them to react to opportunities (Maruska and Fernald 2010), allowing a submissive fish to become a breeding male when the suppression imposed by the dominant individual disappears (Maan et al. 2008; Fernald 2009).

Interestingly, such suppression of reproduction also occurs in species without a hierarchical social structure, as shown in the collembolan *Orchesella cincta*. Males of this soil arthropod have been shown to decrease the spermatophore production in the presence of other males (Zizzari et al. 2013). Exactly how chemical cues of a male collembolan affect the ejaculate production of another male remains to be determined. It is plausible, however, that the inhibition of spermatophore production is triggered by a compound emitted by males that evoke an endocrine response. That is, stress hormone levels might entail the inhibition of physiological processes related to reproduction, as shown in several social birds and mammals (Creel 2001).

Sperm removal

We define sperm removal as a set of behaviors that results in elimination of rival sperm, which does not require direct interaction with the rival. That eliminating sperm of competitors increases a male's fertilization success is documented (see e.g., Parker 1998; Simmons 2001; Wigby and Chapman 2004). The mechanism that allows males to enhance their own success by eliminating rival sperm is generally referred to as sperm displacement. It should be noted here that sperm displacement generally refers to sperm removal from the storage organs of mated females, the most famous example being the zygopteran penis adapted for the removal of rival sperm stored by the female (Waage 1979). However, as we point out in the following, another often ignored mechanism of sperm removal is known to occur

outside the female body (i.e., in the environment). This is where our paper's focus lies; we purposefully do not review taxa displaying sperm displacement of stored sperm, because in species where interactions between the mating partners determine a rival's loss of fitness, a reproductive suppression strategy might be confounded by other mechanisms, like cryptic female choice (Peretti and Aisenberg 2015). Thus, in species where a male's reproductive success is determined by a complex male–female interplay, it is difficult to disentangle the effect of male–male competition and female preference.

In social animals, to the best of our knowledge, reproductive suppression via sperm removal is only due to interactions with the mating partner. The reason for this can be uncovered by looking at the mode of sperm transfer of a species. Indeed, the category of animals performing sperm removal is relevant to understand the diversity in male reproductive suppression strategies. In animals with internal fertilization, gametes are transferred to the recipient via 2 main routes: they are carried in unencased ejaculates or encased in packages (Zizzari et al. 2014). In the latter case insemination might not occur in the conventional way by using a copulatory organ to transfer the ejaculate into the female reproductive tract. For example, species whose ecological niche is represented by humid habitat, evolved an indirect way of sperm transfer by means of ejaculates (spermatophores) deposited on the substrate. Males that deposit more spermatophores will be more likely to have their ejaculates taken up by females (Zizzari et al. 2009). Interestingly, these animals have evolved an additional offensive tactic to suppress reproduction of rivals: physical destruction of a rival's spermatophores. In many soil arthropods and salamanders, when a male encounters a previously deposited spermatophore he will trample, crush, or eat it and typically deposit a new spermatophore near or even on top of the crushed one (Schuster and Schuster 1970, 1977; Alberti 1974; Arnold 1976; Proctor 1992, 1998; Stam et al. 2002). In sum, the way in which the sperm are transferred can enable the evolution of this mechanism of reproductive suppression.
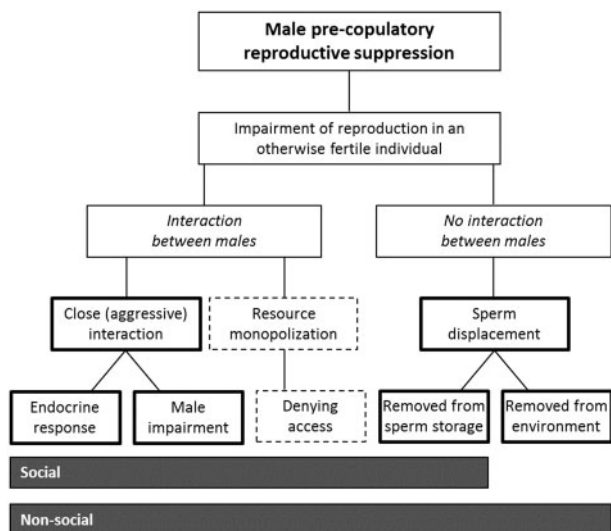
Broadening the View of Reproductive Suppression

The preceding brief overview shows that in order to properly define possible reproductive suppression mechanisms, extensive knowledge about the reproductive biology of a given system and its environment is required. Depending on their mating pattern, animals employ a wide array of mechanisms to suppress reproduction in rivals (Figure 1).

The examples of reproductive interference in Table 1 show that males of non-social animals are able to depress the fitness of a rival, though some behaviors are more harmful than others. For instance, nematodes of the genus *Steinernema* remove a rival from the reproductive population by killing him (Zenner et al. 2014). Less extreme examples are provided by males of acanthocephalans and some nematodes, whose males have been observed to perform a homosexual rape or place a cement plug on the rivals' reproductive organ making them incapable of reproducing at least temporarily (Coomans et al. 1988; Gems and Riddle 2000; Hassanine and Al-Jahdali 2008). Although several instances of same-sex sexual behavior are suspected of being related to male dominance in vertebrates, such behaviors are often attributed to cases of mistaken identity in invertebrates (see review by Bailey and Zuk 2009). Yet, Preston-Mafham (2006) excluded that the homosexual mounting behavior he observed in the scatophagid fly *Hydromyza livens* occurred through mistaken identity. Male–male sexual behavior is a

widespread phenomenon that needs certainly a more accurate analysis because there might be species where this represents a strategy to increase male reproductive success, as suggested in the hemipteran *Xylocoris maculipennis* (Carayon 1974) and in the flour beetle *Tribolium castaneum* (Levan et al. 2009). Males of *X. maculipennis* have been reported to traumatically inseminate other males and it has been hypothesized that the injected ejaculate (i.e., seminal fluid plus sperm) mixes up with the ejaculate of the inseminated male (Carayon 1974), although this remains to be demonstrated. So, while it remains unknown whether sperm from both males actually inseminate the female in the latter case, the transferred SFPs could also act on the reproductive physiology of the inseminated male, similarly to what was discovered in *L. stagnalis* (Nakadera et al. 2014). More information is available for *T. castaneum*. Levan et al. (2009) showed that male homosexual copulatory behavior may lead to indirect sperm transfer to females through a male intermediary. Although the male's homosexual partner contributed only 0.5% to each female's total progeny (Levan et al. 2009), the transfer of a small quantity of non-self sperm might decrease a males' reproductive success. Alternatively, albeit speculatively, a male might be induced to perform a same-sex encounter by female mimicry of a rival to make the mounting male temporary unable to inseminate a female, which has been described in salamanders (Arnold 1976). In this case the indirect sperm translocation would represent a male counter-adaption. However, this line of thought has not been taken into account and the homosexual copulation was explained by Levan et al. (2009) as a way to discard older sperm, indicating that more work is required to understand this in full.

In other systems, rivals are able to reproduce but their capacity to compete for females is impaired (i.e., the amount of ejaculate available to females is reduced). Such is the case of male reproductive inhibition in *L. stagnalis* (Nakadera et al. 2014) and the active ejaculate removal of soil arthropods and salamanders (Schaller 1971; Arnold 1976).

The behaviors described above potentially impose loss of reproductive fitness on the rival. Therefore, co-evolution to prevent this might be expected. In this respect, the great diversity of indirect sperm-transfer modes displayed by some animal taxa offers the opportunity to observe this phenomenon. In the most extreme form of indirect sperm transfer, namely dissociated sperm transfer, males and females need never make contact for reproduction (Proctor 1998), because males deposit their spermatophores in the environment without meeting the females (Zizzari et al. 2009, 2013). Such spermatophores are more at risk for sperm removal than spermatophores transferred directly to the female (Proctor 1998; Stam et al. 2002). Thus, selection upon spermatophore destruction by rivals might have resulted in counter-selection upon spermatophores to be laid preferentially in the presence of a potential partner. In fact, in many soil arthropods and salamander species, spermatophores are released only during or after a more or less elaborated courtship behavior with the mating partner (Schaller 1971; Arnold 1976; Proctor 1998).

In such cases males might use their antennae, legs, or heads to guide the female on the spermatophore and encourage her to pick it up (see e.g., Thomas and Zeh 1984; Tallarovic et al. 2000; Kozlowski and Aoxiang 2006; Walter and Proctor 2013). This behavior is referred to as associated sperm transfer (Proctor 1998). Moreover, differences among several species of salamander suggest that the longer the courtship time per spermatophore, the greater the chance the female will pick it up (Halliday 1974). Considering this evidence, it seems that in species where sperm transfer is indirect, and therefore sperm removal occurs outside the female body, an evolutionary transition has taken place toward avoidance of sperm removal by rivals.

Conclusions and Outlook

Current thinking emphasizes the importance of sociality as the primary driving force of reproductive suppression. This view stems from the idea that sociality leads to higher selection pressures on more developed secondary sexual traits or behaviors that enhance the success of individuals in a competitive situation (Clutton-Brock and Huchard 2013).

Here, we argue that irrespective of whether males belong to non-social or social animals, the suppression of reproductive fitness can be achieved via similar offensive behaviors (Figure 1). That non-social animals employ offensive behaviors is not surprising. What we found remarkable is that, despite the strong parallels with reproductive suppression strategies in social animals, these mechanisms are labeled pre-copulatory strategies in non-social animals. With our selection of taxa displaying a very high diversity of male interference strategies we highlight that male pre-copulatory reproductive suppression and male pre-copulatory competition overlap and are independent of whether animals live in (complex) social groups or not. While it can be useful to identify different forms of pre-copulatory male–male competition (e.g., defensive versus offensive mechanisms), it is not a useful dichotomy to reserve male reproductive interference for animals with a social hierarchy. Such a distinction rather obscures important similarities and may obstruct elucidating why different proximate mechanisms have evolved.

It should be noted that the species listed in our table represent by no means an exhaustive list of animals exhibiting male reproductive suppression behaviors, but simply provides a variety of groups of non-social animals and mating patterns in which pre-copulatory offensive behavior (i.e., reproductive suppression) are more likely to

Figure 1. Classification scheme to identify male pre-copulatory reproductive suppression categories (in italics) and their major subcategories. Various mechanisms of male pre-copulatory reproductive suppression are shown per category. Heavy boxes indicate offensive mechanisms, while dashed boxes indicate defensive mechanisms (see text for details). The two gray bars show that impairment of reproduction is independent of whether animals live in social groups or not. Examples of offensive mechanisms are given in Table 1.

be found. For instance, among arthropods and amphibians we have the greatest diversity of modes of sperm transfer. Yet, the diversity of intra-sexual offensive mechanisms and their selection are very often overlooked in these groups.

Even though male offensive behaviors in social and non-social animals serve the same ultimate goal, in the latter they might be more difficult to detect. For instance, in cooperative breeders the prevention of reproductive activity in subordinates by the territorial male is a phenomenon observable over multiple reproductive seasons, provided that the subordinates are not separated from the colony (Pruett-Jones and Lewis 1990). Crucially, in non-social animals, a male's reproduction might be suppressed for the duration of a single mating episode. Thus, in these taxa it is difficult to properly define possible reproductive suppression mechanisms without an extensive knowledge on their ecological niche and life history. Also, while we focused on male–male competition, the patterns examined could potentially be extended to female–female competition. However, whether female–female competition is equivalent to male–male competition is still debated (see e.g., Rosvall 2011; Clutton-Brock and Huchard 2013), mainly because females are expected to compete over breeding resources, while males over mate quantity.

Finally, a broad, inclusive approach should be used to spawn insights into the evolutionary pressures that are likely to have shaped different form of offensive mechanisms. In this respect, more studies should explicitly set out to also examine non-conventional offensive mechanism. We hope that our insights will generate discussion and inspire new avenues of research aimed at understanding variation across species in the evolution of male reproductive suppression.

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