

## Review



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# Sperm and alternative reproductive tactics: a review of existing theory and empirical data

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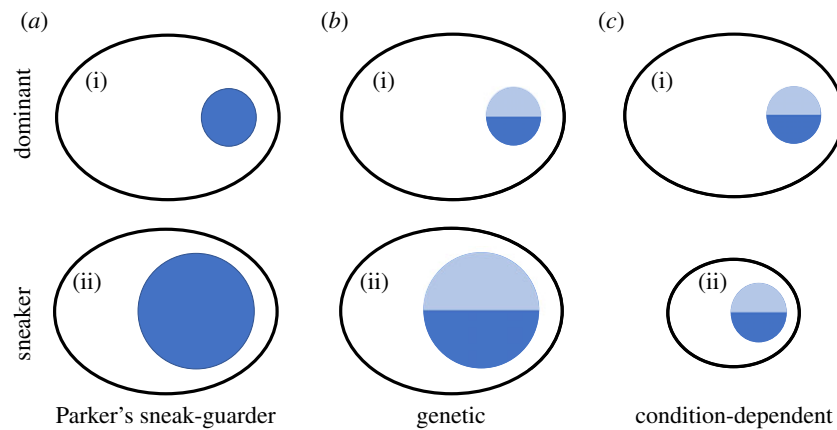
Males that exhibit alternative reproductive tactics (ARTs) often differ in the risk of sperm competition and the energetic trade-offs they experience. The resulting patterns of selection could lead to between-tactic differences in ejaculate traits. Despite extensive research on male ARTs, there is no comprehensive review of whether and what differences in sperm traits exist between male ARTs. We review existing theory on ejaculate evolution relevant to ARTs and then conduct a comprehensive vote-counting review of the empirical data comparing sperm traits between males adopting ARTs. Despite the general expectation that sneaker males should produce sperm that are more competitive (e.g. higher quality or performance), we find that existing theory does not predict explicitly how males adopting ARTs should differ in sperm traits. The majority of studies find no significant difference in sperm performance traits between dominant and sneaker males. However, when there is a difference, sneaker males tend to have higher sperm performance trait values than dominant males. We propose ways that future theoretical and empirical research can improve our understanding of the evolution of ejaculate traits in ARTs. We then highlight how studying ejaculate traits in species with ARTs will improve our broader knowledge of ejaculate evolution.

This article is part of the theme issue ‘Fifty years of sperm competition’.

## 1. Introduction

Alternative reproductive tactics (ARTs) are discrete tactics performed by individuals within a sex to obtain reproductive success and are the result of disruptive selection on traits affecting reproductive success [1]. ARTs can involve discontinuous variation in behaviour, physiology and/or morphology [1,2]. ARTs can be fixed, sequential or reversible [1]. They can be maintained as a genetic polymorphism (in which case we expect ARTs to achieve equal fitness at equilibrium) or through condition dependence (in which case ARTs are not expected to achieve equal fitness [2,3]). Male ARTs often manifest as two distinct behavioural tactics: a dominant tactic and a sneaker tactic that sneaks mating opportunities from the dominant male [1,2]. Male ARTs may experience divergent selection on ejaculate traits owing to differences in the risk of sperm competition—when sperm from two or more individuals compete for the fertilization of the same set of eggs [4]—with sneaker males typically facing a higher risk of sperm competition than dominant males.

Sperm are one of the most diverse cells across taxa, and the processes generating this divergence are of great interest [5,6]. Selection could favour differences in sperm traits (e.g. sperm morphology) between ARTs. Males adopting ARTs may face different fertilization environments [7], spatio-temporal fertilization dynamics [8–10] and/or risks of sperm competition [11]. Despite a growing number of studies, to our knowledge, there is no recently published comprehensive review or meta-analysis. While Montgomerie and Fitzpatrick [12] reviewed differences in sperm traits and relative testes size of male ARTs, this review focused exclusively on fish and many additional studies on this subject have been published since 2009.



**Figure 1.** (a) Parker's [11] sneak-guarder (dominant) model predicts sneaker males to have higher ejaculate expenditure in the form of sperm quantity (this figure is adapted from [19]). (b,c) Future models should incorporate differences in sperm quality and total reproductive budgets. We might expect ARTs that are genetically determined to have equal reproductive budgets (b), while condition-dependent ARTs will likely have unequal reproductive budgets (c). Differences in energy budgets could influence our predictions about differences in absolute ejaculate investment between males adopting either a dominant or sneaker tactic. The large unfilled oval represents a male's total reproductive budget, while the filled circle represents energy allocated towards ejaculates. The dark fill represents energy allocated to sperm count, and the light fill represents energy allocated to sperm quality (e.g. sperm velocity). Although the figure shows a 50/50 split between sperm count and sperm quality, we do not necessarily predict this will be the case. (Online version in colour.)

Below, we first review the existing sperm competition theory relevant to male ARTs. We then report the results of a comprehensive literature review synthesizing empirical studies that examined differences in sperm traits (i.e. morphology and performance) between male ARTs. Finally, we discuss gaps in both theory and empirical research, and highlight ways to address these gaps that will improve our understanding of ARTs and the evolution of ejaculate traits in general.

## 2. What does theory predict about sperm allocation and alternative reproductive tactics?

During our literature search (described §3a), we screened for theory papers that predict how male ARTs should differ in ejaculate allocation. We also performed a forward and backward search on Parker and Pizzari [13], the most recent comprehensive review of sperm competition theory. We only included sperm competition models that explicitly model different male roles. Sperm competition models that do not explicitly include males in different roles will not necessarily apply to species with ARTs. For example, sperm competition models without explicit male roles generally assume males have the same expected risk or intensity of sperm competition, which is usually not the case in species with ARTs [3,14,15]. We found only five sperm competition models relevant to species with ARTs. The first four models use a game-theoretical approach [9,11,16,17], while the fifth is an individual-based model [18].

Parker [9] considered sperm competition games when males occupy one of two roles, favoured or unfavoured, where the sperm from males in a favoured role is more competitive (in terms of fertilization) than sperm from males in a disfavoured role. In this model, males have the same reproductive energy budget and trade-off energy between mating and ejaculate production. Males face the same risk of sperm competition, and there is no sperm limitation. This model is relevant to the many species with ARTs in which the dominant male tactic has a competitive mating advantage over subordinate

males during sperm competition [9,10,12,14]. If the roles of males are constant and sperm costs are equal, males in the disfavoured role are predicted to allocate more to ejaculate expenditure than males in the favoured role [9].

Ball & Parker [17] developed an extension of this constant 'roles model' that was coevolutionary in that the roles were explicitly determined by females. Females could increase the strength of sperm selection (i.e. the proportion of unfavoured male sperm eliminated) at the cost of fecundity, while males can increase sperm allocation at the cost of mating opportunities. Each female is assumed to mate with exactly two males, and males in the unfavoured roles are assumed to produce fewer progeny than males in the favoured roles. This model is relevant to many species where the dominant ART is preferred by females [3]. Similar to Parker [9], if male roles are constant, males in the disfavoured role are predicted to allocate more to ejaculate expenditure than males in the favoured role [17].

Parker [11] examined sperm competition games between males adopting either a guarder or sneaker role. In this model, sneakers know they are spawning in sperm competition, while guarders only know the average risk of sperm competition. Both males have the same reproductive energy budget and trade-off energy spent on obtaining mating opportunities with energy spent on ejaculate expenditure. This model assumed a fair raffle—each sperm from each male has an equal chance of fertilization—and that females mate with at most one other male (i.e. a risk model). This model predicts that if the relative cost per sperm for a sneaker is equal or greater to that for a guarder, sneakers should allocate more energy to ejaculate expenditure than guarders regardless of the average risk of sperm competition in the population (figure 1a). If the relative cost per sperm for a sneaker is less than for a guarder, then the difference in ejaculate allocation between sneakers and guarders is predicted to depend on the population-level risk of sperm competition. At higher risk, guarder ejaculate expenditure may equal or even exceed that of sneakers. If the relative cost per sperm is low for sneakers, they will allocate less sperm in a given mating to achieve more mating opportunities (electronic supplementary material, figure S1).

Gage *et al.* [16] expanded this model to include the intensity of sperm competition (i.e. more than one sneaker) and relaxed the assumption of a fair raffle. Like the original sneaker-guarder model, when sperm competition is a fair raffle and costs are equivalent, sneakers invest more in ejaculate expenditure than guarder males, with the difference being highest at intermediate sperm intensities. If sperm from sneaker males have a higher probability of fertilization than sperm from guarder males, then guarder males invest more in ejaculate expenditure at higher intensities of sperm competition. When the cost of producing sperm relative to the cost of obtaining a mate is equal or lower for sneakers, sneakers are predicted to have higher relative ejaculate expenditure across all intensities of sperm competition. However, if the cost of producing sperm relative to obtaining a mate is higher for sneakers, guarders are predicted to have higher relative ejaculate expenditure at higher intensities of sperm competition (electronic supplementary material, figure S1).

The individual-based model by Engqvist & Taborsky [18] considered a trade-off between sperm production and individual growth, that in turn affects mating success, fertilization success and mortality. Body size is assumed to affect mortality, sneaking success and the ability of males to hold territories. In this model, ARTs could evolve as either being genetically determined or condition dependent. They found that sneaker males evolved higher relative sperm expenditure independent of the risk of sperm competition for territorial males and regardless of whether the ARTs were genetic or condition dependent. ARTs were more likely to evolve when sperm competition was a fair raffle as opposed to a loaded raffle (sperm from ARTs have different probabilities of fertilization).

In most situations, sneakers are predicted to invest more in their ejaculate than dominant males [11,16,18]. Males in a disfavoured role (all else being equal) are similarly expected to invest more in their ejaculate than males in a favoured role [9,17]. Dominant males are only predicted to have higher ejaculate expenditure than sneaker males if the average sperm competition intensity is high and sperm costs are different for sneakers and/or the raffle is loaded in favour of sneakers [16] (see electronic supplementary material, figure S1 for more in-depth predictions). However, we did not find any theory that made predictions about sperm quality or traits *per se* [9,11,16–18].

### 3. How do males adopting alternative reproductive tactics differ in ejaculate traits?

Given that sneaker males are expected to invest more in their ejaculate overall, they might also be expected to produce higher quality sperm. To determine whether this expectation is supported, we synthesized data using a vote counting approach on whether and how male ARTs differ in sperm traits. We were interested in two main categories of sperm traits, which we refer to as sperm morphology and sperm performance (higher values of these traits should result in higher fertilization success).

#### (a) Methods

We searched the 'Web of Science' with the phrase: '(Alternative Reproductive' OR 'Alternative Mating') AND ('Sperm'). Our search resulted in 364 articles, which we read for relevancy. We

considered papers relevant if they had direct statistical comparisons of sperm traits between ARTs. For sperm morphology, we collected data on sperm total length, head length, midpiece length and flagellum length; for sperm performance traits, we collected data on the per cent of sperm cells motile/viable, sperm velocity, sperm longevity, and the amount of adenosine triphosphate or ATP—a measure of energy in a sperm cell. We performed a forward citation search on articles that were relevant based on these criteria. Finally, we conducted a targeted backward citation search on papers that had sperm trait data to find data on sperm quantity or ejaculate investment (e.g. sperm count) from the same species. This resulted in 55 relevant studies on 29 species (electronic supplementary material).

To ensure comparability, we categorized the ARTs of these species into either a dominant or sneaker tactic, such that dominant males experienced lower sperm competition on average than sneaker males. We excluded species that did not fit well into this categorization (see electronic supplementary material for species that were excluded). In species with more than two ARTs, we compared the most dominant male that experiences the lowest risk of sperm competition to the least dominant male. For experimental studies, we present the results from the comparison between the dominant and sneaker males without any manipulation. For each variable, we recorded whether the studies found that sneaker males were significantly higher than dominant males, there was no significant difference, or dominant males were significantly higher than sneaker males. For species with multiple studies of the same variable or multiple dominant morphs, we averaged these scores.

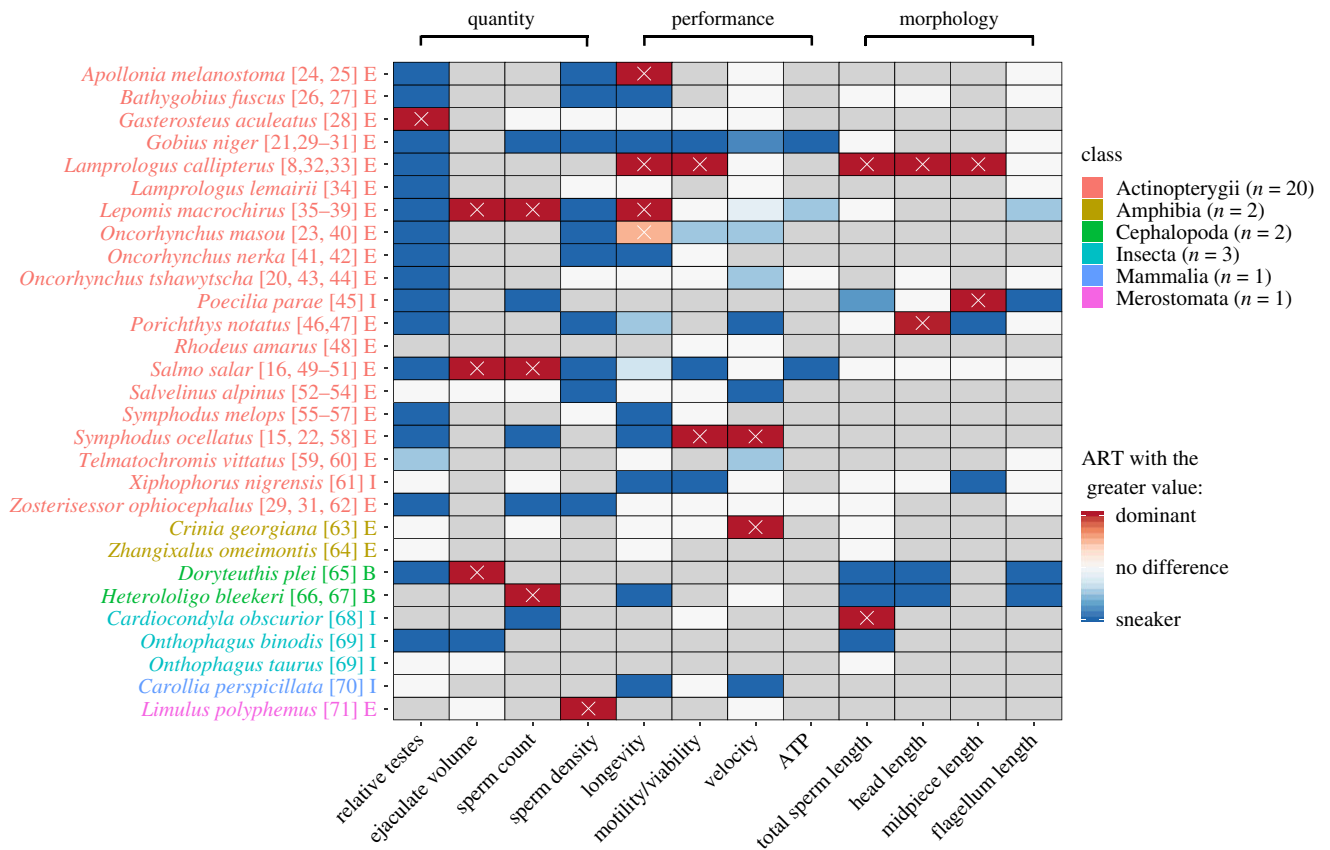
#### (b) Results

We found sperm trait data for 29 species, with the majority of species ( $n=20$ ) being within Actinopterygii (ray-finned fishes; figure 2). The remaining nine species with sperm trait data were spread across five other taxonomic classes: Amphibia, Cephalopoda, Insecta, Mammalia and Merostomata.

Following theoretical predictions [9,11,16,18] and earlier syntheses [12,72], relative ejaculate expenditure, as gauged by relative testes size and sperm density, were usually higher in sneaker males (figure 2; table 1). There were more species in which the dominant male had larger ejaculate volumes than sneaker males (figure 2; table 1).

We found sperm morphology data for 20 species (figure 2; table 1). Flagellum length was the most studied aspect of morphology (figure 2; table 1). The majority of studies found no significant difference between dominant or sneaker males in sperm morphology (figure 2; table 1). If there was a difference, sneaker males tended to have longer sperm than dominant males (figure 2; table 1). For species with data on sperm morphology measurements broken down into different parts (i.e. head, midpiece and flagellum length), three species showed no significant differences across all measurements, one species showed a significant difference in only midpiece length, two species showed significant differences between tactics that differed in a direction depending on the sperm morphology trait, and three species showed significant differences in a consistent direction across multiple sperm morphology traits (figure 2).

Across all sperm performance traits recorded, the majority of species showed no significant differences between dominant and sneaker males (figure 2; table 1). When there was a significant difference, there were more species with sneaker males having higher sperm performance trait values than dominant males (figure 2; table 1). For species in which multiple sperm performance traits were measured, we looked for evidence of a trade-off among performance traits. A pattern consistent with a trade-off would be one ART having a significantly higher sperm performance trait value in one trait but lower values in another (i.e. blue



**Figure 2.** Studies comparing the sperm traits of male ARTs are mostly on fish [8,15,16,20–71]. Sneaker males generally have larger relative testes, and if there is a difference in sperm performance traits or morphology, sneakers tend to have higher mean trait value. This heatmap shows whether or not there was a significant difference and in what direction for different species (colour coded by ART) and different ejaculate traits of interest. Grey values indicate that those data were not reported in any of the articles we found. Light blue and light red indicate that there were multiple studies of the same species that did not consistently find a significant difference. White crosses indicate dominant > sneaker; E's indicate external fertilization; I's indicate internal fertilization; B's indicate that sneaker males deposit spermatophores externally and dominant males deposit spermatophores internally. Species names are colour-coded by taxonomic class.

**Table 1.** Across all studies, sneaker males have larger relative testes than dominant males. Sneaker males tend to have higher quality sperm. This table summarizes figure 2 and does not take phylogeny or biological information (e.g. mode of fertilization) about the species into account. The per cent of species (rounded to nearest whole number) is based on number of species for which the empirical search found data on a given trait.

type of trait	trait	% species (# species) no difference	% species (# species) dominant >	% species (# species) sneaker >
quantity	relative testes	24% (6)	4% (1)	72% (18)
	ejaculate volume	43% (3)	43% (3)	14% (1)
	sperm count	33% (4)	25% (3)	42% (5)
	sperm density	26% (4)	7% (1)	67% (10)
performance	longevity	36% (8)	18% (4)	46% (10)
	motility/viability	65% (11)	12% (2)	23% (4)
	velocity	52% (11)	10% (2)	38% (8)
	ATP levels	40% (2)	0% (0)	60% (3)
morphology	total length	62% (10)	13% (2)	25% (4)
	head length	56% (5)	22% (2)	22% (2)
	midpiece length	20% (1)	40% (2)	40% (2)
	flagellum length	73% (11)	0% (0)	27% (4)

and red cells in performance traits on the same row in figure 2). The majority of species (13) showed no evidence of a trade-off or evidence for one tactic having consistently better-performing sperm across multiple traits (figure 2). Three species showed evidence of a trade-off among sperm performance traits. In five species,

sneaker males had significantly better sperm performance than dominant males across multiple sperm performance traits, while dominant males had significantly better sperm performance than sneaker males across multiple performance traits in only one species (figure 2).



In summary, the majority of studies from our empirical literature search found that sneaker males have higher values of relative sperm quantity traits such as sperm density and relative testes size (figure 2; table 1). However, this trend was weaker in absolute sperm count and reversed for ejaculate volume (figure 2; table 1). Although the majority of studies found no significant difference in sperm morphology or sperm performance traits, if there was a difference, sneaker males tended to have significantly longer sperm and higher sperm performance trait values than dominant males.

#### 4. How can we improve our understanding of when, how and why alternative reproductive tactics differ in ejaculate traits?

Existing sperm competition models on ARTs [9,11,16,18] make predictions about relative ejaculate expenditure but do not consider energetic trade-offs between ejaculate traits and assume males have equal reproductive budgets (figure 1a). Despite this theoretical gap, there is a general expectation that sneaker males should have sperm of higher quality because they experience more sperm competition. Yet, the majority of studies from our literature search found no significant difference in sperm morphology or sperm performance traits between males adopting ARTs. Our results are also consistent with an unpublished master's thesis that performed a meta-analysis on how ejaculate traits differ between ARTs in fish species [73]. We suggest the following six possible explanations for this mismatch and ways to address them with future research.

##### (a) There should be a difference, but there is not enough data to detect it

Our empirical literature review revealed a strong taxonomic bias towards Actinopterygii (ray-finned fish). Although ARTs are well documented and possibly more abundant in fish [12,14], ARTs are found in many other taxonomic groups [3]. A broader understanding of how ARTs differ in sperm traits will require more studies that compare sperm traits of ARTs, especially in species outside Actinopterygii. While any sperm trait data would be informative, we especially need data on sperm morphology, ideally broken down by sperm components (i.e. head length, midpiece length and tail length, figure 2). Additionally, the absence of significant differences in some studies may be owing to low statistical power, which in our qualitative review is recorded as no difference. More data and a formal phylogenetically corrected meta-analysis are needed to determine whether the overall effect size of male ART on sperm traits across taxa is significantly different from zero.

##### (b) Our expectations could be wrong: we need new theory

The expectation that sneaker males should invest more in sperm and therefore have higher quality sperm ignores trade-offs between ejaculate traits and assumes ARTs have equal energy budgets. It is not clear how these assumptions affect predictions and explicit theoretical modelling is needed.

We suggest expanding the Parker [11] model to make predictions about relative sperm quality (morphology or performance traits that increase the probability of fertilization)

by allowing ejaculate expenditure to be split between sperm count and sperm quality as opposed to just sperm count (figure 1b,c). In this hypothetical model, more investment in sperm quality results in higher costs per sperm, but each sperm has a higher chance of fertilizing ova. Similar models on the evolution of sperm size outside of ARTs show that the evolutionarily stable investment in sperm quality can be independent of the risk of sperm competition [74,75]. Analogously, sneakers and dominant males may not be generally predicted to differ in sperm quality.

ART game theory models [9,11,16] can also be expanded by relaxing the assumption of equal reproductive budgets between sneakers and dominant males (figure 1b,c). We know theoretically [76] and empirically [77,78] that ejaculate traits are influenced by male condition, independent of sperm competition risk. In many species with condition-dependent ARTs, sneaker males tend to be of lower quality [3], in which case they may have a smaller reproductive budget and lower sperm quality even if they have higher relative ejaculate expenditure (figure 1c).

##### (c) The divergence of sperm traits may be evolutionarily constrained

Ejaculate traits are multivariate, and ARTs may differ in the optimal combination of traits. The evolution and expression of tactic-specific optima could be constrained by both genetic correlations between ejaculate traits and genetic correlations of traits across tactics (i.e. intertactical genetic correlation). Intralocus tactical conflict would occur when the optimal phenotype of sperm traits differs between males adopting ARTs that share the same genome [79] and is analogous to intralocus sexual conflict, where sexes have different optimal phenotypes [80,81].

Conducting quantitative genetic breeding designs on species with ARTs (reviewed in [79]) to estimate both genetic correlations between ejaculate traits and intertactical genetic correlations of these traits would greatly improve our understanding of potential constraints on the evolution of divergent ejaculate traits. While shedding light on the evolution of ARTs, this would also inform our broader understanding of the evolution of ejaculate traits. To understand how the evolution of divergent sperm traits will be constrained, we need to develop quantitative genetic models that integrate realistic estimates of between-trait and intertactical genetic correlations.

##### (d) Other ejaculate components were not considered

Ejaculate components besides sperm, such as seminal fluid proteins, sugars, salts, fats and hormones, play an important role in the fertilization process and investment into these aspects may be favoured over sperm traits [82]. To our knowledge, there are only three papers investigating the effects of seminal fluid (or seminal plasma) on sperm performance in ARTs [20,21,83]. These studies show that sneaker seminal fluid can negatively affect dominant male sperm performance [20,83]; dominant male seminal fluid can positively affect both their own sperm performance [21], and even the sperm performance of rival sneaker males [83]. Conducting more empirical studies of this kind will be necessary to show how generalizable these dynamics are and to what extent selection may be acting on seminal fluids in ARTs. A recent study on seminal plasma protein composition in Chinook salmon

(*Oncorhynchus tshawytscha*) identified differential protein abundance of 29 proteins between sneaker and dominant males [84]. Conducting more proteomic studies like this will be important in getting at mechanisms that underly these interesting dynamics as well as identifying the specific genes that selection may be acting on. Additionally, developing a theoretical framework to understand when male ARTs should be selected to invest in seminal fluid over other ejaculate traits will help generate better *a priori* hypotheses for these future empirical studies. Furthermore, negative effects of sneaker seminal fluid on dominant male sperm could select for females to somehow counteract this effect to either avoid potential sperm limitation (e.g. [85]) and/or to bias sperm competition games to favour the dominant male (assuming the dominant male is of higher quality).

### (e) Female influences

Our current analysis ignores female influences; however, there is growing empirical evidence that female traits (e.g. eggs and the reproductive tract) influence both sperm performance and fertilization outcomes both in general [5,86,87], but also in species with ARTs [22,23,88,89]. For example, Alonzo *et al.* [22] show that ovarian fluid increases sperm performance for both sneaker and dominant males. However, ovarian fluid biases sperm competition games by reducing the effect of sperm count, which likely favours the dominant male who releases faster but fewer sperm in natural mating events (figure 2). To better understand how widespread female influences on sperm performance and ultimate fertilization outcomes between male ARTs are, we need to conduct similar experiments on other taxa, especially in species with internal fertilization (as all current examples are in externally fertilizing fish). A better understanding of these female processes will greatly inform the assumptions made and scenarios modelled in future theory.

Although female influences on fertilization outcomes via sperm selection were modelled by Ball & Parker [17], cryptic female choice may act more subtly than the sperm selection mechanism assumed in this model. Rather than killing off sperm from the disfavoured male (i.e. sneaker male), the female environment may change the relative importance of different ejaculate traits as in Alonzo *et al.* [22], which could favour one tactic over the other. This could hypothetically lead to a coevolutionary chase. Taking the dynamics of Alonzo *et al.* [22] as an example, selection could act on sneakers to invest more in sperm velocity than sperm count, which would in turn select for some other mechanism for females to bias paternity towards the preferred dominant male. Developing more theory to model the coevolutionary dynamics between cryptic female choice and sperm allocation in ARTs will greatly improve our understanding on the evolution of ejaculates in ARTs.

### (f) Additional differences among species must be considered

Making sense of the observed variation among species could greatly improve our understanding of the evolution of ejaculate traits (figure 2). One approach would be to conduct a formal phylogenetically corrected meta-analysis to look at how certain modifiers influence the degree and direction that ARTs differ in sperm quality. One important modifier

could be the category of ART. Simultaneous ARTs may not show differences in sperm traits because these traits would have to be plastic, which is less well demonstrated than plasticity in sperm count and ejaculate volume [90]. How the ARTs are determined may also affect whether they differ in sperm quality (figure 1b,c). Additionally, spatio-temporal differences in mating between ARTs may be an important driver in how ARTs optimally balance trade-offs between sperm traits (e.g. performance and longevity [8]). We also need to consider the average risk of sneak matings when conducting a formal meta-analysis, as theory predicts this will affect the degree to which dominant and sneaker males differ in ejaculate allocation [11,16]. Collecting and/or compiling data on these crucial modifiers will be important for conducting a meta-analysis to provide insight into the processes that influence the divergent evolution of ejaculate traits.

## 5. Conclusion

Despite 50 years of research on sperm competition, we still have gaps in our understanding of the evolution and maintenance of variation in sperm traits. Studying sperm traits in ARTs will aid our understanding of the evolution of sperm traits in general, as differences between ARTs likely reflect recent trait divergence and within-species comparisons have inherently fewer confounding variables than across-species comparisons. Existing theory predicts—all else being equal—that sneaker males should have higher ejaculate investment than dominant males [11,16]. Although existing theory does not make explicit predictions about sperm quality, there is a general expectation that sneaker males should have higher sperm quality than dominant males. We find that the majority of species showed no significant differences in sperm traits between ARTs. However, when there is a significant difference, there is a trend for sneaker males to have significantly longer sperm and higher sperm performance trait values than dominant males. The variation among species highlights a gap in our understanding of the underlying dynamics involved in the evolution of ejaculate traits. Future empirical and theoretical research into this variation that integrates the reproductive ecology, female influences, how tactics are determined and the underlying genetic architecture of ejaculate traits in species with ARTs will significantly improve our understanding of the evolution of ejaculate traits.

**Data accessibility.** Supporting data are provided as electronic supplementary material.

**Authors' contributions.** M.C.K. and S.H.A. conceived of the review. M.C.K. and S.H.A. designed the literature search and heavily discussed the ideas and arguments presented in this review. M.C.K. collected the data presented in this review. M.C.K. drafted the manuscript and S.H.A. critically revised the manuscript. Both authors approve of the publication of this article.

**Competing interests.** We declare we have no competing interests.

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