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Review

It's all in your head: the role of quantity estimation in sperm competition

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The study of animal cognition has provided valuable data throughout the years, yet its reliance on laboratory work leaves some open questions. The main question is whether animals employ cognition in daily decision-making. The following discussion uses sperm competition (SC) as a test case for demonstrating the effect of cognition on routine choices, in this case, sexual selection. Cognition is manifested here by males' ability to represent the number of rivals competing with them. I claim that response to SC is driven by quantity estimation and the ability to assess competition magnitude cognitively. Hence, cognition can determine males' response to SC, and consequentially it can be selected within this context. This supports the argument that cognition constitutes an integral part of an individual's toolbox in solving real-life problems, and shows that physical and behavioural phenomena can expose cognition to selection and facilitate its evolution.

Keywords: animal cognition; sperm competition; quantity estimation; evolution; sexual selection; cognition

1. WHAT IS QUANTITY ESTIMATION?

Quantity estimation (QE) encompasses the range of perceptual and cognitive aptitudes allowing individuals to respond to the quantity aspect of stimuli in various degrees of accuracy [1]. A fundamental distinction is made between quantity and amount: amount describes the physical attributes of stimuli (density, surface area, etc.) and provides information on the magnitude of such continuous indices. In contrast, quantity exclusively refers to the discrete dimension of exact number, and allows increments in integer units only [2]. For example, in foraging, amount reports on the magnitude of physical food features, while quantity conveys information on the number of individual food items. I suggest that the transition from processing amount to processing quantity entails a transition from the automatic and non-cognitive to the progressively more cognitively complex [3]. This is demonstrated by QE's role in sperm competition (SC).

2. WHAT IS SPERM COMPETITION?

SC is the struggle between sperm of different males for the fertilization of a given set of ova [4]. SC affects the evolution of many taxa and induces a variety of adaptations at behavioural, morphological and physiological levels [5–7]. Parker and co-workers [8–11] modelled the resource allocation a male is expected to invest in sperm production when faced with different number of rivals. These models make three predictions: the first states that males should invest minimally in the absence of competition. Secondly, investment should be maximal in the presence of a single competitor. This situation is known as SC risk (SCR), and it is a dichotomy between absence and presence of rivals, thus not requiring QE. Finally, sperm expenditure is expected to progressively decline as the mean number of rivals exceeds one. This is SC intensity (SCI), and here a subtle distinction of quantity is required in order to qualify for the progressive decline condition. These predictions rely on two debatable assumptions: the first is that individuals can assess the magnitude of their competition, be it accurately or vaguely (what I call the 'estimation conjecture'). The second assumption posits that there exists, in every species, a given knowledge of an average number of competing males (what I call the 'innate mean conjecture').

SC models address population-level SC and, consequently, do not consider how individuals perceive, process and act upon the number of rivals. However, it is clear that by alluding to assessment, these models should focus on individuals. Population analyses are limited in explicating the role cognition might play in behaviour, since they average out individual differences in performance. As a result, SC models neglect the questions of the mechanisms of assessment, who performs the assessment, or what is assessed. This is a substantial lacuna, since without the ability to estimate competition size, an organism cannot be said to truly respond to SCI [12]. The following discussion bridges this gap by showing that individuals can gauge the magnitude (intensity) of a competition, by using a range of perceptual and cognitive aptitudes, and that this assessment process determines their response to SC.

3. LINKING QUANTITY ESTIMATION AND SPERM COMPETITION

Males' ability to estimate competition magnitude determines ejaculate size and composition. Sperm does interesting things post copula, yet those chemical actions

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Table 1. Experimental design for species tested for SC intensity. Species: H, hermaphrodite. Competition size: 1v0-2 means a focal male was presented with 0, 1 or 2 other males. 1v1/5 means it was one or five males; m, males; f, females; s, small; l, large. Traits: CD, copula duration; VST, various sperm traits; SE, sperm expenditure. Model: support/refute SCI model predictions. Population-level analyses are not included.

species	competition	trait inspected	model	ref.
Schistocephalus solidus (H)	1v1/3	sperm storage volume	support	[16]
Macrostomum lignano (H)	1v1/2/3/7	sex allocation	support	[17,18]
Ophryotrocha diadema (H)	1v1/11	sex allocation	support	[19]
Helobdella papillomata (H)	1v0/1/3/7	testisac volume	support	[20]
Ophryotrocha diadema (H)	1v2/6/12	sex allocation	refute	[13,21]
yellow dung fly	1v1/3	testis size	support	[22]
fruit fly	1v0/1/3	CD	support	[23]
	1v1/2/4	seminal fluid composition	support	[24]
golden egg bug	1v1/2	CD, SE	support	[25]
rice weevil	1v1/5/10	courtship duration, CD	support	[26]
monarch butterfly	1v3, 1s:1l	VST	refute	[27]
tropical house cricket	1v0/1/6	SE	refute	[28]
spring field cricket	1v0/1/6	SE	support	[28]
Southwestern field cricket	1v0/1/6	SE	refute	[28]
Australian field cricket	1v0/1/5	SE	support	[29]
	1v0,1,5,10,15	VST	refute	[15]
house cricket	1v0/1/7	SE	refute	[30]
tropical house cricket	1v0/1/7	SE	refute	[30]
Cordylochernes scorpioides	1v0-3	SE	refute	[14]
mealworm beetle	1m:2f/3/4f, 2mv4f	time near scent origin	refute	[31]
peppermint shrimp (H)	1v1/2/5/10	sex allocation	refute	[32]
sailfin mollies	1m:3f, 3m:1f	SE	refute	[33]
guppy	1v0/1/2/4	VST	refute	[34]
European bitterling	1v0/1/3/5	ejaculation rate	support	[35]
	not specified	SE	support	[36]
grass goby	1v0/1/2/4	ejaculate size	support	[37]
	1v0/1/4	territoriality, aggression & SE	refute	[38]
black goby	1v0/1/2/4	ejaculate size	support	[37]
	1v0/1/4	territoriality, aggression & SE	support	[38]
rainbow darter	1v0/1/4	ejaculate size	refute	[39]
freshwater crayfish	1v0/1/3/	ejaculate size	refute	[40]
red-spotted newt	1v0/1/3/7	courting display	support	[41]
small-mouthed salamander	1v0/1/2	courtship duration, spermatophore number	support	[42]
Australian quacking frog	1v0/1/2/4	fertilization success	support	[43]
	1v0/1/2	ejaculate & testis size	refute	[12]
meadow vole	1v5	SE	support	[44]
bank vole	1v1/4	VST	support	[45]

are out of cognition's reach. Estimation is not performed by sperm, and once sperm is delivered, cognition takes a back seat. Thus, the time window under investigation here includes only the events leading up to ejaculation. Cognitively speaking, assuming *a priori* that males can estimate quantity in SC contexts is non-trivial. Schleicherova *et al.* [13] report that the worm *Ophryotrocha diadema* modifies its sex allocation through a finely tuned, concentration-based threshold. Here, response to SC is wholly dependent upon amount and requires no cognitive processing. Bonilla *et al.* [14], report that sperm allocation in the pseudoscorpion *Cordylochernes scorpioides* decreased almost monotonically as the number of different male olfactory cues increased from 0 to 3. Thomas & Simmons [15] observed that sperm viability decreased in males of the cricket *Teleogryllus oceanicus* as the number of different male scents on a virgin female partner increased. Evidently, different species rely on different cues to assess SC; those cues are perceived at varying levels of accuracy and sophistication; and assessment determines if and how males modify their behaviour and/or sperm traits (table 1).

4. THE ESTIMATION CONJECTURE

SC models provide a framework for examining cognition's role in SC. These models consider two scenarios: in the first, sperm allocation is shaped by the mean level of SC, and males can assess only whether the number of competitors is smaller or greater than such an average [13]. In QE nomenclature, this is called relative quantity judgement. Many species possess basic QE aptitudes, where amount and quantity are significantly confounded (for a review see [46]). In SC, relative quantity judgement is manifested, for example, by males measuring females' reproductive tract content [47,48]. In the second SC scenario, males have precise information concerning the number of competitors (akin to [15]). In QE terminology, this is counting.

To tackle the estimation conjecture, I examine the role quantity plays in males' assessment of SCR/I, and begin by looking at the issue of quantity versus amount. While SCR has substantial experimental support, SCI garners only a fragmented one [49–51] (see also table 1). As an explanation, I suggest that whereas SCR relies on a binary distinction between absence and presence (in which both amount and quantity provide cues of equivalent reliability), SCI demands a representation of the actual number of rivals, entailing the cognitive function of counting. Since counting is more complex, it is expected to be less phylogenetically frequent.

To substantiate the argument for QE, I investigate what is the element assessed by males: if stimuli are continuous (e.g. spermatheca content) and evaluation is concentration-based [27,52], amount is the dominant cue. If stimuli are males themselves, then the cue becomes quantity, and it can be said (given appropriate experimental controls) that males effectively count their rivals.

Next, I use Gelman & Gallistel's counting principles [53], in which ordinality and cardinality are prerequisite to counting. Ordinality is the representation of order within a stimulus array [54]. In QE, ordinality means that tagging of stimuli is continuous and sequential. Cardinality dictates that the last tag assigned represents the sum of all items in an array. To exhibit ordinality in SC, males need to distinguish rivals tallied from rivals to be tallied. Such ability is plausible given several lines of evidence. First, many species can correctly establish mating status [55] or mating order [6] using various mechanisms. Second, males are aware of not simply the presence of observers, but also of their composition ([56] and references therein). Cumulatively, it is safe to presume that males of several species can actively distinguish between individuals, tag them and represent them ordinally. Third, with respect to cardinality, it is observed that, in nature, males are often encountered sequentially [57]. Next, selected reports explain how males can benefit from relegating the execution of sexual behaviour to a later stage: Grant *et al.* [58] introduced male Japanese medaka to simultaneous and sequential presentations, and concluded that sexual behaviour indices were more prominent following sequential presentation. Reinhardt [59] reports that the summative number of male–male encounters reliably predicts variation in ejaculate size in the grasshopper *Chorthippus parallelus*. Thus, it is plausible to identify cardinality aptitude employed in SC context. Together, these lines of evidence provide a tentative, albeit indirect, backing to an ability to track and manipulate quantity over time in a manner qualifying to the principles of counting.

Overall, there is experimental support for the existence of a continuum of various fashions of gauging competition magnitude, ranging from crude perceptual sensing of chemical concentration through more elaborate processing of amount cues, and culminating in cognitive processing of quantity and counting. These aptitudes are employed contextually in some individuals and species to respond to SCI.

5. THE INNATE MEAN CONJECTURE

SC models assume the existence of a given knowledge of an average number of competing males. Clearly, if males use innate means, they need not estimate the number of their rivals, and automatic response to perceptual amount cues (such as concentration thresholds) suffice. Indeed, some species rely upon an *a priori* value, embedded either prenatally or during a critical period in development [60,61]. This option may apply to males who lack plasticity in accommodating for changes in competition size [23,62]. Nonetheless, innate means cannot be assumed to be global, since the composition and magnitude of competition may vary substantially [12]. Additionally, data show that local responses can rely on the phenotypic plasticity of sperm traits [63–65].

If averages are not used, males need to form their estimation during some point in time, be it prior to or during copula, thus allowing temporal cognition to enter the equation. The role of interval timing in QE has been thoroughly substantiated [2,66,67]. Therefore, identifying interval timing's involvement in SC supports the argument for QE's role in SC. I focus on estimations prior to copula [24,68], since estimations during copula rely predominantly on probing spermatheca content, which is amount estimation. There are two alternatives to the innate mean conjecture concerning timing's role in SC: the first is estimation according to *ad hoc*, local conditions [69], and the second is decision reached locally via a comparison to a hardcoded value [70,71]. Interval timing is important in both cases, as shown, for example, by the observation that mating duration prolongs as males' exposure to rivals prior to copula progressively extends [72]. Further cementing the role of interval timing in connecting QE and SC is the observation that phenotypic plasticity of various sperm traits is triggered only by a specific stimulus and a threshold exposure time to it [73,74], even at adulthood [75,76].

As an interim conclusion, the QE analysis of SC supports the idea that males can estimate the magnitude of their competition. At the very least, SC assessments require males to perform relative quantity judgements, where males can distinguish between more or less rivals. Occasionally, assessment might entail a more sophisticated QE aptitude, where males need to perform a continuous real-time monitoring of the number of individuals they encounter. Such aptitude involves exact representation, it is sequential (and thus requires handling interval timing), and it meets the requirements of the basic principles of counting [53]. Such an aptitude has yet to be addressed in the QE literature. Thus, current QE models fail to describe fully the impact quantity has on males' assessment of SCI.

As table 1 indicates, this analysis goes beyond Parker *et al.*'s models: some species' response to SC, while not obeying Parker's predictions, still supports the argument that assessment is crucial for apprehension of competition size. Hence, the assertion that cognitive processes at the individual level tailor behavioural and physiological response to SCR is extended to data that contradicts SC models. Furthermore, the modelling of other phenomena also presupposes males' ability to gauge competition magnitude: mosquito fish males' mate choice [77] and giant danio's and zebra fish's resource defence [78] echo Parker *et al.*'s assumptions to the dot. Thus, it becomes even more pertinent to explore the role the cognitive functions of QE have in various behaviours and their evolutionary trajectories.

6. EVOLUTIONARY ANALYSIS OF SPERM COMPETITION AND QUANTITY ESTIMATION

Based on the suggested link between SC and QE, possible evolutionary corollaries could be considered. To do so, further elaboration of QE theory is needed. QE is a composite behaviour, comprising quasi-independent building blocks (perceptual or cognitive elements; e.g. temporal cognition) brought together by exaptation [2]. The operation of a building block within a cognitive complex does not negate its own independent, parallel and simultaneous effect. Here lies the source of quasi-independence: amount functionality is tapped by various amount networks *and* by quantity networks of which they are part. If an animal can process both amount and quantity, then stimuli may activate either amount or quantity networks. However, quantity has amount as one of its constituents; thus, the same amount-network is stimulated, but it supports different tasks. This contingent characteristic of the choice between quantity and amount allows various environmental conditions to determine which cue is used per given task. Such an outline suggests that QE aptitudes (such as relative quantity judgement and counting) are punctuated across phylogeny in a way that defies a linear schematization of its evolution: counting most probably have used the QE aptitudes preceding it, and evolved independently in several lineages. Therefore, the evolutionary processes that had shaped the continuum of QE aptitudes are nonlinear and promote convergence [2].

Data show that males' cognitive aptitude directly affects their mating success [79] and that females can infer such aptitudes via behavioural or morphological proxies [80]. Some studies document a direct association between learning and plasticity of sperm traits in SC context [81,82]. A ubiquitous observation in the study of animal behaviour is that individuals differ in cognitive performance. These lines of evidence suggest a viable link between individuals' cognitive capacity and their mating success, thereby exposing their cognitive system to selection, be it directly or indirectly.

Parker *et al.* argue that males who can accurately assess the number of their competitors use sperm more efficiently than those who cannot. Cognition's role in SC via QE suggests that cognitive traits can be selected [83]. Changes in sperm traits can translate into competitive ability [22,84,85] and sperm competitiveness can become heritable [86,87]. If estimation of quantity is males' assessment mechanism, then cognition is the cause of their response to SC and, consequentially, it could be selected. The interwovenness of quantity and amount dictates that cues generated by rival males activate multiple modalities [88] and processing processes. Such multitude could either improve decision-making [89] and facilitate attainment of perfect knowledge if cues are of the same nature (amount *or* quantity [14]), or it might stymie the estimation process, and favour averaged responses. Under ecological conditions where amount cannot provide reliable information, and/or when the interaction between quantity and amount jeopardizes swift and trustworthy response, a gradual shift from processing amount towards processing quantity is expected. Pertaining to this, a direct association between learning and plasticity of sperm traits in SC has been reported [81], and even argued to be the only probable cause of an increase in sperm expenditure [82]. Finally, given the observation that profound environmental differences predict vastly different selective forces on sperm traits [90], evolutionary advancements should become possible if some individuals collect a multitude of environmental cues [24,72], and if they can contingently alternate between quantity and amount as salient features. Evolutionarily phrased, QE can complexify if individuals exploit their plastic perceptual and cognitive responses in a way that is canalized towards preferring quantity to amount. Note, however, that currently there is no information on mechanisms translating the cognitive process of QE into actual behavioural or physiological SC modifications.

7. ECONOMICS OF SPERM EXPENDITURE

QE does not inform males about rivals' quality. Decision-making in sexual competition scenarios requires additional information, such as female availability and status, time of season, etc. Only the combination of all lines of information forges a reliable appraisal of the investment a male should allocate per competition event. Furthermore, sperm production is costly [91], and an ejaculate's competitive value changes during competition [92]. Hence, sperm expenditure is not trivial. It is probable that an economic regulation principle selects which plastic modification is executed in response to SC, such that it would be the one where minimal energy investment is required [93]. A support for this argument comes from meadow voles, where males' preference for the more receptive female was reversed when males had the choice between the more receptive females accompanied by 0 or 1 males compared with the less receptive females accompanied by five males. Here, the number of males was a cue overriding the chemical signal of female receptiveness [94].

8. FUTURE RESEARCH

The methodology in the studies reported here has been QE-*un*aware, hence lacking crucial controls required to consolidate quantity's role in SCI. This leaves the issue of alternative hypotheses to the QE argument open until future studies design methods to incorporate QE data and theories. Numerous ways could assist in achieving this goal.

(a) *Design modifications*

- It is only the number of *males* that need be manipulated in future experiments, and done so only in the presence of a single female, in order to eliminate the effect of female availability. Additionally, it has to be the *same* male who is presented with the choice alternatives, since only the individual level is important, and thus individual differences in performance are crucial.
- Future designs should present graded multi-player scenarios, in which both absolute numbers as well as a wide range of ratios are examined, and subjects are forced to perform a comparison (as in [20,75]). Figure 1 graphically depicts the predictions of SC models in terms of QE. From 0 to 1 rivals, the situation is SCR, which is limitedly informative concerning QE. As the number of rivals exceeds 1, SCI can be assessed by either amount or quantity. If males estimate quantity (and conform to SC models' predictions), then we expect a decreasing linear relationship between the number of rivals and energy expenditure towards sperm traits or sexual behaviour. If males process amount, then the relationship is nonlinear, and depends

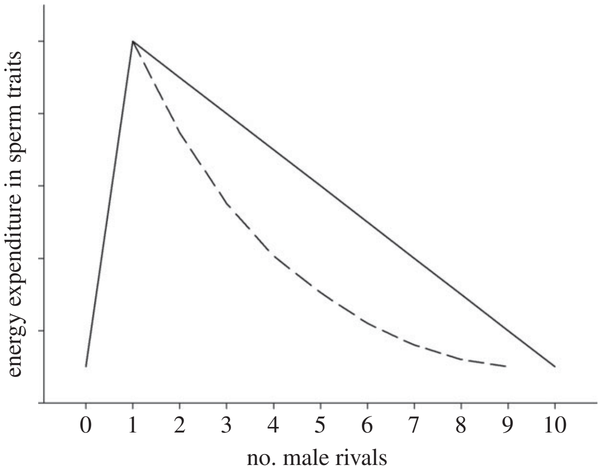

Figure 1. The relation between number of rival males and energy expenditure towards sperm traits as predicted by SC models.

on the nature of the amount cue used (figure 1 uses an arbitrary relationship, illustrating nonlinearity). Future work should be designed to generate data that could be inserted into graphs such as figure 1.

— Current designs boast a substantial variance in choice of observed traits, leading to non-unitary outcomes within and between species [17,26,29,45,93,95]. Future studies should establish a cohesion and standardization (enough to allow comparative studies), and observe a wide range of variables (as in [96]).

(b) *Choice of animal models*

— *Hermaphrodites*. Males are a minority in hermaphrodites, thus exposed to relaxed SC [97], yet theory still predicts sex allocation to respond to the actual number of rivals [98]. In simultaneous hermaphrodites, competitors are also potential partners, and therefore competition may occur between related and/or unrelated sperm [99]. In outcrossing simultaneous hermaphrodites, sex allocation depends on mating group size $K+1$, where K is the number of different sperm donors [100]. When $K=1$ (i.e. a single, self-fertilizing individual), there is local SC and an individual should invest minimally in sex allocation [16]. When $K>1$, things get complicated. If $K=2$, the effective mating group size depends on mating type: under cross-fertilization, mating group size is one and the optimal investment in sperm depends on the number of eggs of the partner. If both self- and cross-fertilizations occur, mating group size will be two, as sperm from both male functions compete for the fertilization of one's ova. With more individuals, competition scenarios complexify further [16]. While there is considerable amount of data on hermaphrodite sex allocation, investigating more closely the SC aspect, with an emphasis on the QE issue, should provide interesting observations.

An intriguing case is protandric-simultaneous hermaphrodites, where individuals reproduce first as males and later as simultaneous hermaphrodites [18,32]. Here there are two profoundly different QE phases, since in the first QE is performed by a male and in the second by a hermaphrodite. Exposing the same individual under these two phases to different number of rivals could provide precious data.

— *Spermatophore depositing species*. Spermatophores are interesting for QE because they are sperm encapsulated into discrete entities that can thus serve as a quantity cue. Spermatophores are used by both internal and external fertilizers, and for QE the question is whether rival males can detect them. If spermatophores are deposited internally, detection requires probing the female reproductive tract, thus making it, most likely, an amount cue. If spermatophores are deposited externally, then they can serve as a discrete quantity cue, facilitating counting. Additionally, spermatophore production time varies drastically across species and taxa, and can be remarkably swift [101], extremely slow [102] or impeding on remating interval [103]. Furthermore, there are data tying SC to spermatophore traits [42,104]. In several species, once a spermatophore is fully formed, males are committed to a fixed ejaculate expenditure [30]. This leads to several questions: When do these males form the decision leading to spermetophoregenesis? What is the quantity stimulus to which they respond, and what is the lag between formation and deposition? Will there be a deposition if there has been a change in the assessment of SCR/I in the interim between genesis and copula? Answering those questions could provide data discerning the role amount and quantity play in the estimation process, and might support the argument that QE is guiding the physiological changes in response to SC.

— *Diapause*. Multivoltine insects can have diapause larval development under harsh conditions, forcing differential energy allocation to hibernation and subsequent development. Consequently, individuals of different generations are expected to differ substantially in many traits, including spermatogenesis [65]. Comparing males of different diapause generations could elucidate the role of environmental amount/quantity cues on adults' SC performance.

9. CONCLUSION

Cognition can affect behaviour and physiology in a complex web of ecological and evolutionary parameters. Through this prism, I argue that males' response to SC is driven by their cognitive ability to gauge the magnitude of their competition. Thus, QE has improved males' sexual competitiveness and, reciprocally, SC has contributed to the complexification of QE. This discussion strengthens current models of sperm expenditure by highlighting the cognitive components shaping it. It also suggests that an evolutionary analysis of cognition within ecological and behavioural contexts may consolidate theories concerning phylogenetic complexification of cognitive systems.

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REFERENCES

1 Shifferman, E. M. 2009 Its own reward: lessons to be drawn from the reversed-reward contingency paradigm. *Anim. Cogn.* **12**, 547–558. (doi:10.1007/s10071-009-0215-2)

2 Shifferman, E. M. 2011 The evolution of quantity estimation in the animal kingdom. PhD Thesis, Tel Aviv University, Tel Aviv.

3 Shima, J. S. 2002 Mechanisms of density- and number-dependent population regulation of a coral-reef fish. *Mar. Fresh Res.* **53**, 175–179. (doi:10.1071/MF01133)
4 Parker, G. A. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525–567. (doi:10.1111/j.1469-185X.1970.tb01176.x)
5 Birkhead, T. R. & Møller, A. P. 1998 *Sperm competition and sexual selection*. San Diego, CA: Academic Press.
6 Simmons Leigh, W. 2001 *Sperm competition and its evolutionary consequences in the insects*. Princeton, NJ: Princeton University Press.
7 Wedell, N., Gage, M. J. G. & Parker, G. A. 2002 Sperm competition, male prudence and sperm-limited females. *Trends Ecol. Evol.* **17**, 313–320. (doi:10.1016/s0169-5347(02)02533-8)
8 Parker, G. A. 1982 Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J. Theor. Biol.* **96**, 281–294. (doi:10.1016/0022-5193(82)90225-9)
9 Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1996 Sperm competition games: individual assessment of sperm competition intensity by group spawners. *Proc. R. Soc. Lond. B* **263**, 1291–1297. (doi:10.1098/rspb.1996.0189)
10 Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1997 Sperm competition games: a prospective analysis of risk assessment. *Proc. R. Soc. Lond. B* **264**, 1793–1802. (doi:10.1098/rspb.1997.0249)
11 Ball, M. A. & Parker, G. A. 1998 Sperm-competition games: energy dependence and competitor numbers in the continuous-external-fertilization model. *IMA J. Math. Appl. Med. Biol.* **15**, 87–96. (doi:10.1093/imammb/15.1.87)
12 Byrne, P. G. 2004 Male sperm expenditure under sperm competition risk and intensity in quacking frogs. *Behav. Ecol.* **15**, 857–863. (doi:10.1093/beheco/arh098)
13 Schleicherová, D., Lorenzi, M. C., Sella, G. & Michiels, N. K. 2010 Gender expression and group size: a test in a hermaphroditic and a gonochoric congeneric species of Ophryotrocha (Polychaeta). *J. Exp. Biol.* **213**, 1586–1590. (doi:10.1242/jeb.041814)
14 Bonilla, M. M., Zeh, D. W., White, A. M. & Zeh, J. A. 2011 Discriminating males and unpredictable females: males bias sperm allocation in favor of virgin females. *Ethology* **117**, 740–748. (doi:10.1111/j.1439-0310.2011.01928.x)
15 Thomas, M. L. & Simmons, L. W. 2009 Male-derived cuticular hydrocarbons signal sperm competition intensity and affect ejaculate expenditure in crickets. *Proc. R. Soc. B* **276**, 383–388. (doi:10.1098/rspb.2008.1206)
16 Schärer, L. & Wedekind, C. 2001 Social situation, sperm competition and sex allocation in a simultaneous hermaphrodite parasite, the cestode *Schistocephalus solidus*. *J. Evol. Biol.* **14**, 942–953. (doi:10.1046/j.1420-9101.2001.00350.x)
17 Janicke, T. & Schärer, L. 2010 Sperm competition affects sex allocation but not sperm morphology in a flatworm. *Behav. Ecol. Sociobiol.* **64**, 1367–1375. (doi:10.1007/s00265-010-0951-y)
18 Schärer, L. & Ladurner, P. 2003 Phenotypically plastic adjustment of sex allocation in a simultaneous hermaphrodite. *Proc. R. Soc. Lond. B* **270**, 935–941. (doi:10.1098/rspb.2002.2323)
19 Lorenzi, M. C., Sella, G., Schleicherová, D. & Ramella, L. 2005 Outcrossing hermaphroditic polychaete worms adjust their sex allocation to social conditions. *J. Evol. Biol.* **18**, 1341–1347. (doi:10.1111/j.1420-9101.2005.00916.x)
20 Tan, G. N., Govedich, F. R. & Burd, M. 2004 Social group size, potential sperm competition and reproductive investment in a hermaphroditic leech, *Helobdella papillornata* (Euhirudinea: Glossiphoniidae). *J. Evol. Biol.* **17**, 574–580. (doi:10.1111/j.1420-9101.2004.00692.x)
21 Schleicherová, D., Lorenzi, M. C. & Sella, G. 2006 How outcrossing hermaphrodites sense the presence of conspecifics and suppress female allocation. *Behav. Ecol.* **17**, 1–5. (doi:10.1093/beheco/ari093)
22 Hosken, D. J. & Ward, P. I. 2001 Experimental evidence for testis size evolution via sperm competition. *Ecol. Lett.* **4**, 10–13. (doi:10.1046/j.1461-0248.2001.00198.x)
23 Bretman, A., Fricke, C. & Chapman, T. 2009 Plastic responses of male *Drosophila melanogaster* to the level of sperm competition increase male reproductive fitness. *Proc. R. Soc. B* **276**, 1705–1711. (doi:10.1098/rspb.2008.1878)
24 Fedorka, K. M., Winterhalter, W. E. & Ware, B. 2011 Perceived sperm competition intensity influences seminal fluid protein production prior to courtship and mating. *Evolution* **65**, 584–590. (doi:10.1111/j.1558-5646.2010.01141.x)
25 García-González, F. & Gomendio, M. 2004 Adjustment of copula duration and ejaculate size according to the risk of sperm competition in the golden egg bug (*Phyllomorpha laciniata*). *Behav. Ecol.* **15**, 23–30. (doi:10.1093/beheco/arg095)
26 Flay, C. D., He, X. Z. & Wang, Q. 2009 Influence of male density on the courtship and mating duration of male rice weevils, *Sitophilus oryzae*. *N. Z. Plant Prot.* **62**, 76–79.
27 Solensky, M. J. & Oberhauser, K. S. 2009 Male monarch butterflies, *Danaus plexippus*, adjust ejaculates in response to intensity of sperm competition. *Anim. Behav.* 77, 465–472. (doi:10.1016/j.anbehav.2008.10.026)
28 Schaus, J. M. & Sakaluk, S. K. 2001 Ejaculate expenditures of male crickets in response to varying risk and intensity of sperm competition: not all species play games. *Behav. Ecol.* **12**, 740–745. (doi:10.1093/beheco/12.6.740)
29 Thomas, M. L. & Simmons Leigh, W. 2007 Male crickets adjust the viability of their sperm in response to female mating status. *Am. Nat.* **170**, 190–195. (doi:10.1086/519404)
30 Gage, A. R. & Barnard, C. J. 1996 Male crickets increase sperm number in relation to competition and female size. *Behav. Ecol. Sociobiol.* **38**, 349–353. (doi:10.1007/s002650050251)
31 Carazo, P., Font, E., Forteza-Behrendt, E. & Desfilis, E. 2009 Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate? *Anim. Cogn.* **12**, 463–470. (doi:10.1007/s10071-008-0207-7)
32 Baeza, J. A. 2007 No effect of group size on sex allocation in a protandric-simultaneous hermaphroditic shrimp. *J. Mar. Biol. Assoc. UK* **87**, 1169–1174. (doi:10.1017/S0025315407057542)
33 Aspbury, A. S. 2007 Sperm competition effects on sperm production and expenditure in sailfin mollies, *Poecilia latipinna*. *Behav. Ecol.* **18**, 776–780. (doi:10.1093/beheco/arm044)
34 Evans, J. P. 2009 No evidence for sperm priming responses under varying sperm competition risk or intensity in guppies. *Naturwissenschaften* **96**, 771–779. (doi:10.1007/s00114-009-0529-6)
35 Candolin, U. & Reynolds, J. D. 2002 Adjustments of ejaculation rates in response to risk of sperm competition in a fish, the bitterling (*Rhodeus sericeus*). *Proc. R. Soc. Lond. B* **269**, 1549–1553. (doi:10.1098/rspb.2002.2055)
36 Smith, C. H., Reichard, M. & Jurajda, P. 2003 Assessment of sperm competition by European bitterling,

Rhodeus sericeus. *Behav. Ecol. Sociobiol.* **53**, 206–213. (doi:10.1007/s00265-002-0576-x)

37 Pilastro, A., Scaggiante, M. & Rasotto, M. B. 2002 Individual adjustment of sperm expenditure accords with sperm competition theory. *Proc. Natl Acad. Sci. USA* **99**, 9913–9915. (doi:10.1073/pnas.152133499)

38 Scaggiante, M., Rasotto, M. B., Romualdi, C. & Pilastro, A. 2005 Territorial male gobies respond aggressively to sneakers but do not adjust their sperm expenditure. *Behav. Ecol.* **16**, 1001–1007. (doi:10.1093/beheco/ari081)

39 Fuller, R. C. 1998 Sperm competition affects male behaviour and sperm output in the rainbow darter. *Proc. R. Soc. Lond. B* **265**, 2365–2371. (doi:10.1098/rspb.1998.0585)

40 Galeotti, P., Rubolini, D., Pupin, F., Sacchi, R., Altobelli, E., Nardi, P. A. & Fasola, M. 2009 Presence of rivals reduces mating probability but does not affect ejaculate size in the freshwater crayfish *Austropotamobius italicus*. *Behaviour* **146**, 45–68. (doi:10.1163/156853908x390922)

41 Verrell, P. A. 1983 The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Behav. Ecol. Sociobiol.* **13**, 307–313. (doi:10.1007/bf00299678)

42 McWilliams, S. R. 1992 Courtship behavior of the small-mouthed salamander (*Ambystoma texanum*): the effects of conspecific males on male mating tactics. *Behaviour* **121**, 1–19. (doi:10.1163/156853992X00417)

43 Byrne, P. G. & Roberts, J. D. 1999 Simultaneous mating with multiple males reduces fertilization success in the myobatrachid frog *Crinia georgiana*. *Proc. R. Soc. Lond. B* **266**, 717–721. (doi:10.1098/rspb.1999.0695)

44 delBarco-Trillo, J. H. & Ferkin, M. H. 2006 Male meadow voles respond differently to risk and intensity of sperm competition. *Behav. Ecol.* **17**, 581–585. (doi:10.1093/beheco/ark001)

45 Lemaître, J.-F., Ramm, S. A., Hurst, J. L. & Stockley, P. 2010 Social cues of sperm competition influence accessory reproductive gland size in a promiscuous mammal. *Proc. R. Soc. B* **278**, 1171–1176. (doi:10.1098/rspb.2010.1828)

46 Reznikova, Z. & Ryabko, B. 2011 Numerical competence in animals, with an insight from ants. *Behaviour* **148**, 405–434. (doi:10.1163/000579511x568562)

47 Rondeau, A. & Sainte-Marie, B. 2001 Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. *Biol. Bull.* **201**, 204–217. (doi:10.2307/1543335)

48 Siva-Jothy, M. T. & Stutt, A. D. 2003 A matter of taste: direct detection of female mating status in the bedbug. *Proc. R. Soc. Lond. B* **270**, 649–652. (doi:10.1098/rspb.2002.2260)

49 delBarco-Trillo, J. H. 2011 Adjustment of sperm allocation under high risk of sperm competition across taxa: a meta-analysis. *J. Evol. Biol.* **24**, 1706–1714. (doi:10.1111/j.1420-9101.2011.02293.x)

50 Kelly, C. D. & Jennions, M. D. 2011 Sexual selection and sperm quantity: meta-analyses of strategic ejaculation. *Biol. Rev.* **86**, 863–884. (doi:10.1111/j.1469-185X.2011.00175.x)

51 Bode, M. & Marshall, D. J. 2007 The quick and the dead? Sperm competition and sexual conflict in sea. *Evolution* **61**, 2693–2700. (doi:10.1111/j.1558-5646.2007.00232.x)

52 Engqvist, L. 2007 Male scorpionflies assess the amount of rival sperm transferred by females' previous mates. *Evolution* **61**, 1489–1494. (doi:10.1111/j.1558-5646.2007.00107.x)

53 Gelman, R. & Gallistel, C. R. 1978 *The child's understanding of number*. Cambridge, MA: Harvard University Press.

54 Arnold, K. & Zuberbühler, K. 2008 Meaningful call combinations in a non-human primate. *Curr. Biol.* **18**, R202–R203. (doi:10.1016/j.cub.2008.01.040)

55 Sandner, P. & Schärer, L. 2010 No plastic responses to experimental manipulation of sperm competition *per se* in a free-living flatworm. *Ethology* **116**, 292–299. (doi:10.1111/j.1439-0310.2010.01746.x)

56 Bierbach, D. *et al.* 2011 Male fish use prior knowledge about rivals to adjust their mate choice. *Biol. Lett.* **7**, 349–351. (doi:10.1098/rsbl.2010.0982)

57 Barry, K. L. & Kokko, H. 2010 Male mate choice: why sequential choice can make its evolution difficult. *Anim. Behav.* **80**, 163–169. (doi:10.1016/j.anbehav.2010.04.020)

58 Grant, J. W. A., Bryant, M. J. & Soos, C. E. 1995 Operational sex ratio, mediated by synchrony of female arrival, alters the variance of male mating success in Japanese medaka. *Anim. Behav.* **49**, 367–375. (doi:10.1006/anbe.1995.9998)

59 Reinhardt, K. 2001 Determinants of ejaculate size in a grasshopper (*Chorthippus parallelus*). *Behav. Ecol. Sociobiol.* **50**, 503–510. (doi:10.1007/s002650100398)

60 Yamane, T. & Miyatake, T. 2008 Strategic ejaculation and level of polyandry in *Callosobruchus chinensis* (Coleoptera: Bruchidae). *J. Ethol.* **26**, 225–231. (doi:10.1007/s10164-007-0051-2)

61 Martel, V., Damiens, D. & Boivin, G. 2008 Strategic ejaculation in the egg parasitoid *Trichogramma turkestanica* (Hymenoptera: Trichogrammatidae). *Ecol. Entomol.* **33**, 357–361. (doi:10.1111/j.1365-2311.2007.00973.x)

62 Loher, W. & Dambach, M. 1989 Reproductive behavior. In *Cricket behavior and neurobiology* (eds F. Huber, T. E. Moore & W. Loher), pp. 43–82. Ithaca, NY: Comstock Pub. Associates.

63 Immler, S., Pryke, S. R., Birkhead, T. R. & Griffith, S. C. 2010 Pronounced within-individual plasticity in sperm morphometry across social environments. *Evolution* **64**, 1634–1643. (doi:10.1111/j.1558-5646.2009.00924.x)

64 McNamara, K. B., Elgar, M. A. & Jones, T. M. 2010 Adult responses to larval population size in the almond moth, *Cadra cautella*. *Ethology* **116**, 39–46. (doi:10.1111/j.1439-0310.2009.01714.x)

65 Vermeulen, A., Engels, S., Engqvist, L. & Sauer, K. P. 2009 Phenotypic plasticity in sperm traits in scorpionflies (Mecoptera: Panorpidae): consequences of larval history and seasonality on sperm length and sperm transfer. *Eur. J. Entomol.* **106**, 347–352.

66 Meck, W. H. & Church, R. M. 1983 A mode control model of counting and timing processes. *J. Exp. Psychol. Anim. Behav. Proc.* **9**, 320–334. (doi:10.1037/0097-7403.9.3.320)

67 Walsh, V. 2003 A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn. Sci.* **7**, 483–488. (doi:10.1016/j.tics.2003.09.002)

68 Ziege, M., Mahlow, K., Hennige-Schulz, C., Kronmarck, C., Tiedemann, R., Streit, B. & Plath, M. 2009 Audience effects in the Atlantic molly (*Poecilia mexicana*): prudent male mate choice in response to perceived sperm competition risk? *Front. Zool.* **6**, 17. (doi:10.1186/1742-9994-6-17)

69 Pettersson, L. B., Ramnarine, I. W., Becher, S. A., Mahabir, R. & Magurran, A. E. 2004 Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* **55**, 461–468. (doi:10.1007/s00265-003-0727-8)

70 Montrose, T. V., Edwin Harris, W., Moore, A. J. & Moore, P. J. 2008 Sperm competition within a

dominance hierarchy: investment in social status vs. investment in ejaculates. *J. Evol. Biol.* **21**, 1290–1296. (doi:10.1111/j.1420-9101.2008.01570.x)

71 Oku, K. 2009 Effects of density experience on mate guarding behavior by adult male Kanzawa spider mites. *J. Ethol.* **27**, 279–283. (doi:10.1007/s10164-008-0117-9)

72 Bretman, A., Fricke, C., Hetherington, P., Stone, R. & Chapman, T. 2010 Exposure to rivals and plastic responses to sperm competition in *Drosophila melanogaster*. *Behav. Ecol.* **21**, 317–321. (doi:10.1093/beheco/arp189)

73 Stoltz, J. A. & Andrade, M. C. B. 2009 Female's courtship threshold allows intruding males to mate with reduced effort. *Proc. R. Soc. B* **277**, 585–592. (doi:10.1098/rspb.2009.1554)

74 Edward, D. A., Fricke, C. & Chapman, T. 2010 Adaptations to sexual selection and sexual conflict: insights from experimental evolution and artificial selection. *Phil. Trans. R. Soc. B* **365**, 2541–2548. (doi:10.1098/rstb.2010.0027)

75 de Jong, K., Wacker, S., Amundsen, T. & Forsgren, E. 2009 Do operational sex ratio and density affect mating behaviour? An experiment on the two-spotted goby. *Anim. Behav.* **78**, 1229–1238. (doi:10.1016/j.anbehav.2009.08.006)

76 Price, A. C. & Helen Rodd, F. 2006 The effect of social environment on male–male competition in guppies (*Poecilia reticulata*). *Ethology* **112**, 22–32. (doi:10.1111/j.1439-0310.2006.01142.x)

77 Mautz, B. S. & Jennions, M. D. 2011 The effect of competitor presence and relative competitive ability on male mate choice. *Behav. Ecol.* **22**, 769–775. (doi:10.1093/beheco/arr048)

78 Chapman, M. R. & Kramer, D. L. 1996 Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Anim. Behav.* **52**, 83–94. (doi:10.1006/anbe.1996.0154)

79 Keagy, J., Savard, J. F. & Borgia, G. 2011 Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Anim. Behav.* **81**, 1063–1070. (doi:10.1016/j.anbehav.2011.02.018)

80 Shohet, A. J. & Watt, P. J. 2009 Female guppies *Poecilia reticulata* prefer males that can learn fast. *J. Fish Biol.* **75**, 1323–1330. (doi:10.1111/j.1095-8649.2009.02366.x)

81 Lyons, C. & Barnard, C. J. 2006 A learned response to sperm competition in the field cricket, *Gryllus bimaculatus* (de Geer). *Anim. Behav.* **72**, 673–680. (doi:10.1016/j.anbehav.2005.12.006)

82 Matthews, R. N., Domjan, M., Ramsey, M. & Crews, D. 2007 Learning effects on sperm competition and reproductive fitness. *Psychol. Sci.* **18**, 758–762. (doi:10.1111/j.1467-9280.2007.01974.x)

83 Boogert, N. J., Fawcett, T. W. & Lefebvre, L. 2011 Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behav. Ecol.* **22**, 447–459. (doi:10.1093/beheco/arq173)

84 Clark, A. G. 2002 Sperm competition and the maintenance of polymorphism. *Heredity* **88**, 148–153. (doi:10.1038/sj.hdy.6800019)

85 Simmons, L. W. & García-González, F. 2008 Evolutionary reduction in testes size and competitive success in response to the experimental removal of sexual selection in dung beetles. *Evolution* **62**, 2580–2591. (doi:10.1111/j.1558-5646.2008.00479.x)

86 Hosken, D. J., Garner, T. W. J. & Ward, P. I. 2001 Sexual conflict selects for male and female reproductive characters. *Curr. Biol.* **11**, 489–493. (doi:10.1016/s0960-9822(01)00146-4)

87 Holland, B. & Rice, W. R. 1999 Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088. (doi:10.1073/pnas.96.9.5083)

88 Lickliter, R., Bahrick, L. E. & Markham, R. G. 2006 Intersensory redundancy educates selective attention in bobwhite quail embryos. *Dev. Sci.* **9**, 604–615. (doi:10.1111/j.1467-7687.2006.00539.x)

89 Johnstone, R. A. 1996 Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Phil. Trans. R. Soc. B* **351**, 329–338. (doi:10.1098/rstb.1996.0026)

90 Smith, C. C. & Ryan, M. J. 2010 Evolution of sperm quality but not quantity in the internally fertilized fish *Xiphophorus nigrensis*. *J. Evol. Biol.* **23**, 1759–1771. (doi:10.1111/j.1420-9101.2010.02041.x)

91 Nakatsuru, K. & Kramer, D. L. 1982 Is sperm cheap? Limited male fertility and female choice in the lemon Tetra (Pisces, Characidae). *Science* **216**, 753–755. (doi:10.1126/science.216.4547.753)

92 Pizzari, T., Worley, K., Burke, T. & Froman, D. 2008 Sperm competition dynamics: ejaculate fertilising efficiency changes differentially with time. *BMC Evol. Biol.* **8**, 332. (doi:10.1186/1471-2148-8-332)

93 Awata, S., Takeyama, T., Makino, Y., Kitamura, Y. & Kohda, M. 2008 Cooperatively breeding cichlid fish adjust their testis size but not sperm traits in relation to sperm competition risk. *Behav. Ecol. Sociobiol.* **62**, 1701–1710. (doi:10.1007/s00265-008-0598-0)

94 Vaughn, A. A. & Ferkin, M. H. 2011 The presence and number of male competitor's scent marks and female reproductive state affect the response of male meadow voles to female conspecifics' odours. *Behaviour* **148**, 927–943. (doi:10.1163/000579511x584375)

95 Vaughn, A. A., delBarco-Trillo, J. H. & Ferkin, M. H. 2010 Self-grooming by male meadow voles differs across copulation but is not affected by the risk and intensity of sperm competition. *Behaviour* **147**, 259–274. (doi:10.1163/000579509x12523920754410)

96 delBarco-Trillo, J. H. & Ferkin, M. H. 2007 Risk of sperm competition does not influence copulatory behavior in the promiscuous meadow vole (*Microtus pennsylvanicus*). *J. Ethol.* **25**, 139–145. (doi:10.1007/s10164-006-0008-x)

97 LaMunyon, C. W. & Ward, S. 1998 Larger sperm outcompete smaller sperm in the nematode *Caenorhabditis elegans*. *Proc. R. Soc. Lond. B* **265**, 1997–2002. (doi:10.1098/rspb.1998.0531)

98 Petersen, C. W. 1991 Sex allocation in hermaphroditic sea basses. *Am. Nat.* **138**, 650–667. (doi:10.1086/285240)

99 Schärer, L. 2009 Tests of sexual allocation theory in simultaneously hermaphroditic animals. *Evolution* **63**, 1377–1405. (doi:10.1111/j.1558-5646.2009.00669.x)

100 Charnov, E. L. 1982 *The theory of sex allocation*. Princeton, NJ: Princeton University Press.

101 Ootsubo, T. & Sakai, M. 1992 Initiation of spermatophore protrusion behavior in the male cricket *Gryllus bimaculatus* De Geer. *Zoo. Sci.* **9**, 955–969.

102 Locher, R. & Baur, B. 1999 Effects of intermating interval on spermatophore size and sperm number in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Ethology* **105**, 839–849. (doi:10.1046/j.1439-0310.1999.00452.x)

103 Reinhold, K. & Von Helversen, D. 1997 Sperm number, spermatophore weight and remating in the bushcricket *Poecilimon veluchianus*. *Ethology* **103**, 12–18. (doi:10.1111/j.1439-0310.1997.tb00002.x)

104 Voight, J. R. 2009 Differences in spermatophore availability among octopodid species (Cephalopoda: Octopoda). *Malacologia* **51**, 143–153. (doi:10.4002/040.051.0110)