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Essay

Sexual stereotypes: the case of sexual cannibalism

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There is a long-standing debate within the field of sexual selection regarding the potential projection of stereotypical sex roles onto animals by researchers. It has been argued that this anthropomorphic view may be hampering research in this area, for example by prioritizing the study of male sexual adaptations over female ones. We investigated how males and females are described in the sexual cannibalism literature. Sexual cannibalism is a specific form of sexual conflict and is highly gendered, with females generally cannibalizing males. We found that females were more likely to be described using active words and males with reactive words. This is contrary to recent results from a survey of the sexual conflict literature. While this reversed gender bias may arise from the nature of sexual cannibalism, our results nevertheless indicate an alternative form of sexual stereotyping. A number of the words used to describe cannibalistic females were highly loaded and suggestive of a negative stereotype of sexually aggressive females. To make progress we suggest first that animal behaviour researchers recognize both the costs and benefits of looking for general patterns as part of the scientific method. Although necessary, the search for general patterns may validate existing stereotypes or provide the basis for new ones. Additionally, we suggest that the field of sexual behaviour research is neither wholly bad nor good in terms of language use but that we should work towards a consensus of how and when we use particular terms to describe sexual behaviour.

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Research in animal behaviour faces the continual challenge posed by the fact that those of us doing the research are animals as well. The subjectivity provided by anthropomorphism (endowing nonhuman animals with human-like attributes), zoomorphism (the converse, endowing humans with nonhuman animal-like attributes), and the sociocultural surroundings researchers finds themselves in, can bias what research is done, how it is done and how the resulting data are interpreted. While no means unique to animal behaviour (or indeed biology), the problem of maintaining scientific objectivity is perhaps more immediate in behavioural research, especially when that research crosses human and nonhuman animal boundaries (e.g. in primatology; for an influential critique see Kennedy 1992). Perhaps the clearest case in point concerns the study and interpretation of sexual behaviour in nonhuman animals (presented in detail by Zuk 2003). Since the resurgence of interest in sexual selection and related phenomena following Trivers's (1972) seminal paper, there have been repeated calls for the terminology and language used to describe or explain sexual behaviour to be free from either anthropomorphic

connotations (avoiding such words as 'rape' or 'homosexuality': Gowaty 1982; Bailey & Zuk 2009) or stereotypical sex roles that might have more to do with prevailing human cultural norms than biological reality (Gowaty 1982; Hrdy 1986; Martin 1991; Zuk 1993; Fox Keller 2004).

Recently, Karlsson Green & Madjidian (2011) extended the critique of how we use language by surveying the sexual conflict literature and scoring the language used in describing sexually antagonistic traits in males and females. Sexual conflict is said to occur when the optimum value of a given trait differs for males and females (Parker 1979; see Arnqvist & Rowe 2005 for a thorough review). Sexual conflict is therefore the result of conflicting patterns of selection in the two sexes, selection that may be the result of natural selection (in the narrow sense, i.e. fertility and viability selection: Endler 1986), sexual selection (Andersson 1994) or both. Depending on the traits involved, the sexually antagonistic selection underpinning sexual conflict may engender cycles of sexually antagonistic coevolution (SAC: Rice 1996; Rice & Holland 1997), as females and males in turn evolve trait values that change the pattern of selection in the other sex. Alternatively, sexually antagonistic selection may be resolved without prolonged coevolution (for instance through the sex-limited expression of genes associated with sexual dimorphism: Fairbairn et al. 2007). Sexual conflict may arise over any trait, but conflicts over parental care and over mating have perhaps attracted the most attention

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(the evolution of sexual dimorphism notwithstanding), with sexual conflict over mating having perhaps the biggest impact in behavioural ecology in recent years (Chapman et al. 2003; Arnqvist & Rowe 2005; Tregenza et al. 2006).

Karlsson Green & Madjidian (2011) showed in their survey of the most cited papers on sexual conflict that male traits were more likely to be described using 'active' words, whereas female traits were more likely to be described with 'reactive' words, that is, in terms of female traits being a response to male behaviours or male-imposed costs. They ascribed this difference (at least in part) to the anthropomorphic imposition of conventional sex roles on animals by researchers (caricatured as males active, females passive). They argued that maintaining or propagating stereotypical gender roles is detrimental to the field of sexual conflict as a whole, stifling new ideas and discoveries (see also Madjidian & Karlsson Green 2012).

The original Karlsson Green & Madjidian (2011) paper has already been discussed by Perry & Rowe (2012), particularly in terms of their treatment of the theory base (for a response see Madjidian & Karlsson Green 2012). In this paper, we do not wish to add to that critique; instead we would like to add to the more general conversation about how we use words when studying sexual behaviour. Although they briefly mention it in their discussion (Karlsson Green & Madjidian 2011, page 905), one particularly notable instance of sexual conflict did not appear in the 30 most cited papers and thus was not covered in their literature survey: sexual cannibalism. Sexual cannibalism can, at least in some cases, be seen as an extreme example of a conflict of interest between the sexes. It is usually defined as an individual of one sex killing and consuming a conspecific individual of the other sex before, during or after copulation (with the female typically being the cannibal: Elgar 1992). Sexual cannibalism is generally much rarer than other forms of cannibalism (Elgar 1992), and has a fairly limited distribution taxonomically, occurring most widely in spiders and other arachnids (Elgar 1992), but also in insects such as mantids (Lawrence 1992), dipterans (Downes 1978) and orthopterans (Johnson et al. 1999; for a review see Elgar 1992) and potentially in cephalopods (C. Widmer, personal communication). Sexual cannibalism of females by males is not unknown but it is much rarer, having been recorded in crustaceans (Elgar 1992; Dick 1995; Tsai & Dai 2003) and in two species of spider (Schutz & Taborsky 2005; Aisenberg et al. 2011).

There are several hypotheses for the evolutionary origin of sexual cannibalism. First, it has been suggested that sexual cannibalism is adaptive to females, either as part of an adaptive foraging strategy (Newman & Elgar 1991) or as an extreme form of mate choice (Elgar & Nash 1988; Prenter et al. 2006). Under these scenarios, sexual cannibalism is not the optimal outcome for the male, and so there is sexual conflict over sexual cannibalism. Second, sexual cannibalism may be adaptive for males if it increases their likelihood of gaining fertilizations and/or if the female gains nutritional benefits from consuming the male (Buskirk et al. 1984; Andrade 1996). The extent to which there is sexual conflict will be determined by factors that influence the costs and benefits to males of being eaten, such as the likelihood of a male encountering multiple partners (i.e. opportunity costs of cannibalism) and the (related) extent to which females mate multiply. Therefore, under some circumstances there will be no conflict between the sexes. Third, sexual cannibalism may not be adaptive for either males or females, arising instead as a by-product of selection for aggressiveness in juveniles: the 'aggressive spillover' hypothesis (Gould 1984; Arnqvist & Henriksson 1997). Under this scenario, there would be no sexual conflict over sexual cannibalism (although one might argue that there would be conflict over female aggression).

Here, using similar methods to Karlsson Green & Madjidian (2011), we surveyed the sexual cannibalism literature to look for patterns of language bias when describing behaviour. We assessed which terms were used to describe the way in which males and females respond to each other, and whether there was a gender bias in active or reactive terms. Sexual cannibalism provides a useful counterpoint for the study of language use and sex role stereotypes for two reasons. First, such extreme behaviour (i.e. the consumption of partners), whether on purpose or not, might be expected to result in the use of strong, colourful or emotive language. Second, in the majority of cases it is the male being cannibalized by the female. Thus the sexual cannibalism literature might be expected to provide an interesting exception to the patterns of language bias found in the sexual conflict literature as a whole, as females should take an ostensibly active role in the process. However, if the active male/passive female stereotype is truly pervasive, we may predict active words again to be associated with male behaviours.

METHODS

Literature Search: Sexual Cannibalism Terminology

We searched ISI Web of Science (Thomson Reuters) using the search term 'sexual cannibalism' (initial search undertaken in February 2012; search used for analysis 17 September 2012). This search resulted in 556 papers. However, not all of these papers were relevant to our study: the search also brought up papers on other types of cannibalism (e.g. filial cannibalism in fishes) and infanticide in primates. Those papers deemed not relevant were removed from the list, leaving 210 papers. Following Karlsson Green & Madjidian (2011), we initially took the 30 most-cited papers, including reviews, empirical papers and theoretical studies. However, these 30 most-cited papers (not counting reviews) considered only 13 species. Therefore, we went further down the list in order of citations adding studies that added a new species until we had a total of 30 study species, from a total of 47 papers (number of citations per paper ranged from 17 to 152; see Table A1 in Appendix 1). Of the 43 nonreview papers, 17 studies were concerned with cannibalism during and after copulation (postcopulatory cannibalism), whereas 26 studies considered species in which cannibalism may occur before copulation (precopulatory cannibalism; Table A1 in Appendix 1). The four review papers all included references to both pre- and postcopulatory cannibalism. In terms of the taxonomic coverage, 23 of the species were spiders (35 papers and two reviews), six were mantids (six papers) and one was an orthopteran (one paper, concerning the sagebrush cricket, *Cyphoderris strepitans*). Two of the papers contained mathematical models of the evolution of sexual cannibalism: Buskirk et al. (1984) modelled postcopulatory cannibalism in which males could increase their inclusive fitness by allowing themselves to be cannibalized, while Newman & Elgar (1991) modelled precopulatory cannibalism as a female foraging strategy. In addition, Arnqvist & Henriksson (1997) presented a verbal model that considered precopulatory cannibalism as an indirect result of selection on high female aggression in earlier life stages. See Table A1 in Appendix 1 for the full list of references and study species.

In their paper, Karlsson Green & Madjidian (2011) selected terms used to describe sexually antagonistic traits. Here, for each paper we recorded the words used to describe males and females, and the words used to describe behaviours performed by either sex during cannibalistic or potentially cannibalistic sexual interactions. As such there was some judgement involved in which words we

selected for analysis. For instance, we decided to exclude any purely descriptive words such as 'approach' and 'kill', and several words associated with the act of eating, such as 'eat', 'decapitate' and 'cannibalize' (as this word came up in almost every paper in our list). We also excluded the word 'devour', again because of its association with eating, although some may argue this is also potentially a loaded term (or at least unnecessarily colourful). Across all papers surveyed, we identified 72 terms used to describe the behaviour of males and females during sexual cannibalism. After excluding those terms not deemed relevant, we were left with a list of 49 valid terms (see Appendix 2 for the excluded words). Each word was scored once for each paper, so that the frequency of use within each paper was not recorded.

Once we had identified our terms we asked three independent parties to classify them as active, reactive or neutral (for a full description of the meanings of active, reactive and neutral see Karlsson Green & Madjidian 2011). Any words classified differently by two people were excluded from the analysis, leaving us with 31 consistently classified terms: 13 active, 11 reactive and seven neutral. We then performed chi-square tests to determine whether the usage of active and reactive terms varied for males and females. We note that there is the potential for pseudoreplication in these kinds of data: terms used in the same paper may not be independent of each other, and word use among papers written by the same authors might also not be independent. However, our main aim was to explore the association between words and gender that might be experienced by readers of those papers as a whole, rather than ascribe a given level of gender bias (if present) to a particular paper or author.

RESULTS

Active words were significantly more likely to be used to describe females than males in the context of sexually cannibalistic behaviour (chi-square test: $\chi_1^2 = 13.78$, $P < 0.001$; Table 1, Fig. 1). Likewise, reactive words were significantly more likely to be used to describe males ($\chi_1^2 = 33.98$, $P < 0.001$). In terms of neutral and unclassified words, females were significantly more likely to be described using neutral words than males ($\chi_1^2 = 3.86$, $P = 0.049$), but significantly less likely to be described using unclassified (i.e. equivocal) words than males ($\chi_1^2 = 43.2$, $P < 0.001$).

We also considered papers concerning pre- and post-copulatory cannibalism separately, as there are different theories regarding their adaptive significance and so we expected there to be different language used when describing behaviour, especially for males. The patterns of language were the same as the above in both subsets (females more likely to be described with active words and males with reactive words: all $P < 0.03$). Considering specific words though did reveal some interesting patterns of usage (Fig. 2). For example, while words such as 'sacrifice', 'suicide' and 'complicit' were used to describe males with similar frequency across both groups (Fig. 2), words such as 'caution' and 'avoid' were more commonly used in species with

precopulatory cannibalism. For females, 'rapacious' and 'indiscriminate' were only used in reference to precopulatory species, and these species were more commonly termed 'voracious'. In contrast the words 'attack' 'aggressive' and 'predatory' were used similarly across instances of pre- and postcopulatory cannibalism.

DISCUSSION

Among the most highly-cited papers in the field of sexual cannibalism, females are more likely to be described using active terms, whereas males are more likely to be described in reactive terms. This is in contrast to a survey of the more general sexual conflict literature presented by Karlsson Green & Madjidian (2011), which found the opposite result: males are typically portrayed as the active sex while females are portrayed as the reactive sex (Fig. 1). Instead, our results confirm the caveat that Karlsson Green & Madjidian (2011) themselves included in their paper, namely that a gender bias in the use of language may depend upon which particular sexual conflict is being studied. As such, our results argue against there being a general male–female sexual stereotype that pervades all studies of sexual conflict. However, as we discuss below our results do not necessarily contradict the broader point that language may reflect or influence sexual stereotyping.

Within the phenomenon that is sexual cannibalism, there is a clear distinction between cannibalism that occurs before copulation and cannibalism that occurs during or after copulation (Elgar & Schneider 2004). Our survey shows that authors have used slightly different language in these two instances. For example, in species that show precopulatory cannibalism, males are more likely to be described as 'cautious' and 'avoiding' females, compared to species that show postcopulatory cannibalism. The words 'rapacious' and 'indiscriminate' were used exclusively in reference to females showing precopulatory cannibalism, and these females were more likely to be termed 'voracious'. This may follow from the nature of cannibalism in these species: precopulatory cannibalism cannot be adaptive for males, and so cannibalism is hypothesized to represent a female foraging strategy (Newman & Elgar 1991) or emerge as a by-product of selection on female aggression (Gould 1984; Arnqvist & Henriksson 1997). If cannibalism is not considered in the male's interest, then male–female interactions are perhaps more likely to be interpreted a certain way: aggressive, predatory females killing cautious, helpless males.

Yet for other terms the usage is not so straightforward. Words such as 'sacrifice', 'suicide' and 'complicit' were used at similar frequencies to describe males being cannibalized before or after copulation. The terms 'attack', 'aggressive' and 'predatory' were also used similarly to describe females across the different timings of cannibalism. But why should precopulatory cannibalism by a female also be described as male 'sacrifice'? The phrase 'male sacrifice' or 'male suicide' might be taken to imply that there is some benefit to the male from being cannibalized (despite the lack of evidence for such a benefit). Here then is an example of how words might lead to an implicit inference about behaviour being presented, whether deliberately so by the authors or not.

To what extent is the language used in studies of sexual cannibalism justified? Let us consider males first. In the Australian red-back spider, *Latrodectus hasselti*, males appear to perform a 'somersault' during mating that brings their abdomen within reach of the female's jaws, and they are subsequently cannibalized (Forster 1992; Andrade 1996). This behaviour occurs in all copulations observed, and results in male death (Forster 1992). Phrases such as 'male suicide' and 'self-sacrifice' might seem reasonable to describe a behaviour that seems unequivocal: the male does appear to present himself to the female. However, 'suicide' and 'self-

Table 1
Frequency of terms used to describe males and females across the 47 papers used in our study

	All words	Active	Reactive	Neutral	Unclassified
N	49	13	11	7	18
Male	203	43	56	8	96
Females	136	85	9	18	24

There were 49 terms in total. Each term was scored once for each sex if it appeared in a paper. Words in the unclassified category are those that were not classified the same by three independent parties.

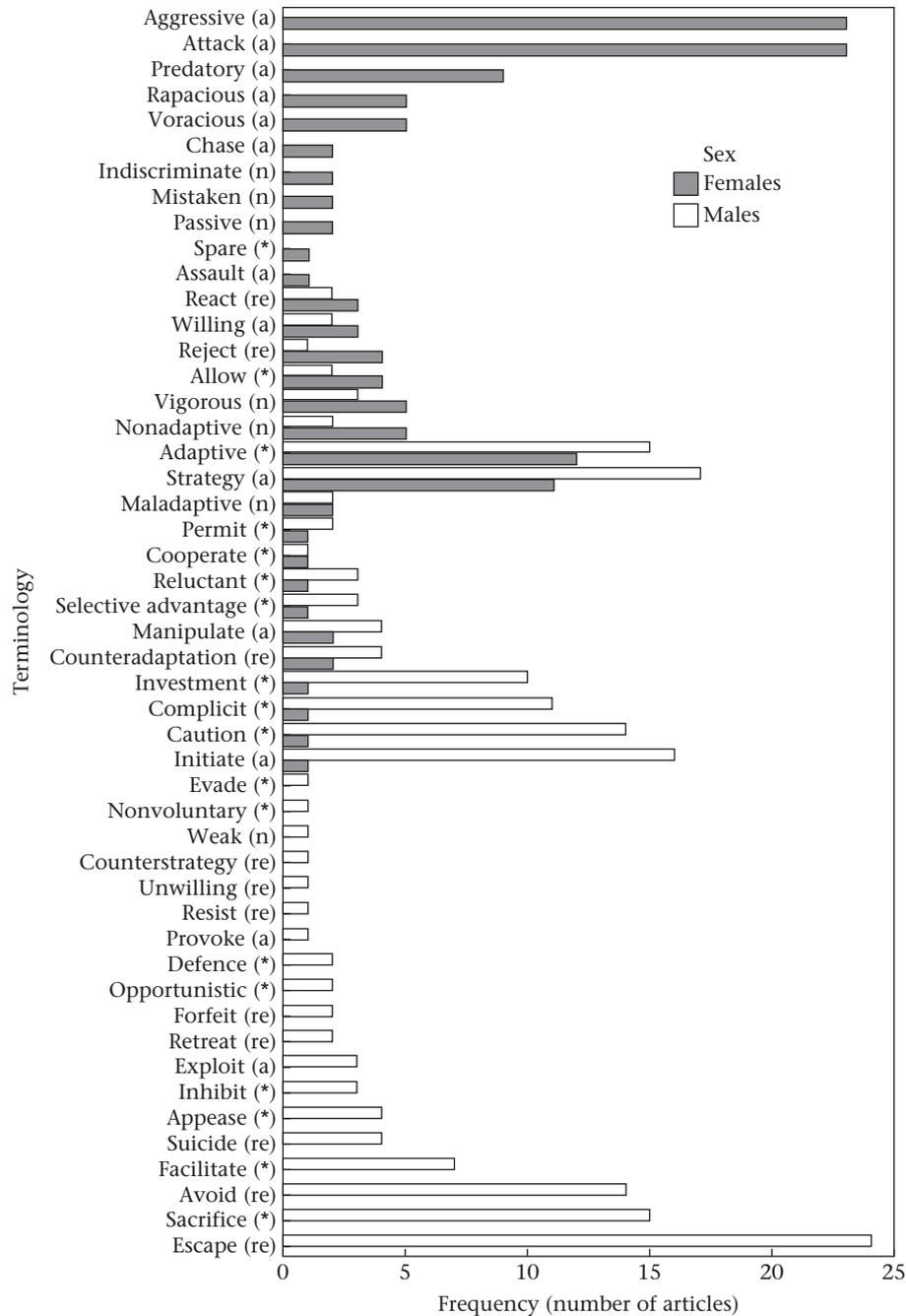


Figure 1. Frequency of terms used when describing male and female behaviour of sexually cannibalistic species across the 47 articles surveyed (30 most cited articles, plus 17 further studies). See the appendices for references and excluded words. The frequency for each sex is the number of articles the term appears in, in the context of describing behaviour. Words were also classified by three independent observers as active (a), reactive (re) or neutral (n). Terms marked with an asterisk were classified differently by at least two of the parties and so could not be given an overall classification.

sacrifice' are rather loaded terms. As mentioned above, 'sacrifice' might imply a benefit to males. Alternatively, the use of 'sacrifice' may present males in a rather noble, selfless manner (to be contrasted with the female sexual predator). Finally, such terms at the very least suggest a level of anthropomorphic goal orientation we should be wary of (Kennedy 1992). Instead, why not just say that males present themselves to females during copulation with a particular manoeuvre?

In terms of the words used to describe females, while sexual cannibalism is predicated on the fact that one of the pair ends up being the meal of the other, some of the words used to describe

female behaviour are a long way short of being value free: for instance, females have been called 'voracious' or 'rapacious' more than once. Moreover, if we are concerned with either the causes or consequences of negative sexual stereotyping more generally, the use of such words suggests that there may be scant comfort in our findings here of the assignment of active agency to female animals in the context of sexual cannibalism. Not least this is because it is well-known across human culture that sexually aggressive or violent females are themselves a negative stereotype: from the Gorgons of Greek myth to the femme fatale, the 'black widow' or the 'lethal seductress' of today (Sjoberg &

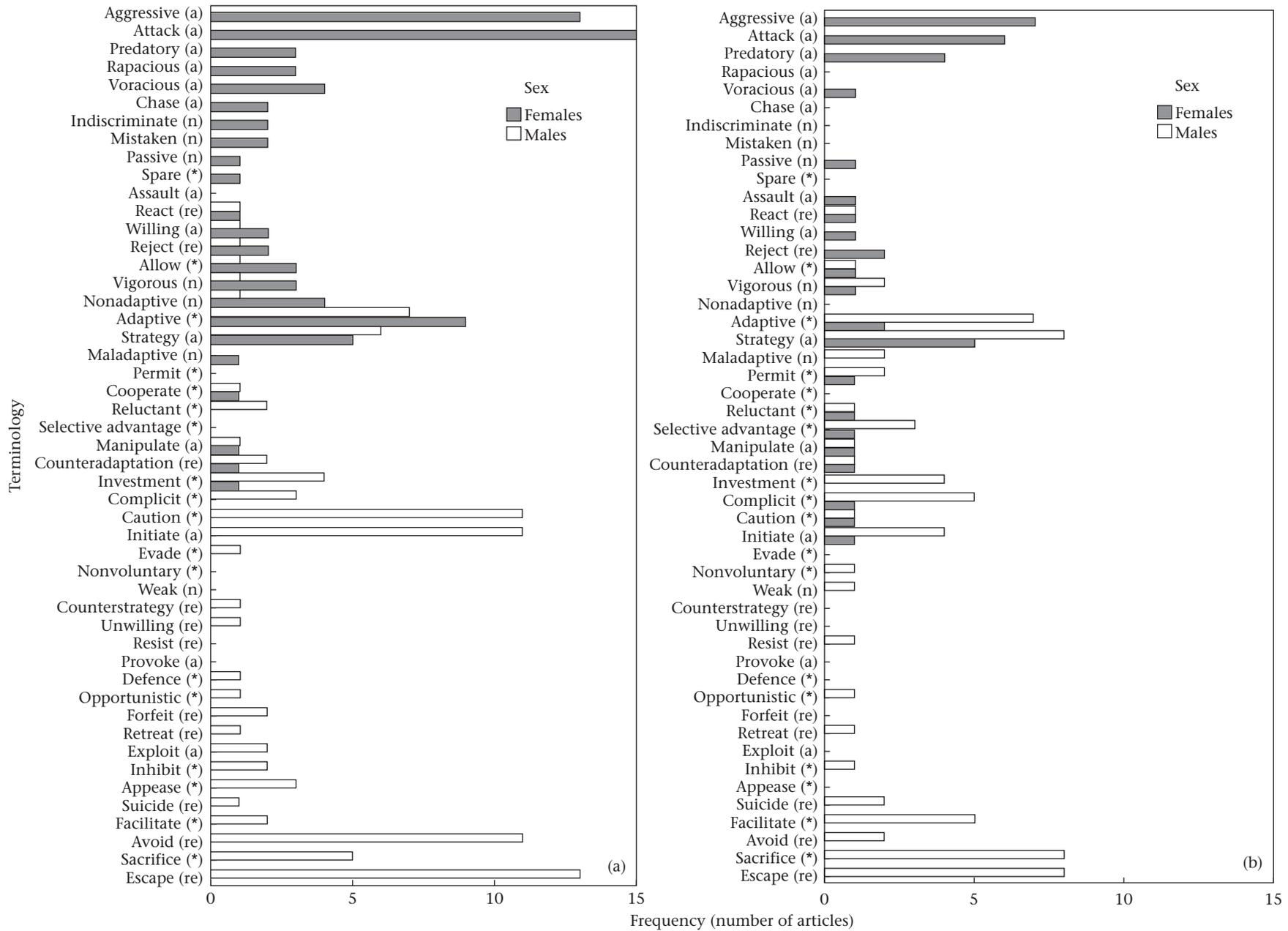


Figure 2. Frequency of terms used when describing male and female behaviour of sexually cannibalistic species considered separately for (a) studies in which cannibalism occurs before and/or during copulation (26 papers) and (b) studies in which cannibalism occurs only during and/or after copulation (17 papers), excluding reviews. See the appendices for references and excluded words. The frequency for each sex is the number of articles the term appears in, in the context of describing behaviour. Words were also classified by three independent observers as active (a), reactive (re) or neutral (n). Terms marked with an asterisk were classified differently by at least two of the parties and so could not be given an overall classification.

Gentry 2008). These negative stereotypes are clear in many forms of modern entertainment (e.g. film noir: Boozer 1999) and also in the media, where they may engender narratives that both reflect and influence associations between sexuality, gender and violence (Oliver 2007; Sjöberg & Gentry 2008). As such we appear to be in something of a dilemma when it comes to sexual behaviour and gender, caught between different negative stereotypes of females.

To help us go forward and address dilemmas such as this, we wish to make three points. First, we need to discriminate between looking for general patterns and stereotyping. As scientists, much of what we do is to look for general patterns in the natural world, from which theory and eventually understanding can be drawn. According to the Oxford English Dictionary on the other hand (online version: www.oed.com), a stereotype is 'a preconceived and oversimplified idea of the characteristics which typify a person, situation, etc.'. Clearly there is potential for tension here: an unsophisticated grasp of general patterns might lead to preconceptions or oversimplifications, yet the search for simple rules is also a valid one. Only history can tell us how well we get the balance right in any particular case. However, this is to frame the discussion only in terms of academic research. The dialogue between academic and nonacademic communities is also of concern (e.g. Barron & Brown 2012; Madjidian & Karlsson Green 2012). First and foremost, scientists may bring preconceptions and oversimplifications from their sociocultural surroundings, with 'general principles' merely serving to validate those preconceptions. This will forever be an inescapable part of science, and something that we must always be aware of and try and guard against as much as we can. However, there is also the concern that scientific findings about sexual behaviour (or indeed anything else) may travel the other way and provide the basis for sociocultural norms that are chauvinistic, demeaning, or that justify oppression and violence towards some members of society (for instance women or in terms of sexual identity: Barron & Brown 2012). While animal behaviour researchers cannot change the natural world to fit any particular cultural worldview, we can be careful about how we present that natural world to the nonacademic community and avoid easy sensationalism (Barron & Brown 2012). We suggest that the key message that we should put across is that there are no easy lessons about how we should live or love to be learned from nonhuman animals (Huxley 1893; Zuk 2003).

Second, we need to remain grounded on the extent to which progress has been impeded by the cultural baggage of researchers. Even though we accept the critiques of how research into sexual behaviour has progressed since Darwin (1871; e.g. Cronin 1991; Birkhead 2010), clearly there has been considerable progress in our understanding of animal sexual behaviour and mating systems (for example as reviewed in major edited volumes and monographs: Bateson 1983; Thornhill & Alcock 1983; Bradbury & Andersson 1987; Birkhead & Møller 1993; Andersson 1994; Eberhard 1996; Simmons 2001; Arnqvist & Rowe 2005; Oliveira et al. 2008; Leonard & Córdoba-Aguilar 2010). Perhaps ironically, the rise of one particular cultural artefact, feminism, may well have helped contribute to this progress (Hrdy 1986; Fox Keller 2004). This is neither to be complacent of future progress nor to suggest that we currently have all the answers. Such confidence would be foolish, and the last few years have shown that there is still plenty to talk about (e.g. Roughgarden & Akçay 2010; Shuker 2010; Rubenstein 2012). But it would also be wrong to overinterpret current trends and fashions. For instance, Madjidian & Karlsson Green (2012) are correct to point out that the wonderful review of Bonduriansky (2001) on male mate choice has helped make male mate choice a 'hot topic' (in their words). And we recommend that review paper

unreservedly. But hot topics are themselves as much a phenomenon of how we do science as anything else, providing something new (or at least something old enough to have received limited attention for a while) to write grants and papers about. In terms of sexual selection, the problem that females have been ignored in studies of sexual mating systems has been addressed at least three times over the last three decades or so, from the initial renaissance of female mate choice in the early 1980s (e.g. Bateson 1983; Bradbury & Andersson 1987), the appreciation of the role of females in postcopulatory sexual selection in the early to middle 1990s (e.g. Birkhead & Møller 1993; Eberhard 1996), to the current revival of interest in females in sexual selection (e.g. Clutton-Brock 2007, 2009; Rosvall 2011; Rubenstein 2012). In summary, we think animal behaviour researchers have made, and will continue to make, significant advances in how we understand the reproductive behaviour of animals, and that the role of females has actually been increasingly appreciated since Trivers (1972; Bonduriansky 2011). As highlighted by Perry & Rowe (2012), those advances are perhaps most clearly seen in terms of our theory.

Third, while we fully recognize the risks presented to our thinking and understanding by the traps laid for us by our own societal influences and cultural baggage (Karlsson Green & Madjidian 2011), we would hope that does not necessitate the removal of all words and terminology beyond the starkest of descriptions of behaviour. Words are powerful, but while we need to be aware of the implications they carry we need not be beholden to them. For instance, consider the widespread acceptance of one phrase that was previously considered loaded: mate choice. The typical definition for mate choice is now generally given as any aspect of the phenotype of one sex that leads to nonrandom mating success of the other (after Halliday 1983; Maynard Smith 1987). The phenotype may be behavioural, physiological or morphological. Importantly, that mate choice can result from a phenotype need not be the evolutionary cause of that phenotype (Maynard Smith 1987), an awareness of which perhaps deflects criticism of the potentially goal-oriented nature of the word (Kennedy 1992). Given what has happened over the last 30 years or so, one might argue that emancipating 'choice' from only 'conscious' (i.e. human) decision making allowed modern studies of mate choice to flourish (Bateson 1983; Andersson 1994). Moreover, when we realized how morphology and physiology could act as arbiters of choice (particularly female reproductive tracts: Eberhard 1996), so the full extent of female agency in sexual selection became clearer. Choice has thus proved a useful word to cover the sexual selection outcomes engendered by all these phenotypes, once freed from the anthropomorphic baggage about conscious choice, aesthetics and so on, and progress has probably been swifter for it. We therefore join Perry & Rowe (2012) in urging the animal behaviour community not necessarily to proscribe words, but rather to encourage consensus in how we define behaviours and the contexts in which we use them. Some words will be easier to reach consensus on than others (probably not 'rapacious' for example), but we should also not delude ourselves that words will not continue to have double lives. The authors of this paper are happy to be thought of as animals, but not necessarily happy to be thought of as *animals*.

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Appendix 1. Literature used in terminology analysis

Table A1

The 47 papers used in our literature survey, including species studied and the type of cannibalism

Author	Title	Times cited	Class	Family	Species	Pre- or postcopulatory cannibalism?	Notes
Andrade 1996	Sexual selection for male sacrifice in the Australian redback spider	152	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Andrade 1998	Female hunger can explain variation in cannibalistic behaviour despite male sacrifice in redback spiders	46	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Andrade 2003	Risky mate search and male self-sacrifice in redback spiders	65	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Andrade & Banta 2002	Value of male remating and functional sterility in redback spiders	67	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Arnqvist & Henriksson 1997	Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints	73	Arachnida	Pisauridae	<i>Dolomedes fimbriatus</i>	Pre	Includes verbal model
Barry et al. 2008	Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity	19	Insecta	Mantidae	<i>Pseudomantis albobimbriata</i>	Pre	
Birkhead et al. 1988	Sexual cannibalism in the praying mantis <i>Hierodula membranacea</i>	55	Insecta	Mantidae	<i>Hierodula membranacea</i>	Pre	
Brautigam & Persons 2003	The effect of limb loss on the courtship and mating behaviour of the wolf spider <i>Pardosa milvina</i> (Araneae: Lycosidae)	18	Arachnida	Lycosidae	<i>Pardosa milvina</i>	Pre	
Buskirk et al. 1984	The natural selection of sexual cannibalism	71	N/A	N/A	N/A	Post	Model
Elgar 1991	Sexual cannibalism, size dimorphism and courtship behaviour in orb-weaving spiders (Araneidae)	63	Arachnida	Araneidae	Orb-weaver sp.	Pre	

Table A1 (continued)

Author	Title	Times cited	Class	Family	Species	Pre- or postcopulatory cannibalism?	Notes
Elgar 1992	Sexual cannibalism in spiders and other invertebrates	129	N/A	N/A	N/A	N/A	Review
Elgar et al. 2000	Female control of paternity in the sexually cannibalistic spider <i>Argiope keyserlingi</i>	80	Arachnida	Araneidae	<i>Argiope keyserlingi</i>	Post	
Elgar & Fahey 1996	Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider <i>Nephila plumipes</i> Latreille (Araneae: Araneoidea)	57	Arachnida	Araneidae	<i>Nephila plumipes</i>	Pre	
Elgar & Nash 1988	Sexual cannibalism in the garden spider <i>Araneus diadematus</i>	69	Arachnida	Araneidae	<i>Araneus diadematus</i>	Pre	
Elgar & Schneider 2004	Evolutionary significance of sexual cannibalism	50	N/A	N/A	N/A	N/A	Review
Elias et al. 2005	Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae : Salticidae)	36	Arachnida	Salticidae	<i>Habronattus dossenus</i>	Pre	
Fahey & Elgar 1997	Sexual cohabitation as mate-guarding in the leaf-curling spider <i>Phonognatha graeffei</i> Keyserling (Araneoidea, Araneae)	30	Arachnida	Araneidae	<i>Phonognatha graeffei</i>	Post	
Foellmer & Fairbairn 2003	Spontaneous male death during copulation in an orb-weaving spider	26	Arachnida	Araneidae	<i>Argiope aurantia</i>	Post	
Forster 1992	The stereotyped behaviour of sexual cannibalism in <i>Latrodectus hasselti</i> Thorell (Araneae, Theridiidae), the Australian redback spider	61	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Fromhage & Schneider 2005	Safer sex with feeding females: sexual conflict in a cannibalistic spider	41	Arachnida	Araneidae	<i>Nephila fenestrata</i>	Pre	
Fromhage & Schneider 2006	Emasculation to plug up females: the significance of pedipalp damage in <i>Nephila fenestrata</i>	39	Arachnida	Araneidae	<i>Nephila fenestrata</i>	Pre	
Fromhage et al. 2003	Fitness consequences of sexual cannibalism in female <i>Argiope bruennichi</i>	34	Arachnida	Araneidae	<i>Argiope bruennichi</i>	Post	
Gaskett et al. 2004	Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae : Araneidae)	44	Arachnida	Araneidae	<i>Argiope keyserlingi</i>	Post	
Huber 2005	Sexual selection research on spiders: progress and biases	86	N/A	N/A	N/A	N/A	Small section on sexual cannibalism
Johnson 2001	Sexual cannibalism in fishing spiders (<i>Dolomedes triton</i>): an evaluation of two explanations for female aggression towards potential mates	46	Arachnida	Pisauridae	<i>Dolomedes triton</i>	Pre	
Johnson & Sih 2005	Precopulatory sexual cannibalism in fishing spiders (<i>Dolomedes triton</i>): a role for behavioural syndromes	61	Arachnida	Pisauridae	<i>Dolomedes triton</i>	Pre	
Johnson et al. 1999	Female remating propensity contingent on sexual cannibalism in sagebrush crickets, <i>Cyphoderris strepitans</i> : a mechanism of cryptic female choice	26	Insecta	Prophalangopsidae	<i>Cyphoderris strepitans</i>	Post	Nonlethal cannibalism
Knoflach & van Harten 2001	<i>Tidarren argo</i> sp nov (Araneae : Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism	50	Arachnida	Theridiidae	<i>Tidarren argo</i>	Post	
Kynaston et al. 1994	Courtship, mating behaviour and sexual cannibalism in the praying mantis, <i>Sphodromantis lineola</i>	26	Insecta	Mantidae	<i>Sphodromantis lineola</i>	Pre	
Lawrence 1992	Sexual cannibalism in the praying mantid, <i>Mantis religiosa</i> : a field study	52	Insecta	Mantidae	<i>Mantis religiosa</i>	Pre	
Liske & Davis 1987	Courtship and mating behaviour of the Chinese praying mantis, <i>Tenodera aridifolia sinensis</i>	46	Insecta	Mantidae	<i>Tenodera aridifolia</i>	Pre	

(continued on next page)

Table A1 (continued)

Author	Title	Times cited	Class	Family	Species	Pre- or postcopulatory cannibalism?	Notes
Maxwell 1998	Lifetime mating opportunities and male mating behaviour in sexually cannibalistic praying mantids	31	Insecta	Mantidae	<i>Iris oratoria</i> , <i>Stagmomantis limbata</i>	Pre	
Moya-Larano et al. 2003	Mating patterns in late-maturing female Mediterranean tarantulas may reflect the costs and benefits of sexual cannibalism	19	Arachnida	Lycosidae	<i>Lycosa tarantula</i>	Unclear	
Newman & Elgar 1991	Sexual cannibalism in orb-weaving spiders: an economic model	74	Arachnida	Araneidae	Orb-weaver sp.	Pre	Model
Persons & Uetz 2005	Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters	47	Arachnida	Lycosidae	<i>Schizocosa ocreata</i>	Pre	
Prenter et al. 1994	Male exploitation of female predatory behaviour reduces sexual cannibalism in male autumn spiders, <i>Metellina segmentata</i>	22	Arachnida	Tetragnathidae	<i>Metellina segmentata</i>	Pre	
Pruitt & Riechert 2009	Male mating preference is associated with risk of precopulatory cannibalism in a socially polymorphic spider	17	Arachnida	Theridiidae	<i>Anelosimus studiosus</i>	Pre	
Sasaki & Iwahashi 1995	Sexual cannibalism in an orb-weaving spider <i>Argiope aemula</i>	48	Arachnida	Araneidae	<i>Argiope aemula</i>	Post	
Schneider & Elgar 2001	Sexual cannibalism and sperm competition in the golden orb-web spider <i>Nephila plumipes</i> (Araneioidea): female and male perspectives	64	Arachnida	Araneidae	<i>Nephila plumipes</i>	Pre	
Schneider & Elgar 2002	Sexual cannibalism in <i>Nephila plumipes</i> as a consequence of female life history strategies	39	Arachnida	Araneidae	<i>Nephila plumipes</i>	Pre	
Schneider & Lubin 1998	Intersexual conflict in spiders	53	N/A	N/A	N/A	N/A	Small section on sexual cannibalism
Schneider et al. 2000	Sperm competition and small size advantage for males of the golden orb-web spider <i>Nephila edulis</i>	74	Arachnida	Araneidae	<i>Nephila edulis</i>	Pre	
Schneider et al. 2006	Sexual conflict over copulation duration in a cannibalistic spider	37	Arachnida	Araneidae	<i>Argiope bruennichi</i>	Post	
Shillington & Verrell 1997	Sexual strategies of a North American 'tarantula' (Araneae: Theraphosidae)	21	Arachnida	Theraphosidae	<i>Aphonopelma</i> sp.	Post	Species undescribed
Snow & Andrade 2004	Pattern of sperm transfer in redback spiders: implications for sperm competition and male sacrifice	40	Arachnida	Theridiidae	<i>Latrodectus hasselti</i>	Post	
Stalhandske 2001	Nuptial gift in the spider <i>Pisaura mirabilis</i> maintained by sexual selection	34	Arachnida	Pisauridae	<i>Pisaura mirabilis</i>	Pre	Males give nuptial gifts
Uhl & Vollrath 1998	Little evidence for size-selective sexual cannibalism in two species of <i>Nephila</i> (Araneae)	20	Arachnida	Araneidae	<i>Nephila edulis</i> , <i>Nephila clavipes</i>	Pre	

We chose the top 30 most cited papers from Web of Science (including reviews) resulting from the keyword search 'sexual cannibalism' performed on 17 September 2012, and after excluding results not deemed relevant. After the top 30, we also included another 17 studies of species that were not already in our list (excluding reviews), so that we covered a total of 30 species, across 47 papers. Cannibalism was classed as precopulatory when it was recorded before copulation at least once, regardless of whether it also occurs after copulation. Postcopulatory cannibalism only includes those cases in which cannibalism occurs after insemination by the male, but can occur during or after copulation. In all species females are larger than males.

APPENDIX 2. WORDS EXCLUDED FROM ANALYSIS

Approach
Benefit
Cannibalize
Capture
Consume
Conflict won
Cost
Decapitate
Decide/decision
Devour
Eat

Elaborate (courtship)

Gift
Ignore
Injure
Indirect result
Kill
Profit
Response
Sated
Spillover
Survive
Wait