



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

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