On the accurate description of social and genetic mating systems

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Abstract

Mating systems are critical determinants of the intensity of sexual selection and sexual conflict, but understanding how variation in reproductive behavior influences these phenomena requires consistent, accurate descriptions of the array of mating arrangements observed in nature. As understanding of animal mating systems has evolved, behavioral ecologists have shifted from using behavioral information to an increasing reliance on genetic data to characterize patterns of reproductive behavior and success. Although genetic data are critical for an accurate accounting of parentage and reproductive success, they exclude critical information regarding the nature of behavioral relationships among reproductive partners, thereby potentially confounding fundamentally different types of mating systems. I contend that the ability to identify common evolutionary trends and their underlying selective pressures is significantly enhanced by using a terminological framework that differentiates explicitly between social and genetic mating systems. Furthermore, inclusion of both types of information can reveal new and intriguing relationships between behavior and fitness that further our understanding of how selection shapes mating systems. Here, I offer behavioral ecologists a new terminological framework for the study of mating systems that allows us to more appropriately merge genetic with behavioral data in an attempt to improve our understanding of this critical aspect of animal behavior. Lastly, I suggest a potential way in which we can begin to fully embrace the complexity of animal mating systems, in part via the adoption of a more quantitative framework for behavioral and genetic data.

Introduction

Mating systems describe the behavioral patterns (and their genetic outcomes) through which reproduction, the fundamental process by which evolutionary success is measured (Clutton-Brock, 1989; Greenwood, 1980). As such, an understanding of animal mating systems is critical if one hopes to understand why, and how, individual lineages, and consequently, populations, persist over generational time. Mating systems are intertwined with patterns of sexual selection, with specific systems being linked to specific patterns of sexual dimorphism (Clutton-Brock, 2007), and sexual conflict (Chapman et al., 2003; Holland and Rice, 1998; Clutton-Brock and Parker, 1995). Additionally, because of their effect on effective population size (Bateman, 1948; Anthony and Blumstein, 2000; Falconer, 1996), mating systems are intimately linked with natural selection, genetic drift,

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and other population genetic parameters.

Mating systems describe the distribution, defined in both behavioral and genetic terms, of individual reproductive success within a population (Clutton-Brock, 2007, 1989; Cerchio et al., 2005; Greenwood, 1980; Reeve et al., 1998; Wingfield et al., 1990). Consequently, understanding how selection has shaped a species' mating system requires some knowledge of the strength of sexual selection (Bateman, 1948; andersson, 1994; Darwin, 1871), the intensity and outcome of sperm competition (Clutton-Brock, 2007; Moller and Briskie, 1995), and mate choice. Although mating systems have now been studied within an evolutionary framework for decades (Emlen and Oring, 1977; Greenwood, 1980; Orians, 1969; Kleiman, 1977; Arnqvist and Nilsson, 2000; Griffith et al., 2002; Bateman, 1948), only since the widespread use of microsatellite based parentage analysis have we begun to recognize the complexity of this component of animal behavior.

As our knowledge of mating systems has increased, the associated growth in the number of factors known to influence reproductive success has blossomed. However, our ability to synthesize these factors within a common terminological framework has not experienced concomitant growth. In fact, I believe that the lack of a new framework that incorporates the synergy between the genetic and behavioral perspectives may have hindered our ability to draw generalizations regarding the actions of selection on reproductive behavior. Moreover, the frequent misuse of terminology (e.g., Portnoy et al. (2007); Arnqvist and Nilsson (2000); Baer and Schmid-Hempel (1999); Zeh and Zeh (2001); Parker and Birkhead (2013)) stemming from this deficit may hinder researchers ability to make generalizations based on data.

The assertion that terminological misuse is important is particularly exemplified by the inappropriate use of the term polyandry. Though in its classical use, polyandry refers to the situation where one female is socially bonded to more than one male, it is more common to see polyandry used to describe multiple female mating. Confusion over the use of these terms has resulted in a body of literature that, while interesting and important, is often difficult to interpret due to the conflation of behavioral and genetic data. A cursory literature search using the keyword 'polyandry' (e.g. http://goo.gl/HZAEx) is illustrative of this point– both the traditional meaning of polyandry (e.g. regarding social behavior) and the more novel use regarding multiple mating are represented on the very first page of results. As a result of this confusion, our existing terminology fails in one of its primary purposes—to allow researchers to cluster similar behaviors under a common term.

The goal of this paper is to increase awareness and engender discussion. The misapplication of fundamental behavioral terms (e.g. polyandry), along with the conflation of social and genetic systems has become a massive problem. While I encourage the adoption of the terminological framework described below, I believe that the appropriate model for the study of mating systems is one that includes both behavioral and genetic aspects of mating systems as a quantitative, continuous variable (Bertram and Gorelick, 2009). Although much work is needed regarding the latter point, using existing indices (e.g. I_s Arnold and Wade (1984) and percent extra-pair or extra-group copulations) to quantitatively characterize genetic and behavioral systems may be an important first step.

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A brief history of mating systems

Ethology—Though undoubtedly true that animals of the genus *Homo* have been avid observers of behavior since their origin, modern studies on behavior can be traced back to Darwin's work on natural (Darwin, 1859) and sexual (Darwin, 1871) selection. To these studies, R.A. Fisher (1930) and others (Mayr, 1942; Dobzhansky, 1937) provided a theoretical backbone, which was in turn formed the basis for descriptive and empirical works of the late 20^{th} century (Tinbergen, 1963; Von Frisch, 1967; Verner and Willson, 1966; Orians, 1969; Bradbury and Vehrencamp, 1977; Altmann et al., 1977; Kleiman, 1977). Importantly, it was this period during which mating behavior was studied intensively, and the terms monogamy, polygyny, polyandry, polygynandry, and promiscuity began to be frequently used by researchers to describe sociosexual relationships.

An ecological framework—Emerging from this period of intense interest, Emlen and Oring (1977) published the first theoretical treatment of mating systems. In their seminal paper, they argued that mating systems are driven by a combination of ecological conditions (i.e., the distribution of resources – including mates – in time and space and parental (i.e., uni- versus bi-parental) care requirements. With different combinations of resource requirements and availability as the context, sociosexual relationships are formed, and classified as either monogamous, polygynous, polyandrous, polygynandrous, or promiscuous. Interestingly, this conceptual model remains the foundation for ecological studies of mating systems, now, over 30 years later. Between 1977 and the mid-1990's, the study of mating systems proceeded in what Kuhn (1962) would have called normal science, where researchers attempted to fit observational data into the established framework. Researchers collected behavioral data that resulted in detailed information on social relationships then binned relationships into one of these five categories (e.g. (Wittenberger and Tilson, 1980; Foltz, 1981; Davies, 1985; Ostfeld, 1986). This type of study seemed justified because social relationships were believed to accurately reflect sexual relationships and thus actual paternity.

The molecular revolution—Though paternity analysis in a non-human animal was first reported in 1984 (Smith et al., 1984), ABO blood type (Dodd and Lincoln, 1978), immunoglobulins (Schanfield, 1989), and HLA genotyping (Heise et al., 1983) had been used in cases of disputed human paternity for several years before that. Despite this, molecular studies of parentage were not commonplace in the behavioral literature until the 1990's (Lifjeld et al., 1991; Ribble, 1991). These studies, typically using microsatellite DNA have increased in popularity until this day.

Currently, the ease with which molecular data on parentage are now collected and analyzed means that many researchers interested in mating systems, especially as they relate to sexual selection are now able to describe the genetic mating system very precisely (McEachern et al., 2009; Rios-Cardenas and Webster, 2008; Webster et al., 2008; Simmons et al., 2008; Soulsbury, 2010). Impressively, microsatellite based parentage analysis have been conducted in thousands of species (for example, DeYoung et al. (2009); Shurtliff et al. (2005); Koopman et al. (2007). The increase in sample size and complexity of the hypotheses being tested has beget a series of extremely sophisticated methods for analysis of molecular paternity including maximum likelihood (Kalinowski et al., 2007) and Bayesian (Jones and Wang, 2009) solutions.

Though molecular parentage analysis has advanced the field of mating systems in innumerable ways, deepening our understanding of both pattern and process, one undesirable consequence has

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been the demise of the behavioral study (but see DuVal (2013); Sousa and Westneat (2012); Bird et al. (2012)). While this shift is undoubtedly multifactorial, the ease with which molecular genetics allow quantification of parentage, coupled with the difficulties in funding long-term behavioral research has frequently resulted in a limited ability for researchers to assess the underlying behavioral and ecological phenomena that lead to observed genetic outcomes.

The problem—Research conducted during the past 15 years has revealed more variation in mating systems than can be accommodated by the traditional categorical set of behavioral terms, especially when attempting to unite social and genetic mating systems under a single term (e.g. polygyny). Furthermore, although a mating system continuum seems to exist, where monogamy gradates into polygyny or promiscuity, we continue to be limited by the categorical framework that has been traditionally used. Taking monogamy as an example, while the social relationship can be defined as either monogamous or non-monogamous depending on the nature of the pair bond (i.e. behavioral data), even systems characterized by strong pair bonds and intense mate guarding can vary widely in their genetic mating system, which may be characterized by multiple female mating, multiple male mating, or genetic promiscuity (Dixon et al., 1994; Mulder et al., 1994). High variance in reproductive success, and thus enhanced sexual conflict or dimorphism, may be common in social monogamy, and yet the binary categorization (monogamous or non-monogamous) based on behavioral data alone does not reflect important variation in genetic system.

Both socio-sexual relationships and their genetic outcome influence sexual selection. Because the nature of the social relationships is often not a reliable predictor of parentage (Dale et al., 1999; Goossens et al., 1998; Moller and Tegelstrom, 1997; Soukup and Thompson, 1997; Webster et al., 2001; Solomon et al., 2004), having either genetic or behavioral information in isolation necessarily means that our understanding of mating systems as a dynamic process is shortsighted. We are now faced with a Kuhnian crisis (Kuhn, 1962). Specifically, that mating systems are too complex to fit into the traditional categorical classification system. This limits the clarity with which we can think about mating systems, and our ability to make accurate predictions about the strength and nature of critical evolutionary parameters like sexual selection and sexual conflict.

Although the utility of genetic data is obvious, behavioral studies that provide the ecological context are often incomplete. As opposed to using both types of information in a complementary fashion, the field has largely been fractionated into two non-overlapping areas of study. I hold the viewpoint that classically-defined mating systems fundamentally describe the socio-sexual relationship between individuals in a population. These relationships have genetic consequences that may or may not correlate with behavioral observations. Unless we consider both sources of information, our ability to make predictions on critical evolutionary parameters like sexual selection is limited. While there are many examples of confusion resulting as a direct result of incomplete information, one of the most salient examples is of the genetic system characterized by multiple female mating, inappropriately labeled as polyandry.

Polyandry is essentially ubiquitous across the animal kingdom
(Taylor et al., 2008)

Polyandry—The classical definition of polyandry is that of a social mating system. Specifically, behavioral (classical) polyandry describes the case where a single female is pair-bonded to,

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and mates with, multiple males who in turn, typically mate with a only single female (Emlen et al., 1998). Because access to males is often limiting in polyandry, more intense sexual selection in females is typical. Classically, this specific social mating system is characterized by sex-role reversal including male pregnancy, and reverse sexual dimorphism (Emlen and Oring, 1977; Alcock, 1975), although this is not always the case (e.g. tamarins, Terborgh and Goldizen (1985)). In contrast with the notion that polyandry is ubiquitous (Taylor et al., 2008), this social mating system is thought to be amongst the most rare of forms in nature.

Increasingly, however, the term polyandry is being used to describe individual reproductive behavior characterized by multiple female mating; to represent the case where multiple males sire offspring in a single brood, clutch, or litter (Dibattista et al., 2008b,a; Firman, 2011; Leonard and Boake, 2008; McNamara et al., 2008). This use of the word is problematic because the two systems, both labeled polyandrous, are predicted to have opposite characteristics (Table 1). Indeed, predictions about sexual selection based on the assumption of social (classical) polyandry include more intense sexual selection in females, sex-role reversal and uni-parental, typically obligate male care (Emlen and Oring, 1977). These predictions are exactly opposite to what one might expect when studying a system characterized by multiple female mating (i.e. polyandry in the common use, inappropriate sense), where, for instance, males are the more sexually dimorphic species.

A particularly salient example of terminological confusion is found in a 2010 study of Trinidadian guppies (*Poecilia reticulata*) by Barbosa and colleagues (2010). There, sexually selected phenotypic diversity of sons was examined in two treatment groups. In the monoandrous group, females were mated with a single male while in the 'polyandrous' group, females mated with multiple males. The resultant sons were raised to sexual maturity, after which color and sexual behavior were quantified. Barbosa found that sons of 'polyandrous' females were different that sons of monoandrous females—they were more colorful. While an extremely interesting result, linking 'polyandry' with enhanced sexually selected characters in males is opposite of what we would expect in classically polyandrous species where females typically show more elaborate sexually selected traits. To the naïve reader—or the meta-analyst, the conflation of terms—polyandry with multiple female mating may be confusing, or error provoking. As described below, a more appropriate description of the genetic mating system described here is multiple female mating.

In summary, the field of Behavioral Ecology, and more specifically behavioral ecologists who study mating systems are currently forced to apply terms meant to describe social relationships to genetic data. This problem has manifested itself in many studies where behavioral data are discordant with genetic data. Particularly affected are systems where multiple female mating is conflated with polyandry. Below, I offer a set of terms and recommendations that will help to resolve this conceptual dilemma.

Definitions

Science has a way of inventing terminology, and the field of mating system research is no exception. The terminology has become cumbersome to the point of being dysfunctional, with different researchers using the same term to indicate different phenomena. Terminology is only useful if it allows us to effectively communicate and group similar phenomena together, in order to identify

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common cause and consequence. My goal is to propose a set of definitions, operational in nature, that will allow researchers and readers alike to use data to form opinions and make judgments about the ecological and evolutionary processes.

Although I posit that both genetic and social mating systems vary continuously (Bertram and Gorelick, 2009), categorical variables are valuable tools enabling us to group similar systems together. As such, I recognize their utility, as well as the inevitability of their use. So long as researchers continue to use the terms monogamy, polygyny, polyandry, polygynandry, and promiscuity, appropriate use will be critical.

Social Relationships

Social Monogamy. Social monogamy is characterized by an exclusive socio-sexual relationship (=pair bond) between two animals. The pair bond exists outside the times of courtship and copulation, either before or after mating. Paternal care may or may not exist. The maintenance of a socio-sexual relationship does not preclude the possibility for extra-pair mating by either sex. This system appears to be the most common in passerine birds (Griffith et al., 2002; Lack, 1968).

Polygyny. Polygyny describes the socio-sexual relationship where one male has a specific relationship or bond with more than one female that may or may not last outside the period of courtship and mating. This male typically mates with all sexually mature females to which he is bonded. Paternal care may or may not occur. The maintenance of a relationship does not preclude the possibility for extra-group mating by either sex. Classic examples of this type of mating system includes red-winged blackbirds (Westneat, 1993) and black-tailed prairie dogs (Hoogland, 1983). Note that lekking systems (e.g. Duval (2012); Reynolds et al. (2009); Lebigre et al. (2007)) do not fall under this system, as they lack the requisite pair bond.

Polyandry. Polyandry describes the socio-sexual relationship where one female has a relationship or bond with more than one male that lasts outside the period of courtship and mating. This female typically mates with all sexually mature males to which she is bonded. Paternal care may or may not occur. Sex-role reversal is typical, with females often having more exaggerated phenotypes. The maintenance of a social relationship does not preclude the possibility for extra group mating by either sex. Examples of this social mating system include Jacanas (Emlen et al., 1998), Phalaropes (Dale et al., 1999), the Galapagos hawk (Faaborg et al., 1995), and a cichlid fish (Kohda et al., 2009).

Social Promiscuity. Promiscuity is the socio-sexual system that is characterized by the lack of pair bonding. Both males and females may mate with multiple individuals of the opposite sex. Classical lekking species belong in this social mating system, as a result of the distinct lack of pair bind, rather than in polygyny.

Polygynandry. Polygynandry describes the socio-sexual relationship between >1 male and >1 female that lasts outside the period of courtship and mating. All animals typically mate with all other opposite-sexed animals. Paternal care may or may not occur. The maintenance of a social relationship does not preclude the possibility for extra-group mating by either sex. Classic examples include acorn woodpeckers (Haydock and Koenig, 2002), and pipefish (Jones and Avise, 2001; Mobley and Jones, 2009).

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Genetic Relationships

Genetic monogamy. Genetic monogamy describes the genetic outcome of mating, and is characterized by (1) the absence of extra-pair offspring in the resultant clutch, brood, or litter and (2) the absence of paternal representation in any other female clutch, brood, or litter. This genetic outcome may be associated with social monogamy (Brotherton et al., 1997), but this link is not necessary (Wilson and Martin-Smith, 2007).

Multiple male mating (MMM). Multiple male mating describes the system where only males may mate with multiple individuals, and critically, these matings result in fertilizations at some frequency (perhaps 5%) within the population as evidenced by molecular parentage data. Many socially polygynous systems and system where socially monogamous males engage in extra pair fertilizations with other females would fall into this category (Benedict, 2008).

Herein lies the issue of attempting to apply a categorical variable to continuous data–researchers working on systems characterized by a rate of multiple male mating of slightly less than the arbitrarily chosen 5% fall into somewhat of a grey area. Are these instance of MMM so infrequent so as to represent aberrant behavior or worse yet technical error (sample labeling or genotyping error), or do they speak to some low-frequency alternative mating strategies? Though this concern is presented in conjunction with multiple male mating, the distribution of maternity or paternity may frequently fall into this grey-zone, not always lending itself to straightforward classification.

Multiple female mating (MFM). Multiple female mating describes the system where only females may mate multiply, and critically, these matings result in fertilizations at some discernible frequency. Examples may be found in social polyandry as well as in systems where socially monogamous females solicit matings from unpaired males in addition to their social mates.

Genetic Promiscuity. Genetic promiscuity describes the situation in which some males sire offspring with multiple females, and females bear multiply sired clutches, broods, or litters. Polygynandry cannot be distinguished from promiscuity when looking only at genetic data.

To enhance the clarity and thus usability of these social and genetic definitions, I propose that social and genetic mating systems be characterized separately, using terms unique to each domain. For instance, in the common scenario where both social and genetic systems are known, and social monogamy is coupled with multiple mating by both males and females (e.g. genetic promiscuity), the appropriate descriptor would be social monogamy with genetic promiscuity.

The way forward

Mating systems are critical determinates of the intensity of both sexual selection and sexual conflict, but accurate predictions require accurate definition. It is my hope that increased regard for the way in which we define systems will consequently increase our ability to group natural phenomena more accurately. Indeed, more accurate categorization will allow researchers to highlight differences, recognize similarities, and in turn, more efficiently form hypotheses regarding underlying phenomena.

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The development of a fully quantitative framework within which mating systems can be defined, and compared is beyond the scope of this paper, yet ironically may represent a fundamental solution to the terminological confusion I have outlined. Indeed, a major limitation in the conceptualization of a quantitative framework is a lack of empirically derived data, which ideally would consist of complete and unequivocal assignment of maternity and paternity for large numbers of individuals as well as an accurate accounting of social interactions across a variety of taxa. Remarkably, the advent of high throughout genotyping coupled with automated GPS-based telemetry may make such idealized datasets possible.

In contrast to empirical work, there has been a substantial amount of theoretical work done looking at the variation in (mostly male) mating success. Indeed, much of this work will be useful for characterizing mating systems, in addition to their intended use—to characterize the strength of sexual selection. Early works by Arnold (Arnold and Wade, 1984) and by Mackenzie and colleagues (1995) demonstrated how modeling biotic and abiotic factors– many of them key to the Emlen–Oring model of mating systems (Emlen and Oring, 1977), is critical to understanding variation in mating success. That the same factors influencing variation also seem to be important to mating systems should suggest that conceptual overlap may be substantial. Following this point, several authors have made explicit these links between variation in mating success and mating systems (Kokko et al., 1999; Kokko and Linstrom, 1997; Bertram and Gorelick, 2009; Arnold and Duvall, 1994). I suggest that testing the theoretical predictions with empirically derived data is an important next step for interested researchers.

I propose that genetic mating system be quantified by researchers conducting microsatellite or SNP based studies of parentage using, for example, the index of the opportunity for sexual selection I_s, first described by Arnold and Wade (Arnold and Wade, 1984). This index describes variance in relative mating success, and therefore, is a fully quantitative measure of the genetic mating system of a population when both males and females are adequately sampled. Several researchers have quantified I_s and rates of extra-pair/group fertilization within single studies, of socially monogamous and polygynous songbirds (Otter et al., 1998; Yezerinac et al., 1995; Kempenaers et al., 1992), reviewed in Albrecht et al. (2006), and although these represent only a small sample of the total number of studies completed, they suggest the general utility of using I_s as a quantitative index, inasmuch as it can be calculated for all types of mating system with data typically collected in studies of genetic parentage. When using this index, combined with an accurate, quantitative description of social mating system (e.g., percent extra-pair/group fertilizations in monogamous or polygynous species), we may begin to have the ability to develop quantitative hypotheses about sexual dimorphism and conflict, as well as to understand the variation within specific social and genetic mating systems.

Conclusions

Descriptive work on mating systems has shown that, using the traditional terminology, a tremendous amount of variation exists in the way that authors describe mating systems. Contained within a single traditionally defined category, the entire range of genetic outcomes has been observed and

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yet, more often than not, these outcomes have not been presented in a way that allows for easy comparison between studies. I urge strict adherence to traditionally defined social mating system definitions along with adoption of a new set of terms that explicitly consider and label genetic processes. Additionally, I propose that researchers conducting studies of parentage describe their systems using quantitative methods—using, for instance, variance in relative mating success I_s.

Acknowledgments

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Table 1

	Classic polyandry	Inappropriate polyandry
Operational Sex Ratio	Female biased	Male biased
Sexual dimorphic	Females	Males
Parental Care	Male biased	Female biased
Strength of Sexual Selection	Higher in females	Higher in males

Table 1 describes the predictions based on classical polyandry versus the more common, inappropriate use of the term on several key evolutionary parameters.

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