Quantifying and comparing mating systems using normalized mutual entropy

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Methods for quantifying mating systems have been debated for over 30 years. Existing quantification methods rely on inequality indexes, producing a single number from a vector of data for all females or males in a population. Such methods do not account for interactions between members of the two sexes because they do not use the natural matrix (dyadic) structure of the data, where each matrix entry reflects how often a given pair of individuals mated or how many offspring they produced. These inequality indexes also suffer from being a function of population size. Here, we propose mutual entropy as a way to account for the matrix structure, along with a normalization that makes this index independent of population size, thereby robustly quantifying the continuum between monogamy and polygyny/polyandry. Normalized mutual entropy: (1) is a measure of diversity, so it can serve as an upper bound for sexual selection and (2) can accommodate hermaphrodites and self-fertilizing individuals. Normalized mutual entropy thereby provides a measure of mating systems, promiscuity, inbreeding and social cohesion.
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Mating systems are generally defined by the number of sexual partners acquired during the breeding season. Mating systems are often pigeon-holed into monogamy, polygyny, polyandry or polygynandry, despite the general realization that these form a continuum. Similar realizations have been formally recognized in pigeon-holing the gender of plants, where we now typically assign gender to a continuum between zero and one (Lloyd 1980). While qualitative definitions of four or more mating systems are useful, molecular genetic techniques have revealed true complexities in mating systems. These complexities suggest that polygynandry may be the most common mating system in animal populations. Unfortunately, polygynandry is an overly broad category. Furthermore, the continuum between polygynandry and other mating systems is so broad that the boundaries can be difficult to distinguish (Jones & Avise 2001). While the proximate purpose of this paper is to introduce a new method for quantifying mating systems, we also wish to address other important but related questions. Along a continuum of mating systems, how can we determine, in a statistically rigorous fashion, when two populations differ, especially when the populations are of different sizes? How do we account for not just numbers of matings, but also numbers of offspring, which combined provides a superior measure of the population's fitness? Can we account for self-fertilizing individuals and hermaphrodites?

A primary use for mating system indexes has been to measure levels of selection, especially sexual selection. The motivation here is clear. It is difficult to measure selection gradients directly. Instead, we estimate upper bounds for selection by computing the variability over space or time in a trait. Then, invoking Fisher's fundamental theorem, the rate of evolution can be no larger than this variability. The important point is that a measure of diversity can be used to quantify mating systems because of its utility in predicting possible evolutionary outcomes. A good measure of mating systems will therefore be a continuous function that quantifies the diversity of interactions within the mating system.

Many indexes have been proposed to quantify mating systems (summarized in Kokko et al. 1999; Fairbairn & Wilby 2001). These indexes all take a sequence of measurements (e.g. how many males each female mates with in a population) and produce a measure of diversity. The most famous of these indexes is the opportunity for selection, I, which is the square of the coefficient of variation. To compute I for females or males, one must first calculate the mean and standard deviation of the number of mates amongst all individuals of that sex. I is then computed as the square of the ratio of standard deviation divided by the mean. If all males mate with the same number of females, then I equals zero (no variance). If 'dominant' males mate with more females than 'subordinate' males, then I can grow as large as the number of males (Fairbairn & Wilby 2001). Many modifications of the coefficient of variation have been proposed, often called inequality indexes, all of which convert a vector input for each sex into a single number to quantify the mating systems for that sex (reviewed in Kokko et al. 1999; Gorelick & Bertram 2007).

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Inequality indexes do not utilize the detailed data about how each female reacts with each male, even though mating systems are dyadics between all individuals of both sexes in a population (Altmann 1997). Inequality indexes are therefore incapable of capturing interactions that occur between the two sexes. For example, consider the following pair of populations, each represented by a matrix, that each include two females and two males: $\begin{pmatrix} 99 & 1 \\ 1 & 99 \end{pmatrix}$ and $\begin{pmatrix} 50 & 50 \\ 50 & 50 \end{pmatrix}$, where the rows are females, columns are males, and the matrix entries represent either how often a given female mates with a male or the number of offspring produced by that couple. In both populations, every individual either mates a hundred times or produces 100 offspring. Each individual also mates with both members of the opposite sex. All previous mating system indexes operate on the sums of the rows and columns of these matrices or their respective presence/absence vectors (summarized in Kokko et al. 1999; Fairbairn & Wilby 2001). Notice that both matrices have identical row and column sums, thus all previous indexes of mating type operate on the vector (100, 100) (or, for presence/absence data, the vector (2, 2) because each female mates with two males and each male mates with two females). Vector-based statistics will therefore yield identical measures of mating systems for these two very different populations. Vector-based statistics cannot account for the indiscriminate nature of individuals in the second population or strong (pre- or post-copulatory) assortative mating, an interaction between opposite-sex individuals, in the first population. Vector-based statistics such as I, the square of the coefficient of variation, yield values of zero for both populations, even though the first population is virtually monogamous while the second population is polygynandrous. It would, therefore, be advantageous to use a measure of diversity whose input is a matrix of interactions (Moniz et al. 2007), at least if this data matrix is available (Fig. 1a).

METHODS

In a previous publication, we showed that diversity of a matrix of data is the inverse of its division of labour (Gorelick et al. 2004). Monogamy is extreme division of labour, where each female chooses only one male (performs only one task) and all females specialize on different males (tasks) as mates. Likewise, polygynandry is equivalent to a lack of division of labour, where each female mates with all males (performs all tasks) and does not specialize on any given male (task). Virtually all aspects of sex, from anisogamy to mate choice have been conceptualized as divisions of labour, so it is sensible to think of mating systems as division of labour. In our previous work we also compared various families of indexes of division of labour, including several modifications of coefficients of variation that operate on vector inputs, and indexes that naturally have matrix inputs (Gorelick & Bertram 2007). Here, we combine our two earlier results to introduce a mating system index that has matrix inputs and is also a measure of diversity and hence applicable to studies of selection.

Diversity amongst all entries p_{ij} in a matrix of probabilities ($1 = \sum_{i,j=1}^{m,n} p_{ij}$) can be quantified by $1 - I(i,j)/H(i)$, where $I(i,j) = \sum_{i=1,j=1}^{m,n} p_{ij} \times \log(p_{ij}/p_i \cdot p_j)$ is mutual entropy, $p_i = \sum_{j=1}^{m} p_{ij}$, and $H(i) = -\sum_{i=1}^{m} p_i \times \log(p_i)$ is marginal entropy (Shannon 1948; Cover & Thomas 1991). (Note the nomenclatural confusion that inequality indexes (vector-based) are designated by I, while mutual entropy (matrix-based) is designated by $I(i,j)$. Both designations are traditional, and we are reluctant to deviate from that tradition, so always doubly index mutual entropy herein to preclude further confusion). For mating systems, the rows and columns represent all the individuals in the population, while components of the matrix represent whether the pair of individuals mated or produced offspring. These probabilities can be binary yes/no data or can be real numbers representing the number of times the pair mated or the number of offspring they produced. Divide all entries of the matrix by the total number of matings or offspring produced so that $1 = \sum_{i,j=1}^{m,n} p_{ij}$. Because $\lim_{p \to 0} p \log(p) = 0$, we can eliminate all rows and columns that contain only zeroes before carrying out further computations. Thus, the remaining rows and columns will only contain the individuals that actually mated or produced offspring. This method can accommodate self-fertilization and hermaphroditic matings that occur in many plants, fungi, protists, prokaryotes and animals (Fig. 1b). This method could also be generalized to explicitly handle more than two mating types: instead of a two-dimensional array (matrix) of two sexes, we could have an n-dimensional array of n mating types and then compute mutual entropy of that array (Cazelles 2004; Gorelick 2006). Regardless of details, which we discuss below, normalized mutual entropy, NME $= 1 - I(i,j)/H(i)$, yields a number between zero and one that is proportional to mating system's diversity and is asymptotically F-distributed (Gorelick et al. 2004). Maximum values of NME occur when all individuals mate with all other individuals and do so equally often. Intuitively, this makes sense in that such a scheme would guarantee maximal genetic diversity. Normalized mutual entropy has been used as a measure of ecological diversity (Colwell & Futuyma 1971; Gorelick 2006) and genetic diversity (Liu & Lin 2005). Minimal values of NME occur when all mated individuals are strictly monogamous. That is, monogamy yields a NME value of zero and polygynandry yields a NME value of one, when all individuals mate equally often with everyone else (Fig. 2).

Although NME is asymptotically F-distributed, in practice one would use resampling statistics to analyse whether two values of NME differ from one another. The elements in the probability matrix are randomized (permuted), NME computed for each permutation, and an empirical distribution created of all the permutations. One can then use goodness-of-fit tests, such as Cramer-von Mises, to test whether two matrices have a statistically significant difference in their NME values (D'Agostino & Stephens 1986).

Mutual entropy is a natural measure of promiscuity in the following sense. High mutual entropy means that if we know which row (or column) of the matrix is selected, then we should be able to predict which columns (or rows) will be non-zero. Similarly, monogamy means that if we select one female (or male), then we should be able to predict which male (or female) they mated with. On the other hand, if males are polygynous, or females are polyandrous, then it will be nigh impossible to predict who they mated with. Correspondingly, NME will be close to one. Note, however, that if NME is close to one, we cannot discern which sex was responsible for this because of their promiscuity.

Mutual entropy is a natural measure of mating systems insofar as it is a measure of how disparate female and male mating tactics are from one another. This follows from mutual entropy being a special case of the Kullback–Leibler distance (Kullback & Leibler 1951) between the vectors of female and male mating data. Remember, mutual entropy yields a single number for the entire population. To obtain measures of female and male promiscuity from this distance between the two sexes, as we will see below, we have to divide mutual entropy by the marginal entropy (Shannon's index) of the vector for the opposite sex.

DISCUSSION

Normalized mutual entropy should be considered better than other indexes at distinguishing differences between monogamy and other mating systems for the following six reasons. First, and
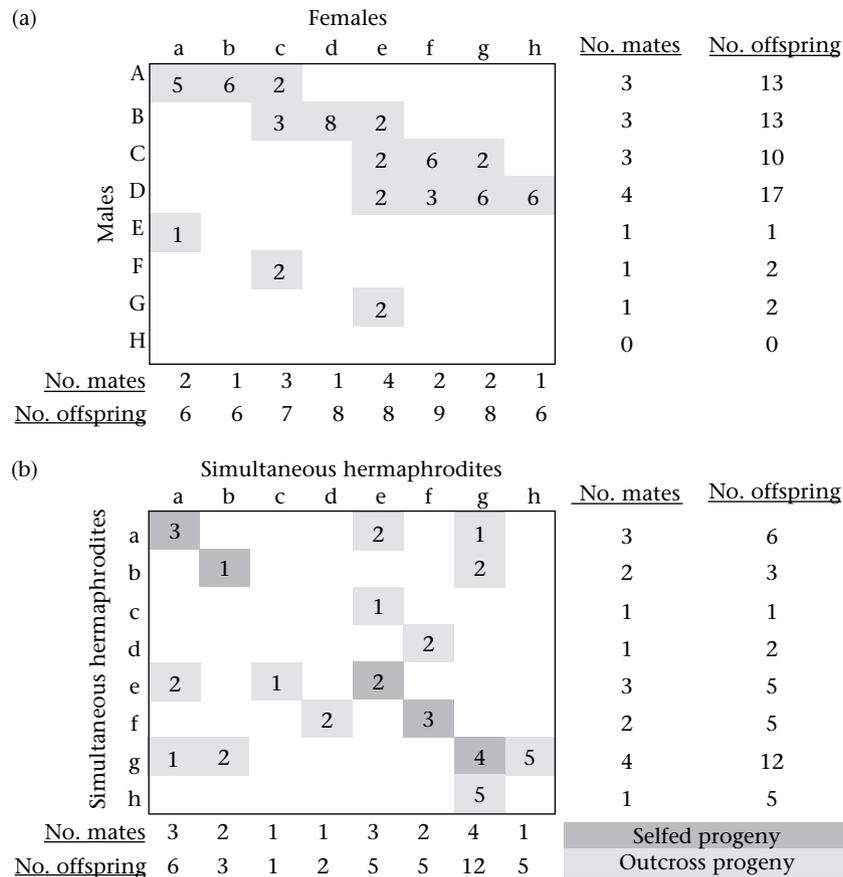
Figure 1. Mating system examples. (a) Describes a mating system between males and females with no inbreeding. Each of the eight males is represented by his own row; each of the eight females is represented by her own column. Each cell represents the number of progeny produced by the pair. Beside the matrix is a list summarizing the number of times each male mated and the number of offspring produced. These are also summarized for females below the data matrix. (b) Describes a mating system with inbreeding. The cells that lie along the diagonal (dark grey) represent the offspring produced via inbreeding.

foremost, because it uses matrix inputs and thereby captures potential interactions between all mates. Second, because it is a measure of diversity, and can therefore serve as an upper bound when studying sexual selection. Third, because it has sound statistical properties (asymptotically *F*-distributed), and can hence be used to test whether two populations have statistically different mating systems. Fourth, because it lies between zero and one, and thereby allows comparisons between populations that have different numbers of individuals. Fifth, because it can incorporate data on number of matings or offspring produced by each pair of mates, rather than just the binary variable of whether the two individuals mated or produced offspring (Fig. 3). Sixth, because mating populations that include hermaphrodites or individuals that can self-fertilize may be analyzed using this statistic just as simply as any other mating system.

The form of data collected and interpretation of NME vary depending on context. Someone focusing only on reproductive output of dioecious (gonochoristic) taxa, divorced from notions of kinship and Hamilton's rule, would have the rows of the data matrix represent males, the columns represent females, and the matrix entries (cells) represent the number of viable offspring produced by that pair. Someone studying monoecious (hermaphroditic) taxa would have to include all individuals in the rows and all individuals in the columns. In this case, while the matrix entries would still represent the number of viable offspring produced by each pair, the diagonal entries would represent the number of viable offspring produced via self-fertilization. Any rows or columns that only contain zeroes would be automatically

eliminated from consideration by the computation of mutual entropy, as would always happen for some individuals of one sex in gynodioecious or androdioecious taxa. When matrix entries are the number of viable offspring produced by a given pair divided by the total number of viable offspring in the population, NME can be conceptualized as an upper bound for genetic variation. Minimal NME (equal to zero) arises from obligate selfing populations and from obligately monogamous populations. Maximal NME (equal to one) arises when all individuals mate equally often with all other members of the population or with all other members of the opposite sex. With hermaphroditic input data, normalized mutual entropy is a form of inbreeding coefficient. However, there is at least one potential weakness: NME cannot distinguish obligate selfing from obligate monogamy without selfing. However, NME for either of these two scenarios would be greater than NME for a population that includes individuals that reproduce both via selfing and via outcrossing with another individual.

An alternative form of input data structure and interpretation of NME arises when focusing on social structure. Here, we might also have the rows be all individuals, the columns be the same individuals, but have the matrix entries be number of matings or other sexual encounters. Along the diagonal, we can include the number of times each individual masturbated. At a minimum, this should be of interest in studies of mammals (e.g. Darling 1937). A population composed exclusively of monogamous individuals that also masturbate would be considered more promiscuous than a population of monogamous individuals that never masturbate. We can also include same-sex matings. This could be very useful for
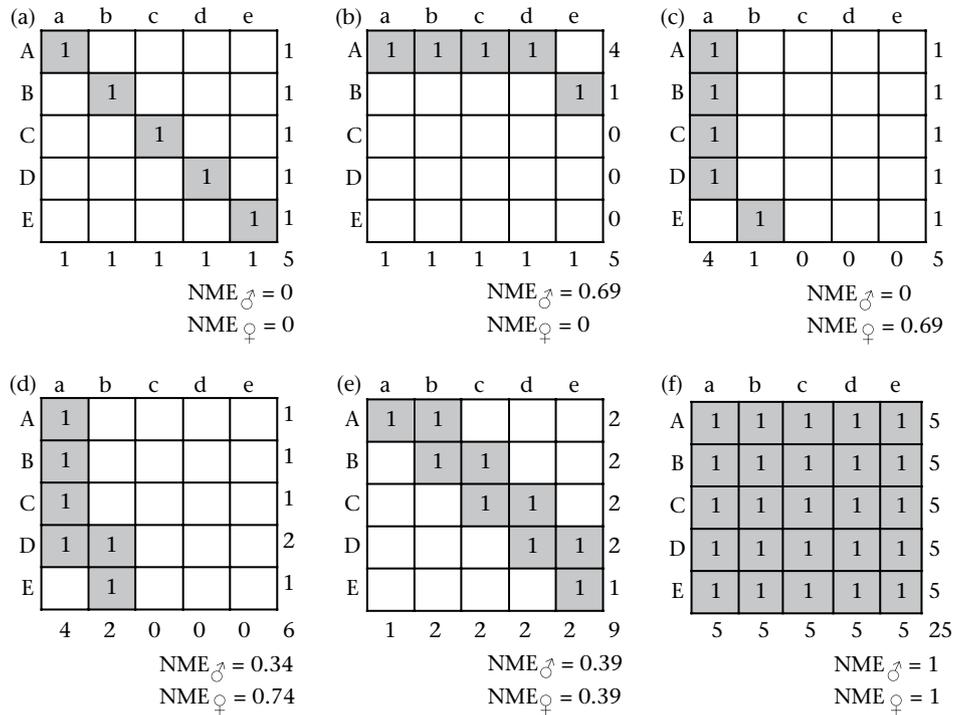
Figure 2

(a) Monogamy

	a	b	c	d	e	
A	1					1
B		1				1
C			1			1
D				1		1
E					1	1
	1	1	1	1	1	5

$NME_{\male} = 0$
$NME_{\female} = 0$

(b) Polygyny

	a	b	c	d	e	
A	1	1	1	1		4
B				1		1
C						0
D						0
E						0
	1	1	1	1	1	5

$NME_{\male} = 0.69$
$NME_{\female} = 0$

(c) Polyandry

	a	b	c	d	e	
A	1					1
B	1					1
C	1					1
D	1					1
E		1				1
	4	1	0	0	0	5

$NME_{\male} = 0$
$NME_{\female} = 0.69$

(d)

	a	b	c	d	e	
A	1					1
B	1					1
C	1					1
D	1	1				2
E		1				1
	4	2	0	0	0	6

$NME_{\male} = 0.34$
$NME_{\female} = 0.74$

(e)

	a	b	c	d	e	
A	1	1				2
B		1	1			2
C			1	1		2
D				1	1	2
E					1	1
	1	2	2	2	2	9

$NME_{\male} = 0.39$
$NME_{\female} = 0.39$

(f)

	a	b	c	d	e	
A	1	1	1	1	1	5
B	1	1	1	1	1	5
C	1	1	1	1	1	5
D	1	1	1	1	1	5
E	1	1	1	1	1	5
	5	5	5	5	5	25

$NME_{\male} = 1$
$NME_{\female} = 1$

Figure 2. Examples of how the different mating systems influence the NME statistics. These mating systems include only binary data (mating or no mating), so it is apparent how the two NME indexes change with different mating systems. Each female is each represented by a column; each male is represented by a row. In each example (a–f), two NME indexes are included, one for the males and one for the females. The NME is high when the male or female mates multiply, highest when all individuals of one sex mate multiply, and zero when all individuals of one sex only have one mating partner. (a) Monogamy. (b) Polygyny. (c) Polyandry. (d–f) Different forms of polygynandry.
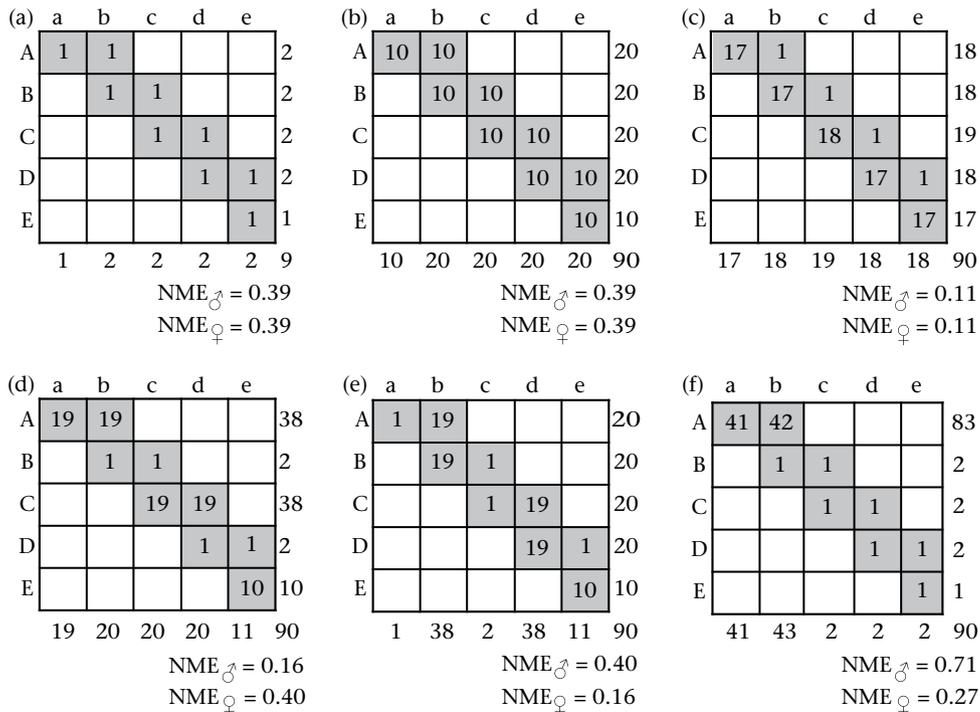
Figure 3

(a)

	a	b	c	d	e	
A	1	1				2
B		1	1			2
C			1	1		2
D				1	1	2
E					1	1
	1	2	2	2	2	9

$NME_{\male} = 0.39$
$NME_{\female} = 0.39$

(b)

	a	b	c	d	e	
A	10	10				20
B		10	10			20
C			10	10		20
D				10	10	20
E					10	10
	10	20	20	20	20	90

$NME_{\male} = 0.39$
$NME_{\female} = 0.39$

(c)

	a	b	c	d	e	
A	17	1				18
B		17	1			18
C			18	1		19
D				17	1	18
E					17	17
	17	18	19	18	18	90

$NME_{\male} = 0.11$
$NME_{\female} = 0.11$

(d)

	a	b	c	d	e	
A	19	19				38
B		1	1			2
C			19	19		38
D				1	1	2
E					10	10
	19	20	20	20	11	90

$NME_{\male} = 0.16$
$NME_{\female} = 0.40$

(e)

	a	b	c	d	e	
A	1	19				20
B		19	1			20
C			1	19		20
D				19	1	20
E					10	10
	1	38	2	38	11	90

$NME_{\male} = 0.40$
$NME_{\female} = 0.16$

(f)

	a	b	c	d	e	
A	41	42				83
B		1	1			2
C			1	1		2
D				1	1	2
E					1	1
	41	43	2	2	2	90

$NME_{\male} = 0.71$
$NME_{\female} = 0.27$

Figure 3. Examples of how the number of progeny (or the number matings) influences NME. These examples all use the same mating data but differ in the number of progeny produced by each mated pair. These examples show how the NME is influenced by progeny number. NME changes with increasing variance among the parents in the number of offspring they produce.

Table 1
Description of normalized mutual entropy (NME) variations

Statistic	Columns	Rows	Marginal entropy[*]	Description of statistic[†]
$NME_{S\female}$	Females	Males	Males	Female promiscuity (social mating system)
$NME_{S\male}$	Females	Males	Females	Male promiscuity (social mating system)
$NME_{S\female\male}$	Both	Both	Either	Hermaphrodite promiscuity (social mating system)
$NME_{G\female}$	Females	Males	Males	Female promiscuity (genetic mating system)
$NME_{G\male}$	Females	Males	Females	Male promiscuity (genetic mating system)
$NME_{G\female\male}$	Both	Both	Either	Hermaphrodite promiscuity (genetic mating system)

[*] The marginal entropy to use when calculating the normalized mutual entropy statistic.

[†] Social mating system quantifies data on the number of matings; genetic mating system incorporates data on the number of progeny. Subscripts: S = social mating system, G = genetic mating systems; male and female symbols represent whether the NME statistic is for males, females or hermaphrodites.

comparative analyses of social structure in primates, where same-sex matings are believed to contribute to social cohesion and where female–male matings that do not result in offspring may help ensure that the male does not kill the female's offspring (Parish 1996). With same-sex matings and with opposite-sex matings that do not result in offspring, normalized mutual entropy can be conceptualized as an index of social cohesion.

Notice that we propose dividing mutual entropy by marginal entropy, but have thus far not specified which marginal entropy. If rows of the data matrix correspond to males and columns to females, then people will want to compute NME in two separate ways; using marginal entropy of females and using marginal entropy of males. If the data matrix represents how often each female–male pair mated, then the two statistics measure male and female promiscuity, respectively (e.g. Fig. 2). On the other hand, if the rows and columns of the data matrix both contain information about both sexes, as when we consider same-sex matings, then marginal entropy of the rows equals marginal entropy of the columns; that is, there is only a single measure of promiscuity for the population. In this case, it is possible to separately determine the promiscuity measures for each sex by taking the original matrix and creating two new matrices. The first new matrix would have all the rows associated with the males redacted. Mutual entropy divided by marginal entropy of the rows would then yield promiscuity of females. The second new matrix would have all the columns associated with the females redacted. Mutual entropy divided by marginal entropy of the columns would then yield promiscuity of males. It is also possible to determine how strongly self-fertilization or self-sex influences the promiscuity statistic. In this case, quantify the promiscuity measure for the entire population with the self-fertilization and/or self-sex data included. Then create a new data matrix that has the diagonal data, representing the same sex or self-fertilization data, all set to zero. Renormalize this new data matrix so that the sum of all entries adds up to one and then calculate the NME. The difference between this promiscuity measure and the one that includes the entire data set would represent the importance of inbreeding. While it is much more ad hoc to eliminate effects of self-fertilization or self-sex from such an analysis than to separately analyse female and male promiscuity, this comparative approach of setting the diagonal to zero would provide a measure of how strongly self-fertilization or self-sex influences the promiscuity statistic.

Promiscuity has pejorative and andocentric connotations, but we have not come up with a better or equally evocative term. Following Hrdy (1999), the phrase 'assiduously parental' may be appropriate but is hardly euphonious. Likewise, the phrase 'social mating system' may raise anthropocentric flags (Parish 1996; Roughgarden 2004). Humans, bonobos, and probably several other taxa use sex as a form of social activity, often divorced from reproduction, but the adjective social seems inappropriate with many other taxa, such as matings in flowering plants; pollen deposition on stigmas is hardly social. Thus, with trepidation, we call NME a measure of promiscuity.

We recommend that when there are data sets on both mating frequency and progeny production, NME for male and female mating promiscuity (using number of matings), and NME for male and female progeny promiscuity (using number of progeny) should all be calculated (Table 1). Differences between male mating promiscuity and male progeny promiscuity or between female mating promiscuity and female progeny promiscuity will indicate the degree to which the social mating system and the genetic mating system differ. For example, if all females were to each mate with multiple males, NME for female mating promiscuity would be greater than zero. If the males were to each mate with only one female, the NME for male mating promiscuity would be zero. Together, these two numbers would reveal that the social mating system is polyandrous (Table 2). However, if postcopulatory female choice or sperm competition strongly influence the number of viable progeny, the resulting NME for female progeny promiscuity would drop (to zero if each female's progeny came from only one

Table 2
Relation between the NME mating statistics and the conventional mating statistics (adapted from: Searcy & Yasukawa 1995; Jones & Avise 2001)

Mating system	No. of mates per male	$NME_{S\male}$ or $NME_{G\male}$	No. of mates per female	$NME_{S\female}$ or $NME_{G\female}$	Gender or sex experiencing more intense selection[*]
Monogamy	1	0	1	0	Neither
Polygyny[†]	>1	>0 to 1	1	0	Males
Polyandry[‡]	1	0	>1	>0 to 1	Females
Polygynandry[§]	>1	>0 to 1	>1	>0 to 1	Either or neither

[*] The NME statistics simultaneously reflect the intensity of sexual selection. The sex with the larger NME statistic has the potential to experience more intense sexual selection.

[†] The level of polygyny depends on how large the male NME statistic is ($NME_{S\male}$ or $NME_{G\male}$). A population or species with a high male NME statistic (close to one) would be more promiscuous than a population or species with a low male NME statistic (close to zero).

[‡] The level of polyandry depends on how large the female NME statistic is ($NME_{S\female}$ or $NME_{G\female}$). A population or species with a high female NME statistic (close to one) would be more promiscuous than a population or species with a low female NME statistic (close to zero).

[§] The level of polygynandry depends on how large both the male and female NME statistics are. A population or species with high female and male NME statistics (close to one) would be more promiscuous than a population or species that with low female and male NME statistics (close to zero). When one sex has a high NME statistic (close to one) and the other sex has a low NME statistic (close to zero), that population or species would be polygynandrous but have more intense polygyny (males close to one) or polyandry (females close to one).

male). The difference between the NME for mating promiscuity and the NME for progeny promiscuity represents the difference between the social mating system and the genetic mating system (i.e. the degree to which sperm competition and/or post-copulatory female choice influences the genetic mating system).

The NME method we introduce here has an obvious drawback. It requires the collection and use of a data matrix whose entries are either the number of times each individual mated with every other individual (minimally, mated/not mated data) or the number of offspring produced by possible combinations of males and females. While the former type of data matrix may be less available because of the number of hours required to observe all the matings, the latter has become commonplace. Molecular genetic techniques have advanced to the point that diagnosing maternity and paternity in natural populations has become routine.

We do not claim that the NME statistic we present can be used to derive a measure for the potential for sexual selection. The Bateman gradient already does a good job of that (Arnold & Duvall 1994). Furthermore, we also do not claim that the NME statistic can be used in a manner similar to the Bateman gradient for calculating how many offspring a male is likely to produce after a specific number of matings. Instead, NME can best be used to account for sexual interactions between individuals because it allows us to encapsulate the dyadic structure of mating systems by having the inputs be a matrix instead of a vector.

CONCLUSION

Mating systems are dyadic interactions between female and male individuals in a population. Existing methods for quantifying mating systems do not account for this dyadic structure, but only capture essences of each sex separately. Our primary contribution here is to introduce an index, normalized mutual entropy (NME), that encapsulates the dyadic structure of mating systems by having the inputs be a matrix rather than a vector. Of course, we also wish to obtain traditional mating structure indexes separately for both females and males, albeit without throwing out the dyadic baby with the bath water, and so we divide mutual entropy by marginal entropy of males and females, respectively. With this normalization of mutual entropy, we have an index of mating systems that lies between zero and one and is asymptotically *F*-distributed. This allows for comparisons between different populations and even between different studies because this index is normalized for the number of mating individuals in the population. Normalized mutual entropy can then also be interpreted as a measure of diversity and even of inbreeding. We had to slightly modify these methods for taxa that are simultaneous or sequential hermaphrodites. Here, unless we suitably modify the matrices, we only have one marginal entropy to divide by, marginal entropy of all individuals.

Hermaphrodites provided a nice segue to extending the above methods to more than just a heterosexist perspective, in which matings are always between opposite sexes where only reproduction is important, by allowing for same-sex matings and self-sex.

Normalized mutual entropy then provides an index of social cohesion, as well as promiscuity. We hope these extended methods will be used by mammalogists, primatologists, sociologists, and those interested in gender studies.

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