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How effective is recognition of siblings on the basis of genotype?

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Abstract

The ability to recognize kin based on genetic markers has been widely proposed as a mechanism to facilitate altruistic behaviour and inbreeding avoidance. Siblings are an important group of relatives to discriminate from unrelated individuals but present a problem, because siblings can share 0, 1 or 2 alleles at any single recognition locus. Here, we present a Bayesian model of kin recognition that defines the potential for genotypic information to convey kinship. Under the direct comparison model, where the signaller's genotype is compared with that of the receiver, the odds ratio that a pair of individuals were siblings was substantially increased if they shared both alleles at a single locus, but only a minority of siblings were recognized; increasing the number of recognition loci used could not increase both the odds ratio and the proportion of siblings recognized. A maternal comparison model, where the signaller's genotype is compared with that of the receiver's mother, performed poorly when only a single recognition locus was considered, but became increasingly effective with more recognition loci. Nevertheless, incorporating partial-matching information across multiple, independent loci are likely to be difficult. Further empirical work needs to establish the mechanistic basis of genetic kin recognition used by different taxa.

Introduction

A large body of evolutionary theory describes the fitness benefits that should accrue to animals if they can help their kin, avoid mating with kin or act spitefully to non-kin (Hamilton, 1964a,b). The ability to exhibit any of these behaviours in nature often requires the ability to distinguish relatives from unrelated individuals in a mixed population (Hamilton, 1964a; Maynard Smith & Szathmary, 1995). One mechanism by which kin recognition might occur is by the comparison of polymorphic genetic markers between signaller and receiver, as relatives are more likely than unrelated individuals to share alleles (Grafen, 1990; Rousset & Roze, 2007). Genetic-based kin recognition would be potentially useful where animals are not able to rely on individual familiarity, as for example where morphological phenotypes change substantially over time or where siblings come from different litters. In vertebrates, considerable interest has focussed on the use of polymorphic loci such as those of the major histocompatibility complex (MHC) or of the gene cluster encoding the major urinary proteins (MUPs), which can influence odour profiles of individuals and have been implicated as genetic cues for inbreeding avoidance (Potts *et al.*, 1991; Potts & Wakeland, 1993; Hurst *et al.*, 2001; Sherborne *et al.*, 2007). Full-siblings represent an important group of relatives to recognize because: first, they share half their genome and so the costs of inbreeding and benefits of altruism are likely to be high (Hamilton, 1964a); and, second, they often form part of the same cohort of potential mates or of con-specifics competing for resources (Frank, 1998; Griffin *et al.*, 2004). Moreover, while natural populations will also include individuals of varying degrees of relatedness, any mechanism of kin recognition that is unable to distinguish siblings from unrelated individuals is unlikely to recognize other, more distant relatives.

The problem for genetic-based kin recognition of siblings is that, while on average two siblings share 50% of their alleles identical by descent (i.e. derived from

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the same parental chromosome), the number of alleles shared at any single locus is a matter of chance. Direct comparison of the genotypes of full-siblings at a single polymorphic locus will reveal 0, 1 or 2 alleles identical by descent with probabilities 0.25, 0.5 and 0.25 respectively. Thus, the use of a single recognition locus will falsely exclude siblings that share no alleles. Assessment of sharing across multiple independent recognition loci could reduce the number of siblings falsely excluded because of lack of allele sharing. In practice, however, kin recognition will be based on recognition of alleles that are identical by state, not identical by descent. This means that some unrelated individuals may be falsely assigned as siblings because of chance sharing of alleles according to the number of different alleles at each polymorphic locus in the population. Comparison of genotypes between the signaller and the receiver's familiar mother provides an alternative model of kin recognition through behavioural imprinting on the maternal phenotype during rearing (Holmes & Sherman, 1982; Beauchamp *et al.*, 1988; Penn & Potts, 1998). This has the advantage that all offspring share an allele identical by descent with their mother. No full-siblings would therefore be falsely excluded under this model, while incorporation of genotypic information from multiple loci should reduce the proportion of unrelated individuals falsely assigned as siblings.

Here, we consider the effectiveness of genotype information from one or more independently assorting loci in discriminating between siblings and unrelated individuals under two models; (i) 'direct comparison', where the genotypes of signaller and receiver are compared directly and (ii) 'maternal comparison', where the genotype of the signaller compared with that of the receiver's mother.

Materials and methods

A kin recognition system should ideally minimize two sources of error: false assignment, where unrelated individuals share x alleles at signaller and receiver genotypes (p(unrelated|x)); and false exclusion, where sibs do not share x alleles (p(siblings|not x)). These sources of error are minimized where the probability of an unrelated individual sharing x alleles (p(x|unrelated)) is low and where the proportion of sibs sharing x alleles (p(x|siblings)) is high. Equation 1 describes the posterior odds ratio (p(siblings|x)/p(unrelated|x)) that two individuals are siblings given that the signaller and reference genotypes, for a single locus, share x alleles and is based on the product of: (i) the prior odds ratio ($r/(1-r)$), which is the expectation in the absence of genetic data that the two individuals are siblings and in the simplest case is calculated from the frequency of encounter, r, between siblings in the population; and, (ii) the Bayes factor (p(x|siblings)/p(x|unrelated)), which is the odds ratio that signaller and reference genotype will share x alleles given that signaller and receiver are or are not siblings.

$$\frac{p(\text{siblings}|x)}{p(\text{unrelated}|x)} = \frac{r}{1-r} \times \frac{p(x|\text{siblings})}{p(x|\text{unrelated})} \qquad (1)$$

Of particular interest is the Bayes factor. This describes how new genotypic information modifies prior expectations. If the Bayes factor is close to one, comparing the genotypes of the two individuals is not informative as the posterior odds ratio remains unchanged. Whereas, if the Bayes factor deviates greatly from one, genotypic information substantially alters the posterior odds ratio. Nevertheless, even if a sib can be recognized with high confidence, if it share x alleles, the proportion of sibs capable of being recognized as such will be low if p(x|siblings) is low. We considered kin recognition based on the direct comparison model, where the reference genotype is that of the receiver, and based on the maternal comparison model, where the reference genotype is that of the receiver's mother. This framework was also extended to multiple, unlinked recognition loci such that sib recognition was considered where signaller and reference genotypes shared; (i) both alleles at any of these multiple loci under the direct comparison model, (ii) 1 or more alleles at all loci under the direct comparison model and (iii) 1 or more alleles at all loci under the maternal comparison model.

To estimate p(x|siblings) and p(x|unrelated), separate simulations were performed for different numbers of alleles at a locus (or at multiple loci) present within a population. For each simulation, 1000 allele frequency distributions were drawn at random, $\{p_1, \ldots, p_i, \ldots p_n\}$ such that $p_i = p'_i / \sum_{j=1}^{n} p'_j$, where p'_i is drawn from a uniform distribution. This model therefore does not consider how diversity at such recognition loci has evolved or been maintained (Rousset & Roze, 2007). From each allele frequency distribution, p(x|siblings) and p(x|unrelated) were estimated from 250 samples from which two genotypes were picked randomly from a large population under Hardy–Weinberg equilibrium. These genotypes were set as parents from which offspring were generated and the following determined; (i) the proportion of full-sib pairs sharing 0, 1 or 2 alleles and (ii) the proportion of unrelated individuals sharing 0, 1 or 2 alleles. All simulations were performed in R v2.7.0 (http://www.r-project.org) and the code used is available as supporting information.

Results

Direct comparison model

For a single locus under the direct comparison model, sharing of both alleles between two individuals substantially increased the Bayes factor (i.e. increased the odds ratio that two individuals were siblings, Equation 1) but sharing a single allele did not (Fig. 1a). Furthermore, the

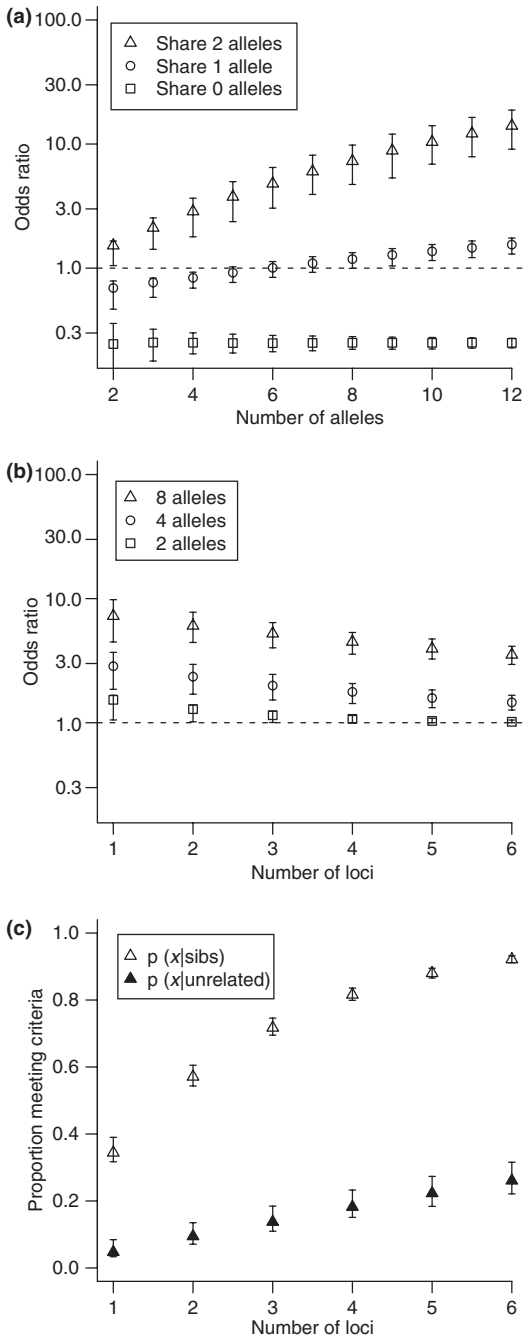

Fig. 1 The odds ratio or Bayes factor p(*x*|siblings)/p(*x*|unrelated), of sharing *x* alleles under the direct comparison model (see text) under different levels of polymorphism for (a) a single recognition locus for sharing 0, 1 or 2 alleles (squares, circles and triangles respectively); (b) multiple recognition loci such that both alleles are shared at least one locus given 2, 4 or 8 alleles at each locus within the population (squares, circles and triangles respectively); and (c) proportions of sibs (open triangles) and unrelated individuals (closed triangles) sharing both alleles at least one locus given 8 alleles at each locus in the population. Medians are shown with 95% confidence intervals for variation between randomly sampled allele frequency distributions.

Bayes factor associated with sharing both alleles increased rapidly with increasing polymorphism but for sharing one allele the Bayes factor only increased slowly. However, the error of falsely excluding siblings was high because the probability that sibs shared both alleles (p(x|siblings)) tends towards 0.25 as polymorphism increased (Fig. 1c and Table S1). Using multiple, unlinked loci increased the proportion of siblings that would share two alleles at any one (or more) of such recognition loci, but at a cost of falsely assigning an increasing proportion of unrelated individuals matching at both alleles for any of these loci (Figs 1b and c and Table S1).

An alternative means of combining genotype information across multiple loci for the direct comparison model is to recognize siblings only where each of these multiple recognition loci shares one or both alleles. Here, the information carried by each locus was relatively modest (Fig. 2a) but combined multiplicatively such that the Bayes factor increased with the number of loci (Fig. 2b). However, because failure to share either allele at a locus excluded some siblings, increasing numbers of loci led to the false exclusion of an increasing proportion of siblings (Fig. 2c and Table S2).

Maternal comparison model

In the maternal comparison model, genetic similarity was compared between the signaller's genotype and that of the receiver's mother – on the basis that all offspring share one allele identical by descent at every locus with their mother. Under this model, sharing at least one allele at a single polymorphic locus was only modestly effective at distinguishing siblings as a result of the false inclusion of a high proportion of unrelated individuals (Figs 3a and c). However, the maternal comparison model became increasingly effective when a greater number of independent loci at which at least one allele is shared was considered (Fig. 3b). Thus, as all siblings share an allele with their mother across all their loci, incorporating more loci excluded more unrelated individuals (Fig. 3c and Table S3).

Discussion

These results indicate that there is no simple system to distinguish all siblings from unrelated individuals on the basis of genotype. A simple system (i.e. one based on a single recognition locus) can correctly identify siblings that share both alleles under the direct comparison model, but this is only capable of identifying a minority of siblings. Most siblings do not share both alleles at a particular recognition locus and so are indistinguishable from unrelated individuals. Nevertheless, such a system has recently been demonstrated in a semi-natural population of wild-bred house mice (*Mus musculus domesticus*) (Sherborne *et al.*, 2007), where females avoided mating with males sharing both MUP haplotypes

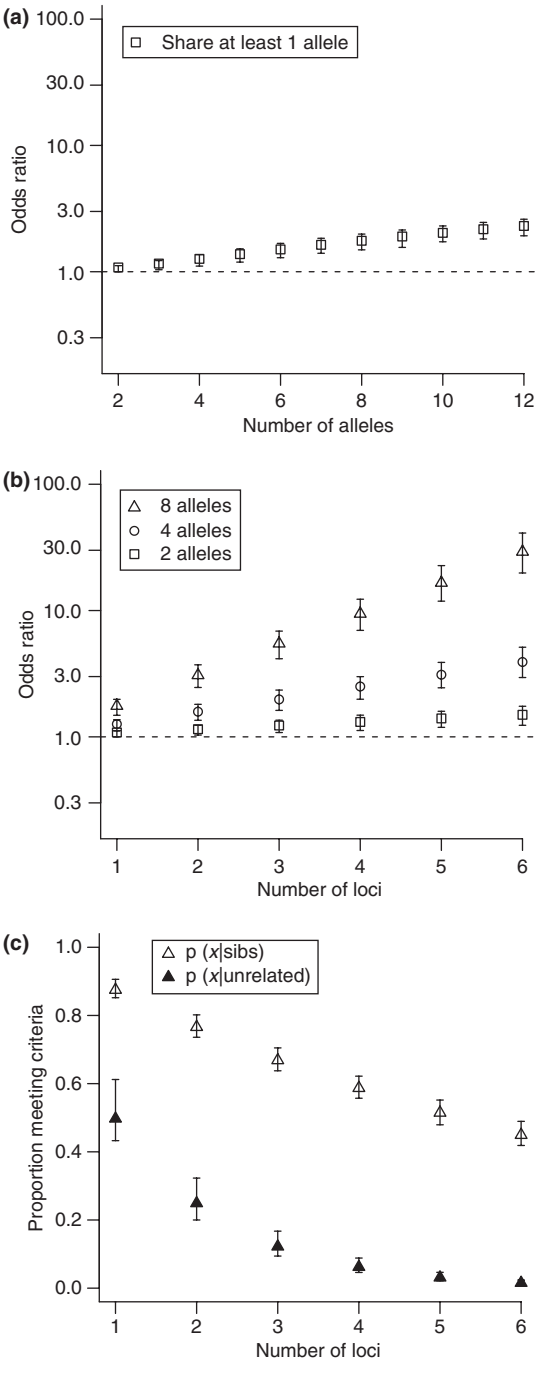

Fig. 2 The odds ratio or Bayes factor p(x|siblings)/p(x|unrelated), of sharing $x \geq 1$ alleles under the direct comparison model (see text) under different levels of polymorphism for (a) a single recognition locus for sharing of at least one allele; (b) multiple recognition loci such that at least one allele is shared at all loci given 2, 4 or 8 alleles at each locus within the population (squares, circles and triangles respectively); and (c) proportions of sibs (open triangles) and unrelated individuals (closed triangles) sharing at least one allele at all loci given 8 alleles at each locus in the population. Medians are shown with 95% confidence intervals for variation between randomly sampled allele frequency distributions.

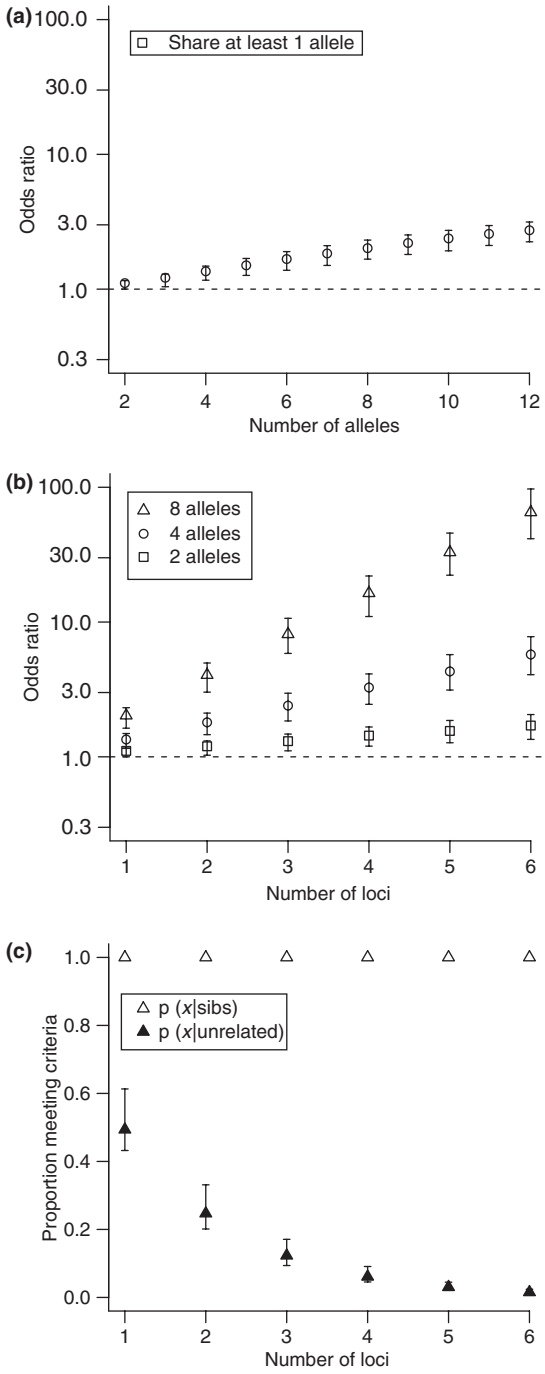

Fig. 3 The odds ratio or Bayes factor p(x|siblings)/p(x|unrelated), of sharing $x \geq 1$ alleles under the maternal comparison model (see text) under different levels of polymorphism for (a) a single recognition locus for sharing of at least one allele; (b) multiple recognition loci such that at least one allele is shared across all loci given 2, 4 or 8 alleles at each locus within the population (squares, circles and triangles respectively); and (c) proportions of sibs (open triangles) and unrelated individuals (closed triangles) sharing at least one allele at all loci given 8 alleles at each locus in the population. Medians are shown with 95% confidence intervals for variation between randomly sampled allele frequency distributions.

as themselves but did not avoid mating with full-siblings that shared only one MUP haplotype as themselves. Interestingly, the Bayes factor for animals sharing no alleles is constant around 0.25, which indicates that sharing of no alleles could potentially be used in systems where the objective is to identify unrelated individuals rather than sibs. Increasing the number of recognition loci used under the direct comparison model does not provide a ready means to both increase in the proportion of siblings recognized and reduce the proportion of unrelated, matching individuals. By contrast, recognizing siblings on the basis of sharing alleles with a maternal genotype is effective, in the sense that it is able to identify all full-siblings and maternal half-siblings. However, this is not a simple system since it relies on allele sharing across multiple, independent recognition loci. It also requires information on maternal genotype to be retained beyond any period of maternal care.

The two vertebrate genomic regions previously implicated in kin recognition, MHC and MUP, are notable in that they are each complexes of tightly linked loci, each of which may have multiple alleles (Trowsdale, 1995; Hurst *et al.*, 2001; Beynon & Hurst, 2004; Piertney & Oliver, 2006; Mudge *et al.*, 2008). With respect to the models presented here, MHC or MUP haplotypes (i.e. the set of alleles present on closely linked loci on a single chromosome) can be viewed as equivalent to alleles at a single locus. Mechanistically, however, recognition of a single 'familiar' haplotype when this is combined with another unknown haplotype, as required for the maternal comparison model, may be very difficult. Thus, a MUP genotype gives rise to a readily identifiable phenotype from the expression of 8–14 (Hurst & Beynon, 2004) distinct, polymorphic proteins present in the urine of mice, which provides a very high level of polymorphism (Hurst *et al.*, 2001; Beynon *et al.*, 2002). Previous work indicates that mice recognize and respond to such phenotypes in the recognition of individuals and to avoid inbreeding (Hurst *et al.*, 2001; Cheetham *et al.*, 2007; Sherborne *et al.*, 2007). However, it would seem extremely difficult to disentangle this complex protein expression phenotype into underlying haplotypes since the polymorphic MUP proteins present in the phenotype cannot be resolved into two separate sets of alleles expressed from a series of loci. This is because both different individuals may express different numbers of loci from each chromosome and because highly similar, paralogous loci are expressed from the same chromosome (Mudge *et al.*, 2008). Similarly, the MHC also contains many clusters of functionally similar, paralogous loci, such as DRB loci, with complex expression patterns (Vincent *et al.*, 1996; Traherne *et al.*, 2006). MHC type has complex effects on the urinary volatile odour profile of animals such as mice, which depend strongly on interaction with the genetic background, while the odours of MHC heterozygotes are not an additive combination of the two homozygous profiles (Willse *et al.*, 2006). MHC type may be more specifically detected through the pattern of peptide ligands that bind to the MHC proteins that an individual expresses (Leinders-Zufall *et al.*, 2004; Spehr *et al.*, 2006), but again it is unclear how this could be resolved into two separate haplotypes and there appears to be no empirical evidence that animals can recognize the separate MHC haplotypes carried by a heterozygous animal. Thus, partial matching across multiple recognition loci envisaged in the maternal comparison model presented here requires that such recognition loci both recombine independently of each other and that the products of such loci are separately identifiable within the recognition system of the receiver. The reliance on such loci to recognize more distant relatives than siblings becomes even more problematic, as more distant relatives are less likely to share even a single haplotype with either the receiver or the receiver's mother.

Getz (1981) presented a model of kin recognition based on 'kingrams', defined as the expected distributions for the numbers of alleles shared by either related or unrelated individuals and proposed that an optimal threshold that minimized the overlap between these distributions could be used as a criterion for deciding kinship (i.e. two individuals are accepted as kin if they share more than a certain number of alleles summed across all loci). Related models have also been presented by Beecher (1982), Lacy & Sherman (1983) and by Queller & Goodnight (1989). Under Getz's model, recognition alleles need not be identifiable to particular loci [although estimates of kinship are more accurate if this can be achieved (Queller & Goodnight, 1989)]. However, estimates of kinship still require loci to be inherited independently of each other, which may be unlikely if, as appears for MHC and MUP loci, new recognition loci evolve via duplications within gene clusters (Hughes & Yeager, 1997; Mudge *et al.*, 2008). Furthermore, any threshold number of alleles for acceptance of kinship will vary between populations depending on allele frequencies and so, consequently, requires a considerably more complex recognition model than the allele matching model that we present here. Nevertheless, the allele matching model that we propose here is not exclusive or other mechanisms, and could be used in conjunction with information on allelic or phenotypic similarity or with familiarity cues to improve kin recognition.

It is likely that both the ability to recognize kin and the associated benefits of doing so will vary between species (Pusey & Wolf, 1996; Sherborne *et al.*, 2007). Thus, in some species individuals may encounter siblings frequently while in other species such encounters may be rare. Given this, if the prior odds ratio (Eqn 1), based on the frequency of encounters between siblings, is very low, the evidence provided by the Bayes factor has to be correspondingly high to raise the posterior odds ratio above one (i.e. more likely that the two individuals are

siblings than not). Moreover, if the frequency of encounters between siblings is very rare, the fitness benefits of kin recognition will only be experienced by a small proportion of the population and so, perhaps, is unlikely to evolve. Similarly, kin recognition is only likely to evolve and be maintained where it leads to a behaviour that enhances fitness. Given this, it is likely that some species exhibit mechanisms to recognize kin while others do not, depending for example, on the extent of dispersal or on the advantages of co-operation between relatives (Hamilton, 1964a; Pusey & Wolf, 1996). Discovering which species exhibit kin recognition and why should be a fruitful topic for future study. Equally, those species that do exhibit kin recognition may not all use the same recognition system. Thus, although a great deal of research has been conducted on the MHC because this set of polymorphic loci is common to all vertebrates (Piertney & Oliver, 2006), recent research from house mice indicates that MUPs are far more important for kin and individual recognition in this species (Cheetham *et al*., 2007; Sherborne *et al*., 2007). However, the expansion of MUPs into a polymorphic gene cluster appears to have occurred recently and independently in the two highly social murid species *Mus musculus* and *Rattus norvegicus* (Logan *et al*., 2008; Mudge *et al*., 2008). As yet, the loci used by other vertebrates remain unclear and should be a priority for future studies.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Performance of the direct comparison model to correctly recognize siblings and to falsely assign unrelated individuals as siblings, where recognition is based on sharing both alleles at one or more of multiple recognition loci.

Table S2 Performance of the direct comparison model to correctly recognize siblings and to falsely assign unrelated individuals as siblings, where recognition is based on sharing at least one allele at all of multiple recognition loci.

Table S3 Performance of the maternal comparison model to falsely assign unrelated individuals as siblings, where recognition is based on sharing at least one allele with the receiver's mother for all of up to six loci under the maternal comparison model.

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