



Fostering clarity in kin recognition designs: reply to Todrank & Heth

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Todrank & Heth (2006) raise several issues about the proximate basis of kin recognition in their critique of our Commentary paper (Mateo & Holmes 2004) on the use of cross-fostering to study kin recognition. In that methods paper, we outlined several cross-fostering designs and discussed how the results using each design could be interpreted. We certainly agree with Todrank & Heth's (2006, page e1) observation that '... the theoretical, methodological and empirical issues are too complex for a thorough analysis in this brief response...' Accordingly, we will focus our comments on what we take to be the central issue in their critique of our paper (Mateo & Holmes 2004): how cross-fostering can be used to study kin recognition by phenotype matching (PM). In PM (Holmes & Sherman 1982), an individual learns some of the phenotypic traits of its rearing associates and/or its own traits ('kin referents') and stores them in memory as a 'kin template'. Later, the individual compares the phenotypes of unidentified conspecifics to its acquired kin template (the 'matching' process) and uses some type of matching rule (e.g. Lacy & Sherman 1983; Getz 1991) as a proxy for their degree of relatedness. In PM, when an individual uses a template acquired from its rearing associates, we refer to it as rearing-associates phenotype matching (RAPM) and when an individual uses a template acquired from itself, we refer to it as self-referent phenotype matching (SRPM).

In functional terms, one reason for distinguishing between RAPM and SRPM is that these two mechanisms can mediate recognition of different categories of kin. Both types of PM can mediate recognition of never-before-encountered (unfamiliar) kin, but in terms of PM, SRPM can mediate discrimination between full siblings and maternal half-siblings whereas RAPM cannot (see Hauber & Sherman 2001, Box 1, for examples in which SRPM

might mediate kin recognition). Furthermore, because individuals are more closely related to themselves than they are to their rearingmates, SRPM may provide more accurate estimates of an animal's relatedness to conspecifics than would RAPM. In our methods paper (Mateo & Holmes 2004), we described experimental designs using cross-fostering to distinguish between recognition via RAPM and SRPM. In one paragraph (pp. 1454–1455), we critiqued a design used by Heth et al. (1998) that purported to demonstrate SRPM. Todrank & Heth's (2006) Forum article, stimulated in part by our critique (Mateo & Holmes 2004), indicates that they may not have understood our argument, so we attempt to clarify the issue again here.

One of the most potent ways to investigate both RAPM and SRPM is to manipulate kin templates by altering the social makeup of early rearing environments so as to produce predictable kinds of discrimination behaviour in later tests (e.g. Buckle & Greenberg 1981; Mateo & Johnston 2000). Accordingly, cross-fostering techniques in which one newborn (single-transfer design) or more than one newborn (multiple-transfer design) is taken from its genetic parent and given to an unrelated foster parent have been used to study PM because they allow investigators to manipulate kin templates by exposing test animals to different individuals' phenotypes during early development (e.g. siblings and nonsiblings) and determining how this exposure affects subsequent discrimination abilities (e.g. Holmes 1986; Penn & Potts 1998; reviewed in Mateo & Holmes 2004). That kin templates can be acquired from an individual's rearing associates, including its nestmates and parent(s), and/or its own phenotype has consequences for how cross-fostering studies are designed if one wants to distinguish between RAPM and SRPM. We (Mateo & Holmes 2004, pp. 1453–1455) argued that the best way to investigate SRPM is to use the single-transfer design, whereas Todrank & Heth (2006) assert that the multiple-transfer design could also be used to study SRPM (see also Todrank & Heth 2003). We reasoned that the multiple-transfer design should not be used to

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investigate SRPM because a kin template could be acquired from the relative(s) transferred along with the test animal. To study self-matching, an animal should be transferred so that it is reared without exposure to kin cues (other than its own) to prevent 'social learning' from other kin (Alexander 1991), which cannot be prevented if two or more relatives are transferred together (e.g. see Figure 2 in Mateo & Holmes 2004).

Using the multiple-transfer design, fostering halves of litters between golden hamster, *Mesocricetus auratus*, mothers, Todrank & Heth (Heth et al. 1998; Todrank & Heth 2003) apply the following logic to claim that their results demonstrate SRPM, which we questioned in our cross-fostering article (Mateo & Holmes 2004). A test animal discriminates between its unfamiliar kin and the unfamiliar kin of its foster nestmates, but it fails to discriminate between the unfamiliar kin of its foster nestmates and unfamiliar individuals from another family that is unrelated to the test animal and to its foster nestmates. Todrank & Heth (2006) interpret these results to mean that the test animal did not incorporate its foster nestmates' cues into its recognition template. Then they extrapolate from their results to argue that the test animal also did not incorporate cues from its familiar kin (transferred along with the test animal) into its recognition template, because if the test animal had incorporated cues from its familiar kin during early rearing, then there is no reason that it would not also have incorporated the cues of its foster nestmates during that period. According to Todrank & Heth (2006), this set of results implies discrimination based on SRPM, because no cues of rearing-mates were learned.

We believe that there are two flaws in Todrank & Heth's argument, which lead us to reject the claim that SRPM can be studied effectively with a multiple-transfer cross-fostering design. First, their claim is based on 'negative evidence'; that is, the apparent absence of differential responses to cues from the unfamiliar kin of the test animal's foster nestmates and unfamiliar individuals from another family. Failure to find evidence of discrimination cannot be used to infer that recognition did not and could not occur (e.g. Gamboa et al. 1991) and thus that certain types of phenotypic cues were not incorporated into a recognition template. A test animal may fail to respond differentially to two stimuli because testing conditions are inadequate to reveal a recognition ability that is present or because the animal is simply not motivated to discriminate. Therefore, the negative results of Heth et al. (1998) do not allow the authors to conclude that the cues of rearingmates were not incorporated into recognition templates, nor can they assume that if cues from one category of rearingmates were not incorporated into a template (e.g. fostermates), then all other rearingmates' cues would also be excluded (e.g. familiar kin transferred with the test animal).

Second, even if we were to grant that negative evidence could be used to conclude that certain cues were not incorporated into a kin template, we believe that a multiple-transfer design is inefficient for studying SRPM because self-referencing can only be revealed under a restricted set of conditions. Todrank & Heth (2006) argued

for the operation of SRPM based, in part, on their finding that test animals failed to discriminate between unfamiliar kin of their foster nestmates and unfamiliar individuals from another family (see above). The problem is that the authors could not know whether their multiple-transfer design would reveal SRPM until after they had determined that test animals failed to discriminate between unfamiliar kin of their foster nestmates and unfamiliar individuals from another family. In other words, the results of one kind of discrimination test had to be known before the investigators could be confident that their multiple-transfer design could reveal SRPM if it were to operate. If test animals had discriminated between the unfamiliar kin of their foster nestmates and unfamiliar individuals from another family, then, according to their logic, Todrank & Heth's efforts to study SRPM with a multiple-transfer design would have been doomed from the outset. In contrast, if one uses a single-transfer design and finds that test animals discriminate between their unfamiliar kin and the unfamiliar kin of their foster nestmates, then one can infer the operation of SRPM without having to also determine whether test animals will fail to discriminate between unfamiliar kin of their foster nestmates and unfamiliar individuals from another family. Indeed, in another study with golden hamsters using a single-transfer design and a larger sample size than Heth et al. (1998), Mateo & Johnston (2000) found that the cues of foster siblings were incorporated into templates. Thus, if one were to set out to test for SRPM, one should not use a design that depends on negative results to support a conclusion.

We have focused our reply to Todrank & Heth (2006) on what we believe is the most crucial issue that they raise in their critique of our paper (Mateo & Holmes 2004), but there are also some lesser issues that require comment. Todrank & Heth (2006) assert that we '... do not explain how an animal could use a template acquired from all nestmates to distinguish between full siblings and half-siblings from litters of mixed paternity' (page e1). We have never suggested that a template acquired from both full siblings and maternal half-siblings could be used to discriminate between these kin classes, and, indeed, we wrote (Mateo & Holmes 2004) that 'Self-matching could mediate recognition when multiple paternity occurs within litters, for example, to discriminate between equally familiar full and maternal half-siblings' (page 1453).

Throughout their Forum article, Todrank & Heth refer to 'composite templates' and criticize some of our ideas (Mateo & Holmes 2004) by referring to such templates. They write, for example, 'Mateo & Holmes's (2004) criticisms are based on their assumptions about the use of composite templates acquired from their nestmates ...' (page e1). We did not use 'composite templates' in our 2004 paper, and Todrank & Heth have not defined it, so we are not clear about how to respond to their critique. That said, one way to describe a composite template would be to specify that it comprises phenotypic cues from multiple individuals, for example, two different sibling nestmates or one sibling and one maternal half-sibling nestmate, and various questions could be posed about such templates. For example, do templates comprise individually distinct cues that vary from one kin referent

to the next or do they only comprise cues shared in common by all close genetic relatives (e.g. siblings). If templates are acquired during early development, are all the phenotypes encountered (e.g. own, agemates, mother) equally likely to be represented in the composite template or do some phenotypes have privileged access to templates? If a composite template exists, will each of its components be weighted equally in the matching process or might some cues (e.g. a individual's own traits) be weighted more heavily? (Note that these issues, and appropriate cross-fostering designs for studying some of them, were addressed in our 2004 paper.) We know that composite templates as we described them above do exist (e.g. Buckle & Greenberg 1981; Holmes 1986; Mateo & Johnston 2000), but we are not sure how to respond to Todrank & Heth's (2006) critique of the term because they did not define it and we did not use it in our paper (Mateo & Holmes 2004).

We appreciate this opportunity to clarify further one of the design issues that we raised in our Commentary (Mateo & Holmes 2004), and we hope that readers find helpful this exchange on empirical and conceptual concerns about cross-fostering and phenotype matching.

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