passive by-product of related individuals aggregating in the same area, but apparently through the active recognition of kin. In their daily activities, female goldeneye ducks were more likely to occur together with their old birth nest mates than with other females, and these pairs lasted longer than did pairs of other goldeneye ducks. Hence, old nest mates seemed to recognize each other in the field, and females parasitized their birth nest mates more often than would be expected by chance alone.

This study not only suggests that the relatedness among individuals is a crucial factor in the evolution of brood parasitism in

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ducks and other species with related females breeding in the same area., but it also shows brood parasitism in a new light: as an active strategy based on social interactions and recognition of kin. Ultimately, it leads us to ask whether the female dumping her eggs in the nest of another female should even be labelled as a 'parasite' – perhaps the foster female actually benefits from looking after next-door's kids?

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Letters

Self referencing in hamsters

Comment from Heth & Todrank

Kin recognition by self-referent matching in hamsters[1] has gained prominence with the recent publication of two papers[2,3]. Hauber and Sherman[3] suggest that self-referent matching might be more widespread than was previously suspected. However, there are several limitations to Mateo and Johnston's study[2], which we address here.

Cross-fostering only one individual from each litter to minimize prior social experience with kin[2] prevents subjects from becoming familiar with phenotypes of their genetic relatives. Differential responses to kin and non-kin could be affected by differential familiarity with the phenotypes of the target individuals, precluding adequate distinctions between learned family templates and self-referent matching (see the alternative procedure[1] in which familiarity and relatedness were not confounded because halves of litters were cross-fostered).

Although tested on their pro-oestrous 'highest' scent-marking day, females averaged less than one flank scent mark in five out of the six tests performed[2]. Such low response levels cannot provide a conclusive test of differential scent marking. Furthermore, scent marking as a measure of differential agonistic motivation or solicitation would predict more marking in response to non-kin odours than to kin odours (as was found previously[1]), rather than the reverse[2]. Significant differences in vaginal scent marking[1] would also be expected rather than no differences[2]. Mateo and Johnston[2] tested the differential responses to odours of unfamiliar sisters and sisters of foster-siblings 'to assess the relative weighting of odours in kin templates', yet such 'weighting' contradicts the idea of self-referent matching, which uses the own odour rather than a family template. The differential investigation found (longer investigation of sibling odours)[2] was in the opposite direction than would be expected with self-referent matching, namely, stronger responses to non-kin odours. Subjects showed no differential investigation of female odours, yet discriminative responses are needed to substantiate a claim of self-referent matching-based nepotism. Differential investigation of male odours demonstrates discrimination between odours, but does not enable unequivocal distinctions among possible mechanisms underlying the responses. The differential latencies data might indicate differences in the qualities of the odours of kin and non-kin, but it is unclear whether this differential interest is necessarily indicative of using self-referent matching in either agonistic behaviour or mate choice.

Mateo and Johnston[2] also claim to have demonstrated two recognition mechanisms (one based on familiarity, the other on genetic relatedness) in hamsters, as was suggested in ground squirrels[4], despite not testing two mechanisms. However, the discussions of this issue in their report[2] and in that of Hauber and Sherman[3] do not acknowledge that our two papers with Johnston[1,5] demonstrated these two separate mechanisms in hamsters.

We hope these additional comments will help guide future designs and interpretations.

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Self referencing in hamsters

Reply from Mateo & Johnston

We thank Heth and Todrank[1] for their interest in our research, and wish to clarify some of the issues that they raised. First, we disagree with their assertion that they have shown self-matching and familiarity-based mechanisms for kin recognition in previous papers. As explained by Hauber and Sherman[2], the design used by Heth *et al.*[3] was inappropriate for demonstrating

self-matching. Furthermore, experiments that they claim show a role of familiarity in distinguishing kin from non-kin only examine how familiarity is important for discriminating between odors of siblings[4,5].

Second, recognition is the result of an individual's perception of the phenotypes of conspecifics and their degree of correspondence with the individual's recognition 'template'. The subsequent action taken by the individual depends both on the match between its template and the stranger's phenotype and on the context (e.g. mating, nepotism)[6]. This action component is not involved directly in the initial recognition process. In our study[7], self-matching was demonstrated through behaviors involved in the perception of odors by hamsters (e.g. latency to and duration of investigation of both male and female odours), rather than through their subsequent scent-marking behaviors.

We suggested that differential agonistic flank-marking might indicate a mating preference, but did not elaborate further because we were more interested in the mechanism rather than the function of recognition. However, from an ultimate perspective, we would expect pro-estrous and estrous females to be less agonistic toward unrelated males (potential mates), in contrast to the pattern predicted by Heth and Todrank[1,3] (although females in other reproductive states might show different trends). We did not find differential vaginal marking to male odors, but this is difficult to interpret because females were not tested in a mate-choice context.

Additional research is needed to determine the process mediating self-matching (e.g. habituation or sensitization to own odors). However, it is important to bear in mind that, functionally, the outcome of a self-matching mechanism (accurate assessments of relatedness) is independent from its underlying processes.

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Self referencing in hamsters

Reply from Hauber & Sherman

Mateo and Johnston's study[1] is important for three reasons. First, they devised a novel methodology to untangle the effects of social learning and self-referencing in the ontogeny of kin recognition. They cross-fostered single golden hamster pups <12 hrs after birth, so that each individual had only itself as a source of information about how genetic relatives would smell. By using three separate families, Mateo and Johnston created groups that were, to each cross-fostered pup, familiar non-kin, unfamiliar kin, or unfamiliar non-kin. Previous cross-fostering protocols, which involved rearing juveniles with littermates or their mother[2,3], confounded familiarity and self-referencing because recognition cues could have been learned from associates, self, or both[4]. Only by preventing subjects from becoming familiar with the phenotypes of genetic relatives can the two mechanisms be disentangled.

Second, Mateo and Johnston found that cross-fostered females approached flank-gland odors of unfamiliar non-kin significantly faster than they approached odors of unfamiliar siblings. This indicates that these hamsters used their own smell as a standard against which to compare novel odors, that is, self-referent phenotype matching.

Third, Mateo and Johnston found that cross-fostered hamsters investigated odors of familiar non-kin more slowly and for less time than they investigated odors of unfamiliar non-kin, indicating that the animals had also learned recognition cues from foster littermates. We see no reason why self-matching and familiarity-based mechanisms are incompatible[3]. To determine the relative importance of the two sources of cues, Mateo and Johnston compared the behavior of females toward odors of unfamiliar sisters and unfamiliar sisters of foster littermates. Test subjects investigated odors of unfamiliar sisters significantly longer, suggesting differential weighting of their own odors over those of their foster family. We cannot comment on the direction of the specific response measures because cues learned from nestmates and self could be used in different recognition contexts[3], and the functions of hamster kin recognition in nature are unknown[1,5].

We hope that future lab studies of self-referencing adopt Mateo and Johnston's methodology, and that this exchange encourages field studies of when and why hamsters recognize relatives.

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Low testosterone in new fathers

Comment from Place

In a recent review in *TREE*, Wynne-Edwards and Reburn[1] suggest that the decrease in serum testosterone levels of new fathers immediately after the birth of a child is associated with the expression of paternal behavior. Another explanation warrants consideration. A key variable that often changes dramatically with the shift from expectant to actual fatherhood is the duration and quality of sleep. Levels of testosterone were lower in men sampled in the three