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

weeks after birth than in men sampled before birth, and sleep deprivation can certainly develop during that interval (personal experience). Sleep deprivation has been associated with a reduction in the concentration of testosterone in men[2], and this might explain the drop in testosterone levels of new fathers. Additionally, the largest decreases in testosterone were noted in men who reported pregnancy symptoms and strong emotional responses to stimuli, such as holding a soft doll wrapped in a soiled receiving blanket, listening to recorded cries and watching a breastfeeding video[3]. These findings were taken to suggest that father–offspring interactions cause the decreased testosterone levels observed in new fathers. However, men who are more emotionally involved with the care of their baby are likely to share more in the night-time duties of parenting. Such activity will add to the severity of sleep deprivation, and perhaps to lowering of testosterone levels in these dedicated fathers. The degree of sleep deprivation among new fathers could be controlled for statistically if this confounding variable was measured. Alternatively, one might provide new fathers with supplemental childcare at night (e.g. a nanny) to determine if improved sleep prevents a decrease in testosterone levels in fathers after birth. The pool of expectant fathers who would volunteer for such a study should be vast.

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Low testosterone in new fathers

Reply from Wynne-Edwards

Ned Place raises an interesting point about the proximate stimuli that might be responsible for hormone changes in men becoming fathers[1,2]. Specifically, he speculates that sleep deprivation, which can decrease androgens[3], is responsible for the significantly lower free testosterone concentration reported for men sampled during the three-week interval immediately following the birth[1]. He finds additional support for his hypothesis in the complex relationship between psychometric measures that might reflect greater paternal involvement and lower free testosterone concentrations.

Sleep deprivation is an obvious candidate for a proximate stimulus effecting a change in testosterone concentrations (although acute sleep deprivation does not always reduce free testosterone[4]). There is also a circadian pattern in free testosterone[5] and sleep deprivation might alter testosterone concentrations by disrupting activity patterns[6]. Other lifestyle changes, including a decrease in coital frequency[7,8] or a hormonal response to time away from work[9], might affect testosterone. Similarly, anticipation of a major, stressful event (which the birth of one's first child probably is) will acutely lower testosterone immediately before, and for some time after, the event[10].

Supplying a 'night-nanny' might clarify the proximate stimuli influencing testosterone concentrations in new fathers (although this mother suspects that it might have collateral effects on testosterone through increased coital frequency too). However, understanding the proximate stimuli is not a prerequisite for studies of the role that decreased testosterone concentrations might play in the behavioural neuroendocrinology of fatherhood.

Individual men might reach 'low testosterone concentrations immediately after the birth' by different stimulus pathways. Nevertheless, all men who are bathed in lower testosterone concentrations for a period of several weeks are likely to experience subtle modifications in neuroendocrine circuits affecting learning and behaviour. Reduced testosterone concentrations precede direct paternal care in passerine birds[11]. In men, short-term decreases in free testosterone concentrations might also lower thresholds for parental bond formation or behaviour to occur.

Place is correct that a causal relationship between reduced testosterone concentrations and parental behaviour is neither established nor claimed. Longitudinal studies of individual men, cross-cultural studies representing different levels of direct paternal care by men and experimental manipulations of testosterone in 'natural fathers' are the next steps towards testing any 'causal' hypothesis.

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Sex-ratio theory in conservation biology

Comment from Tella

In a *TREE* review, Courchamp *et al.*[1] illustrated the Allee effect, resulting from stochastic sex-ratio fluctuations in small populations, with the case of the Kakapo, *Strigops habroptilus*. This parrot is now considered extinct in its original quarters in