speculation that desiccation tolerance had essentially been explained: "Now it is clear that we were optimistic in this conclusion, and that what we had thought to be a simple solution is not so simple at all" [2].

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Animal Behavior: Social Recognition in Crickets

A recent study of social recognition in crickets shows that decorated cricket females use self-referenced recognition information in their choice of mates. This allows the polyandrous females to choose novel, diverse mates.

**Michael D. Breed*
and Helen F. McCreery**

Social recognition is a powerful tool that allows animals to make important decisions about affiliations, aid-giving behavior, and mates. A key element of social recognition is to gain information about key individuals, or types of individuals, in an animal's social milieu. One use for this information is to be able to relate past social interactions to current or future social interactions. Another key use is to be able to assess genetic similarity with other animals as they are encountered. In these contexts, self-referencing — comparing conspecifics' phenotypes with one's own — is potentially important, but is poorly understood. Self-referencing may be especially useful for assessing genetic similarity.

Self-Referencing in Mate Choice

A study by Capodeanu-Nägler *et al.* [1] reported in this issue of *Current Biology* breaks new ground by providing empirical support for self-referencing in mate choice [2]. A common mechanism for recognizing how similar a conspecific is to oneself is phenotype matching, which can occur either by referencing the phenotypes of family members or by referencing one's self [3–5]. Recognition by phenotype matching [3–5] occurs when an animal learns phenotypes — common modes are vision, sound, or odor — and applies that information to assess its similarity with newly encountered animals, which can coincide with genealogical relatedness. Self-referent phenotype matching occurs if an animal uses its own phenotype as the basis for its template.

Phenotype matching is not the only way individuals can self-reference in the context of social recognition. It is possible to compare a conspecific's phenotype with ones own in real time, without a template, using on-line processing. On-line processing does not require high-level integration of sensory information, and is therefore a simpler process than template formation [3]. On-line processing is a recently proposed and compelling model for recognition that questions the axiom that templates are necessary. Self-referencing is difficult to experimentally assess and requires particularly shrewd designs for convincing tests.

The few studies on self-referencing in mate choice have focused on immunocompatibility of potential mates [6,7]. Decorated crickets (Figure 1) present an interesting study system to look at self-referencing in a different context. Female decorated crickets are polyandrous, and prefer not to mate with males with whom they have previously mated.

Cuticular Hydrocarbons as Mate Choice Cues

Crickets use cuticular hydrocarbons (CHCs) in mate choice decisions, and because CHCs are transferred during mating, they can assess whether they have previously mated with a particular male by self-referencing, by comparing a male's CHC profile with their own [8]. CHCs, which form the waxy or greasy surface on an insect's exoskeleton, probably first evolved as waterproofing, as did the analogous waxy cuticle of plant leaves. Individuals of any given insect species have a mixture of a few to dozens of such compounds on their surface. The blend is typically species-specific but variation often exists among individuals. This variation carries information about sex, mating status, age, and family membership. Obviously much of this information is potentially useful in choosing mates.

Figure 1. A mating pair of decorated crickets. (Photograph courtesy of Dave Funk.)

Capodeanu-Nägler *et al.* looked at self-referencing of CHC profiles in mate choice using some important facts from previously published research. CHCs are transferred from females to males during copulation and female crickets use these cues to avoid repeated matings with the same males. The CHC profile of a cricket can be modified by applying extracts of CHCs from another cricket. In their new study inbred lines of crickets are used to reduce within-family variation in CHCs and reduce potential overlap in cue profile among families, making it easier to assess the impact of changes in CHC profile on within- and between-family behavior.

Capodeanu-Nägler *et al.*'s clever experimental design modifies the CHC profile of female decorated crickets. These females' phenotypes were altered so that they smelled like mates that would be offered to them later in the experiment. Females made mating decisions based on these new phenotypes, preferring to mate with males that smelled like the females used to smell, rather than mate with new males that shared their current smell. This experiment disentangles whether females use contemporaneous self-referencing or compare potential mates' profiles to a static template (i.e., phenotype matching).

In these crickets, the use of self-referencing in mate choice is robust to rapid changes in the self-referenced phenotype. While the authors did not rule out the possibility that females memorize a template of their phenotype while updating it rapidly, the simplest explanation for the results is that the crickets use on-line processing, comparing males' phenotypes to their own with no high-level integration.

The Importance of Self-Referencing

Capodeanu-Nägler *et al.* investigated self-referencing in female decorated crickets in the context of maximizing polyandry in mate choice. Nevertheless, since CHC profiles are similar among close relatives, this same self-referencing mechanism may be important in avoiding inbreeding in this species as well.

This paper provides clear evidence for rapidly updating self-referencing in the context of mating for this species. Given that self-referencing is potentially widespread among animals and important in critical contexts such as mating, the results of Capodeanu-Nägler *et al.* suggest that studies in which similar misdirection is employed could reveal the use of similar mechanisms in other species.

Ozaki *et al.* [9] proposed a similar on-line mechanism in nestmate recognition systems of the ant *Camponotus japonicus* and such mechanisms may be important in other eusocial insects. Ants, bees, wasps and termites all need to discriminate nestmates from non-nestmates and most species exclude non-nestmates from their nest. This behavior prevents robbing and social parasitism.

Most studies of nestmate recognition have been interpreted to reflect learned cuticular hydrocarbon profiles, but recently Ozaki [9] and van Zweden [10] have questioned the necessity for learning as a step in making these comparisons. Instead, eusocial insects, like the decorated crickets, could be making an on-line comparison between self and the potential intruder. This would explain the rapidity with which honeybee guards change their perception of nest membership when their cue profile is changed [11] and the lack of ability of these guards to use both an old and a new cue template. Rather than replacing a learned template with a new template, perhaps they are always self-referencing and simply use whatever cues are available on their own surface at the moment they encounter an intruder.

An advantage of using contemporaneous self-referencing over template comparison is that it does not require special adaptations for learning and memory and does not involve longterm storage of recognition information. For insects and other invertebrates, which possibly have limited learning and memory capacity, this may have been an easier evolutionary solution to the problem of inbreeding avoidance than elaborate mechanisms of template learning. Self-habituation at the sensory level is one possible on-line processing mechanism and would be particularly parsimonious; an animal whose sensory system stops responding to its own cuticular cue profile would then still be able to perceive non-matching profiles [9]. Capodeanu-Nägler and colleagues' exciting study contributes to our understanding of social recognition by demonstrating that female decorated crickets self-reference in the context of mate choice in a way that rapidly updates, suggesting on-line processing of recognition information.

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