Dispatches

Animal Behavior: Stay Close for Comfort

Mate guarding — a male staying near a female for a while after mating — has traditionally been interpreted in the context of sexual conflict. New observations of wild field crickets suggest instead that guarding males provide protection from predators, enhancing female fitness.

Marlene Zuk

With many animals, mating is not over even well after copulation is finished. Male bluebirds and flycatchers, for instance, perch near their mates for the days surrounding the fertile period; male tiger beetles grasp females with their jaws and move with them for several hours after copulation; and, male crickets attempt to remain in contact with females after spermatophore attachment, antennating the female and blocking her path if she moves away. Such post-insemination behavior, called ‘mate guarding’, is usually interpreted as a means by which males ensure that their own ejaculates, rather than those of rivals, fertilize a female's eggs [1]. Mate guarding has even been suggested to occur in humans, with sexual jealousy on the part of either men or women as one of its manifestations [2].

Geoff Parker [3] developed the theory about the evolution of mate guarding, and numerous studies have since documented its occurrence as well as quantified the costs and benefits to males of relinquishing future mating opportunities but increasing the likelihood of paternity from the current mating [4,5]. Initially, looking at mate guarding as a way of a male gaining an edge in sexual competition was part of the increasing recognition of selection at the level of the individual, in contrast to a ‘good-of-the-group’ rationale [1].

Following this perspective, although some researchers have emphasized a role for female choice in mate guarding [6], much of the more recent work has assumed that mate guarding is a manifestation of sexual conflict, in which opposing selective forces act on males and females [7]. According to this view, females would be better off left alone to choose additional mates, and hence should be expected to oppose attempted mate guarding. Males, by contrast, benefit by protecting their investment and are expected to attempt to override any such female resistance. But is mate guarding always a bad deal for females? A recent study in *Current Biology* by Rolando Rodríguez-Muñoz, Amanda Bretman and Tom Tregenza [8] suggests otherwise.

The scientists used a wild population of the field cricket *Gryllus campestris*, a species in which both females and males occupy burrows dug into the soil [9]. Burrows are defended against conspecifics and are only shared by an opposite-sex pair around the time of mating. Each cricket in the population has been tagged and was monitored with video, as well as genotyped so that the reproductive success of every individual could be tracked [8,9]. This meticulous monitoring over the lifetime of the individual crickets meant that the population could be studied much like those of large vertebrates such as lions or primates, with generations telescoped for a better understanding of the evolutionary trajectory for the insects.

Like many insects, the crickets are subject to predation, mainly by birds, and the burrows serve as a refuge when predators strike. If a predator attacked a pair of crickets occupying a burrow, as occurred more often than a predator striking a lone individual, the male allowed the female first access to the shelter, a practice that resulted in much lower mortality for the female than the male (Figure 1). In turn, the male cricket was likely to mate more frequently with a female sharing his burrow, and thereby fathered more offspring [8]. Males that spent more time sharing a burrow mated more times with the same female, but were not more likely to have multiple mates [8]. The ‘guarding’ by males thus benefitted both sexes, rather than representing a conflict of interest.

Figure 1. The cost of cricket ‘chivalry’.

Female cricket 6J entering the burrow she shared with her last partner, male 9A. His scattered remains are the result of a lethal attack by a nabid bug. Photo courtesy of www.wildcrickets.org.

The authors [8] suggest that postinsemination associations in other species could evolve either via the previously described more conventional pathway of sexual conflict and coercion, or through cooperation and mutual benefit, such as in crickets. An important component to their study is the natural setting in which it was conducted; most studies of mate guarding in crickets and other insects have taken place in small laboratory cages that do not allow the participants much mobility. Females thus confined might have been unable to evade the efforts of males to prevent them leaving or removing a spermatophore, making it difficult to evaluate the effectiveness of mate guarding under natural circumstances.

Variation in features such as the availability of suitable burrow habitat, the sex ratio, or the population density will influence the probability of finding a new mate and hence the costs and benefits of mate guarding for both sexes [10]. For example, if females are relatively scarce, males would benefit by remaining with mates longer than if females were common. In species that form pair bonds but also engage in extra-pair copulations, such as many songbirds, males must balance the gains of prolonged mate guarding against the costs of losing opportunities to find extra-pair mates, while females might be less able to exercise mate choice when being guarded [10].

The generality of the findings by Rodríguez-Muñoz and colleagues [8] also remains to be seen. In many animals, including many species of crickets and other insects, males do not have a resource such as the refuge of a burrow to offer to females, and remaining with a mate after copulation could simply prolong a period of vulnerability to predators [11]. Regardless, 'mate guarding' may be too narrow a term, as the behaviors exhibited may include activity, as well as benefits, to both sexes [12].

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Neuroscience: How Is Three-Dimensional Space Encoded in the Brain?

A recent study in the rat has shown that hippocampal place cells and entorhinal grid cells exhibit vertically-elongated firing fields, indicating that the rat's brain may encode the animal's elevation less accurately than its horizontal position.

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We live in a three-dimensional world. Questions about how we perceive and represent the three-dimensional world that surrounds us have occupied humankind for centuries. In art, the perception of three-dimensional space has been a central theme, from the gradual development of geometrical perspective methods, in antiquity and the Middle Ages, to modern three-dimensional films. In philosophy, many thinkers have debated the nature of three-dimensional space: While Newton argued that space is an objective, absolute entity, Kant argued that space is an *a priori* mental framework that our mind uses to coordinate external sensations [1]. In science, the physicists of the 20th century, from Einstein onward, have made great progress in understanding the nature of three-dimensional space and its distortions. Very little progress, however, has been made in understanding the mental representation of three-dimensional space in the brain. A recent study by Hayman *et al.* [2] starts to close this gap between the physics and neuroscience of three-dimensional space.

While few previous studies have examined the neural representation of three-dimensional space, the representation of two-dimensional planes in the brain has been studied extensively for the past 40 years [3,4]. The neural machinery that represents two-dimensional spatial planes includes 'place cells' in the hippocampus — neurons that become active when the animal traverses a particular location in space, termed the 'place field' [3–5] — and 'grid cells' in the entorhinal cortex and adjacent regions — neurons that are activated when the animal passes through the vertices of a hexagonal two-dimensional lattice that spans the environment [4,6]. Together with neurons that encode the animal's head-direction [7], and neurons which encode the positions of the geometric borders of the environment [8], these types of space-coding cells form the essential components of the brain's 'navigation circuit' for two-dimensional environments. But what about the third dimension?

Previous experiments in three-dimensional environments included a study of hippocampal place cells in rats walking on a surface titled