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LETTER TO THE EDITOR

Dart Shooting in Helicid Snails: An 'Honest' Signal or an Instrument of Manipulation?

In some species of helicid land snails, a snail pushes a calcareous spear, or "love dart", through the body wall of its partner during courtship. Recently Leonard (1992 p. 513) proposed a novel explanation for the occurrence of this behaviour, the functional significance of which has been debated for over a century (Ashford, 1883; see Leonard, 1992). She suggests that the dart "... serves to induce a (snail's mating) partner to act as a male by acting as an honest signal of an individual's willingness to reciprocate in a sperm-trading mating system". We feel that the available data do not support this conclusion and we wish to suggest an alternative hypothesis, namely, that snails have evolved dart-shooting behaviour in order to manipulate sperm utilization and/or oviposition in their mating partners (Charnov, 1979; Tompa, 1980). In other animals from different phyla, males influence female reproduction indirectly by stimulating the female's sensory systems (Becker *et al.*, 1993). We suggest that snails have evolved the additional ability to influence fertilization directly by manipulating the endocrine system of their partners.

Terrestrial snails of the genus *Helix* are simultaneous reciprocal hermaphrodites that do not self-fertilize (Frömming, 1954). Sperm received during copulation can be stored for at least 2 years (Tryon, 1882). Copulation does not necessarily lead to oviposition, and the time between copulation and oviposition can vary greatly (Moulin, 1980). Moreover, two or more copulations may occur between successive oviposition events (Moulin, 1980). Given these conditions of sexual reproduction, a helicid snail has the potential to "choose" which sperm it will use to fertilize its eggs. Therefore, a snail could enhance its reproductive fitness by increasing the chance that its own sperm will be used to fertilize its partner's eggs (Charnov, 1979).

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In *Helix aspersa*, both mating partners shoot a dart. Each pushes a calcareous dart through the body wall of its partner. The dart is coated with a mucus that is secreted by the digitiform gland. It is usual for the dart to become lodged in the skin of the partner, thus providing an opportunity for the mucus to dissolve in the haemocoel (Adamo & Chase, 1988, 1990). Factors present within the mucus can facilitate courtship by increasing behavioural synchrony between the two mating snails (Adamo & Chase, 1990). It has also been speculated that the dart may increase the reproductive fitness of the dart-shooter by somehow influencing fertilization (Charnov, 1979; Tompa, 1980).

Dart-shooting occurs towards the end of courtship. During the initial stages of courtship, snails evert their normally internal genital apparatus. Once the eversion has reached its maximal level, a snail pushes against its partner, then rapidly everts its muscular dart sac. After dart-shooting, the snail everts its penis and attempts to copulate. Its partner soon fires its own dart, and then it too begins to evert its penis. After a variable number of copulation attempts, simultaneous intromission is achieved (Chung, 1987; Adamo & Chase, 1988). Snails exchange spermatophores whenever there is successful simultaneous intromission (Chung, 1987; Adamo & Chase, 1988), suggesting that snails do not copulate without exchanging spermatophores.

Leonard (1992) proposes that dart-shooting is a metabolically expensive (and hence honest) signal affirming a snail's intention to mate as a male. She argues that the male is the less preferred role in this system because of the uncertainty that its sperm will be used to fertilize eggs. The female, on the other hand, has a more sure investment for her reproductive effort. Leonard (1992) makes explicit predictions about what should be observed if her hypothesis was correct. For example, she predicts that individuals that do not dart-shoot should deliver little or no sperm to their partner. Fortunately this prediction can be tested in *H. aspersa* because these snails

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occasionally court without dart-shooting (Guisti & Lepri, 1980; Chung, 1987). Because snails require 5–7 days to make another dart once it has been shed during mating (Dillaman, 1981; Tompa, 1982) snails that court before the dart has been re-formed do not dart-shoot. During courtships in which either one or both snails did not shoot darts, both Guisti & Lepri (1980) and Chung (1987) noted that both snails produced and exchanged spermatophores, and Chung (1987) observed that these spermatophores were full. This is contrary to Leonard's prediction.

Leonard (1992) also argues that courtship by these recently mated dartless snails represents their attempt to 'cheat' their partners, because after copulation, snails make undesirable mates. If this were the case, then the evolution of a mechanism to signal honest intent might be adaptive because dart-shooting snails would gain preferential access to mates by eliminating uncertainty about their (i.e. the dart-shooter's) reproductive status. However, Leonard's (1992) argument fails on two grounds. First, there is little reason to believe that recently mated snails make undesirable mates. Recently mated snails are capable of making both sperm and spermatophores (Chung, 1987). Recently mated snails are also likely to have unfertilized eggs available, since snails (*Helix aspersa*) tend to oviposit 1–2 weeks after copulation (Moulin, 1980) and fertilization occurs at the time of oviposition (see Tompa, 1984). Moreover, Baur (1994) has found that in the related land snail *Arianta arbustorum*, the second male to mate sires 0% to 100% of the offspring (with an average of about 32% $\pm$ 14%), suggesting that mating with a recently mated snail would not necessarily result in lowered reproductive fitness. Second, there is no evidence that snails avoid copulation with dartless partners (i.e. potential cheaters) (Lind, 1976; Guisti & Lepri, 1980; Chung, 1987). If anything, copulation occurs more rapidly without dart shooting, provided both snails have a high level of sexual arousal (Adamo & Chase, 1990). The observation by several researchers (Lind, 1976; Guisti & Lepri, 1980; Chung, 1987) that dartless snails are readily accepted as mating partners does not support Leonard's (1992) hypothesis.

Furthermore, if the female were the preferred role in *H. aspersa*, it would be expected that snails would prefer to act unilaterally as females. In fact, the evidence suggests the opposite. Both Guisti & Lepri (1980) and Chung (1987) observed that if the penis is unilaterally inserted during mating, the mating partner appears to push it out. Chung (1987) observed that in rare cases in which unilateral intromission was achieved, the partner that was acting as a male adopted the normal copulatory posture that the animals exhibit when passing a spermatophore. The animal that was acting unilaterally as a female, however, did not adopt this posture but instead pulled away from its partner and attempted to bite the penis until it was dislodged.

Contrary to Leonard's (1992) prediction, the evidence suggests that the male role is preferred in *H. aspersa*. After dart-shooting, a snail everts its penis and attempts to copulate with its partner. However, the partner does not permit intromission until it is ready to intromit. In other words, intromission does not occur before the second male has begun to evert its own penis (Chung, 1987; Adamo & Chase, 1988). Moreover, snails will copulate unilaterally as males when they are with partners that have had their penes surgically removed (Jeppesen, 1976). In these cases, it is likely that the operated snail allows unilateral intromission only because it is incapable of perceiving that it has not achieved intromission. Together, these observations are most consistent with the hypothesis that the male, not the female role, is preferred.

Regardless of which sexual role may be preferred in hermaphroditic snails, 'cheating', i.e. acting as only a male or female, appears to be prevented by the reciprocity required for copulation. The entrance to the vagina is normally closed by a sphincter muscle which is relaxed only when the snail is everting its own penis (Chung, 1987). Presumably animals that have had their penes surgically removed were able to participate in unilateral matings because they relax this sphincter when they evert their "phantom" penes in the same way that snails that have had their dart sacs removed evert the stump of the dart sac during dart-shooting (Adamo & Chase, 1990).

Not only is Leonard's hypothesis not supported by the available data, but it fails to demonstrate how the dart could be used as a "signal". In animal communication systems, signals are "honest" either because there is a cost to cheating (Dawkins & Guildford, 1991) or because cheating is impossible as the signal is an unavoidable correlate of the animal's physiological condition (Zahavi, 1977). Expensive signals are "honest" not simply because they are metabolically costly, but because they are a reflection of the animal's physiological status. For example, roaring in stags is both an expensive and honest signal because the ability of a stag to roar depends on its strength (see Burk, 1988). Dart-shooting, on the other hand, although expensive, is not necessarily correlated with either male sexual behaviour or spermatophore production. This makes dart-shooting a "conventional signal" (Maynard Smith & Harper, 1988), if it is a signal at all, and therefore it is a system that is open to cheating. Leonard (1992) does not

discuss what would prevent a snail from shooting a dart, signalling its intention to mate as a male, but then withholding its spermatophore from its partner during copulation. In this way a snail could induce its partner to mate *and* avoid having to fulfill the male role. Without some explanation as to how cheating could be prevented, it is unclear how the dart could have evolved as a signal of a snail's intent to mate as a male.

The known features of snail reproduction, briefly reviewed above, are consistent with the hypothesis that the dart serves to increase the likelihood that the recipient will use the shooter's sperm to fertilize its eggs (Charnov, 1979; Tompa, 1980). According to this hypothesis, the substance(s) passed by the dart influences female reproduction, but not courtship *per se*. We suggest that the digitiform gland mucus contains some of the same hormonal factors that otherwise control snail reproduction (see Joose & Geraerts, 1983), and that by introducing them into the mating partner's haemocoel, snails can directly manipulate their partner's reproductive physiology, thereby increasing their own reproductive success.

This hypothesis explains why both snails expel darts, as opposed to just one, since both snails will benefit by inducing the other to use its sperm. It also accounts for the fact that courtship can occur normally without dart-shooting. If, for example, a snail has received inferior sperm and attempts to mate again without dart-shooting, our hypothesis predicts that it will still be a desirable mating partner. Although the dartless snail has less chance of manipulating its mating partner because it cannot inject it with digitiform gland mucus, it can still produce and receive sperm (Chung, 1987). Therefore the cost of mating with a dartless snail is borne by the dartless snail, not by the snail's partner. We also suggest that the lack of ability of dartless snails to manipulate their partners is the main reason why few snails mate while lacking a dart. A clear and testable prediction of our hypothesis is that snails that succeed in penetrating their partners with a dart will sire more offspring than snails that are unsuccessful in dart-shooting.

Understanding male and female sexual strategies demands an integrative approach (Ryan, 1990). For example, some species, such as *H. aspersa*, may have evolved anatomical, physiological and behavioural specializations that allow an individual to manipulate its partner's endocrine system. The potential for this exists in any animal with internal fertilization. It is known that the spermatophore or seminal fluid of many animal species contains endocrine factors that are involved in female reproduction (see Loher *et al.*, 1981; Gormendio & Roldan, 1993; Chapman *et al.* 1994). Thus, to interpret the functional significance of some traits may require an understanding of the animal's physiology as well as its behaviour (Gomendio & Roldan, 1993).

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