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The function of dart shooting in helicid snails*

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Abstract: Some stylommatophoran species, including several helicid snails common to Europe and North America, drive sharp, calcareous darts into their sexual partners prior to copulation. Why any animal would treat a prospective mate in this manner has been the subject of considerable speculation. One widely held belief is that the dart stimulates the partner. Here, I review evidence showing that this hypothesis, along with several others, is almost certainly incorrect. On the other hand, there is strong empirical support for the idea that the dart increases the reproductive fitness of the successful shooter by promoting the survival and utilization of its sperm. How the dart works to produce this effect is an open question; current evidence indicates that it injects a chemical agent into the recipient and that this substance contracts the female tract in such a manner as to facilitate the passage of allosperm to the spermatheca. Although successful dart shooting clearly benefits the shooter, there is little evidence to suggest either a cost or a benefit to the recipient.

Key words: sexual selection, sperm competition, courtship, sexual conflict, *Cantareus aspersus*

According to recent phylogenetic studies (Koene and Schulenburg 2005, Davison *et al.* 2006), a dart is used in only 4-9 families within the Stylommatophora, which comprises approx. 60 families of snails and slugs in total. It is noteworthy that all the dart-bearing families mate in a simultaneous, reciprocal manner (Davison *et al.* 2006). Most of the research on molluscan darts has been done on helicid snails, in particular *Cantareus aspersus* (Müller, 1774; formerly *Helix aspersa*). Therefore, the present review relates specifically to *C. aspersus* unless otherwise noted.

The dart, like other reproductive structures, differs greatly in size and shape among species (Koene and Schulenburg 2005). Individuals of a few species even possess multiple darts, all of which are released in a single courtship episode. In *Cantareus aspersus,* the dart is sharply pointed; it has a fluted shaft and a corona by which it attaches to the dart sac while in storage (Fig. 1). The dart from the first shooter is released about 30 min before the initiation of courtship (Fig. 2). About 25 min later, the second animal releases its dart. Copulation (mutual intromission) ensues after a further 10 min (Chung 1987, Adamo and Chase 1988). Although the act of releasing the dart is often described as "shooting," in fact the dart does not travel through the air. It is forcefully externalized, but its corona remains lightly attached to the dart sac until it is pulled away after the tip becomes embedded in the partner's skin. Approximately one-half of the darts strike the body wall of the partner and remain lodged there for hours, whereas the rest of the darts either miss the intended target altogether or strike only weakly, then fall out. In the former cases, the dart is retracted. Significantly, copulation occurs regardless of the fate of either partner's dart.

From appearances, it would seem that the dart is harmful, but this has not been proven. Although I have observed hundreds of matings, I have never seen any reaction to the dart apart from a momentary reflexive withdrawal of the body. Never has an animal suffered a noticeable long-term effect, let alone death. However, I have seen one dart penetrate cleanly through the head of its target (Fig. 1 in Chase and Blanchard 2006) and another dart lodge in the cerebral ganglion.

The possibility of interactions between the two dart shooting events of a courtship was examined in a recent study (Chase and Vaga 2006). We found that neither the timing, accuracy, nor location of the second shot was influenced by the success or failure of the first shot. This result, and others, indicates that dart shooting is not a source of conflict during the mating process: the protracted courtships cannot be interpreted as attempts to shoot without being shot. Rather, each snail appears to be interested only in getting off the best possible shot, evidently one that penetrates deeply near the genital pore, for reasons to be explained below. Although we found no evidence for direct costs of dart receipt, the possibility of indirect, post-copulatory costs remains a possibility; this too will be discussed below.

FOUR FALSIFIED HYPOTHESES

The striking behavior of dart shooting has occasioned numerous commentaries through the ages, with no paucity

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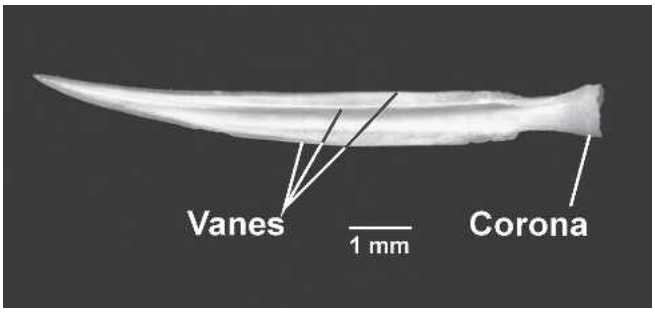

Figure 1. Photograph of a dart from *Cantareus aspersus*. The corona remains attached to the tubercle of the dart sac until the dart strikes its target. As the dart is expelled, mucus collects in the fluted cavities created by the vanes.

of speculation as to its function. Here, I briefly review several hypotheses which, although once plausible, may now be rejected (see also Landolfa 2002).

1. Sexual stimulation

Swammerdamm described the dart in the mid seventeenth century, but he was apparently unaware of its role in reproduction (for references, see Kothbauer 1988). The first written account of dart shooting is by Maupertuis (1753). Maupertuis' interpretation of the dart's function was precisely that of most modern authors, namely that it stimulates the partner to proceed with mating. Kothbauer (1988) has drawn our attention to the fact that Maupertuis' view of dart shooting in snails, as well as that of many subsequent authors, corresponds to the main idea behind Eros, the Greek god who was able to cause other gods to fall in love by shooting them with arrows. Indeed, although I have no evidence, I suspect that the ancient Greeks created Eros after observing *Cantareus aspersus* (or perhaps *Helix pomatia* Linnaeus, 1758) shooting darts in their gardens. Maupertuis asserted that the snail's use of the dart is necessary and justifiable due to the snails' lethargic disposition, but he argued that for humans to use similar violent means to arouse passions would be immoral.

An immediate objection to the idea that the dart's function is to stimulate the partner is that by the time the dart is shot, *i.e.*, late in the courtship ritual, the partner is already highly aroused; indeed the partner is nearly ready to shoot its own dart. Hence, at this point, there is no need to further stimulate the partner.

Several empirical studies have examined whether the receipt of a dart does, in fact, quicken the activity of the targeted partner. Adamo and Chase (1988) found that the interval between the two dart shots was slightly reduced when the first shot hit the partner compared to when it missed the partner; these data suggested a stimulatory effect of the dart. However, other studies (*e.g.*, Lind 1976, *Helix pomatia*) reported either an absence of stimulation or an actual diminution in the level of arousal after a snail was hit by a dart. Additionally, in a recent study with a large sample size and strictly defined measures, we found no significant effect of successful dart shooting on the interval between dart shots (Chase and Vaga 2006). Nor did we find that the outcome of either dart shot affected the duration of courtship (measured from the first dart shot to intromission).

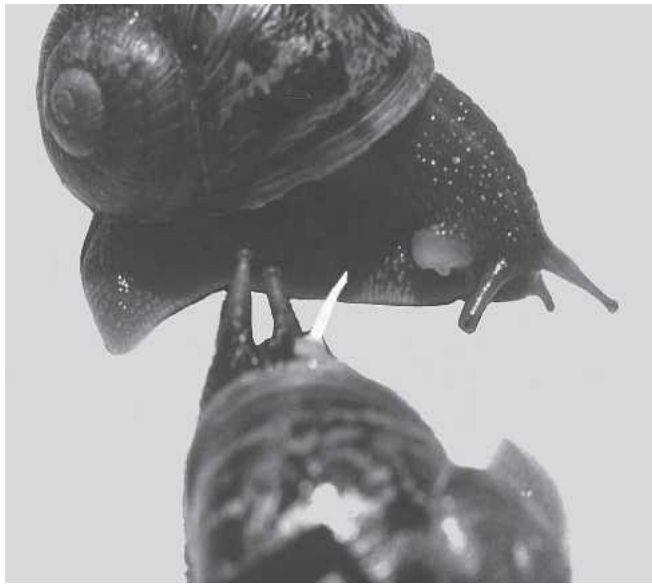

Figure 2. An individual of *Cantareus aspersus* photographed at the moment of dart release. Because this dart did not penetrate the partner, it was retracted by the shooter and digested. The peculiar squeezed appearance of the shooter's tentacles is the consequence of elevated hydrostatic pressure. Note also the everted genital apparatus of the intended target snail. The photograph was digitally edited to eliminate background and to enhance contrast; the dart was colored white. Shell length of the upper snail is ca. 27 mm. Original photograph by Shelley Adamo; photograph reproduced with permission of Oxford University Press.

2. Species recognition

This hypothesis (Diver 1940) is built on the fact that snails lack an auditory sense and have essentially no vision, leaving only touch and chemosensation as instruments by which to distinguish conspecifics from heterospecifics. The hypothesis is effectively disproven by the fact that snails show no reluctance to mate even when untouched by their partner's dart. An alternative, and likely, means of identifying conspecifics is through the extensive body contacts that occur during courtship.

3. A gift of calcium

Charnov (1979) proposed that the dart is a gift of calcium that can be used to promote the development of offspring. It is true, of course, that young snails require an ample supply of calcium to grow their shells, and that environmental sources of the mineral may be limited. On logical grounds, however, it would seem to be a poor strategy to give away as much calcium by shooting a dart as one is likely to get by receiving a dart. In any case, the amount of calcium that can be effectively transmitted to the offspring from a donated dart is too small to make an appreciable difference (Koene and Chase 1998a).

4. A signal of intention

In an attempt to solve the enigma of the dart, Leonard (1992) advanced the idea that snails shoot darts to signal their readiness to deliver sperm to their partner. This hypothesis grew out of earlier work in which she claimed that the male role is the less preferred role in the helicid mating system because the fate of donated sperm is uncertain. Thus, she argued, snails would rather mate as females. The evolution of the dart provided an honest signal of a snail's intention to donate sperm, thus inducing the partner to reciprocate and allowing both snails to benefit. Leonard's bold hypothesis, however, has been contested on both theoretical and empirical grounds. First, the assumed preference for the female role is untenable because, over time, the fitness of male actors and female actors is exactly equal (Greeff and Michiels 1998). Second, several of Leonard's specific predictions have been falsified (Adamo and Chase 1996). Critically, snails that do not receive darts nevertheless intromit and they deliver full spermatophores to their non-shooting or poorly shooting partners (Rogers and Chase 2001, Chase and Vaga 2006).

ONE SUPPORTED HYPOTHESIS

The only hypothesis to receive consistent empirical support states that successful dart shooting enhances male fitness by allowing more of the shooter's sperm to become stored in the recipient's spermathecal sacs, hereafter referred to as the sperm-loading hypothesis. As first proposed by Chung (1987) and later elaborated upon by Adamo and Chase (1996), the sperm-loading hypothesis treats dart shooting as a male manipulative device while ignoring female interests, but I discuss the female point of view below. In addition, neither Chung (1987) nor Adamo and Chase (1996) explicitly referred to the concept of sperm competition, *i.e.*, competition between males to fertilize eggs, although it is in this context that the hypothesis is correctly placed today. Helicid snails are ideal participants for sperm competitions because they mate promiscuously, they store sperm for long periods of time, and they fertilize internally (Chase 2002).

In helicid snails, sperm are packaged inside a spermatophore for transfer during copulation. After the spermatophore is delivered to the partner, the sperm leave the spermatophore and migrate to the storage site, a structure known as the fertilization pouch–spermathecal complex (FPSC). Along the way, digestive enzymes typically digest about 99.98% of the received allosperm (Lind 1973, Rogers and Chase 2001).

Strong evidence in favor of the sperm-loading hypothesis came from the study of Rogers and Chase (2001). Virgin snails were mated one time only with partners that either hit them with their darts or missed them with their darts. Seven days after the mating, the former virgin was dissected and the FPSC was removed. Allosperm in the FPSC were labeled using a fluorescent DNA stain, then counted. Snails that were hit by a dart stored 116% more sperm than snails that were missed (Rogers and Chase 2001). Because helicid snails can produce multiple egg clutches from the sperm of a single donor (Chen and Baur 1993), the results of this experiment imply a fitness advantage to the successful dart shooter because its sperm should remain available for a larger number of clutches than would be the case if its dart had missed.

To see whether the increased sperm storage that we observed after a single mating would provide an advantage when the successful shooter competed with a second sperm donor, we conducted competitive mating trials in which one donor hit the recipient with his dart and the other donor missed. The order of hits and misses was balanced. After the matings, we waited for eggs to be laid and then genotyped the twice-mated mother, each of the two potential fathers, and a randomly chosen sample of the offspring. Note that if the sperm used for fertilization were selected by a raffle-like process, then the donor that has managed to store the most sperm will be the most successful father. Thus, we predicted that the successful dart shooter would father more offspring than the unsuccessful shooter. The experiment was conducted twice, with slightly different conditions, but with very similar results (Landolfa *et al.* 2001, Rogers and Chase 2002). Successful dart shooting significantly improved paternity in this competitive mating situation (Fig. 3). In *Cantareus aspersus,* sperm from the first donor is used preferentially over that from the second donor, regardless of the success or failure of dart shooting (Evanno *et al.* 2005, Chase and Blanchard 2006). As a consequence of this phenomenon, known as first donor precedence, the influence of the dart is most pronounced with respect to the second donor. The paternity of the second donor increased from 17%, when its dart missed and the first donor's dart hit, to 39% when its dart hit

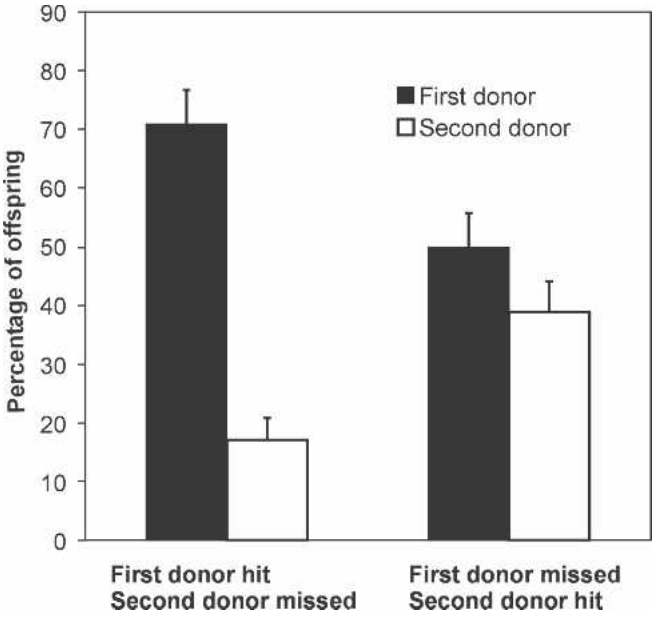

Figure 3. Successful dart shooting increases reproductive success in competitive matings. Snails mated with two sperm donors before producing offspring. One donor hit with its dart, the other missed. Paternities were determined by allozyme genotyping; means ± SE are shown. The effects of the dart are most evident with respect to the second donor (17% paternity *vs.* 39% paternity), owing to first sperm precedence. Data are from Rogers and Chase (2002).

and the first donor's dart missed (Fig. 3; Rogers and Chase 2002).

UNRESOLVED QUESTIONS

While considerable progress has been made in understanding the function of the dart, several questions remain concerning its mechanism of action and its evolution.

1. How does the dart influence sperm utilization?

We suppose that receipt of a dart triggers events in a signaling pathway that ultimately produces effects in the organs that receive sperm. A complete account of the dart's mechanism of action will require descriptions of each step in the signaling pathway. Here, I focus on the initial signal, which is conveyed by the dart. Although the dart itself is a hard structure that will elicit responses in mechanosensory neurons when it penetrates the body wall, the possibility that the dart carries a chemical signal must also be considered because the dart is covered with mucus when it is expelled by the shooter. The presence of mucous glands specifically associated with the dart sac is a consistent feature of the dart-bearing stylommatophoran species (Koene and Schulenburg 2005). The mucus produced by these glands could be used simply to lubricate the passage of the dart out of the animal. However, several pieces of evidence suggest that it contains one or more chemical components that are essential effectors of the dart's function. First, the fluted structure of the dart itself (Fig. 1) can be seen as an adaptation to increase the amount of mucus that can be loaded onto the dart. In *Cantareus aspersus*, the dart carries about 2 mg of mucus (Chung 1986). Second, quantitative analysis has revealed that the effect of dart shooting on sperm storage and paternity are both significantly dependent on the shell volume of the recipient (Rogers and Chase 2001, 2002). The smaller the recipient snail, the larger the dart's effect. One interpretation of this relationship is that the potency of the dart is diminished in larger animals due to chemical dilution. Third, when mucus from the dart gland is applied to the female reproductive tract *in vitro*, contractions occur that cause a reconfiguration of the tract at the critical junction between the organ that receives the spermatophore (the bursa tract diverticulum) and the sperm digestive gland (the bursa copulatrix) (Koene and Chase 1998b). These mucus-induced contractions could allow more sperm to escape enzymatic digestion as they travel from the safety of the spermatophore to the safety of the spermatheca.

Based on the observations summarized above, it is reasonable to suppose that the dart functions by injecting mucus into the recipient and that molecules present in the mucus cause temporary structural changes in the female tract. According to this idea, the dart serves only to convey and inject the chemical agent. To test the hypothesis, Katrina Blanchard and I conducted an experiment to determine whether the dart works by a mechanical means or a chemical means (Chase and Blanchard 2006). As in the experiments described above (Landolfa *et al.* 2001, Rogers and Chase 2002), we arranged for a snail to receive sperm from two donors before producing offspring. In this experiment, however, none of the snails shot darts. Instead, we poked the eventual mother with a hypodermic needle as soon as we detected the partner's intention to dart-shoot. In one of the two matings, we injected saline through the needle; in the other mating, we injected an extract of the dart gland mucus. Thus, in both cases, the mother received mechanical stimulation, but only in the latter case did she receive chemical stimulation. On average, snails delivering sperm in association with injections of mucus fathered 2.3 times the number of babies as did competing snails that delivered sperm to the same mother in association with injections of saline (Chase and Blanchard 2006). This result provides strong evidence that the dart works largely or entirely by injecting mucus, not simply by rupturing the skin. We cannot exclude the

possibility, however, that skin rupture alone may have a small effect on paternity.

2. What is the identity of the bioactive molecule(s) in the dart's mucus?

The next step will be to identify the bioactive molecule(s) in the dart's mucus. Because gastropod molluscs often use peptides as neurotransmitters and hormones (Chase 2002), and because peptides have been found in the secretions of the mucous gland (Börnchen 1967, Chung 1986), the effective agent is likely to belong to this class of molecule. To identify the molecule requires an efficient bioassay. At the present time, a modified procedure to count stored allosperm in once-mated individuals offers the best opportunity. By adopting an approach based on the successive fractionation of mucous extracts, and by using sperm counts as the bioassay, it should be possible to identify the molecule(s) of interest.

3. Does dart shooting either benefit or harm the recipient?

While successful dart shooting almost certainly benefits the shooter, it is not known whether it either benefits or harms the recipient. Benefits to the recipient would occur in either of two scenarios: (1) if successful dart shooting were associated with genes that provide superior viability (the "good genes" model) or (2) if the ability to shoot successfully were heritable, in which case the offspring of the recipient would have a fitness advantage (the "sexy sons" model). Although there is as yet no evidence bearing on these possibilities, suitable tests could be conducted. To test the "good genes" model, it will be necessary to compare the longevity, or viability, of successful and unsuccessful shooters. To test the "sexy sons" model, it needs to be shown that variability in dart structure, mucous content, or dart-shooting behavior is heritable. Until one of these tests provides positive evidence of a benefit to the recipient (and none will be easy to perform), it is not unreasonable to assume a benefit to the shooter alone, in which case dart shooting could be characterized as "male manipulation" (Adamo and Chase 1996).

Rather than benefiting the recipient, the dart could be costly if it reduced the recipient's control over the process of fertilization, if it damaged tissue, or if it increased the chances of infection via the wound. However, none of these possible long-term effects has been documented, and short-term negative effects appear negligible (Chase and Vaga 2006). Thus, current evidence indicates that while successful dart shooting benefits the shooter, its consequences for the recipient are neutral.

Bearing in mind that the recipient is the female partner in this drama, and assuming for the moment that successful dart shooting is associated with high quality genes, it has been proposed (Landolfa 2002) that females perceive the successful dart shot as an indicator of good genes and that they therefore "choose" to store and use sperm from the successful shooter. This would amount to mate selection, but with the choice being made after copulation, *i.e.,* in a "cryptic" manner (Eberhard 1996). It is conceivable that the female function could sort the sperm from various donors to different spermathecal sacs, and later, prior to fertilization, she could selectively release the sperm belonging to the highest-quality donor (see Bojat *et al.* 2001). Attractive though this idea may be, there is no evidence to support it. Furthermore, as noted above, we recently found that injections of mucus through a needle can replicate the benefits to male fitness that ordinarily follow from successful dart shooting. Thus, if females are choosing, they could only be doing so on the basis of the mucus. The use of any other trait, including any present in the shooting behavior, the dart structure, or the sperm, is excluded by the design of the aforementioned experiment.

4. How did the dart evolve?

The steps in the evolution of the dart apparatus are difficult to imagine and probably impossible to confirm. There are many types of "accessory" or "auxiliary" structures associated with the stylommatophoran penis (Tompa 1984). These structures comprise two major groups: (1) the sarcobelum, a fleshy club-like appendage, and (2) the gypsobelum, a hard, sharp instrument, of which the dart is just one example. Although glands are certainly associated with accessory structures in many species, it would be useful to learn the full extent of this association. If glands were invariably associated with accessory structures, then this would support my contention that the primary adaptation is the evolution of a bioactive agent capable of influencing paternity. In ancestral cases, the substance might have been secreted, unaided, out the genital pore. Subsequently, different lineages may have independently evolved accessory structures to improve the efficiency of delivery of the secretion product. Alternatively, if there were taxa that possess either a sarcobelum or a gypsobelum but no gland, then perhaps the accessory structure itself is able to enhance paternity. As mentioned earlier, our experimental evidence in *Cantareus aspersus* is insufficient to rule out this possibility (Chase and Blanchard 2006). In this latter scenario, the glandular product would be a secondary development that increased the power of the manipulation.

If, in fact, the recipient of a dart suffers a cost to its female function, then an evolutionary arms race (Parker 1979) may evolve in which adaptations are selected that on the one hand maximize the dart's efficacy and on the other hand minimize the extent of the harm caused by it. Koene

and Schulenburg (2005) recently reported results that are consistent with this picture. From a phylogenetic analysis, they found an association between a multi-component measure of the dart's shape and a multi-component measure of the "complexity" of the bursa tract diverticulum. Species that have small darts have short diverticula, whereas species with large darts or highly curved darts have long diverticula. This result can be interpreted in light of the fact that longer diverticula make it more difficult for sperm to escape safely (Lind 1973). Thus, it would appear that, as species evolved, the female function selected longer diverticula to defend itself from the harmful effects of more powerful darts. However, until a specific cost of dart receipt is documented, questions relating to sexual conflict and its attendant antagonistic coevolution with respect to the dart will remain controversial.

CONCLUSION

Substantial progress has been made in recent years on the question of why snails shoot darts. In *Cantareus aspersus*, the dart is used to increase the survival and storage of the shooter's sperm in the recipient's spermathecal sacs. As a consequence, successful shooters have greater reproductive success. The phenomenon can be characterized as one of post-copulatory sexual selection in the context of intense sperm competition. To describe it in such terms would have been impossible prior to the bloom of sexual selection theory in the mid-twentieth century, thus explaining, I believe, why it took so long for the riddle of the dart to be solved. Not until empirical work on birds and insects had made known the details of post-copulatory sexual selection in those animals, and theoreticians had elaborated a general context able to accommodate other taxa, could one have imagined the dart's hidden function. Studies on species other than *C. aspersus* are needed to generalize the findings that are summarized in this paper and to provide insights into the dart's evolution.

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