

Courtship and Dart Shooting Behavior of the Land Snail *Helix aspersa*

by

DANIEL J. D. CHUNG¹

Division of Biological Sciences and Museum of Zoology,
University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

Abstract. The dart apparatus, found in a number of pulmonate and opisthobranch gastropods, contains a dart that is used to pierce the flesh of a partner during courtship and mating. It has usually been assumed that dart receipt somehow "stimulates" co-operative courtship behavior, but previous studies have been unable to confirm this hypothesis. In this study, the courtship and dart shooting behavior of the stylommatophoran *Helix aspersa* Müller was studied in order to document in detail the courtship of this snail and to determine whether dart receipt stimulates courtship or has another function. As in *H. pomatia*, there are two basic courtship sequences in *H. aspersa*: one in which dart shooting behavior occurs and one in which it is omitted. The courtship sequence is determined solely by the internal condition of the snail. Young snails have courtship behavior that differs slightly from that of older snails. Quantitative tests show that dart receipt has no effect on the fraction of time spent out of genital contact or the mean rate of biting, but dart receipt appears to decrease the rate of attempted copulation. Dart shooting, by contrast, appears to stimulate the shooter into attempting copulation and into decreasing its rate of biting. It is theorized that the dart may have evolved as a result of sexual selection in hermaphrodites to coerce a mate into acting more as a "female" or to prevent a mate from "cheating" as a "male."

INTRODUCTION

The dart apparatus is a set of organs found in the terminal genitalia of a number of hermaphroditic pulmonate and opisthobranch gastropods. The dart apparatus consists of one or more dart sacs containing a dart—a chitinous or calcareous spear that is thrust into the flesh of a courting partner during "dart shooting"—and associated glands. In general, there are two basic types of dart apparatuses: those with hollow darts perforated at the tip and with a gland at its base, which may be used as hypodermic devices, and those with darts not perforated at the tip and with glands ("mucous glands") near the base. Helicids have the latter type of dart apparatus. Helicids also have deciduous darts; that is, they are cast off during dart shooting and replaced shortly after courtship. It is possible that all non-helicid dart-bearing snails possess non-deciduous darts. Darts may have evolved independently in the helicaceans, ariophantaceans, zonitaceans, philomycids, soleoliferans, nudibranchs, and possibly cephalaspideans and cavoliniids (see

TOMPA, 1980; PRUVOT-FOL, 1960). It has usually been assumed that the dart somehow "stimulates" the courting partner (see TOMPA, 1980, for review), although courtship observations have not been able to demonstrate any function for the dart.

Observations on courtship behavior, with descriptions of dart shooting or use of the dart apparatus, in dart-bearing land snails have been given for a number of species, including: the helicids *Helix pomatia* Linnaeus (MEISENHEIMER, 1912; LIND, 1976; JEPPESEN, 1976), *H. aspersa* Müller (HERZBERG & HERZBERG, 1962); GIUSTI & LEPRI, 1980), *Eobania vermiculata* (Müller), *Tacheocampylaea tacheoides* (Pollonera), *H. lucorum* (Linnaeus) (GIUSTI & LEPRI, 1980); the bradybaenid *Eulota fruticum* Müller (KÜNKEL, 1928); the vitrinids *Vitrina elongata* Draparnard (KÜNKEL, 1933), *V. brevis* Férussac (KÜNKEL, 1929, 1933), *V. major* Férussac (GERHARDT, 1935; see also FORCART, 1949); the parmacellid *Parmacella deshayesi* Moquin-Tandon (GERHARDT, 1935); the zonitid *Ventridens* Binney (WEBB, 1948, 1968b); the helminthoglyptids *Helminthoglypta* Ancey (WEBB, 1942, 1951, 1952b), *Monadenia* Pilsbry (WEBB, 1952a), *Cepolis* Denys de Montfort (WEBB, 1952b), *Humboldtiana ultima* Pilsbry (WEBB, 1980); the

¹ Mailing address: 3324 Wiliama Place, Honolulu, Hawaii 96816, U.S.A.

philomycid *Philomycus carolinianus* (Bosc) (WEBB, 1968a); and the ariophantids *Ariophanta ligulata* (Férussac) (DASEN, 1933), *Macrochlamys pedina* (Benson) (RENSCH, 1955), and *M. indica* Godwin-Austen (RAUT & GHOSE, 1984). With the exception of the studies of LIND (1976) and JEPPESEN (1976), these reports are primarily brief descriptive accounts of courtship.

LIND (1976) provided a detailed ethological analysis of courtship and mating behavior in *Helix pomatia* and attempted to determine the role of dart shooting in the overall courtship sequence through a quantitative analysis of behaviors (1) before and after receipt of a dart and (2) between snails that received versus snails that did not receive a dart. Lind found that dart receipt was not a prerequisite for completion of courtship and copulation and that dart receipt at best appeared to have a slightly negative effect on courtship activity. He found some evidence that dart receipt harmed snails and caused cessation of courtship. JEPPESEN (1976) obtained similar results from observations of courtship in *H. pomatia* that had the dart sac or mucous glands surgically removed.

The more descriptive reports of courtship and dart shooting in land snails provide little evidence for any specific function of dart shooting. WEBB (1952b) suggested that the dart was used by a snail to force its partner to cooperate in courtship by inducing sexual excitement and also to prevent the partner from biting or harming the dart shooter's everted genitals. KÜNDEL (1929, 1933) believed that the dart apparatus in *Vitrina major* was a holdfast organ operating by suction, although GERHARDT (1935) could not verify this hypothesis.

The study reported here is an attempt to understand the function of the dart apparatus through behavioral observations of dart shooting during the courtship of *Helix aspersa*. This study describes in detail the courtship of *H. aspersa*, which had previously been reported in only cursory fashion by GIUSTI & LEPRI (1980) and HERZBERG & HERZBERG (1962), and tests the hypothesis that dart receipt has a stimulatory effect on courtship behavior.

MATERIALS AND METHODS

Specimens of *Helix aspersa* were obtained from College Biological Supply (Escondido, California). The snails were individually isolated in small plastic containers lined with soil and were provided with egg shells and carrot slices. Snails were kept at 21–26°C under a 12 h light: 12 h dark photoperiod for at least two months before being used in courtship observations. This period of isolation appeared to increase the likelihood of snails courting when put together again. Only fully adult snails with a reflected lip and deflected body whorl were used for descriptions of courtship and quantitative analysis of courtship behavior. Courtship in young snails (defined as "subadults" on the basis of conchological characters—large snails without a reflected lip) was observed for qualitative comparison with courtship in older snails. The subadult snails were all

virgins, having been raised from an early juvenile stage in isolation. The field-collected adult snails had an unknown history.

Detailed quantitative observations of courtship were made on 60 pairs of snails, and qualitative observations were made on the courtship and mating of more than 40 other pairs. Of these more than 100 pairs, 10 were pairings of subadults. Of the 60 pairs observed in detail, the data for 36 pairs were detailed enough for quantitative analysis of behaviors presumably related to dart shooting.

Observations on courtship behavior of isolated pairs were taken at night in a lighted room. For each observation session about 12 snails were removed from isolation, washed in water, and placed in an "introductory arena" (a transparent plastic box) where the crawling snails could be observed to identify which snails would court. Snails that exhibited slight eversion of the genitals were noted, and pairs of these snails were transferred to an "observation arena" (a smooth plastic lid, 18 × 13 cm, with upturned sides 2 cm high). Recording of courtship behavior was begun as soon as the pair was placed in the center of the arena and was terminated after the snails attained intromission, one (or both) of the snails withdrew from courtship by crawling out of the arena, or courtship was terminated by the observer. Behavioral records were made on a 20-channel recorder or on a pocket card printer with numerical codes for defined acts. Terminations by the observer were confined to cases where snails had difficulty attaining intromission after 30 min of attempted copulation.

Observations were made on snails courting upright on a horizontal surface. Although snails often mate upside down on the ceilings of laboratory containers, courtship does not appear to be affected by physical orientation to their substrate.

Statistical tests were performed on behavioral data (see below) as described in CONOVER (1980) and SOKAL & ROHLF (1969).

LIST OF BEHAVIORS RECORDED IN COURTSHIP

Labial-head contact (LH) (Figure 1A) occurs when a snail probes the head and labial region of another snail with its mouth and labial palps. The head of the snail is raised off of the substrate, and its tentacles are fully extended. The snail moves its jaws and radula actively, and intermittently bites its partner or nuzzles it. Reciprocation appears to be necessary for prolonged LH behavior. The genital pore shows some swelling, or the genitals may be partially everted.

Labial probing of the region of the genitals (LG) (Figure 1C) occurs when a snail presses its mouth and labial palps on the genitals or on the skin next to the genitals of the partner. The oral probing is focused primarily in a region just posterior to the genital pore of the partner. This behavior can occur with or without genital eversion of either

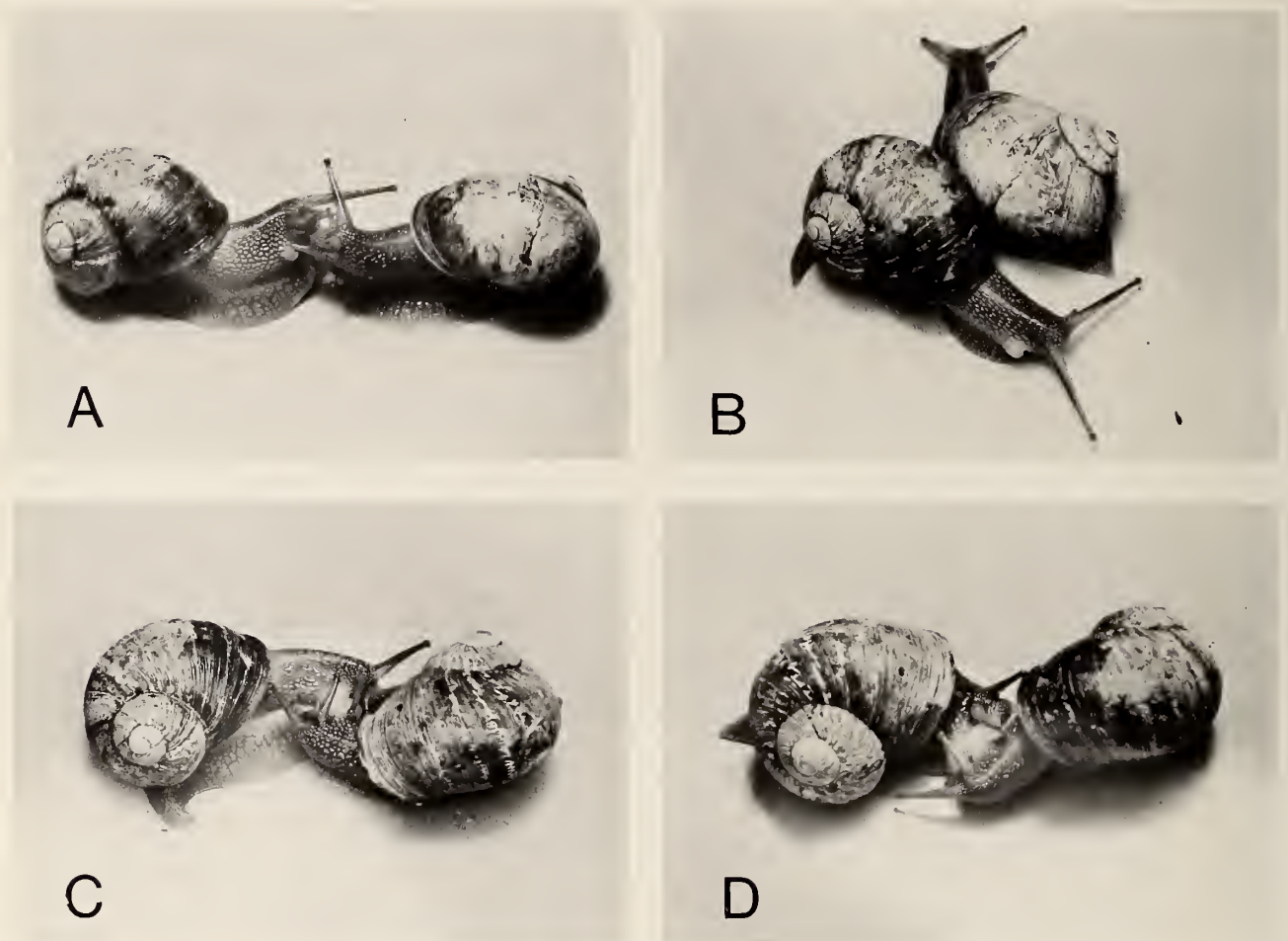


Figure 1

Courtship behavior in *Helix aspersa*. A. Labial-head contact. B. Interruption of courtship. C. Labial-genital contact. This pair is in LG-1. D. IDS behavior is shown by the snail on the left; the snail on the right shows LG behavior.

the actor or recipient, although full genital eversion usually begins at this time. A full genital eversion occurs when the atrium is evaginated and swollen, and the female (vaginal, anterior) and male (penial, posterior) openings are visible. When the behavior occurs simultaneously and reciprocally in both snails, the everted genitals will be appressed and apposed. Genital apposition was not regarded as a separate behavior and was regarded as a result of the simultaneous orientation of the two partners in LG contact, because orientation of the snails towards each other did not appear to depend on genital apposition. LG behavior occurred before and after dart shooting, although with different consequences. LG behavior before dart shooting (LG-1) could not be distinguished from LG behavior after dart shooting (LG-2) except that each led to different behavioral acts in the courtship sequence.

Intention of dart shooting (IDS) (Figure 1D, snail on the left) is a behavior that is seen immediately before dart shooting; the term is borrowed from LIND (1976). A snail

showing well-developed IDS behavior has shortened (but not invaginated) tentacles, a swollen and distended anterior head foot, very swollen and turgid genital eversion with a distension of the anterior (vaginal) region (where the dart sac is located), and a sole that is contracted and reduced in size. The snail in IDS pushes its everted genitals against its partner in a constant pushing motion. There appears to be no oral probing by the snail in IDS of its partner. The everted genitals and anterior headfoot are more swollen at this time than at any other time in courtship; this may be due to increased hydrostatic pressure caused by tensing of the body musculature of the foot and posterior headfoot. IDS persists only as long as the genitals are maintained in contact with the partner's body. The eversion may be pressed against any area of the partner, including the shell, and the pushing may result in the partner even being swept off the substrate and onto the snail in IDS. IDS is terminated by dart shooting. Occasionally, a snail may show very little or essentially no IDS behavior

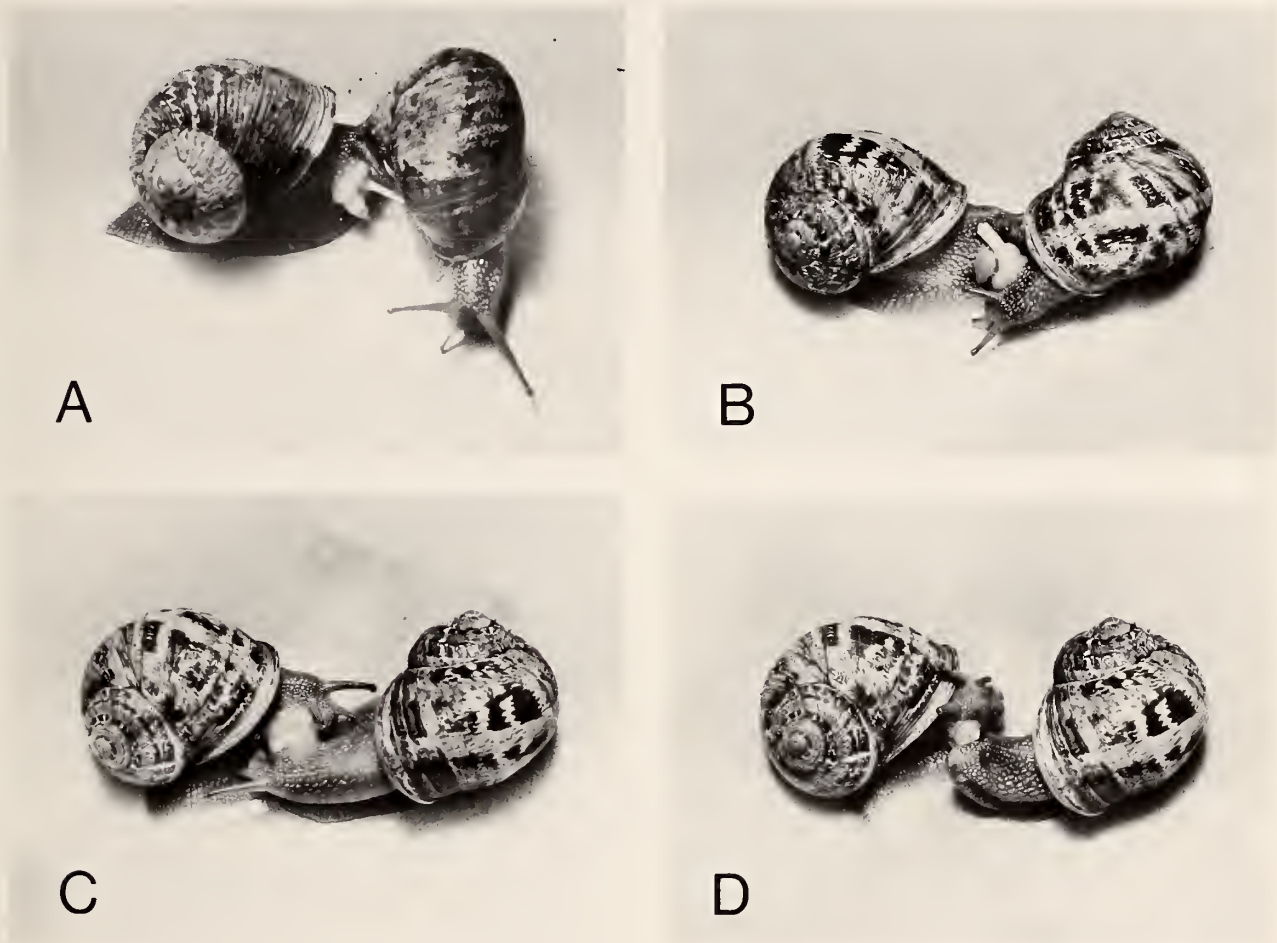


Figure 2

Courtship behavior in *Helix aspersa*. A. Dart shooting behavior shown by snail on the left. The dart of the snail did not penetrate well the partner and was withdrawn back into the dart sac. B. Penial eversion (AC) shown by snail on the right. C. Both snails going through AC. Note the swollen genitals. D. Copulating snails. Both snails have taken the "mating posture."

before dart shooting. Young snails have poorly developed IDS behavior (see below).

Dart shooting (DS) (Figure 2A) occurs when a snail quickly everts the basal tubercle of the dart sac out of its everted genitals. The dart, which is attached by its base to the tubercle in the base of the dart sac, is rapidly pushed from the dart sac and usually pierces the flesh of the partner. Virgin snails possess no dart (see Discussion), and DS behavior leads only to the rapid eversion of the fleshy tubercle in these snails. The eversion of the tubercle takes a fraction of a second, and withdrawal of the tubercle takes 3–10 sec. The dart is never propelled through the air, because it is firmly attached by its base to the tubercle until it is lodged in the partner's tissues. Once lodged in the partner, the dart is detached from the tubercle and is left in the partner. Occasionally, the dart either does not hit the partner or it does not lodge in the flesh and is

withdrawn partially or entirely back into the dart sac. Once DS behavior has occurred, the dart is never used again. Dissections of snails that had withdrawn their darts back into the dart sacs showed that these darts are discarded into the bursal diverticulum shortly before reception of a spermatophore from the partner during copulation. A new dart starts to grow within 6 h after expulsion of a dart and is fully grown within 5 to 7 days after DS (see DILLAMAN, 1981; TOMPA, 1982). During the expulsion of the dart, a globule of whitish mucus, probably from the mucous glands, is usually seen adhering to the dart. Immediately after DS, a snail may evert its penis once.

Penial eversion and attempted copulation (AC) (Figure 2B). Penial eversion occurs repeatedly until a snail either achieves intromission or courtship is broken off. In the normal development of AC behavior, the snail, while oriented with its everted atrium pressed against the body of

the partner, exhibits a momentary tensing of the body wall of the anterior headfoot. This is followed immediately by increased turgescence of the everted atrium and then by penial eversion. The everted penis (about 5–10 mm long) invaginates immediately if the snail does not achieve successful intromission; the total act takes less than 10 sec. After the act is over, the snail pauses before attempting copulation again. Normally, the everted atrium of a snail is pressed against the everted atrium of its partner (*i.e.*, the genitals are apposed) when AC occurs. However, a snail can also evert its penis when the everted atrium is pressed against the tail, shell, or any other part of its partner. Thus, tactile stimulation of the genitals appears to be necessary for AC behavior to be triggered.

Copulation (C) (Figure 2D) was defined by the externally observable behavior of obtaining successful intromission and adoption of the "mating posture." The deposition of sperm in the partner could usually not be verified without dissecting the partner after copulation. In successful intromission, the everted penis of a snail is allowed to penetrate the vagina of a partner and to lodge in the vaginal canal. The snail attaining intromission takes on the mating posture, where the head is lifted off the substrate, the tentacles are shortened and held vertically, and the snail remains immobilized until it deposits its spermatophore into the partner's bursal diverticulum.

In dissected specimens, the intromitted penis (about 2 cm long) is found to lie in the vagina of the partner; the swollen, bulbous head of the penis is lodged at the base of the bursal (spermathecal) stalk and free oviduct. Thirty minutes after achieving successful intromission, the penis is anchored in the vaginal canal to the extent that the snails cannot be pulled apart without physical injury. In this study, if a snail had intromitted and maintained the mating posture for at least half an hour, it was assumed to have gone on to complete copulation.

Tail following (TF). A snail showing tail following behavior follows the tail of its partner, either touching the tail with its oral region or closely following the tail. It is possible that a snail showing TF behavior is following the mucous trail of the partner, but this could not be determined with certainty. Usually, TF behavior is non-reciprocal, but occasionally two snails will follow one another's tail in a circle which eventually tightens up and leads to the snails meeting head to head.

Pauses (P). During a pause, a snail stops courtship activity, does not crawl around, and does not have its head oriented towards its partner. The snail may move its mouth or rasp at the mucus on the substrate. If it has an eversion, the eversion may decline. The muscles of the body are not tensed and the anterior headfoot is not swollen.

Biting (B). Biting was recorded as a separate act during any part of courtship outside of LH contact. The biting snail makes rasping movements against the skin of the partner, and the partner reacts by retracting slightly after each bite.

Interruptions (I) (Figure 1B). During an interruption, a snail crawls away from the partner. The snail may make a tight circling pivot and return within a few seconds, or the snail may crawl far away from the courtship spot. A long interruption may lead to withdrawal from courtship. If a snail has an eversion, the eversion declines.

Withdrawal from courtship (W) occurs when a snail ceases all courtship behavior, persistently avoids all contact with its partner, and crawls away from the courtship site and out of the observation arena.

COURTSHIP SEQUENCE

Two types of courtship sequences are observable in fully mature *Helix aspersa*: primary courtship and secondary courtship (Figure 3; terms from LIND, 1976). In addition, the courtship behavior in young snails just mature enough to court is qualitatively slightly different from that of fully mature snails.

A primary courtship sequence (Figure 3A) includes dart shooting behavior and is seen in courting snails with a fully formed dart and in virgin snails (which possess no dart) courting for the first time. A secondary courtship sequence (Figure 3B) does not include IDS or DS behavior and is seen in snails that have not yet fully grown a replacement for a dart shot in a previous courtship attempt. Whether or not a snail goes through a primary or a secondary courtship sequence appears to depend solely on the internal state of the animal and is not altered by the behavior of the partner it is courting. Thus, one snail of a courting pair may go through a primary courtship sequence while its partner may go through a secondary courtship sequence.

Orientation towards the partner in courtship occurs principally by physical contact with the tentacles and oral region, although some orientation towards mucous trails or the thick patch of mucus that develops at the courtship site may also occur. Orientation towards the partner and a certain amount of synchrony in behavior is necessary for courtship to continue.

Primary Courtship Sequence

The behavior sequences of 34 pairs of snails are summarized in a simplified diagram (Figure 3A). These snails were part of a group of 36 pairs used for quantitative analysis in this study. The number of pairs in which the acting snail made a transition from one behavior to another in the sequence is given next to each arrow. The diagram says nothing about the synchrony or lack of synchrony between the partners. However, because the snails are simultaneous hermaphrodites, and both snails go through the same basic sequence, the numbers given are those for pairs and not individuals.

The diagram does not show pauses, and it does not show two atypical pairs: (1) one pair in which a snail in LG-1 withdrew from courtship after its partner (which had no

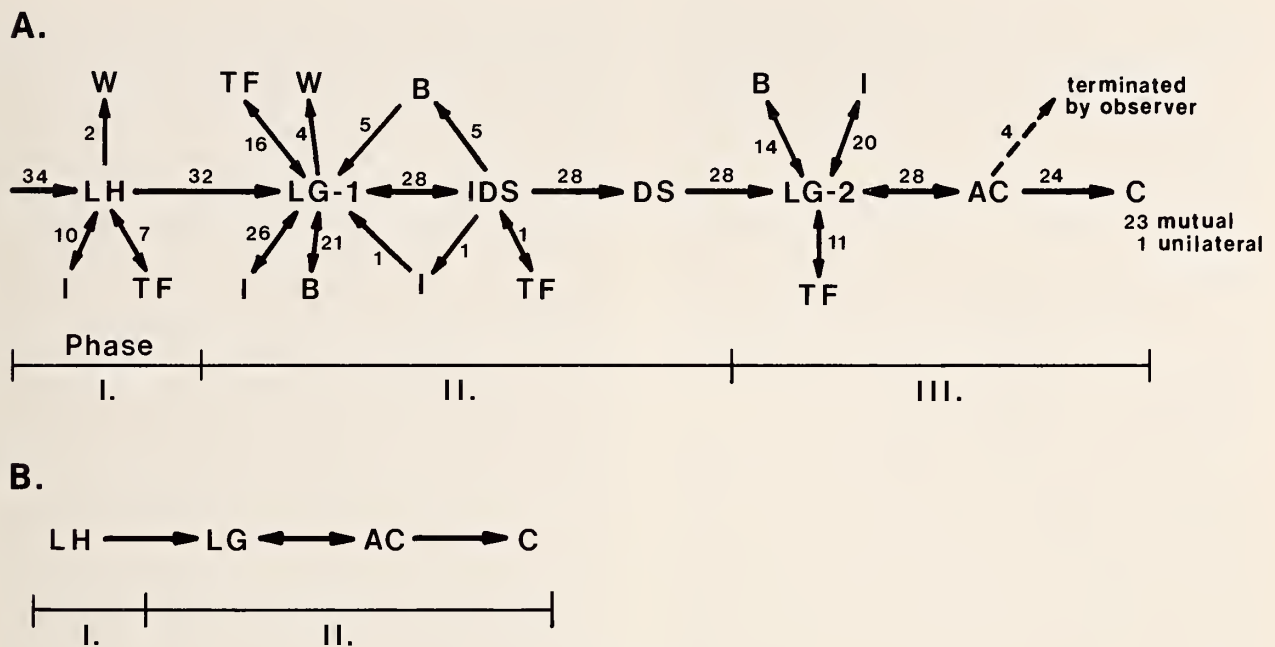


Figure 3

Diagram of courtship behavior in *Helix aspersa*. The number of courting pairs making the transition from one behavior to another is shown next to the arrow. Behaviors of actors (not recipients) are shown. Pauses are not shown. Complicated interactions between B, I, and TF are for the most part not shown. 3A. Primary courtship sequence. 3B. Simplified diagram for secondary courtship sequence. Biting, interruptions, withdrawals, and tail following not shown. LH, labial-head contact; LG-1, labial-genital contact before dart shooting; IDS, intention of dart shooting; DS, dart shooting behavior; LG-2, labial-genital contact after DS; AC, attempted copulation (penial eversion); C, copulation; B, biting; I, interruption; TF, tail following; W, withdrawal from courtship.

dart) went through DS, and (2) a pair in which one snail ejaculated alone without copulating (ignoring its partner) after going through DS. Observations on 4 of the 28 pairs reaching AC were terminated when it was noticed that they had great difficulty achieving mutual intromission. Although these four pairs probably would have eventually attained intromission, the terminations are indicative of the number of snails having difficulty in synchronizing their behavior to effect copulation.

The courtship sequence is basically linear (Figure 3A). There are three phases in primary courtship: (1) an introductory phase (Phase I) which consists of LH behavior, (2) a dart shooting phase (Phase II) which consists of LG behavior (LG-1) leading to DS, and (3) a copulation phase (Phase III) which consists of repeated AC during LG behavior (LG-2) leading to successful intromission.

The diagram of courtship behavior for 34 pairs shown in Figure 3A accurately reflects the variation in courtship behavior of this species. The behavior sequence and certain aspects of courtship related to DS behavior are fairly rigid. Observations of more than 150 courting snails indicate that DS is not a conditional behavior and always occurs in snails with a fully formed dart and in virgin snails courting for the first time. The timing of AC in the court-

ship sequence also appears to be rigid; AC occurs only after the actor has gone through DS and does not depend on receipt of a dart from its partner. The timing of withdrawals may also be constrained; it is noticeable in Figure 3A that no snail withdrew from courtship after it had gone through DS; withdrawals late in courtship may be relatively rare.

Variation in courtship behavior in *Helix aspersa* is seen chiefly in (1) the number of bites (B), interruptions (I), and TF episodes, (2) the degree of development of IDS behavior, (3) the type of dart wound, (4) the number of AC occurring before copulation, and (5) the success of mutual, reciprocal intromission during copulation.

IDS behavior can be virtually absent, partially developed (in young snails), or be fully developed. Omission of IDS behavior was found to be significantly associated with known and presumed virgin snails (snails without darts going through DS): only 5 of 14 snails (36%) showing no IDS possessed darts, while 38 of 44 snails (86%) showing IDS possessed darts ($P < 0.01$, two-tailed Fisher's exact test).

In snails showing normal IDS behavior, maintenance of IDS appears to depend, in part, on the partner's movements. A snail in IDS pushes indiscriminately against the

partner's body and does not orient itself well towards its partner. If the partner does not orient itself towards the snail in IDS, physical contact with the genitals of the snail in IDS will be lost and IDS will cease. Thus, the partner's movements, in large measure, determine where in its body it receives a dart.

Whereas DS behavior always occurs in a primary courtship sequence, the degree and location of dart penetration into the partner varies. In a group of 42 darted snails, penetration varied as follows: the dart was completely lost in the hemocoel of 6 snails (14%), pushed partly into the body and left there in 26 snails (62%), or pushed partly into the body but then withdrawn back into the dart sac of the shooter in 10 snails (24%).

In a group of 57 darted snails, the location of dart penetration varied as follows: 2 snails were darted on the left side of the headfoot (3%); 8 snails were darted on the right side of the headfoot, anterior to the genitals (*i.e.*, in the head) (14%); 19 snails were darted on the right side of the headfoot, posterior to the genitals (33%); 4 snails were darted in the sole close to the mouth or on the mouth (7%); 16 snails were darted in the sole away from the mouth (28%); 1 snail had the dart pierce its everted penis (2%); 1 snail was darted in the penial lobe (2%); 5 snails were darted in the vaginal lobe (9%); and 1 snail was not hit by the dart at all (2%). None of the five darts that hit the vaginal lobe penetrated well; the darts penetrated less than 2 mm and fell out. This may have been due to the fact that the vaginal lobe includes the collar of the dart sac, which is hardened with numerous, tiny calcium carbonate crystals (see TOMPA, 1982). In contrast, in only 3 of the 16 snails darted in the sole and in only 1 of the 19 snails darted in the headfoot posterior to the genitals did the dart penetrate poorly and fall out.

Snails that go through DS behavior but have no dart are virgins and do not inflict a wound on their partners; these snails will begin to grow a dart after this first attempt at DS (see CHUNG, 1986b).

The timing of DS—both the time from the start of courtship to DS and the relative synchrony of DS behavior between partners—is also variable (see quantitative analysis below).

Spermatophore release and reception almost always occur in the context of reciprocal and simultaneous intromission. However, a few pairs intromit non-reciprocally—"unilateral copulation," with one male- and one female-acting snail (3 of 71 pairs, or 4%)—and a few snails were observed to take on the mating posture without intromitting and to ejaculate without a partner, after an otherwise normal courtship (2 of 88 snails, or 2% of individuals). Self-copulation was never observed.

The behavior of snails in AC indicates that copulation is not attained until a snail allows intromission by its partner, and it appears that a snail will normally not allow intromission unless it too achieves intromission at the same time. Copulation cannot apparently be forced on an un-

willing partner in these snails, because the entrance to the vagina is normally closed by a sphincter muscle, which is relaxed only when the snail is also everting its own penis, and the closed sphincter cannot be penetrated by the soft penis. Simultaneous intromission is complicated by the fact that snails of a courting pair rarely shoot darts simultaneously (see below), and thus AC behavior following DS is not synchronized between the snails until after both have gone through DS behavior. To attain copulation, two snails must have their genitals perfectly apposed, go through AC simultaneously, and allow intromission of the partner. The momentary turgescence of the everted genitals immediately preceding AC may be a tactile cue or a stimulus to trigger AC in the partner. However, in spite of this possible cue, AC frequently fails. Transient unilateral intromission is frequent but is almost always terminated. When a snail gains unilateral intromission, it assumes the mating posture, but the partner does not go into the mating posture and immediately pulls away from the first snail or bites at its penis until it is dislodged, or it "ejects" the penis, with the penis appearing to be shoved out of the vagina.

Snails ejaculating without a partner and those allowing unilateral copulation (female-acting snails) behaved similarly to each other in that both acted as though they had attained intromission, although they had failed to penetrate their partners during AC. These snails attempted copulation with their partners, failed to intromit successfully, and then went into the mating posture with their penes everted slightly (3 mm long) and projected anteroventrally. The snails that mated non-reciprocally either remained in the mating posture until they expelled their spermatophores from their penes onto the ground or they eventually came out of the mating posture after 30 min and quietly coupled with their male-acting partners. Because it takes about 30 min for the penis to be anchored and effectively locked in the vaginal canal, it was assumed that these female-acting snails had no alternative but to remain united with their partners after 30 min had passed. The few snails taking on the mating posture without obtaining intromission were considered to be behaving abnormally; snails that did this did not appear to be morphologically abnormal.

The duration of primary courtship varies considerably. The time from start of courtship to DS averages 35 ± 19 min ($\bar{x} \pm SD$; $n = 63$ snails, range: 1–75 min). The time from DS to C usually takes 15–45 min, although a few pairs take more than 4 h to attain copulation after both have gone through DS.

Copulation was not studied in detail and was marked by little external behavior. The duration of copulation was not recorded for most snails but was observed to last from 4 to over 12 h. In a sample of 20 pairs, spermatophores were found forming in the penial flagellum and penis between 1 and 6 h after start of copulation. Transfer of the spermatophore from the penis to the bursal diverticulum of the partner occurs slowly over the last half of the

copulatory period and is usually not strictly simultaneous for both snails. Once a snail transfers its spermatophore, it comes out of the mating posture, retracts its penis, and waits for its partner to finish.

Secondary Courtship

Secondary courtship is seen only in snails that have gone through DS within the previous 5–7 days and have not yet grown a fully formed dart in the dart sac. These are snails that either have recently mated or recently gone through an unsuccessful courtship (through DS). Secondary courtship was not analyzed quantitatively. It is essentially like a primary courtship sequence without a dart shooting phase (Figure 3B) and is of much shorter duration than primary courtship. The first phase is an introductory phase that is qualitatively like the introductory phase of primary courtship. The second phase is a copulation phase that is also qualitatively like the copulation phase in primary courtship. *Helix aspersa* has the ability to mate twice within a 24-h period (one primary and one secondary courtship) and pass two full spermatophores to its partners. This does not occur frequently, as the majority of snails appear to become refractory to mating for at least two days after a primary courtship.

Courtship in Young Snails

Young *Helix aspersa* that have not yet grown a deflected lip on the shell show courtship behavior like that of fully adult snails, except that IDS behavior is not well developed, and snails in IDS tend to slide rather than press their genitals against the body of the partner (10 of 12 snails, or 83%). These snails have mature ovotestes (*i.e.*, they have sperm and mature oocytes), and they have pallial gonoducts that appear to be mature in shape and nearly of adult size. Some of these snails laid fertile eggs after mating. This type of precocious mating has been observed before in *H. aspersa* (COWIE, 1980) and in other stylomatophorans (BAUR, 1984).

Quantitative Analysis of Courtship Behavior Related to Dart Shooting

Of the 34 pairs of snails in Figure 3A that went through a primary courtship sequence, enough data were available on 30 pairs to analyze (1) the timing of DS in courtship, and (2) the effect of dart receipt on courtship behavior. Seventeen of the 30 snails (28%) possessed no darts but showed DS behavior. The histories of these snails were unknown, and the possession of a dart by a snail before DS was unknown to the observer. This natural difference between snails allowed comparisons of courtship behavior to be made between snails receiving darts and those not receiving darts, in addition to the comparisons that could be made between behaviors before and after DS in those snails that received darts.

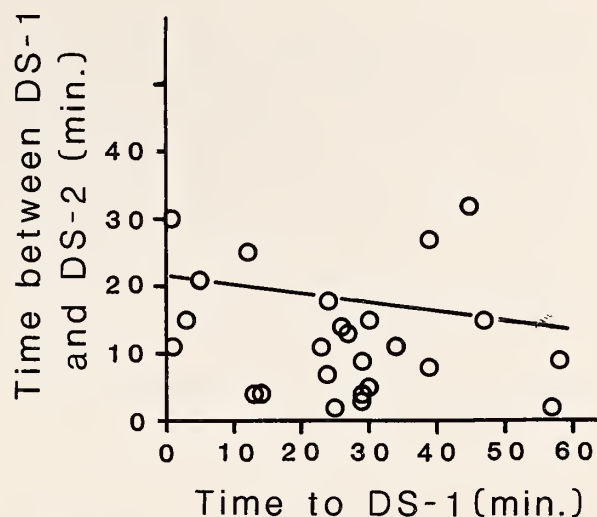


Figure 4

Time between dart shootings (DS-1 and DS-2) vs. time from start of courtship to the first dart shooting. Two groups were pooled—pairs in which both partners possessed darts and pairs in which only the second shooter possessed a dart—because the regression lines for each of the two groups had slopes and y-intercepts not significantly different from one another ($P > 0.10$, two-tailed t -tests). Both shooters with darts: $Y = -0.036X + 13.575$, $r = -0.056$ ($n = 15$). Only second shooter with dart: $Y = -0.285X + 18.222$, $r = -0.300$ ($n = 10$). Pooled data: $Y = -0.13X + 21.29$, $r = -0.186$ ($n = 25$). In all three lines r is not significantly different from zero ($P > 0.10$, two-tailed t -tests).

Data from the 30 pairs could be grouped according to the relative order in which they went through DS and whether or not they possessed a dart (see Table 1). The data indicate that snails probably do not choose their partners assortatively by possession of a dart, because there is no significant difference between the observed and expected numbers of pairs in which both snails possess darts (observed, 15 pairs in which both snails possessed darts, vs. expected, 16 pairs; $P > 0.10$, two-tailed binomial test).

Table 1 shows that the timing of DS during courtship appears to vary greatly and appears to be affected by the condition or age of the snail. The average time from the beginning of courtship to DS in the first shooter varies from 1 to 58 min, with a mean of 26 min. Table 1 shows that in pairs formed of one partner without a dart and one partner with a dart, snails lacking a dart are likely to go through DS first (10 vs. 3 pairs; $P < 0.05$, one-tailed binomial test; assuming *a priori* $p = q = 0.5$). A pair-wise comparison of the row marginals for the time to first DS gives a similar result. There is a significant difference in the time to first DS between snails without darts (16.8 min) and snails with darts (32.4 min) ($P < 0.01$, one-tailed Wilcoxon two-sample test). A comparison of the time to first DS between snails lacking darts and snails possessing darts, both mated to partners with darts (the first column on the left in Table 1), also shows that snails

Table 1

Helix aspersa. Time to DS-1 from start of courtship. $\bar{x} \pm$ SD; sample size in parentheses.

First shooter	Second shooter		Totals
	With dart	Without dart	
With dart	34.4 \pm 13.7 (15)	22.7 \pm 5.1 (3)	32.4 \pm 13.4 (18)
Without dart	14.8 \pm 10.8 (10)	26.5 \pm 30.4 (2)	16.8 \pm 14.2 (12)
Totals	26.6 \pm 15.8 (25)	24.2 \pm 15.8 (5)	26.2 \pm 15.5 (30)

lacking darts go through DS sooner (14.8 min) than snails possessing darts (34.4 min); ($P < 0.01$, one-tailed Wilcoxon two-sample test). This last result is essentially equivalent to the test on the row marginals, because the condition of the second shooter appears to make no difference on the time to DS in the first shooter ($P > 0.05$, two-tailed Wilcoxon two-sample tests on the upper row—34.4 vs. 22.7 min—and column marginals—26.6 vs. 24.2 min). Comparisons involving the data on the two pairs where both partners lacked darts cannot be made, owing to the small sample size of this group.

The time that the second shooter took to go through DS after its partner went through DS is shown in Table 2. A comparison of the column marginals (17.4 vs. 22.8 min) in Table 2 shows that the condition of the second shooter (possession or non-possession of a dart) does not appear to affect the timing of DS in the second shooter ($P > 0.05$, two-tailed Wilcoxon two-sample test). However, comparison of the two cells of the upper row of Table 2 indicates that snails without darts are significantly slower to go through DS (27.3 min) than snails with darts (16.5 min) ($P < 0.025$, one-tailed Wilcoxon two-sample test). These results indicate that snails without darts are perhaps more easily injured or slowed down by dart receipt than snails with darts.

As shown in Table 2, there is no synchrony in DS between the two partners; second shooters take an average of 19 min (range: 4–41 min) to go through DS after the partner has gone through DS. Also, a plot of the time between the first and second DS versus the time to the first DS for the 25 pairs in which the second shooter possessed a dart (Figure 4) shows no correlation between the two variables ($P > 0.05$, two-tailed t -test of H_0 : slope = 0). These results indicate that courting snails tend to space their DS behavior apart, although the data do not indicate what cues the snails use to achieve this. Receipt of a dart does not appear to be the cause of the spacing of DS, because the regression line for the group in which the second shooter received a dart (first shooter possessed a dart) appears to be coincident with the regression line for

Table 2

Helix aspersa. Time between DS-1 and DS-2. $\bar{x} \pm$ SD; sample size in parentheses.

First shooter	Second shooter		Totals
	With dart	Without dart	
With dart	16.5 \pm 10.7 (15)	27.3 \pm 12.3 (3)	18.3 \pm 11.4 (18)
Without dart	19.9 \pm 11.8 (10)	16.0 \pm 11.3 (2)	19.2 \pm 11.0 (12)
Totals	17.4 \pm 11.4 (25)	22.8 \pm 12.1 (5)	18.7 \pm 11.2 (30)

pairs in which the second shooter received no dart (first shooter lacked a dart) (two-tailed t -tests for equal slopes and Y-intercepts, $P > 0.05$).

The data in Table 2 can also be used to test the effect that dart receipt has on subsequent courtship behavior, because the time between the first and second DS can be used as a measure of how quickly the second shooter makes the transition to the copulation phase after the partner has gone through DS. A comparison of the row marginals in Table 2 shows that snails receiving a dart do not take a significantly shorter time to make the transition to the copulation phase than snails not receiving a dart (18.3 min vs. 19.2 min, respectively; $P > 0.05$, two-tailed Wilcoxon two-sample test). The same result is obtained when comparing the cells on the left in Table 2 (second shooter with a dart, first shooter with or without a dart) (16.5 min vs. 19.9 min; $P > 0.05$, two-tailed Wilcoxon two-sample test).

The effect of dart receipt was examined on three other measures of courtship behavior: (1) rate of biting, (2) fraction of time spent away from genital contact (FTC), and (3) rate of AC. Data were most complete for pairs in which the second shooter possessed a dart, and tests for the effect of dart receipt on courtship were performed only on this group (equivalent to the two cells of the column on the left in Table 1). Two types of tests were performed. The first type of test was a comparison of the behavior of snails receiving a dart versus snails not receiving a dart—*i.e.*, the behavior in the group where the first shooter had a dart versus the group where the first shooter lacked a dart. The second type of test, performed on the same variables, was a comparison between the behavior of snails before and after receiving a dart, in the group where both snails possessed darts.

In addition to these tests on dart receipt, the effect of dart shooting on a snail's behavior was examined. The rate of biting and the fraction of time spent out of genital contact (FTC) were each compared for the first shooter before and after it went through DS, in the group where both snails possessed darts.

The variables were defined as follows.

(1) *Biting rate:*

$$(a) \text{ before partner went through DS} = \frac{\text{\# bites initiated by snail from beginning of LG-1 to DS-1}}{T_{\text{before receipt}} - TC_{\text{before receipt}}}$$

$$(b) \text{ after partner went through DS} = \frac{\text{\# bites initiated by snail between DS-1 and DS-2}}{T_{\text{after receipt}} - TC_{\text{after receipt}}}$$

Both (a) and (b) calculated for the second shooter.

$$(c) \text{ before going through DS} = \frac{\text{\# bites initiated by snail from beginning of LG-1 to DS-1}}{T_{\text{before shooting}} - TC_{\text{before shooting}}}$$

$$(d) \text{ after going through DS} = \frac{\text{\# bites initiated by snail between DS-1 and DS-2}}{T_{\text{after shooting}} - TC_{\text{after shooting}}}$$

Both (c) and (d) calculated only for the first shooter.

(2) *Fraction of time spent out of genital contact (FTC):*

$$(a) \text{ before partner went through DS} = \frac{TC_{\text{before receipt}}}{T_{\text{before receipt}}}$$

$$(b) \text{ after partner went through DS} = \frac{TC_{\text{after receipt}}}{T_{\text{after receipt}}}$$

Both (a) and (b) calculated for the second shooter.

$$(c) \text{ before going through DS} = \frac{TC_{\text{before shooting}}}{T_{\text{before shooting}}}$$

$$(d) \text{ after going through DS} = \frac{TC_{\text{after shooting}}}{T_{\text{after shooting}}}$$

Both (c) and (d) calculated only for the first shooter.

(3) *Rate of AC:*

$$(a) \text{ before partner went through DS} = \frac{\text{\# of AC from DS-1 to DS-2}}{\text{time from DS-1 to DS-2 (min)}}$$

$$(b) \text{ after partner went through DS} = \frac{\text{\# of AC from DS-2 to C}}{\text{time from DS-2 to C (min)}}$$

Both (a) and (b) calculated for the first shooter, and (b) also calculated for the second shooter.

$T_{\text{before receipt}}$ = total time the second shooter spent in dart shooting phase before partner went through DS (time from beginning of LG-1 to DS-1, in min)

$T_{\text{after receipt}}$ = total time the second shooter spent in dart shooting phase after partner went through DS (time from DS-1 to DS-2, in min)

$T_{\text{before shooting}}$ = total time the first shooter spent in dart shooting phase before it went through DS (time from beginning of LG-1 to DS-1, in min)

$T_{\text{after shooting}}$ = total time the first shooter spent in copulation phase after going through DS and before being darted by its partner (time from DS-1 to DS-2, in min)

$T_{\text{before receipt}} = T_{\text{before shooting}}$; $T_{\text{after receipt}} = T_{\text{after shooting}}$
 $TC_{\text{before receipt}}$ = time from LG-1 to DS-1 spent in I + TF + P that the second shooter initiated (min)

$TC_{\text{after receipt}}$ = time from DS-1 to DS-2 spent in I + TF + P that the second shooter initiated (min)

$TC_{\text{before shooting}}$ = time from beginning of LG-1 to DS-1 spent in I + TF + P that the first shooter initiated (min)

$TC_{\text{after shooting}}$ = time from DS-1 to DS-2 spent in I + TF + P that the first shooter initiated (min)

DS-1 = first DS, DS-2 = second DS. LG-1 begins for both partners at the same time.

A comparison of snails that received a dart with snails that received no dart shows that there are no significant differences in the means for biting rate and FTC between these two groups (Table 3A). Similar tests for the effect of dart receipt (Table 3B) shows that there are no significant differences in the mean biting rate and mean FTC before and after dart receipt. However, a signed ranks test for equal variances shows that the variance in biting rate is greater in snails that received a dart than in snails that received no dart (Table 3A). There is no statistically significant difference in the variances of snails receiving and snails not receiving a dart in FTC (Table 3A). These results suggest that dart receipt has no influence on FTC but that dart receipt (or a behavioral change associated with DS in one or both of the partners) has an effect on the biting rate. Dart receipt appears to cause a heterogeneous change in the rate of biting—an increase in biting rate in a few snails and a decrease in others, so that the variance in the biting rate increases.

Tests of the effect of dart receipt on the rate of AC (Table 4) yielded results that appear contradictory. Snails receiving a dart have a significantly lower rate of AC than those not receiving a dart (Table 4A; for second shooters). However, the rate of AC after dart receipt is significantly higher after than before dart receipt in first shooters (Table 4B). The differences in the results may possibly be explained by the differences in the two types of tests. Probably the best interpretation of the results is that dart receipt causes a decrease in the rate of AC and that the IDS

Table 3

Helix aspersa. Effect of dart receipt on biting rate and FTC.
 $\bar{x} \pm SD$; n = sample size.

	Received dart	Received no dart
A. Snails receiving a dart (the first snail to receive a dart in pairs in which both snails have darts) vs. snails not receiving a dart (partner did not possess a dart).		
Biting rate ¹	0.24 \pm 0.52 n = 15	0.02 \pm 0.04 n = 10
FTC ²	0.30 \pm 0.25 n = 15	0.14 \pm 0.19 n = 10
B. Before vs. after dart receipt in pairs where both partners possessed darts.		
	Before receipt	After receipt
Biting rate ³	0.08 \pm 0.06 n = 11	0.33 \pm 0.60 n = 11
FTC ⁴	0.17 \pm 0.12 n = 15	0.30 \pm 0.25 n = 15

¹ Variances, but not means, significantly different. $P > 0.10$, one-tailed Wilcoxon two-sample test for means; $P < 0.001$, one-tailed squared ranks test for equal variances.

² Variances and means not significantly different. $P > 0.10$, two-tailed Wilcoxon two-sample test for means; $P > 0.05$, one-tailed squared ranks test for equal variances.

³ Difference between means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

⁴ Difference between means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

behavior of the partner depresses the rate of AC in a snail to a possibly greater degree than that caused by dart receipt. The snails in Table 4A interacted with a partner that had already passed into the copulation phase and was also attempting copulation. In contrast, the snails in Table 4B that had not yet received a dart were interacting with partners in IDS; and it was observed in this study that IDS behavior in a snail frequently made it difficult for a partner to court. If IDS in a snail suppresses the rate of AC in a partner, then the rate of AC in the partner may increase after the snail has gone through DS, in spite of the partner's receipt of a dart wound.

By comparison to the mostly negative effects of dart receipt on the courtship behavior of the receiver, dart shooting has a pronounced effect on the shooter. It has already been noted that penial eversion and attempted copulation never occurs before dart shooting in snails going through primary courtship. Another behavioral change appears to be a decrease in the rate of biting after dart shooting (Table 5). FTC appears to be unaffected by dart shooting (Table 5).

DISCUSSION

Major differences in courtship behavior between *Helix aspersa* and *H. pomatia* are seen in the courtship positions

Table 4

Helix aspersa. Effect of dart receipt on rate of AC. Rate:
 $\bar{x} \pm SD$; n = sample size.

	Received dart	Received no dart
A. Snails receiving a dart vs. snails not receiving a dart. ¹		
	0.53 \pm 0.17 n = 13	0.83 \pm 0.23 n = 8
B. Before vs. after receiving a dart. ²		
	Before receipt	After receipt
	0.47 \pm 0.63 n = 13	0.56 \pm 0.21 n = 13

¹ Means, but not variances, significantly different. $P < 0.05$, two-tailed Wilcoxon two-sample test for equal means; $P > 0.10$, two-tailed squared ranks test for equal variances.

² Differences between means significantly different. $P < 0.05$, two-tailed Wilcoxon test for paired observations.

used to maintain physical contact and in the method of spermatophore transfer. To maintain physical contact, courting individuals of *H. pomatia* lift the anterior region of the soles off the substrate and press them together, while courting *H. aspersa* remain with their soles on the substrate and press their genitals together. Copulation in *H. pomatia* is of brief duration (spermatophores expelled in 4.5 min; intromission lasting 5.6 min), and part of the spermatophore is deposited external to the genital opening (LIND, 1973, 1976), whereas in *H. aspersa* virtually the entire spermatophore is transferred directly into the partner's genitals over a period of an hour or more towards the end of an intromission that lasts 6 h or longer.

A comparison of the overall courtship sequences of *Helix aspersa* and *H. pomatia* shows that major aspects of dart shooting behavior are similar in both species. The integration of DS behavior in the courtship sequence of *H. aspersa* is like that of *H. pomatia* in that (1) the possession of an immature dart is always accompanied by a secondary courtship sequence, (2) DS behavior is never omitted (*i.e.*, is not a conditional behavior) in a primary courtship sequence, and (3) AC never takes place in primary courtship until after a snail has gone through DS. In both species the courtship sequence is fairly rigid, and the type of courtship sequence that a snail goes through is strictly associated with the contents of its dart sac and not with the condition of the partner.

In addition to the association of the type of courtship sequence with the contents of the dart sac, there is an association between the absence of a dart in a snail going through DS and the prior sexual history of the snail. CHUNG (1986b) found that virgin *Helix aspersa* lack darts (an hypothesis proposed in the last century by BOUCHARD-CHANTEREAUX, 1839) and that at least 95% of the virgin snails start growing darts after going through an initial DS. (All fully adult, non-virgin *H. aspersa* possess

Table 5

Helix aspersa. Effect of dart shooting on rate of biting and FTC on snails that shot their dart first. $\bar{x} \pm SD$; n = sample size.

	Before shooting	After shooting	n
Biting rate ¹	0.11 \pm 0.08	0.05 \pm 0.07	11
FTC ²	0.18 \pm 0.10	0.19 \pm 0.23	15

¹ Means significantly different. $P < 0.05$, two-tailed Wilcoxon test for paired observations.

² Means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

darts.) Thus, a snail going through DS but not possessing a dart is likely to be a young snail.

Because the presence or absence of DS and the possession or lack of a dart during DS behavior reflect the reproductive condition of the shooter, a snail might be able to assess the physical condition of a partner by the presence or absence of DS behavior or a dart in the partner. For instance, receipt or non-receipt of a dart might be used by a snail to decide on whether or not to continue with courtship and copulation. However, there is little evidence from either the courtship sequences (Figure 3) or the quantitative tests that this occurs. In only one of 34 pairs going through a primary courtship sequence did a snail withdraw from courtship after its partner went through DS (its partner had no dart); and snails receiving darts appear to be more likely to reduce their rate of attempted copulation rather than increase it (Table 4). The decrease in the rate of AC in snails receiving darts indicate that snails are physically hurt by dart receipt.

DS is unlikely to be used by a shooter to test the vigor or readiness of a partner, because (1) snails appear to be harmed by dart receipt and (2) none of the snails that withdrew from courtship withdrew after receiving a dart. It is unlikely on theoretical grounds that DS is used by a shooter to test the vigor of a partner, because there is a prolonged period of courtship that takes place before dart shooting in which snails can assess one another. Dart shooting is also unlike a final act in an escalated aggressive display, because dart shooting is not a conditional behavior in the courtship of snails that possess a fully formed dart.

The results of the quantitative tests on dart shooting in *Helix aspersa* are similar to the results of tests on *H. pomatia* (LIND, 1976; JEPPESEN, 1976) in that they show that dart receipt apparently has no obvious stimulatory effect on snails of either species. LIND (1976) tested the following hypotheses on the effect of dart receipt: (1) receipt was a prerequisite for carrying through copulation, (2) receipt caused an immediate increase in the intensity of mating activity, (3) receipt caused a decrease in the latency of mating activity after dart receipt, and (4) receipt sped subsequent pre-copulatory behavior. Lind could not prove any of the hypotheses. The first hypothesis was rejected

by both Lind and Jeppesen and is also rejected in this paper, because both *H. pomatia* and *H. aspersa* that have shot darts will attempt copulation whether or not they receive darts. Thus, dart receipt in these two species does not act to trigger copulatory behavior and does not appear to signal a snail's vigor to its partner. The tests of the effect of dart receipt on the rate of AC and on FTC reported here are essentially tests of Lind's second hypothesis, and the results of the tests (Tables 3, 4) do not support this hypothesis.

GODDARD (1962) believed that the injury to the body caused by dart receipt in *Helix aspersa* stimulated an "injury discharge" from the nervous system that subsequently induced penial activity at the time of copulation. His hypothesis appears to be incorrect, as this study and LIND's (1976) study show that dart receipt does not cause penial eversion.

The test of the effect of dart receipt on the biting rate reported here is, in part, a test of WEBB's (1952b) hypothesis that darts are used to stimulate courtship and also prevent a partner from biting the shooter's genitals. Webb's hypothesis could not be verified. The test on biting rate (Table 3) appears to indicate that dart receipt causes some snails to decrease their rate of biting and others to increase their biting rate, although the average rate does not change significantly. The cause of this heterogeneity in response is unknown but may be due to an underlying heterogeneity in the vigor or reproductive condition of darted snails.

The effect of dart receipt may possibly be delayed until after courtship, or the dart may influence the physiology of the snail. TOMPA (1980, 1984) suggested that the effect of dart receipt may be to stimulate maturation and release of ova in a recipient snail, and thereby increase the chances of fertilization of eggs by the dart-shooting snail. This hypothesis has not been tested directly. DORELLO's (1925) and BORCHEN's (1967) hypothesis that darts are used to convey stimulatory substances from the mucous gland secretions into the circulation of a darted snail suggests that the primary effect of dart receipt may be a physiological change that may not greatly affect specific courtship behaviors.

The hypothesis that darts are used to inoculate a snail with bioactive mucous gland secretions was tested by CHUNG (1986a). Injection of mucous gland extract into non-courting snails caused genital eversions similar to those seen in courting snails; topical application of the extract had no effect on the behavior of assayed snails. The results of the study suggested that the bioactive substance in the mucous glands (possibly a peptide) stimulates the simultaneous relaxation of the muscles of the terminal genitals and contraction of the body wall musculature to cause genital eversion. No great changes in genital eversion were seen in courting *Helix aspersa* that received a dart in this study and none were noted in the studies of LIND (1976) and JEPPESEN (1976) on *H. pomatia*. This might be explained by the fact that courting snails almost always have a full

genital eversion at the time of dart receipt, and any further change in the condition of the genitals after dart receipt cannot be detected easily in behavioral observations.

The courtship observations made on *Helix aspersa* and observations made on other dart-bearing land snails suggest two possible effects of dart receipt that are inconsistent with the physical stimulation hypothesis (as defined by GODDARD, 1962, and by LIND, 1976) but are not inconsistent with the chemical stimulation hypothesis (as developed by CHUNG, 1986a). Dart receipt may (1) cause a snail to slow its movements and remain quiescent during the copulation phase of courtship, or (2) affect the functioning of the penis.

The *Helix aspersa* observed in this study appeared to crawl more slowly after receiving a dart, although the average crawling speed could not be quantified. The slowing of movement may be due to the physical injury of dart receipt; however, mucous gland secretions might possibly affect the muscles used for crawling. WEBB (1952b) suggested from courtship observations that dart receipt in helminthoglyptids prevent premature withdrawal during transmission of the spermatophore. However, this hypothesis has never been tested.

Darting of the penis has been observed in a few species and may be a function of the dart in some species. The fusion of the male and female tracts near the genital aperture in stylommatophorans would appear to allow the dart to be shot into the everted genitals of mating partners; and the anatomical placement of the dart sac on the vagina in many species of dart-bearing snails would appear to allow the darting of the penis during copulation. The penis is almost never darted in *Helix aspersa*, and darts are always shot before intromission in this species, but darting of the penis might occur regularly in *Philomycus carolinianus* and species of *Ventridens*. WEBB (1968a) reported that the dart in *Philomycus* injures the partner's penis during copulation. The dart is also reported to pierce the everted penis, along with other organs, during courtship and copulation in *Ventridens* (WEBB, 1968b). Whether the non-deciduous dart in *Philomycus* and *Ventridens* is used to impair the functioning of the male organs or is used as a kind of holdfast was not determined by Webb. In this study, only one *H. aspersa* (about 1% of more than 100 snails observed) received a dart in its everted penis; this snail could not achieve intromission and copulated as a "female" (allowing intromission and accepting a spermatophore but not secreting a spermatophore). This unusual case cannot be regarded as normal, but the suppression of male functioning by the dart in this case is interesting. The dart in *H. aspersa* and other helicids cannot be used as a holdfast, because it is deciduous.

The morphology and anatomical placement of the dart indicate that the darts in most dart-bearing species with non-deciduous darts do not function as purely physical holdfasts, in the way that penial hooks function. None of the published observations of dart shooting behavior clearly

shows a dart being used as a holdfast, although the thin, curved dart of *Ventridens* might theoretically be able physically to restrain a partner. KÜNKEL's (1929, 1933) hypothesis that the hollow, perforated dart of *Vitrina elongata* is used as a suction cup for holding onto the shell of the partner seems unlikely. Künkel did not demonstrate how effective suction could be applied from a dart tip that has a diameter of 0.078 to 0.094 mm, on a partner about 1 cm long; and no one has demonstrated a suction mechanism in the dart apparatus of *Vitrina elongata* or in any other dart-bearing species.

Adaptive Significance of the Dart Apparatus

Observations on the courtship behavior of *Helix aspersa* and other dart-bearing snails have not been able to determine the adaptive significance and evolution of dart-shooting behavior, but the data from this and other studies indicate that the dart apparatus may have arisen in the context of sexual selection in simultaneous hermaphrodites. There are three general evolutionary models that could account for the evolution of the dart apparatus: (1) the reproductive isolation model, (2) the courtship co-ordination model, and (3) the sexual selection model. The data on dart-shooting and reproductive behavior in dart-bearing snails are most consistent with the sexual selection model, least consistent with the courtship co-ordination model, and do not provide any support for the reproductive isolation model.

Both DIVER (1940) and WEBB (1952b) assumed that the dart was used in species recognition during courtship and evolved in this context. However, this hypothesis has never been tested, and appears unlikely on theoretical grounds. *Helix aspersa*, *H. pomatia*, and other dart-bearing snails go through a fairly prolonged period of introductory courtship behavior (with physical contact) before they show dart-shooting behavior. This would argue against the use of the dart as a species recognition device, because both physical cues (e.g., the differences in courtship postures between *H. aspersa* and *H. pomatia*) and probable chemical cues are capable of being passed during the introductory phase before dart shooting. The physical stimulus of dart penetration may not be an ideal signal in species recognition, because the degree and location of dart penetration vary greatly (LIND, 1976; this study). The transfer of a chemical signal used in species recognition by the dart may be an evolutionarily suboptimal strategy, because (1) dart receipt harms a potential mating partner and (2) sexual pheromones, including contact pheromones used in courtship, are usually among the first signals transferred in courtship.

WEBB (1951) noted a single instance of heterospecific courtship between two species of dart-bearing *Helminthoglypta*, where one of the snails died four days after receiving a dart wound during courtship. This is the only observation suggesting that the dart might be used in species

recognition; however, no evidence obtained since Webb's observation has supported his contention that the dart evolved as a species-recognition device.

In the courtship co-ordination model, the behavior of a courting partner is assumed to be an adaptation for promoting co-operative exchange and use of gametes. It is in the context of this model that LIND (1976) implicitly defined the "stimulatory" action of the dart of *Helix pomatia*, and it was in this context that the "stimulation" hypothesis was defined in this paper. The lack of evidence for the stimulation hypothesis, as defined by the courtship co-ordination model, for both *H. pomatia* and *H. aspersa* indicates that the dart is not used to aid co-ordination in courtship. Dart receipt, in fact, appears to cause physical harm: *H. pomatia* is less likely to complete courtship when darts (LIND, 1976), and *H. aspersa* appears to reduce the rate of penial eversion when darts. Dart shooting, by contrast, appears to facilitate the completion of courtship by the shooter: *H. pomatia* and *H. aspersa* attempt copulation only after going through DS in primary courtship, and *H. aspersa* reduces the rate of biting after shooting its dart. Thus, it is the shooter and not the receiver of the dart that appears to be "stimulated" by DS behavior.

Evidence for the evolution of species-specific genital structures through sexual selection is growing (see reviews by WEST-EBERHARD, 1983; EBERHARD, 1985), and species-specific dart morphologies likely reflect sexual selection rather than selection for prezygotic reproductive isolating mechanisms. The data showing that the shooter and not the receiver is stimulated by DS behavior and that the receiver is hurt by dart receipt suggests that there is an evolutionary conflict of interest between the mating partners, similar to that between the males and females of gonochoristic species. Because the variance in male reproductive success is usually greater than variance in female reproductive success (see BLUM & BLUM, 1979; WILLSON & BURLEY, 1983), under certain conditions simultaneous hermaphrodites that act as "males" (those transferring sperm but not using received sperm) may be favored over those acting as pure hermaphrodites. The form of sexual selection occurring in these simultaneous hermaphroditic snails might be of two forms: (1) "cheating" by male-acting hermaphrodites and the use of anti-cheating devices by pure hermaphrodites, and (2) the use of coercion by male-acting hermaphrodites to force partners to behave as a "female." Cheating (acting as a "male," by transferring sperm but not accepting or using received sperm) and the use of anti-cheating strategies have been hypothesized to occur in the hamlet *Hypoplectrus* (FISCHER, 1981, 1984). In this fish, cheating may have given rise to a counter strategy, or anti-cheating strategy, known as egg trading, in which mating partners alternate male and female roles several times in a single spawning bout. Sperm trading in the opisthobranch *Navanax* (LEONARD & LUKOWIAK, 1984) may have evolved under similar sexual selection pressures. In the other form of sexual selection in hermaphrodites,

coercive tactics in courtship and mating (*e.g.*, incapacitating a partner's male organs, or forcefully stimulating the female organs to receptivity) can be simultaneously used offensively and defensively. These two forms of sexual selection are theoretically similar, although cheating does not necessarily involve any type of coercion of the mates. The dart may have arisen either as an anti-cheating mechanism or as a device used in coercion. The dart may have evolved from smaller penial stylets or genital hooks in a kind of evolutionary arms escalation that allowed the evolution of increasingly larger or more effective darts to force the partner to act as a "female." Any destabilizing effect of strong sexual selection on the hermaphroditic condition (see CHARNOV, 1979, 1982) might be reduced by energy recouped from allosperm digested in the gametolytic organs found in pulmonates and many opisthobranchs.

Because dart receipt appears to be harmful to a snail, it does not seem likely that darts evolved through runaway sexual selection by female choice on stimulatory male genital structures (as suggested by EBERHARD, 1985, for darts and other elaborate genitalia). The commonly made assumption that darts (and other spicular genital structures in animals) act to stimulate co-operative mating behavior by mating partners may have to be re-examined.

By comparison with work done on the male accessory gland secretions in insects (see GILLOT & FRIEDEL, 1977; CHEN, 1984), mucous gland pheromones of *Helix* might affect: (1) potentiation of sperm, (2) induction of egg maturation or oviposition (TOMPA, 1980), and (3) the reduction of subsequent receptivity in mating partners (reduction of subsequent "female" receptivity). The possession of separate sperm-digestion and allosperm-storing organs in pulmonates and many opisthobranchs suggest several other theoretical functions of dart receipt, including (1) suppression of allosperm digestion, (2) displacement of previously stored allosperm, or (3) prevention of subsequent allosperm storage. Of these possible effects, a reduction of subsequent mating seems to be unlikely in *H. aspersa*, because snails will mate repeatedly with different partners in a single breeding season in the laboratory (personal observations). The other hypotheses have not been tested directly. The consideration of these and other evolutionary hypotheses may prove to be as profitable to the study of molluscan reproductive biology as they have been to studies on other groups of animals (*e.g.*, see BLUM & BLUM, 1979).

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