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REPRODUCTION OF THE MALONE JUMPING-SLUG, *HEMPHILLIA MALONEI* PILSBRY, 1917 (MOLLUSCA: GASTROPODA: ARIONIDAE): LABORATORY OBSERVATIONS

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ABSTRACT. *Hemphillia malonei* (Malone jumping-slug) from southwest Washington State were maintained in captivity to assess characteristics of reproduction and growth to sexual maturity. We conducted 45 mating trials involving 10 slugs. Prior to copulation the slugs engaged in a prolonged trailing phase that lasted from 45 minutes to 3.5 hours. Throughout this phase, the mouth of the trailing slug was in nearly constant contact with the tail of the leading slug. The copulation phase lasted from 3.5 to 12 hours, and observations indicated that a portion of the penis (the verge) was inserted into the gonopore and that the spermatophore was delivered internally. Our observations suggest that spermatophore delivery occurs asynchronously and that at least occasionally it is non-reciprocal. Eggs were deposited in single or multiple clusters over several weeks. Eggs maintained at 14°C began hatching 47-63 days after oviposition, and hatching continued over a period of 6-20 days. Slugs that were captive-raised from eggs reached sexual maturity in the first year.

Key words: courtship, mating behavior, egg-laying, slug, Washington State, Pacific Northwest.

INTRODUCTION

Jumping-slugs, genus *Hemphillia*, are arionid slugs endemic to western North America. Seven species are currently recognized (Turgeon *et al.*, 1998). Some of these may represent species complexes, and additional, undescribed species may

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exist (Kelley *et al.*, 1999). Ecology, life history, and behavior of this group have received very little attention, and for most species even basic life histories are not known. The aim of this study was to document the reproductive biology of *Hemphillia malonei* Pilsbry 1917, a species of significant conservation interest.

The geographic distribution of *H. malonei* extends from west-central Oregon to the southern Puget Sound region of Washington, United States (Pilsbry, 1917, 1948; Kozloff & Vance, 1958; Kelley *et al.*, 1999). Populations with more-or-less continuous distributions occur west of Mt. Hood, Oregon, and south of Mt. St. Helens, Washington, but elsewhere the species apparently has a patchy distribution (T. Burke, pers. comm.). The species is known from near sea-level to elevations of approximately 1300 m (Kozloff, 1976; W.P. Leonard, pers. obs.), and it is reported to be associated with moist to wet forest conditions (Kelley *et al.*, 1999). *Hemphillia malonei* is listed as a "survey and manage" species under the Northwest Forest Plan (USDA & USDI, 1994 a, b), which in the United States governs the management of federal forest lands from northern California to Washington State (Kelley *et al.*, 1999). Information on its reproductive biology is therefore of interest for conservation purposes.

MATERIALS AND METHODS

In 1999-2000, the breeding observations involved three slugs: one (slug A) was collected on 23 November 1999 adjacent to a tributary of Dougan Creek, Skamania County (elevation 275 m asl; T2N R5E S2); two (slugs B, C) were collected on 22 October 2000 approximately 3 km NW of Morton, Lewis County (elevation 610 m asl; T13N, R4E, S28). In 2001, the breeding trials involved 8 slugs: 5 were collected on 4 September 2001 adjacent to Fisher Creek, approximately 6.5 km west of Morton, Lewis County (elevation 500 m asl; T13N, R3E, S18); three were laboratory-raised from eggs laid by slug B. The slugs ranged from 58-89 mm in extended length while in movement.

In November-December 2000 and in September-November 2001**,** we conducted 45 mating trials. Most of the trials were conducted in Olympia, Washington, but six took place in Victoria, British Columbia. Trials were initiated between 0600 and 1300 hours in an unheated basement with a small exterior window. For each trial we placed two slugs into a covered, clear plastic box (dimensions: 17 cm long, 12 cm wide, 6 cm high) lined with wetted paper towel. We observed pairs intermittently for periods of approximately 5 minutes to 3 hours using an OptiVisor© 3x optical glass binocular magnifier; the duration of observations depended on the activity of the slugs and were longer when the slugs were active or near the end of the copulation phase. Between trials, we maintained the slugs separately in plastic boxes, and provided them with lettuce and carrot; in 2001, dry dogfood was added to supply additional protein.

We transferred eggs into plastic boxes filled to a depth of approximately 5 mm with dechlorinated tap water. Eggs were submerged throughout development, a technique that also has been used to rear eggs of terrestrial salamanders (Bernardo and Arnold, 1999). Upon hatching**,** juvenile slugs were transferred to plastic boxes identical to those used for adults, except that a piece of weathered wood was included for cover. We maintained adults and eggs in an unheated cellar in Olympia, Washington, where the temperature was 14°C (± 1°).

On 9 April 2000 four offspring of slug A were transferred to Victoria, British Columbia, where they were kept until maturation. These slugs were housed together in a 0.5-liter glass jar, loosely filled with moist moss, in an unheated basement room, and were fed a diet of lettuce and carrot. The temperature in the holding room fluctuated seasonally between approximately 12°C and 18°C. After an egg clutch was found on 26 December 2000, the animals were kept in separate jars or plastic shoeboxes. In 2001 four offspring from slug B were kept in Olympia, Washington until maturity.

Two slugs (B, C) were dissected by Lyle Chichester and compared to the illustrations of Kozloff and Vance (1958). These specimens have been deposited in the collection of the Delaware Museum of Natural History (DMNH 221673, DMNH 221674). Two offspring of slug A have been deposited in the Royal British Columbia Museum (RBCM 001-00290-001).

RESULTS

Mating Behavior

The mating behavior will be described in the context of four broad phases (modified from Reise, 1995): recognition phase, trailing phase, copulation phase, and separation phase.

The recognition phase was relatively short, lasting from approximately 30 seconds to 3 minutes. During this phase the slugs came into physical contact, and each secreted (or enlarged) a caudal mucous globule. Mutual mouthing of the tail region and nuzzling of the mantle characterized this phase.

The trailing phase lasted from 45 min to 3.5 hours, averaging approximately 1 hour. Initially, both slugs often crawled off in separate directions, apparently attempting to induce the other slug to follow. Once roles were established, one slug led the other on a crawl along the bottom, sides, and top of the enclosure. The trailing slug followed behind in tandem, while maintaining its mouth in almost constant contact with the tail tip of the lead slug (Fig. 1). Occasionally the trailing slug positioned itself in a more forward position, enabling it to nuzzle and mouth at the mantle of the lead slug. Throughout most of the trailing phase, the leading slug produced copious amounts of caudal mucus, some of which

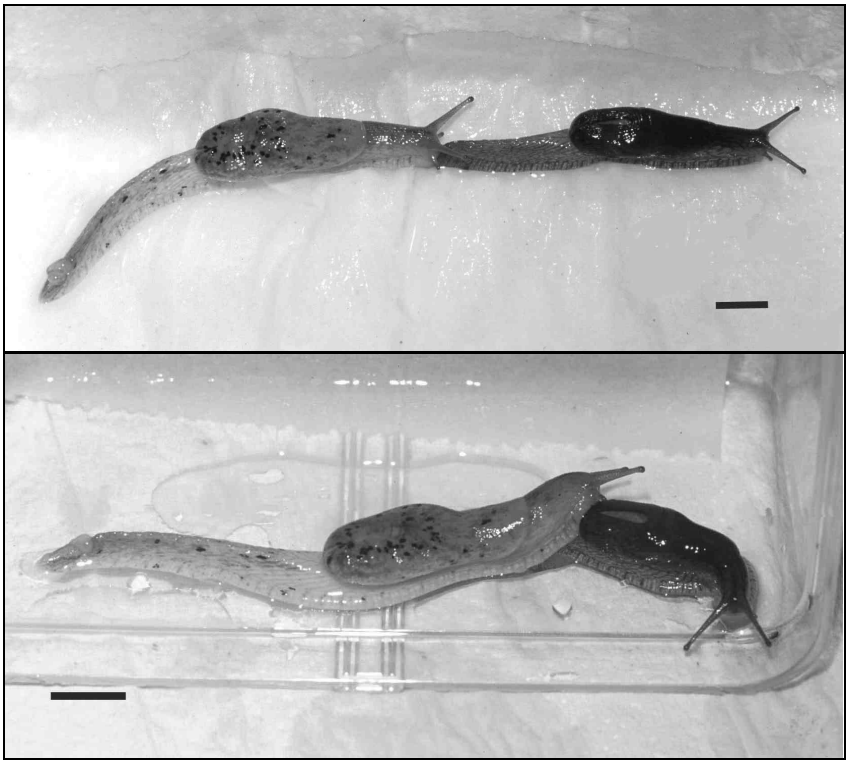

Figure 1. Trailing phase of courtship; bar = ca. 1 cm.

apparently was eaten by the trailing slug. Frequently (22 of 36 trials where trailing was initiated), the paired slugs abandoned courtship in the trailing phase.

The copulation phase lasted from 3.5 to 12 hours. It began when the slugs ceased trailing and curled into a tight circle with their right sides apposed (Fig. 2). The penes were then gradually everted and oriented side-by-side, with the end of each penis touching the posterior edge of the gonopore of the other slug. Subsequently, each slug slowly everted its large penial accessory structure ("stimulator" in the terminology of Kozloff and Vance, 1958). Each slug gradually spread this structure onto its partner's tail or, in some instances, onto the mantle. While one slug always wrapped its penial accessory structure over its partner's tail, the other slug did not always reciprocate. Copulation culminated in the transfer of an approximately 15 mm long, cream-colored spermatophore (Fig. 3). The spermatophore was not apparent as it passed through the similarly colored penis. However, a slow peristaltic pumping action along the basal portion of the penis was visible during the late stages of the copulation phase.

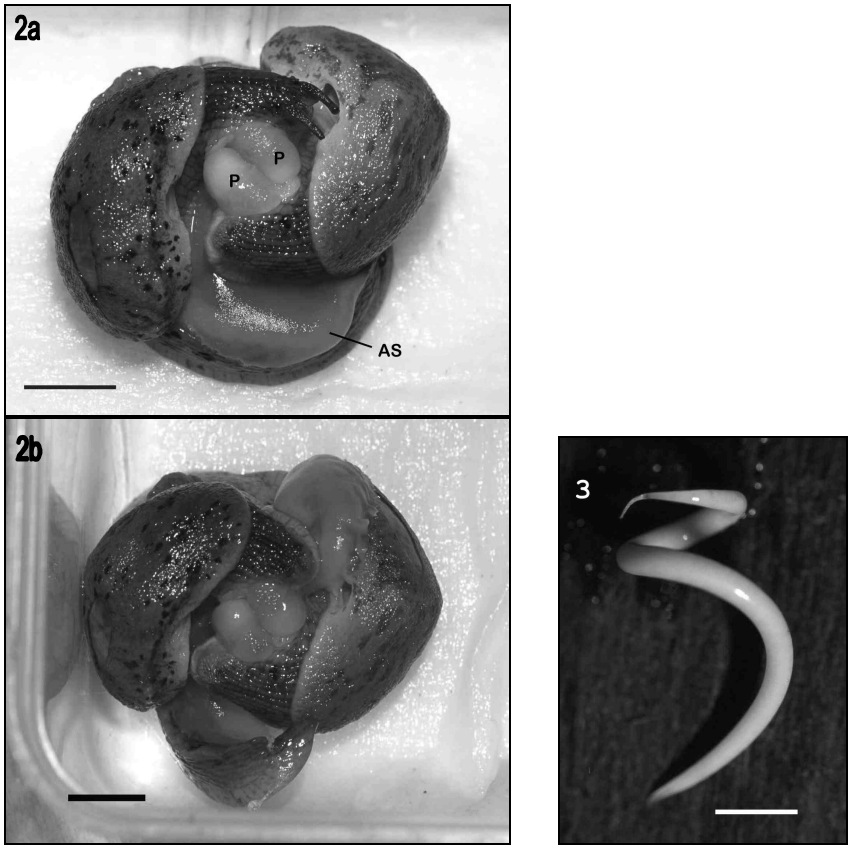

Figure 2-3. *Hemphilia malonea* reproduction. **2a-b.** Copulation phase. P – penis; AS – penial accessory structure; bar = ca. 1 cm. **3.** Spermatophore removed from the gonopore during copulation; bar = ca. 3 mm.

Fertilization was internal, and the verge (an elongated, smoothly tapered structure within the penis sac) penetrated the gonopore of the partner. The verge could not always be seen and was clearly visible only when the slugs began to separate (Fig. 4). During penetration, a small portion of an everted female structure, possibly the base of the bursa copulatrix (spermatheca) could be seen protruding from the gonopore, snuggly wrapped around the verge.

We observed the separation phase on four occasions. It began when the first slug of a copulating pair retracted its penis, and ended when both slugs had retracted their genitalia, including the penial accessory structure. This phase lasted

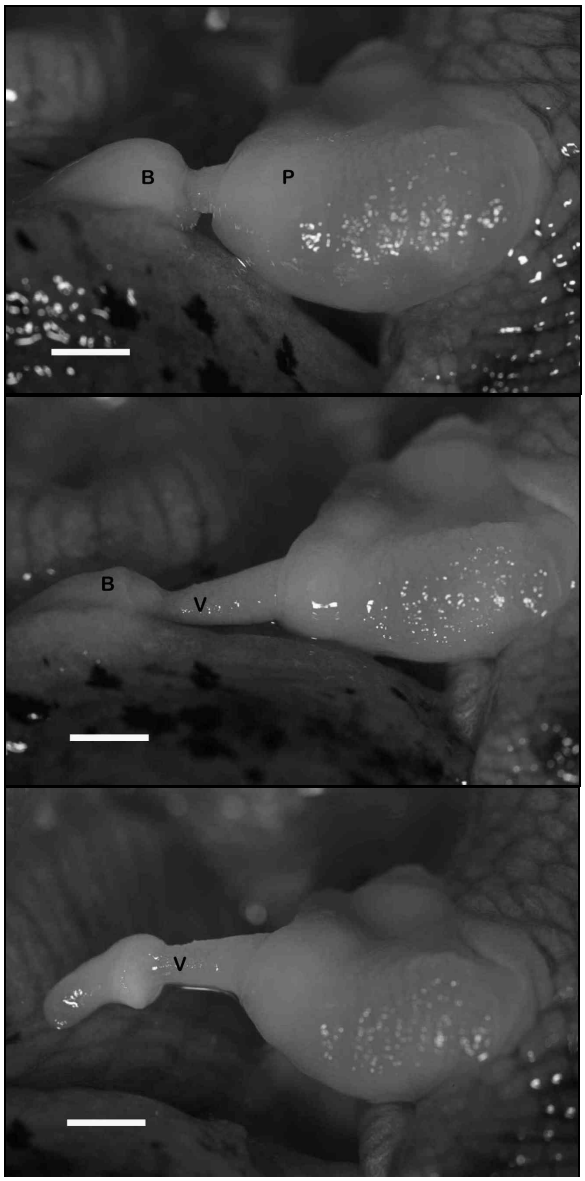

Figure 4. Sequence (top to bottom) of withdrawal of the verge from the partner's partially everted genitalia during the separation phase. V – verge; P – penis; B – partner's partially everted genitalia (probably base of bursa copulatrix); bar = ca. 3 mm.

between 1 and 2.5 hours, in total. The separation was always asynchronous, and typically the other slug's penis remained fully everted after withdrawal by the first slug. The first slug to withdraw its penis tried to crawl away, but was unable to do so as the two slugs were joined where its partner's verge passed through the first slug's gonopore**.** The retreating slug typically turned, reared up, and mouthed its partner's penis, apparently biting it. Between 0.5 and 1.5 hours after the retreating slug had withdrawn its penis, its partner also withdrew, allowing the two slugs to separate (Fig. 4). For approximately 10 seconds after separation, the slender, tail-like portion of a spermatophore protruded from the retreating slug's gonopore. The verge was withdrawn into the penis after approximately 20 seconds, and the majority of the penis was retracted within the subsequent 15 minutes; the penial accessory structure was retracted within the following 10-45 minutes.

While most (36 of 45) mating trials resulted in the initiation of the trailing phase, only 12 pairings (involving 7 different couples) proceeded to the copulation phase. In 10 of the 12 pairings, both slugs had their penes everted, suggesting a mutual transfer of spermatophores. In two instances, however, only a single penis was everted, suggesting non-reciprocal sperm transfer**.** Three slugs mated once, 2 twice, 3 on three occasions, and 2 on four occasions; all matings by individual slugs occurred within a period of 23 to 30 days.

Oviposition and Development

Between 2130 hours on 2 January and 1230 hours on 3 January 2000, slug A deposited a total of 61 eggs in a cluster on the side of the container. Throughout oviposition the slug moved little, keeping tentacles retracted and tail curled forward alongside its body**.** On 5 January, two days after oviposition, the adult was found dead. Hatching of eggs began on 24 February and continued through 2 March. Shortly after oviposition, eggs were round (ca. 3 mm in diameter), translucent, and colorless; after approximately 24 hours, the eggs absorbed water causing the capsules to become larger and oblong (approximately 6 x 4.8 mm) (Fig. 5). On 13 November 2000 slugs B and C each laid the first of what would ultimately be four egg clusters (Table 1). On 19 December 2000 slugs B and C were preserved as voucher specimens.

The time between most recent copulation and oviposition ranged from one to six days (Table 1). For seven egg clusters, the time between oviposition and emergence of the first hatchling ranged from 47 to 63 days ($n = 7$; $\bar{x} = 54.6$ days; SD = 5.2 days; Table 2). Hatchlings emerged from the egg-clusters over 6 to 20 days ($n = 4$; $\bar{x} = 10$ days; SD = 6.5 days). Detailed records on the viability of eggs were not kept, but 8 of 9 egg clusters yielded hatchlings; one egg cluster was inadvertently destroyed by desiccation after the plastic container had been left uncovered.

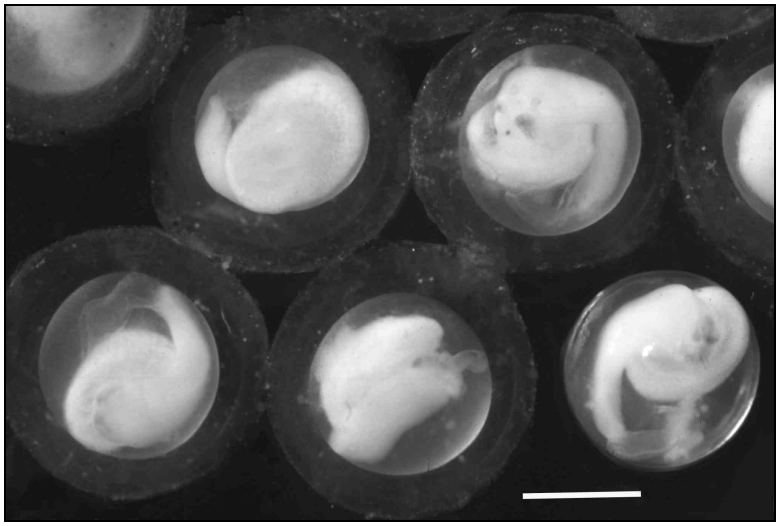

Figure 5. Eggs (in water) approximately 7 days before hatching; bar = ca. 3 mm.

Hatchlings measured 6 mm in extended length. The ocular tentacles were either reddish-brown or dark gray. A faint wash of reddish-brown pigmentation extended onto the mantle and tail.

Table 1. Oviposition dates and number of eggs/clutch deposited by three *Hemphillia malonei* from October 2000 to January 2001. * oviposition dates are accurate to ≤ 5 days before indicated dates; other oviposition dates are accurate to ≤ 24 hours.

Slug	Oviposition dates (Number of eggs in clutch)				Total eggs
A	2 Jan 2000 (61)				61
B	13 Nov 2000 (58)*	23 Nov 2000 (41)	7 Dec 2000 (23)	14 Dec 2000 (25)	147
C	13 Nov 2000 (39)*	25 Nov 2000 (19)	3 Dec 2000 (13)	14 Dec 2000 (19)	90

Table 2. The date of oviposition, date of first egg hatching, and the incubation period of seven *Hemphillia malonei* egg masses maintained at 14°C.

Slug	Date of oviposition / Date of hatching (Days in incubation period)		
A	2 Jan 2000 / 24 Feb 2000 (47)		
B	13 Nov 2000 / 3 Jan 2001 (51)	23 Nov 2000 / 19 Jan 2001 (57)	14 Dec 2000 / 10 Feb 2001 (58)
C	13 Nov 2000 / 5 Jan	25 Nov 2000 / 27 Jan	14 Nov 2000 / 5 Feb

2001 (53) 2001 (63) 2001 (53)

Maturation Period

On 26 December 2000 one of four captive-raised offspring of slug A deposited a cluster of 23 eggs. Three additional eggs were found on 28 December; the same individual probably laid these. Sometime between 24 January and 2 February another individual deposited 9 eggs. At the time of egg-laying, all four slugs ranged in extended length from approximately 65 to 70 mm. On 27 October 2001, 2 offspring of slug B copulated approximately 8 months after hatching. Hence *H. malonei* is capable of reaching sexual maturity in less than one year**.**

DISCUSSION

During courtship mutual examination and partial eating of mucus of various parts of the partner's body occurs in a number of species of terrestrial gastropods: *Ariolimax columbianus* (Gould, 1851) (Richter, 1980); *Arion* species (Adams, 1910; Castillejo, 1992; Chichester & Getz, 1973; Sheridan & Rowland, 1990); *Limax maximus* Linnaeus, 1758 (Langois, 1963; Pilsbry, 1948; Webb, 1950); *Deroceras* species (Reise, 1995 and references therein). The caudal mucus of some stylommatophorans may act as a pheromone that stimulates courtship or indicates sexual readiness by the potential mate (Quick, 1946; Richter, 1980; Murtov, 1999 and references therein). Our observations suggest that caudal mucus has functional significance in courtship of *H. malonei* also.

A trailing phase or "chase" also occurs during the courtship of other species, including *Philomycus carolinianus* (Bosc, 1802) (Webb, 1968), some *Arion* species (Adams, 1910; Castillejo, 1992; Chichester & Getz, 1973; Davis, 1977; Quick, 1946; Richter, 1980; Sheridan & Rowland, 1990), and certain limacids (Barker, 1999; Langois, 1963; Pilsbry, 1948; Webb, 1961). These behaviors occur in at least three families of terrestrial gastropods (Arionidae, Philomycidae, and Limacidae) and may have arisen several times. However, courtship trailing does not occur in all limacids examined so far and is absent from at least two species of *Deroceras* (Reise, 1995).

Our inability to view the actual transfer of the spermatophore during the copulation phase leaves questions about the mechanics of the transfer. However, our observations indicate that the verge is inserted into the partner's gonopore, and that the spermatophore is delivered internally. Additional work is needed to confirm the exact mechanism of sperm transfer and to establish whether the spermatophore is inserted directly into the bursa copulatrix, as we suspect. Anatomical studies are currently underway to investigate these issues (H. Reise, pers. comm.). Our observations also suggest that spermatophore delivery occurs asynchronously and is at least occasionally non-reciprocal. This system may be

conducive for investigating mate choice and the evolution of mating strategies in a hermaphroditic organism.

Accessory structures (*e.g.*, "stimulator," sarcobellum) everted during mating are well known for many stylommatophorans (Barker, 1999; Chichester & Getz, 1973; Davis, 1977; Muratov, 1999; Pilsbry, 1948; Quick, 1946; Tompa, 1984 and reference therein; Reise, 1995, 1996). There are, however, important differences among species in both the structure and function of these accessory structures. Accessory structures may be derived from the free oviduct, atrium, or penis. In some species the accessory structure is waved or stroked across a mate's body during courtship to deliver secretions containing calcium carbonate granules (Tompa, 1984), which presumably stimulate a reproductive response**.** The penial accessory structure of *H. malonei*, however, is not used to stroke the partner, and it is unclear whether it serves a stimulatory function. It may assist in maintaining alignment of the slugs' bodies by adhering to the partner's tail or mantle. Additionally, the adherence of the accessory structure to the partner may also act to deter a slug from "cheating" by crawling away prior to the completion of spermatophore transfer by both individuals.

The spermatophore removed from a slug during copulation (while it was protruding from the penis) was noticeably different in appearance from that shown in an illustration by Kozloff and Vance (1958). It was relatively stout, gradually tapered towards the ends (Fig. 3), and tipped on one end by a short "filament." In contrast, the spermatophore depicted in the earlier illustration, removed from a dissected slug (E. Kozloff, pers. comm.), was very slender for approximately one-half of its length. A spermatophore dissected from the bursa copulatrix from one of our slugs approximately two days after copulation showed a similar narrowing along one end. Most likely the difference in appearance resulted from changes that occurred after the spermatophore had entered the bursa copulatrix.

Our observations suggest that the deposition of eggs in multiple clutches may be a typical mode of oviposition for *H. malonei* (Table 1). Multiple clutches likely provide benefits in unfavorable habitats or under unpredictable weather conditions. While a site may appear suitable at the time of oviposition, the eggs could be destroyed subsequently by desiccation**,** freezing, or fungi, or consumed by predators. By spatially and temporally separating egg masses**,** *H. malonei* may act to "hedge its bets," thus enhancing the survival of at least some young.

Copulation by *H. malonei* was followed by oviposition 1 to 6 days later (Table 1). However, the dates of copulation and oviposition presented in Table 1 should be interpreted with caution because fertilization may have resulted from autospermy (Jordaens *et al.*, 2000; Reise, 1995, 1996) or from previous copulations (Leonard, 1991 and references therein). Self-fertilization occurs in at least some species of stylommatophorans if no mates are available (Duncan, 1975; Runham & Hunter, 1970; Tompa, 1984). Consequently, we cannot be

certain that sperm delivered during copulation immediately prior to oviposition was responsible for fertilizing the eggs.

Gastropods maintained in captivity often exhibit distorted reproductive cycles, including earlier age at first reproduction (Duncan 1975), raising questions about the extent to which breeding activity and embryonic development of *H. malonei* that we observed might have been affected by conditions in captivity. In particular, development, growth, and maturation are probably temperature-dependent**.** Winters in the Cascade Range can be long and severe, especially at higher altitudes, with ambient temperatures at or below the freezing point. The temperatures in microhabitats utilized by *H. malonei*, however, are likely to be less harsh. Refugia such as decaying logs, forest duff, and leaf litter can ameliorate ambient temperatures (Blessing *et al.*, 1999), and additional thermal buffering is likely provided at sites in or near creeks and seeps, or beneath tree canopy, deep talus, or snow pack (Bull & Carter, 1996; Maser *et al.*, 1979). Hence ambient temperature is not an entirely accurate gauge of the temperatures to which slugs or their eggs are subjected under natural conditions.

Arias and Crowell (1963) reported that late-developmental-stage embryos of *Deroceras reticulatum* (Müller, 1774) that had been stored for seven months at 4ºC began hatching within 24 hours after being placed in room temperature. This may parallel the embryonic development of *H. malonei* at montane sites; embryonic development may progress through the fall, be arrested during winter, and completed with the onset of spring. Activity of adults and development of eggs at low-elevation sites with milder winters may progress at a relatively steady rate, which is perhaps comparable to what we observed in captivity. Field observations of growth and reproduction of *H. malonei* and other species of *Hemphillia* would be extremely valuable for complementing observations of captive animals.

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