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Review

Reproductive ecology of predaceous Heteroptera

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ABSTRACT

Reproductive ecology entails relating the physiology and behavior of an organism to its environment and the community in which it lives. Terrestrial predatory Heteroptera (including Anthocoridae, Geocoridae, Miridae, Nabidae, Pentatomidae, Phymatidae, and Reduviidae) display a wide range of reproductive ecologies. But in spite of this variability, a review of the literature reveals certain underlying trends that are useful in understanding how generalist predators function within their environments. First, the reproductive ecology of predatory bugs is inherently coupled to the physiology of the female and her eggs. Second, three population parameters are directly tied to reproduction (maturation rates, realized fecundity, and reproductive diapause) have great bearing on the rate of population increase and reproductive success of a predatory bug, but these three parameters fluctuate widely within and among species. The variables that affect these processes include the physiological status of the mother (mating status, age and size, and nutritional status), the abiotic environment in which she and her eggs live (temperature, photoperiod, water availability), and natural enemies that attack eggs and reproductive females. A final trend observed in the literature involves the hierarchy of events that must occur before a female finds a suitable oviposition site. Females all must locate preferred habitats, plants/substrates, and microsites in which to insert or deposit an egg, but they use a variety of tactics and cues in order to accomplish this, depending on their life history traits. Examining the factors that constrain and promote the reproductive potential of predatory Heteroptera will make biological control programs that center on them more reliable and sustainable.

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1. Introduction

Reproductive ecology examines how an organism's physiology and behavior interact with the biological community and abiotic environment in which it lives to affect its reproductive success. A female's reproductive physiology, and the morphology and physiology of its eggs drive a species' maximum capacity for producing offspring. A series of inter-related constraints restrict this maximum reproductive output, and are grouped in this review as limitations imposed by the mother's physiological status, the environmental conditions experienced by the mother and her eggs, and natural enemies. Ultimately, all of these factors come to bear on the complex and diverse reproductive behaviors that are ultimately observed by the curious naturalist or hardened research scientist.

Predatory Heteroptera are a fascinating group on which to focus because of their diverse biologies and approaches to reproduction (Alomar and Wiedenmann, 1996; Coll and Ruberson, 1998; Fauvel, 1999; Schaefer and Panizzi, 2000). This polyphyletic guild of insects occupies most habitats ranging from the surface of the deep

ocean to freshwater lakes and streams, and from temperate to tropical climates. This review will largely focus on the terrestrial groups of predatory Heteroptera, largely in the Cimicomorpha (Anthocoridae, Nabidae, Reduviidae, Phymatidae, and Miridae) and Pentatomorpha (Geocoridae and Pentatomidae: Asopinae). Occasionally, reference will be given to aquatic, semi-aquatic, and herbivorous taxa to help illustrate key concepts or suggest areas of future research within the focus taxa. Nearly all members of this guild are best described as generalist omnivores, balancing their diet between prey and non-prey food sources to varying degrees. Because of their propensity for consuming insect prey, many of the species under discussion here are viewed as beneficial and several are the focus of mass production operations for biological control of crop and greenhouse pests. A few species that reside toward the phytophagous end of the dietary continuum (e.g., *Lygus* spp.) are even regarded as primary pests, due to the damage they inflict on crops. Their diet inevitably ties predatory bugs to a particular habitat and sometimes to a particular host plant, and this is reflected in their reproductive behavior.

This review is structured into three distinct sections that include Physiology and Morphology Underlying the Reproductive Ecology of the Predatory Heteroptera (including maternal reproductive physiology and egg morphology), Contributing Factors to

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the Reproductive Success of Predatory Heteroptera (including several dynamic processes that influence the reproductive success of the mother, the physiological status of the female, environmental cues, and influence of natural enemies), and oviposition behavior of reproductive females (including patterns in oviposition site selection, mechanisms involved in this selection process, and behaviors involved in oviposition). In spite of the diversity found in predatory bugs, clear patterns in reproductive ecology emerge and will be synthesized at the end of the review that will hopefully help advance future research on this topic. Moreover, the implications of the potentials and constraints for integrating reproductive ecology of predatory bugs into biological control programs in modern cropping systems are introduced.

2. Physiology and morphology underlying reproductive ecology of predatory Heteroptera

It is very difficult to understand the reproductive ecology of the predatory Heteroptera without at least an introduction to the basic physiology and morphology of the female and her eggs. The physiology of the female reproductive tract and morphology of the eggs give insight into why there are certain patterns to their reproduction. For example, clutches of heteropteran eggs are often laid in increments of seven due in part to the presence of seven ovarioles in each ovary of many taxa. Secretions from small accessory glands on the common oviduct glue the eggs in place, transfer symbiotic microbes vertically to the next generation, keep neonates aggregated upon the clutch, all while protecting the eggs from unfavorable climatic conditions. Although numerous factors play a role in reproduction, this review focuses almost entirely on reproductive females and the egg stage. Male and nymphal contributions to the reproductive ecology of a species are discussed only briefly.

2.1. Maternal reproductive physiology

2.1.1. The reproductive tract

The female reproductive tracts of Heteroptera are fairly homogenous in their structure, with distinctions among taxa mostly evident in the structure of their spermathecae and the arrangement of their accessory glands (Pendergrast, 1957; Javahery, 1994; Simiczyjew et al., 1998). All Heteroptera have merostic, telotrophic ovaries; in other words, they all have ovarioles with trophocytes (or nurse cells), and these trophocytes are connected to each oocyte with a nutritive cord. There are four parts to each ovariole: a terminal filament, an apical tropharium (where the trophocytes reside), a basal vitellarium (where the oocytes develop), and a pedicel (Simiczyjew et al., 1998; Lemos et al., 2005). The organization of the trophocytes in the tropharium differs in primitive (e.g., aquatic and semi-aquatic families) and advanced phyla (e.g., most terrestrial groups) (Simiczyjew et al., 1998). In primitive taxa, the trophocytes are mononucleate, whereas in the Cimicomorpha and Pentatomorpha the trophocytes are multicellular and form cytoplasmic lobes in the tropharia (Simiczyjew et al., 1998). Although these different arrangements of the tropharia no doubt have implications for the nutrition of the developing oocyte, the ecological significance of these different physiologies remains unclear.

2.1.2. Ovarioles

The number of ovarioles per ovary varies among taxa, but there are consistencies within certain families. For example, most asopine pentatomids have seven ovarioles per ovary, and often lay clutches with increments of seven eggs (Lemos et al., 2005). Indeed, this pattern of seven ovarioles per ovary is seen in many heteropterans (some or all of Acanthosomatidae, Coreidae, Cydnidae,

Miridae, Pyrrhocoridae, Reduviidae, Scutelleridae, Thyreocoridae) (Woodward, 1952; Javahery, 1994; Ambrose, 1999; Jahnke et al., 2006; Jedlička et al., 2009). Seven ovarioles is certainly not a hard and fast rule for predatory Heteroptera; one naucorid bug has more than 50 ovarioles (Ogorzalek and Trochimczuk, 2009).

2.1.3. Oocytes

The rate at which predatory heteropterans mature eggs and the number of mature oocytes present restricts how quickly a bug can respond reproductively to favorable conditions. There are three general stages to egg development in predatory Heteroptera, and this process is largely governed hormonally. The first stage of egg development is previtellogenetic growth, when the oocyte accumulates nutrients. Next, the oocyte accumulates the specific protein, vitellin, during the vitellogenic growth phase. Finally the mature egg undergoes choriogenesis, where the egg shell is created and sculpted (Adams, 2000; Lemos et al., 2005).

Egg development is initiated by a number of events and is closely tied to the ecology and behavior of the insect. The specific sequences of events that initiate egg development have only been examined for a few taxa, but it appears that any one of a number of occurrences can spur the process forward (Davey, 1997). Mating and transference of stimulatory secretions from the male, ovarian development, or distension of the abdomen (resulting from feeding in *Rhodnius prolixus* Stål, a blood feeding reduviid) can all instigate egg development. These cues act on the brain, which relaxes its normal suppression of juvenile hormone (JH) production by the corpora allata. These cues also inhibit the brain from producing a myo-peptide that normally stops ovulation and oviposition. When JH production increases, it triggers the production of vitellogenesis and is involved with the maturation of the accessory glands (Jedlička et al., 2009). In turn, at least one ecdysteroid (makisterone A) is known to stop vitellogenesis.

The number of oocytes found in each ovariole fluctuates dynamically over the female's life. There is a finite number of oocytes produced by each ovariole (Jahnke et al., 2006) and a finite number of mature oocytes that can be housed in a single ovariole at once (Woodward, 1952; Javahery, 1994). As an extreme example, eggs of *Loricula elegantula* (Baerensprung) (Microphysidae; closely related to anthocorids) are so large that a single egg fills the entire abdomen (Southwood, 1956). Furthermore, oocytes can be resorbed as a female ages; *Perillus bioculatus* (F.) (Pentatomidae) resorbed oocytes when they were reared on a suboptimal diet for 49 days (Adams, 2000). Also, it takes some insects several days to mature eggs, and their phenology of oviposition is punctuated with days of increased oviposition followed by a dearth of oviposition (Anderson, 1962a; Chu, 1969). All this being said, the number of oocytes found in each ovariole is strongly correlated with lifetime fecundity of the female, at least in *Macrolophus caliginosus* (Wagner) (Miridae) (Vandekerkhove et al., 2006).

2.1.4. Spermathecae

The spermatheca and sperm storage allows females of predatory Heteroptera to dissociate from males after mating. Most Heteroptera have a single spermatheca attached to the common oviduct (Javahery, 1994). This notwithstanding, several families pertinent to this review do not have a spermatheca (some Anthocoridae, Miridae, Nabidae, Reduviidae) (Pendergrast, 1957; Jahnke et al., 2006). Another exception is that some reduviids and phymatids that have two pseudospermathecae, which are little more than pouches attached to the common oviduct (Pendergrast, 1957; Ambrose, 1999). In general terms, the spermatheca consists of a terminal bulb, and a duct that connects it to the common oviduct (Pendergrast, 1957). The size and structure of the spermathecal bulb, the presence of a fecundation duct, and the length and complexity of the spermathecal duct have some

usefulness in grouping certain families (Pendergrast, 1957). Traumatic insemination is present in some groups that lack a spermatheca (Cimicidae and possibly some Miridae) (Pendergrast, 1957; Marchini et al., 2010), and a swelling of the vagina into a sperm-storing bursa copulatrix is known in others (Pendergrast, 1957). Finally, some reduviids (and possibly other taxa) are fertilized using a spermatophore (Davey, 1997). In pentatomids, the spermatheca has an elastic spermathecal pouch proximal to the bulb which swells with sperm during mating (Adams, 2001). The duct between the pouch and the bulb restricts sperm from entering the spermathecal bulb. This restrictive duct may partially explain the long mating durations observed in pentatomids (Section 3.2.1). The bulb is further differentiated by sometimes being surrounded by secretory cells of unknown function (these cells are also present surrounding the spermathecal bulbs of Naucoridae, Aphelocheiridae, Corixidae, and Ochteridae; (Pendergrast, 1957). Thus, the structure of the spermatheca varies substantially among predatory Heteroptera, but there are distinctive patterns evident within certain sub-orders and families (Pendergrast, 1957).

2.1.5. Accessory glands

Most predatory groups have 1–2 accessory glands connected near the pedicel (Pendergrast, 1957; Jahnke et al., 2006; Jedlička et al., 2009). Ambrose (1999) recognized both “subrectal glands” and “bursal glands” in reduviids. As the eggs enter the common oviduct, they are coated with accessory gland secretions (Jedlička et al., 2009; Ogorzalek and Trochimczuk, 2009). The bursal gland of reduviids secretes spumaline (or cement), and the subrectal glands secrete a viscous, clear substance with crystalline particles

that coats the eggs. In the non-predatory *Pyrrhocoris apterus* (L.) (Pyrrhocoridae), the accessory glands secrete a variety of triacyl glycerides, acetyls, propionyls, and two forms of Vitamin E (Jedlička et al., 2009). Although the exact mechanisms for how these substances work are poorly understood, these substances function as oviposition pheromones, in shell hardening, as antiseptics, and as adhesive glues (Jedlička et al., 2009); functions that will be discussed at length in Section 4.3.3).

2.2. Egg morphology in predaceous Heteroptera

2.2.1. Morphology of the chorion

In addition to its usefulness in egg taxonomy, the exterior surface of the egg acts as an interface with its environment and thus greatly affects the life histories of the predatory Heteroptera. As a heteropteran egg reaches its final stage of development, it is surrounded by follicular cells that secrete the chorion (Southwood, 1956). The pattern of these follicular cells gives rise to the sculpturing of the chorion, which is often diagnostic of species (Southwood, 1956; Javahery, 1994) (Fig. 1). All heteropteran eggs have an exochorion and an endochorion (Southwood, 1956). A series of invaginations through the chorion called micropyles (these penetrate the entire chorion) or pseudo-micropyles (these end before they reach the endochorion) are important in allowing sperm to reach the embryo (Southwood, 1956). Cobben (1968) distinguishes a third process, the aeropyle, which functions in gas exchange in many cimicomorphan eggs. Some eggs also have a proteinaceous matrix, or “air sponge”, within the chorion that further enhances gas exchange (Southwood, 1956; Cobben, 1968). The

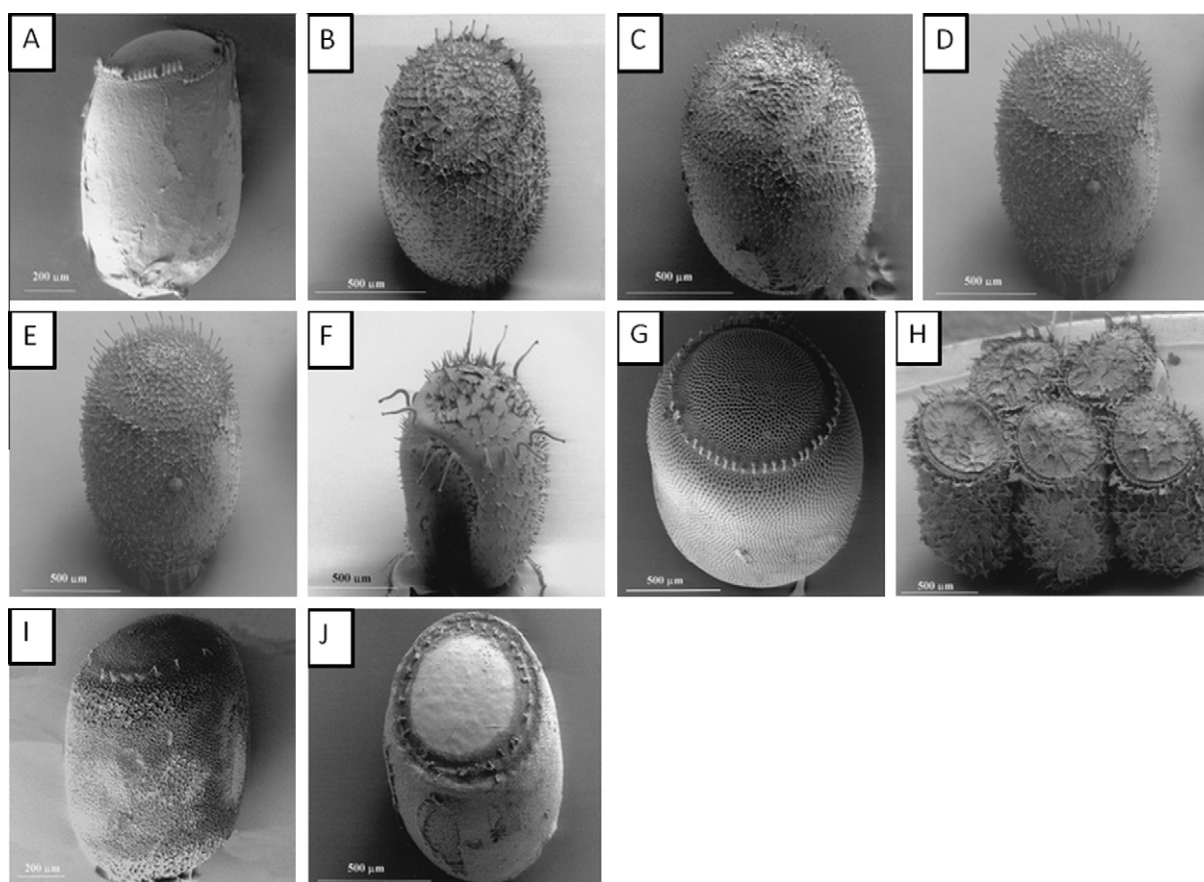


Fig. 1. Scanning electron micrographs illustrating the diversity of chorionic surface sculpturing in Pentatomidae. (A) *Oebalus pugnax*, (B) *Euschistus tristigmus*, (C) *Euschistus servus*, (D) *Euschistus quadrator*, (E) *Euschistus obscurus*, (F) *Podisus maculiventris*, (G) *Acrosternum hilare*, (H) *Piezodorus guildinii*, (I) *Thyanta accerra*, and (J) *Nezara viridula*. Photos reprinted from Bundy and McPherson (2000) with permission from the Entomological Society of America.

number and arrangements of these micropylar processes are further diagnostic of species (Javahery, 1994). Other appendages on the egg surfaces range from spines to long tubes that facilitate air exchange (in aquatic and semi-aquatic taxa) (Esselbaugh, 1946; Southwood, 1956; Cobben, 1968; Blinn and Runck, 1989; Keffer, 2000). Often elongated, the eggs of a species are produced with a range of sizes and dimensions (Hill, 1961; Anderson, 1962a; Cobben, 1968; Chu, 1969; Askari and Stern, 1972; Richards and Harper, 1978; Blinn and Runck, 1989), and egg colors often change as the nymph within develops (Chu, 1969; Carrasco and Kaitala, 2009; Dzerefos et al., 2009).

2.2.2. Structural differences in the eggs of Cimicomorpha and Pentatomorpha

The primary method of escape for hatching nymphs is the most conspicuous difference between eggs of Cimicomorpha and Pentatomorpha (McPherson, 1982). To hatch, the prolarva inhales air and pumps hemolymph into the head. This puts pressure on the chorion of the egg, which breaks at fracture sites (Cobben, 1968; Javahery, 1994; Luo et al., 2010). Eggs of Cimicomorpha all have a true operculum at their apex which detaches during hatching (some cimicomorphan nymphs also have a row of teeth on their crenulum that facilitate breaking of the chorion (Southwood, 1956; Cobben, 1968). Eggs of the Pentatomorpha lack true opercula, but all predatory taxa have a hardened egg burster near their apex that allows the prolarva to push through the chorion (Southwood, 1956; Cobben, 1968; Javahery, 1994). Another important difference between the eggs of these two groups is that eggs of Pentatomorpha often possess true micropyles and lack pseudo-micropyles entirely (Southwood, 1956; McPherson, 1982; Javahery, 1994). Eggs of the Cimicomorpha may have only pseudo-micropylar processes (Southwood, 1956), although some reduviids have both true and pseudo-micropyles (Southwood, 1956; Ambrose, 1999), and all mirids and some nabids have at least one true micropyle (Cobben, 1968). Thus, fertilization must occur

prior to choriogenesis in Cimicomorphans that lack true micropyles (there is no access for the sperm once the chorion is formed in the ovariole). This is not the case in at least some pentatomids (Adams, 2000). General characteristics of the eggs of different predatory families are presented in Table 1.

Cimicomorphan eggs all tend to be elongate and shaped like a wine flask, with a flattened operculum on top (Fig. 2). The operculum on the eggs laid by Cimicomorpha is formed by aeropyles that circumscribe the cephalic end of the egg (Cobben, 1968). This operculum has a sealing bar (observable on a cellular level), and it is distinct from the rest of the egg in the surface pattern on the chorion (Southwood, 1956). Indeed, the shape and surface pattern on the operculum varies sufficiently that it can be used to distinguish species within a habitat or region (Sands, 1957; Hill, 1961; Sanford, 1964). For example, anthocorids found in soybeans have a circular operculum, whereas in nabids and mirids that may occur on the same plants have more elliptical opercula (Southwood, 1956; Isenhour and Yeargan, 1982).

Pentatomid eggs are evenly categorized as either having flattened cephalic ends (i.e., keg-shaped), or with rounded cephalic ends (Esselbaugh, 1946). A hardened egg burster becomes visible in pentatomid eggs just prior to hatch (Javahery, 1994). The shape of the egg burster of the Pentatomorpha varies among species, and can often be used as a reliable taxonomic character (Esselbaugh, 1946; Javahery, 1994). All egg bursters can be categorized as Y- or T-shaped (Javahery, 1994). The pentatomids, which have relatively thick chorions adapted to living exposed on leaf surfaces, tend to have more substantial egg bursters than other taxa (Southwood, 1956). Unquestionably, the Pentatomidae are the best studied group within the Heteroptera in terms of their egg morphology (Southwood, 1956; Bundy and McPherson, 2000), and within the Pentatomidae, the predatory Asopinae boast having the most advanced egg structure (Southwood, 1956). This assignment is based in large part on the well developed pseudoperculum found on asopine eggs. It is similar to a true operculum in that it is

Table 1
Summary of reproductive characteristics of major predatory Heteroptera taxa discussed in the review.

Suborder	Family	Egg burster present?	Operculum present?	Gregarious or solitary eggs	Eggs inserted into substrate?
Pentatomorpha	Pentatomidae:	Yes	Pseudoperculum; lacks true operculum	Gregarious	No
	Asopinae Geocoridae	Yes	No	Both	No
Cimicomorpha	Anthocoridae	No	Yes	Usually solitary	Yes
	Nabidae	No	Yes	Usually solitary	Yes
	Miridae	No	Yes	Usually solitary	Yes
	Reduviidae	No	Yes	Both	No

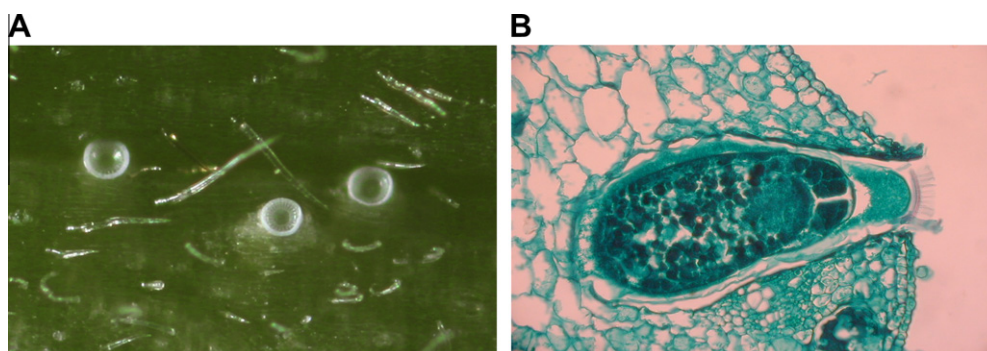


Fig. 2. Photograph of an egg of *Orius insidiosus*, illustrating placement of a cimicomorphan egg. (A) External view of egg and (B) cross section of egg inserted into plant petiole. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

created by a series of micropylar processes that surround the egg (McPherson, 1982; Javahery, 1994). However, the asopine pseudopericulum differs from a true operculum in that it lacks the sealing bar, distinct surface pattern, and additional gas exchange capabilities associated with a true operculum (Southwood, 1956). Asopines tend to have fewer micropyles that are more elaborate than in other subfamilies of the Pentatomidae (Esselbaugh, 1946) (Fig. 1).

3. Contributing factors to the reproductive success of predatory Heteroptera

Many factors contribute to the reproductive success of predatory Heteroptera in this group. After reviewing the diverse literature on this topic, it is useful to categorize the underlying processes that influence the rate and success of reproduction in predatory species. Here, I group these processes as (1) the durations of the pre-oviposition and incubation period, (2) how many offspring a female produces, and (3) successful reproductive diapause, which is necessary for many predatory bugs to attain maximum fecundity and overwinter successfully (especially in temperate habitats).

Initiation, rates, and success of these three general parameters vary tremendously within and among species. The myriad factors that influence these life history traits are easily grouped as either relating directly to the physiological status of the mother (potential and realized fecundity), or to the environmental conditions under which the female or her eggs are exposed. Also, eggs experience heavy mortality inflicted by natural enemies, and avoidance of these natural enemies shape many of the behaviors that will be discussed below, as well as the reproductive success experienced by predatory Heteroptera within their environment. A schematic of the dynamic constraints on reproductive success is presented in Fig. 3.

3.1. Dynamic processes influential to reproductive success

3.1.1. Maturation rates (pre-oviposition and incubation periods)

The duration of the pre-oviposition period in the female and the time required for egg incubation are two parameters critical to the

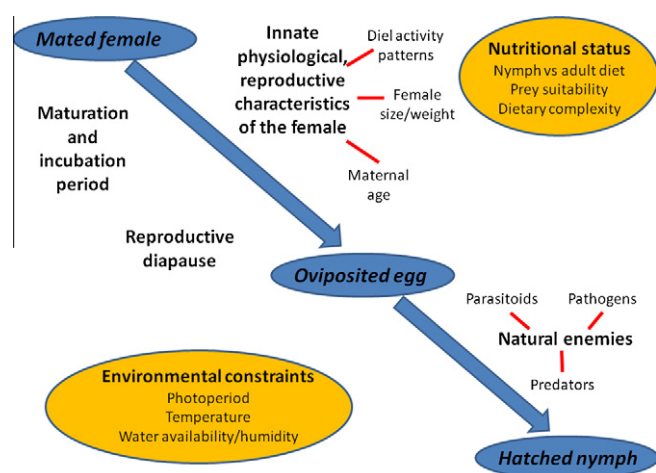


Fig. 3. A schematic of the diverse and dynamic constraints that influence reproductive success between mating and successful hatching of a predatory heteropteran's egg. Once a female is mated, her innate physiological characteristics influence the number of eggs that are laid. After these eggs are laid, natural enemies function as an addition filter that reduces the number of successfully hatched offspring and where and when eggs are laid. Nutritional status and environmental conditions broadly affect many of these parameters to ultimately influence reproductive success. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

reproductive ecology of the predatory Heteroptera that are greatly influenced by myriad factors. Females of predatory Heteroptera are unable to lay eggs directly after eclosion. Rather, they must undergo a pre-oviposition period during which a female mates and matures eggs. Although it depends on the species, physiological status of the female, and the environmental conditions, the pre-oviposition period can extend anywhere from 1.4 to 28 days (Hill, 1957; Anderson, 1962a; Collyer, 1967; Askari and Stern, 1972; Parker, 1981; Horton et al., 1998; Wittmeyer and Coudron, 2001; Carvalho et al., 2006; Vandekerckhove et al., 2006; Bahşi and Tunç, 2008; Das et al., 2008; Fathi, 2009; Neves et al., 2009; Luo et al., 2010). Similarly, eggs that do not overwinter hatch in as few as 5 days and as many as 30 days, depending on the species in question (Anderson, 1962a, 1962b; Javahery, 1994; Das et al., 2008). Egg incubation time can vary intraspecifically as well, depending on the environmental conditions during the incubation period and the physiological conditions of the mother when they were laid (Hill, 1957, 1961; Askari and Stern, 1972; Richards and Harper, 1978; Parker, 1981; Adams, 2000; Jackson, 2003; Luo et al., 2010). For example, eggs of one population of *Anthocoris nemorum* (L.) (Anthocoridae) required anywhere from 9 to 21 days to hatch, depending on the environmental conditions (Collyer, 1967).

3.1.2. Realized fecundity

As mentioned in Section 2.1, potential fecundity (i.e., the total number of eggs a female can lay under optimal conditions) is largely tied to the genetics of the mother and the number of oocytes that are initially present in the ovarioles. Realized fecundity (i.e., the number of eggs a female actually lays over her lifetime) is an extremely plastic characteristic of a female that is strongly influenced by the physiological status of the mother over her life, the environmental conditions the female and her eggs experience, and the mortality inflicted by natural enemies. As will be discussed in Section 4.1, predatory Heteroptera either lay their eggs singly (hereby "solitary"), or in clutches (hereby "gregarious"). Often times, daily and lifetime fecundity varies for females of these two oviposition strategies, with gregarious females laying more eggs than solitary females. By far, the winner for the largest clutch of eggs found in any predatory Heteroptera is the marine gerriid, *Halobates sobrinus* White (Cheng and Pitman, 2002). A single egg mass comprised of nearly 350,000 eggs (laid by 833 females) was affixed to a plastic bucket found at sea! More typically, females of predatory bugs lay between 100 and 1000 eggs over their lives (Hill, 1957, 1961; Anderson, 1962a; Collyer, 1967; Parker, 1981; Liquido and Nishida, 1985; Richards and Schmidt, 1996; Ambrose, 1999; Murai et al., 2001; Wittmeyer and Coudron, 2001; Sisgaard, 2004; Carvalho et al., 2006; Bahşi and Tunç, 2008; Das et al., 2008; Silva and Panizzi, 2008; Hirayama and Kasuya, 2009; Neves et al., 2009; Luo et al., 2010).

3.1.3. Reproductive diapause

Diapause during periods of cold or resource scarcity is typically associated with the reduction or cessation of normal reproductive processes. Species are easily grouped into those that oviposit throughout the year and those that only oviposit during the warmer parts of the year (Woodward, 1952). Predatory Heteroptera typically undergo diapause either as eggs or adults (Harris, 1928; Woodward, 1952; McPherson, 1982). Eggs that overwinter tend to be morphologically distinct from those that do not overwinter and they may require a cold vernalization before they will hatch (Javahery, 1994). For example, eggs of mirids that overwinter tend to have thicker chorions and longer micropyles than mirid eggs that do not overwinter (Southwood, 1956). It may be that females are able to induce diapause in her eggs, possibly through her nutritional status, in order to avoid times of food scarcity for her young (Shintani, 2009).

Diapause is controlled genetically and physiologically, but environmental cues are key in initiating this process. In the herbivorous *Pyrrhocoris apterus* (Pyrrhocoridae), genetic drivers of diapause induction are associated with two gene transcripts (aldose reductase and sorbitol dehydrogenase); these genetic markers are transcribed only during diapause (Košťál et al., 2008). The genetics of individual females within a population also affect diapause initiation. For example, only 80% of one population of *A. nemorum* (Anthocoridae) require cold-induced diapause in order to begin reproduction; 20% of the population can begin laying eggs directly after the pre-oviposition period (Saulich and Musolin, 2009). Cho et al. (2007) found that JH titer was involved in the termination of diapause in *Scotinophara lurida* (Burmeister) (Pentatomidae), but that this hormone was not solely responsible; long-day photoperiods were also necessary for diapause termination.

Diapause is typically characterized by the loss of eggs and the atrophication of the reproductive system, and the increase in fat content in the abdomen; a female's status is easily designated upon dissection (Anderson, 1962b; Elkassabany et al., 1996). This notwithstanding, the reproductive systems of some species continue to develop during the winter, although at a much slower pace than when diapause is ended. This is particularly well described in anthocorids and some aquatic taxa, many of which mature a few eggs during the winter and are ready to reproduce early in the spring (Hill, 1957; Anderson, 1962b; Suchá and Papáček, 2008; Ditrach and Papáček, 2009).

3.2. Physiological status of the mother and reproduction

3.2.1. Mating status

Mating frequency and duration affect the fecundity of female predatory Heteroptera. A single mating is sufficient for many heteropterans to lay eggs (Hill, 1961; Anderson, 1962a; Javahery, 1994), although additional matings will often increase a female's fecundity (Eyles, 1963; Ambrose, 1999; Saulich and Musolin, 2009). Sperm can be stored for long periods of time in some species, thanks in part to sperm-storage organs in the female (Section 2.1.4). In temperate anthocorids, most males die prior to overwintering, and fertilized females are the only ones to successfully overwinter and populate the next generation the following spring (Hill, 1957; Collyer, 1967; Kingsley and Harrington, 1982; Elkassabany et al., 1996; Horton et al., 1998; Saulich and Musolin, 2009). Indeed, fertilization can increase the success of diapause in these bugs (Saulich and Musolin, 2009).

Sometimes, successful mating can take a long time (Javahery, 1994; Himuro and Fujisaki, 2008; Dzerefos et al., 2009); asopine pentatomids are renowned for the long duration of their mating episodes (sometimes, mating can last for days). In *Podisus nigrispinus* (Dallas) (Pentatomidae), it took 11.25 h of mating to fill the spermathecal bulb with sperm, although some insects were able to lay eggs after only 2 h of mating (Rodrigues et al., 2008). This being said, long matings are not the rule for all predatory taxa; *A. nemorum* (Anthocoridae) finishes the job in around 7.5 min (Hill, 1957). In part, long mating durations may be related to sperm competition among males – if a male is mating with a female, he can be sure that someone else is not (Arnqvist, 1988). In *Togo hemipterus* (Scott) (Lygaeidae), an herbivore, the male injects the female with a secretion from one of his accessory glands that inhibits the female from mating again and the longer he mates, the longer it takes her to remate (Himuro and Fujisaki, 2008). The contributions of male accessory glands to female reproductive propensity in predatory taxa merit further attention. Finally, it is noteworthy that not all eggs laid by predatory Heteroptera hatch, which may be related to fertilization levels (Wittmeyer and Coudron, 2001; Das et al., 2008). Unmated females of the phytophagous *Nysius*

huttoni White (Lygaeidae) will occasionally lay eggs (He and Wang, 2000), although this has not been reported in predatory taxa.

3.2.2. Female age and time limitation

Most of the literature suggests that time limitation, or how female longevity constrains maximum reproduction rates, for female predatory heteropterans is an important consideration. Almost invariably, a female's reproductive rate diminishes as she ages (Chu, 1969; Javahery, 1994; Ambrose, 1999), and her offspring's performance may also deteriorate as she gets older (Chu, 1969; Ambrose, 1999). A female typically lives past the duration of her oviposition period (at least in the laboratory), and many species are long lived (especially the univoltine species) (Hill, 1957; Chu, 1969; Chyzik et al., 1995b; Bueno et al., 2006; Carvalho et al., 2006; Bahşi and Tunç, 2008). However, those species whose development is hastened with high temperatures seldom achieve peak fecundity; Chu (1969) found that *Lyctocoris beneficus* (Hiura) and *Xylocoris hiurai* Kerzhner et Elov (= *X. galactinus*) laid fewer eggs at 30 °C than at lower temperatures, largely because these anthocorids survived for a shorter duration at this high temperature. Regrettably, much of the data presented on this topic is conducted in the laboratory, so it is unclear whether sperm-limitation, nutritional or environmental factors may be affecting female longevity or reproductive rates. The question of how a female balances her time and resources between physiological maintenance and reproduction requires substantially more attention from those studying predatory Heteroptera.

3.2.3. Female weight and size

As is the case in many animals, larger predatory heteropterans lay more eggs and over a longer duration (O'Neil, 1992; Honěk, 1993; Oliveira et al., 2005). Much of a female's weight is tied to the number of eggs she has matured; in *Podisus maculiventris* (Say) (Pentatomidae), egg clutches comprised 60% of a female's total weight (O'Neil and Wiedenmann, 1990). This being said, it is not surprising that much of a female's weight gain occurs during their pre-oviposition period, and weight may decrease following the advent of oviposition (Anderson, 1962b). Also, at least one nabid, *Nabis americanoferus*, has a threshold of body weight, below which it does not lay eggs (O'Neil, 1992). It is currently unknown how widespread this restriction on oviposition is within the group. In addition to weight (which fluctuates over the life of an insect), body size is also strongly correlated with reproductive potential. In *P. maculiventris*, as little as 0.5 mm increase in body width is associated with dozens more eggs produced (Evans, 1982a). Thus, factors that affect a female's size (i.e., nymphal nutrition, temperature, etc.), have important implications for reproductive capacity of a bug.

3.2.4. Nutritional status of the female

The mother's diet affects many aspects of her reproductive physiology, most notably the maturation of the oocytes. Not surprisingly, mated females consume more food than unmated ones (Ahmadi et al., 2009), specifically because of the resource requirements for maturing eggs. The frequency of feeding also affects the reproductive capacity of a female; less frequent feeding increases pre-oviposition periods, reduces fecundity, and shortens the duration of the oviposition period (Evans, 1976; Wiedenmann and O'Neil, 1990; De Clercq and Degheele, 1992; Molina-Rugama et al., 1998). The reproductive rates of *Podisus sagitta* (Fab.) (Pentatomidae) fed daily were dramatically improved over those fed every 3, 7, 14, or 21 days (De Clercq and Degheele, 1992). Hill (1961) found that when high quality food disappeared that *Anthocoris sarothamni* Douglas and Scott (Anthocoridae) could not stop laying eggs. Rather than reducing reproductive rates in order to preserve their lives, the females continued laying eggs at their normal rate,

and essentially laid themselves to death. Diet also affects how quickly predatory bugs produce vitellogenin (Shapiro et al., 2000). After diapause, food is necessary for many predatory heteropterans to begin oviposition (Hill, 1961).

The importance of nutritional status of the female is well illustrated by studies that examine the relative fitness of females fed different individual foods, especially prey species. The duration of the pre-oviposition period (Chu, 1969; Ruberson et al., 1991b; Tommasini et al., 2004; Mahdian et al., 2006; Sengonca et al., 2008; Fathi, 2009), the oviposition period (Sanchez et al., 2004; Tommasini et al., 2004; Sengonca et al., 2008; Fathi, 2009), total eggs produced (Chu, 1969; Ruberson et al., 1991b; Chyzik et al., 1995b; Venzon et al., 2002; Sanchez et al., 2004; Tommasini et al., 2004; Mahdian et al., 2006; Xu et al., 2006; Sengonca et al., 2008) and the hatching rate (Chu, 1969; Salerno et al., 2007) are all affected by food type. Lemos et al. (2005) examined the effects of different prey on the reproductive tracts of *P. nigrispinus* (Pentatomidae). Females that were fed larvae of *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) had more and larger oocytes and longer ovarioles than those females fed an artificial diet, likely due to the inability of the diet to support choriogenesis (females fed *Musca domestica* L. [Diptera: Muscidae] or *Tenebrio molitor* L. [Coleoptera: Tenebrionidae] larvae had reproductive tracts of intermediate maturity). Artificial diets are seldom as effective as high-quality prey for supporting reproduction (Wittmeyer and Coudron, 2001; Vandekerkhove et al., 2006). To an extent, females can compensate for poor nymphal nutrition by self-selecting high quality diets, making adult diet as important if not more important than nymphal diet for reproduction (Ruberson et al., 1991b; Vandekerkhove et al., 2006). Finally, some species may display very different life history strategies when presented with high-quality prey resources. *Orius sauteri* (Poppius) and *O. tantillus* (Motchulsky) (Anthocoridae) are adapted to temperate and subtropical climates, respectively. When presented with *Thrips palmi* Karney (Thysanoptera: Thripidae), *O. sauteri* responded very quickly by consuming more prey and maximized egg production as soon as possible, resulting in a hastened death. In contrast, *O. tantillus* paced themselves and laid eggs for a longer period of time when presented prey (Nakashima and Hirose, 1999). This study illustrates that there is a physiological cost to reproduction, and that species where favorable environmental conditions may try to 'make hay when the sun shines', as opposed to those species who live in areas with a more even climate.

Predatory bugs fed diversified diets tend to have greater fitness than those fed simple diets. In part, this is because prey and non-prey foods differ substantially in their nutrient profiles, and predatory insects often require limiting nutrients present in both classes of food (Lundgren, 2009). While prey is often required for reproduction (Anderson, 1962a; Naranjo and Stimac, 1985; Sanchez et al., 2004), adding plant-based foods into a diet often improves a female's fitness over prey-only diets (Salas-Aguilar and Ehler, 1977; Ruberson et al., 1986; Cocuzza et al., 1997; Fritsche and Tamó, 2000; Coll and Hughes, 2008; Lundgren, 2009). Lemos et al. (2009, 2010) found that adding plant material to the diet of prey-fed *Brontocoris tabidus* Signoret (Pentatomidae) increased the number and size of their oocytes, as well as increasing the density of their trophocytes in the tropharium. Moreover, offering more than one prey species is generally superior to offering only a single prey (Herard and Chen, 1985).

3.3. Environmental effects on reproduction

3.3.1. Temperature

Temperature affects most things in the reproductive ecology of predatory Heteroptera. Specifically, temperature has been shown to affect the durations of the oviposition periods, daily and lifetime

fecundities, the hatching rate of the egg, the duration of the incubation times of the egg, and the intrinsic rate of population growth of predatory heteropterans (Chu, 1969; Ambrose, 1999; Bommireddy et al., 2004; Sátiro da Medeiros et al., 2004; Tommasini et al., 2004; Baniameri et al., 2005; Kim and Riedl, 2005; Bahşi and Tunç, 2008; Lu et al., 2009). For each species, there is a distinct high and low temperature threshold beyond which normal biological processes cease. Within this range of temperatures, it is generally the case that warmer temperatures speed maturation processes such as the pre-oviposition period or egg incubation times. Also within this range, there is often an optimal temperature under which reproductive processes function best. Finally, low temperatures are an important cue used by many species in temperate climates to initiate reproductive diapause (Saulich and Musolin, 2009). For example, *Orius albidipennis* Reuter (Anthocoridae) lays eggs until the temperature reaches 15 °C, after which reproduction ceases (Chyzik et al., 1995a). In this species, exposure to short day lengths did not influence egg production rates, although it is often the case that photoperiod and temperature both act as important cues to initiate diapause (Bahşi and Tunç, 2008; Saulich and Musolin, 2009).

3.3.2. Photoperiod

Short day lengths play a key role in the initiation of reproductive diapause in most temperate species of predatory bugs. Each species has a clear threshold of day length below which they enter into a reproductive diapause. This threshold ranges from 10 to 15 h daylight, depending on the species involved (Horton et al., 1998; Braman, 2000; Ruberson et al., 2000). Exposure to long-day conditions and warm temperatures is necessary to resume reproduction in at least some species, although it takes time before they sufficiently mature eggs (Kingsley and Harrington, 1982; Saulich and Musolin, 2009). All of this being said, photoperiod is not universally responsible for the induction of reproductive diapause; reproduction by at least one population of *A. nemorum* (Anthocoridae) was totally unaffected by short day exposures (Collyer, 1967). Indeed, populations of the widely distributed *A. nemorum* typically undergo a winter diapause where reproduction ceases, but 20% of the population does not require an exposure to cold temperatures or short days in order to initiate oviposition (Saulich and Musolin, 2009). Other life history parameters are also influenced by photoperiod; *Orius insidiosus* females experienced shorter pre-oviposition periods as the photophase became longer (Ruberson et al., 1991a). Finally, even species that do not experience reproductive diapause are sensitive to photoperiod. In *Orius thyestes* Herring (Anthocoridae), which does not undergo diapause, daily fecundity decreased as the photoperiod shortened (Carvalho et al., 2006).

3.3.3. Diel activity

Research has revealed that many biological processes (including predation; Lundgren et al. 2006, 2010) observed in natural enemies are tied to the diel cycle, and diel patterns in reproduction in Heteroptera merits further study. In some herbivorous bugs (Lygaeidae and Pentatomidae), oviposition often takes place in the afternoon (between 12:00 and 16:30) (Eyles, 1963). Anthocorids do not seem to conform to this pattern, and will lay equal numbers of eggs during the day and night (Hill, 1957; Chu, 1969). However, Chu observed that eggs of *L. beneficus* and *X. hiurai* (= *galactinus*) hatch in the very narrow window of 08:00–10:00.

3.3.4. Water availability and relative humidity

Generally speaking, eggs of predatory Heteroptera desiccate under dry conditions and require water or humidity to survive (Anderson, 1962a; Chu, 1969; Richards and Harper, 1978; Blinn and Runck, 1989; Ambrose, 1999). The chorion and micropyles of eggs are apparently impervious to water, but if they are soaked

the eggs (or hatching nymphs) will die (Woodward, 1952; Cobben, 1968; Shapiro and Ferkovich, 2006). Some eggs are laid with all of the moisture that they require for development (Woodward, 1952), and others may imbibe water from the substrate. Some species that insert their eggs into plant tissue prefer to lay on plant structures that are less prone to desiccation than their normally preferred sites (Seagraves et al., 2011). Typically, eggs laid on the plant surface have relatively thickened chorions relative to eggs that are inserted into plant material, and presumably this thickness is related to the rate at which eggs lose water under these different conditions (Southwood, 1956). Relative humidity levels are also important for egg survival, and typically around 40–60% seems optimal for the few bugs for which there is data available (Javahery, 1994; Richards and Schmidt, 1996; Riis et al., 2005).

3.4. The effects of natural enemies on reproduction and the egg stage

3.4.1. Pathogens

Females infected with entomopathogens tend to be less fecund than healthy females. In Nabids, virus infection reduces egg production (Braman, 2000). *Beauveria bassiana* (Balsmo) Vuillemin typically kills *Lygus hesperus* (Knight) (Miridae), but at high temperatures the pathogen is unable to kill its host (Noma and Strickler, 2000). However, one of the sublethal effects of the pathogen at these temperatures is to reduce the host's fecundity. Predators often encounter pathogens through infected prey. De Nardo et al. (2001) showed that *P. nigrispinus* is unaffected by *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae) prey infected with nucleopolyhedrovirus (NPV) during their first generation of exposure, but continued exposure to the infected prey eventually had consequences on the predator's fecundity. These effects were observed within a single generation in *Nabis roseipennis* (Nabidae) fed *Pseudoplusia includes* (Walker) (Lepidoptera: Noctuidae) infected with NPV, and were likely tied to prey quality rather than virus infection of the predator (Ruberson et al., 1991b). Females in culture may transmit a pathogen to their eggs; *Aspergillus niger* van Tieghem is transmitted vertically on the ovipositor of *Lygus lineolaris* (Palisot de Beauvois) (Miridae) (Alverson and McCain, 2004). To reduce their offspring's exposure to a pathogen, some females are able to detect and avoid laying their eggs on pathogen-laden substrates. *Anthocoris nemorum* (Anthocoridae) were able to detect *B. bassiana* using proximate cues, and laid significantly fewer eggs onto leaves that were inoculated with the pathogen (Meyling and Pell, 2006).

3.4.2. Egg predation

Cannibalism is a serious problem for many predatory Heteroptera, and likely shapes many of their reproductive strategies. Several descriptions have indicated that species that normally insert their eggs into plant tissue will readily consume conspecific eggs if they are laid exposed on the substrate rather than inserted into plant tissue (Hill, 1957, 1961; Anderson, 1962a; Chu, 1969). Water scarcity may exacerbate this cannibalism. Nymphs of the reduviid, *Agriosphodrus dorhni* (Signoret), readily cannibalize one another (Luo et al., 2010), as do males of *Rhinocoris tristis* (Stål) when females add too many eggs to the brood they are guarding (Gilbert and Manica, 2009). Some species of herbivorous Heteroptera lay trophic eggs (inviolate eggs that are laid to provide food for the rest of the clutch). *Adomerus triguttulus* (Motchulsky) (Cydnidae) lay a large proportion of their brood as trophic eggs (up to 30 trophic eggs per clutch), and this provision by the mother was very important in sustaining nymphs that hatch when resources are scarce (Kudo and Nakahira, 2004, 2005). Whether predatory taxa lay these trophic eggs remains to be described.

Aside from cannibalism, predation on eggs of predatory taxa is likely, but poorly documented (McPherson, 1982; Lattin, 1989,

1999). Some herbivorous taxa (*Phyllomorpha laciniata* [Villers]; Coreidae) lay their eggs onto the backs of conspecifics to avoid ant predation (Katvala and Kaitala, 2003). Mothers of another phytophagous species, *Elasmucha grisea* (L.) (Acanthosomatidae), guard their eggs to reduce predation by ants and earwigs, and the size of her clutch is related to the number of eggs that she can effectively protect (Mappes and Kaitala, 1994). The current dearth of research on egg predation on predatory bugs warrants further attention by entomologists.

3.4.3. Egg parasitoids

If the proportion of literature devoted to a group of natural enemies is any indication of their importance, then parasitoids are the most influential natural enemies of the eggs of predatory Heteroptera. For the most part, these parasitoids belong to the Scelionidae and Mymaridae (Hymenoptera), and there are numerous reports of parasitism rates of various species in various habitats (McPherson, 1982; Lattin, 1989; Javahery, 1994; Jackson, 2003; Torres and Ruberson, 2006). Egg parasitism rates of predatory species can reach 100% in some habitats, and many species have adopted a range of tactics to reduce or avoid parasitism. *Calocoris quadripunctatus* (Villers) (Miridae) embeds its eggs into the scales of dead buds on trees, and the eggs are entirely covered with wood. To overcome this avoidance, the parasitoids of this species have an elongated ovipositor that is able to parasitize the egg through the external covering (Conti et al., 2000). *Lygus hesperus* prefers to lay their eggs on strawberry fruit rather than the vegetative parts of the plant, in large part because *Anaphes iole* Girault (Hymenoptera: Mymaridae) does not parasitize these eggs when the achenes are too close together (Udayagiri and Welter, 2000). *Lygus* and *Nabis* species lay their eggs within the top 30 cm of alfalfa stems, in part to avoid parasitism which was most intense on the middle nodes of the plant (Graham and Jackson, 1982). In contrast to avoidance, some predatory taxa protect their eggs from parasitoids. Females of *Rhinocoris tristis* (Reduviidae) lay eggs exposed on stems or hidden under leaves; the eggs on stems are guarded from parasitoids by the males (Gilbert and Manica, 2009). These male guards are very attractive to females, which add more eggs to the stem-guarded broods than the males can effectively guard. Indeed, the males even eat the eggs in order to stay alive! In spite of his best efforts, eggs laid under male care end up suffering greater parasitism rates than those laid unguarded and concealed beneath leaves. Egg parasitoids also inflict heavy tolls on aquatic and semi-aquatic species (Spence, 1986; Amano et al., 2008; Hirayama and Kasuya, 2009) and phytophagous species (Jones and Westcot, 2002; Reguera and Gomendio, 2002; Rouault et al., 2007; Carrasco and Kaitala, 2009; Dzerefos et al., 2009) of Heteroptera.

4. Oviposition behavior of reproductive females

4.1. Oviposition site selection

Most predatory bugs lay their eggs on plants, although there are many exceptions. Southwood (1956) grouped Heteroptera into four loose categories (based originally on categories developed by Michalk, 1935). These were (1) exposed on plant tissue; (2) semi-exposed on leaves, the soil, or in detritus; (3) embedded in tissue that is dead or dying; and (4) embedded in living and healthy plant tissue. Here, I only discuss two general strategies for oviposition: those species that embed their eggs into tissue (many Cimicomorpha) and those that lay their eggs on the surface of plants and other structures (Asopinae, Geocoridae, Reduviidae, and Phymatidae). Although exceptions exist, eggs of the latter group are gregarious, laid in clutches of numerous eggs, while the former group often inserts solitary eggs into the plant tissue.

This single division of behaviors seems the most appropriate approach to this topic, given the striking differences seen in the physiology and behavior entailed with these two lifestyles. The distribution of these characteristics among predatory families is presented in Table 1.

There are several layers within each landscape that must be filtered through before a predatory bug finds a suitable oviposition site. The first hurdle is that predatory bugs must locate a preferred habitat. Habitat requirements can be very broad (e.g., canopy, forb, or detrital layers) or very restricted (e.g., individual plant species), depending on the species in question. Once a preferred habitat is located, predatory bugs navigate through the vegetation layer in order to locate a preferred plant or substrate. Once this spatial level has been searched, the optimal microsite for oviposition is located on the plant. The ability of predatory Heteroptera to locate specific preferred microsites for oviposition within the complex landscape is particularly impressive when one considers how dramatically an environment changes over the season.

4.1.1. Habitat specialization by predatory bugs

Within a particular landscape, it is clear that predatory Heteroptera prefer to reside within certain habitats (Fauvel, 1999), and this has great bearing on their oviposition patterns. As an example, anthocorids are easily partitioned into species that reside in trees and upper levels of the canopy (e.g., many *Anthocoris* spp.), the forb layer (*Orius* spp.), and the soil (e.g., *Lyctocoris* and *Xylocoris* spp.) (Sands, 1957; Lattin, 1999; Saulich and Musolin, 2009). Within these habitats, some anthocorids move throughout the plant community, while others specialize on specific plants. *Anthocoris sarothamni* resides almost exclusively on broom, *Sarothamnus scoparius* (Koch) and elms, *A. gallarum-ulmi* DeGeer lives in close association with gall-forming aphids on elms, and *A. minki* Dohrn was found only on ash trees (Hill, 1961; Anderson, 1962b). In contrast, at least a few *A. nemorum*, *A. confusus*, and *A. nemoralis* were found on nearly every plant sampled (Sands, 1957; Anderson, 1962b). Other anthocorids are specialists on pine trees, especially *Pinus sylvestris* L. (Pinaceae) (Sands, 1957). In the litter layer, *L. beneficus* preferred drier areas with dead plant material, and *X. hiurai* (= *X. galactinus*) preferred “hot beds” with moist, decomposing material (Chu, 1969). Evans (1982b) found that some species of asopine pentatomids could be found throughout a habitat and some were fairly restricted to specific plant species where a preferred prey could be reliably found. Their degree of habitat specialization influences many of the subsequent steps observed in this behavioral hierarchy.

4.1.2. Plant preferences

Foliar dwelling predatory heteropterans almost always have a narrow range of plants that they prefer to lay eggs on (Coll, 1996; Jackson, 2003; Sanchez et al., 2004; Lundgren and Fergen, 2006). It is clear from the literature that these preferences are species specific (Sisgaard, 2004). For example, *A. nemorum* (Anthocoridae) prefer to lay on apple trees, whereas *A. nemoralis* prefer to lay on pear trees (Sisgaard, 2004). Among plants, soybeans are a very suitable and preferred oviposition site for *Geocoris punctipes* (Say) (Geocoridae) (Naranjo and Stimac, 1985, 1987), but *Orius insidiosus* (Say) (Anthocoridae) performs poorly on soybeans and prefers to lay on several other plants (Lundgren and Fergen, 2006; Lundgren et al., 2009a,b). *Nabis roseipennis* (Reuter) (Nabidae) prefers to oviposit more on soybean than on corn and tomato, but squash was preferred over soybean in the laboratory (Pfannenstiel and Yeargan, 1998). Corn leaves are commonly rejected as an oviposition site by several species that insert their eggs into plant tissue (Pfannenstiel and Yeargan, 1998; Sanchez et al., 2004), although *O. insidiosus* lays its eggs into the silks of corn plants (Barber, 1936). Depending on the variability of plant characteristics in

specific assays, predatory bugs even display preferences for different biotypes of the same plant species (Tingey and Leigh, 1974; Hendricks and Collier, 2003).

4.1.3. Preferred oviposition sites on a specific plant species

In addition to displaying clear preferences for some plant species over others, females also discriminate among potential oviposition sites within a single plant species. A first distinction that is made is how high to lay their eggs on a given plant, a process that is influenced by both the plant and heteropteran species in question. *Nabis roseipennis* prefers to lay its eggs on the bottom 40% of plants when offered corn, tobacco, and tomato (Pfannenstiel and Yeargan, 1998). But they laid throughout the plant on squash (Pfannenstiel and Yeargan, 1998), and the congener *N. alternatus* Parshley only lays on the upper parts of the plant on alfalfa (Richards and Harper, 1978; Graham and Jackson, 1982). In one study on soybeans, *O. insidiosus* laid its eggs on the upper parts of the plants (Isenhour and Yeargan, 1982), yet another study showed that *O. insidiosus* did not discriminate among nodes of green beans (Lundgren and Fergen, 2006). These plant preferences are dynamic over the season (e.g., *A. nemorum* preference for pear trees over apple trees increased as the growing season progressed) (Evans, 1976; Sisgaard, 2004).

Once the preferred region of the plant is found, females select very specific sites on the fruit, flowers, leaves and stems to oviposit. An excellent example of this is in *Lygus* spp., which lay 99% of their eggs on the pedicels of carrot plants under choice conditions (Carlson, 1956). Many species prefer to lay their eggs on the undersides of leaves (Naranjo, 1987; Samsøe-Petersen et al., 1989; Torres and Ruberson, 2006). Exceptions are *P. maculiventris* and *P. bioculatus* (Pentatomidae), which lay more clutches on the upper surface of the plant (Esselbaugh, 1946; Javahery, 1994). Species that insert their eggs into tissues tend to display preferences for the petioles (Sands, 1957; Isenhour and Yeargan, 1982; Benedict et al., 1983; Jackson, 2003; Lundgren and Fergen, 2006) and main leaf veins (Sands, 1957; Anderson, 1962a; Askari and Stern, 1972; Constant et al., 1996; Lundgren and Fergen, 2006; Vandekerckhove et al., 2006). A species' preference for different plant structures varies among the host plants offered (Liquido and Nishida, 1985; Lundgren and Fergen, 2006), and different predators sometimes prefer to lay on different structures on a given plant species (Sanford, 1964; Graham and Jackson, 1982; Isenhour and Yeargan, 1982; Sisgaard, 2004). Fruit and flowers are another preferred oviposition site for some species (Sands, 1957; Udayagiri and Welter, 2000; Rhainds and English-Loeb, 2003; Kim and Riedl, 2005); indeed green bean fruits are a frequently used oviposition site for numerous predatory taxa under mass-production conditions (Schmidt et al., 1995; Richards and Schmidt, 1996; Murai et al., 2001; Shapiro and Ferkovich, 2006; Fathi, 2009). Other taxa will lay their eggs inserted into pine needles (Anderson, 1962a), into stems (Hill, 1961; Sanford, 1964; Evans, 1976), among the scales of dead buds (Sanford, 1964; Conti et al., 2000).

4.1.4. Non-plant oviposition sites of predatory taxa

A number of predatory bugs do not lay eggs on plants. Some subfamilies of reduviids prefer to lay their eggs in the soil, or beneath stones and other structures more commonly found in their habitats (Ambrose, 1999). Chu (1969) describes how *L. beneficus* and *X. hiurai* (= *X. galactinus*) rely heavily on moist barn straw in the wild, but will lay on paddy straw, cherry twigs, filter paper, vermiculite, and cracked corn in the laboratory. Other anthocorids will lay their eggs in bark or on decaying wood (Sands, 1957; Anderson, 1962a; Sanford, 1964). *Loricula elegantula* (Barensprung) (Microphysidae) lays their eggs among lichens (Southwood, 1956). *Geocoris punctipes* prefers to lay their eggs on paper towels or the cage rather than plants in the laboratory (Naranjo, 1987; Naranjo

and Stimac, 1987). Even species that normally lay their eggs on plants will accept certain abiotic materials under laboratory conditions (Parker, 1981; Castane and Zalom, 1994; Shapiro and Ferkovich, 2006; Silva and Panizzi, 2007, 2008, 2009).

4.2. Mechanisms involved in oviposition site selection

4.2.1. Morphological cues in distinguishing preferred oviposition sites on plants

Epidermal thickness and trichome densities are often correlated with a female's preference for a given oviposition site. Lundgren et al. (2008) established that *Orius insidiosus* (Anthocoridae) first discerns among plant species based on their relative epidermal thicknesses (they prefer a thinner epidermis). Once the females have identified a suitable host, epidermal thickness and trichome density (they prefer sparser trichomes) influence where on the plant the eggs are eventually laid. Indeed, *O. insidiosus* cannot oviposit through paraffin that exceeds 0.045 mm thick (Castane and Zalom, 1994). *Nabis alternatus* (Nabidae) laid eggs into the thinnest and weakest stem tissue (measured with a sheer press) on alfalfa, and their preferences for oviposition changes as the plant gets larger and the stem toughens (Richards and Harper, 1978). Likewise, *M. caliginosus* (Miridae) for oviposition sites on *Pelargonium peltatum* (L.) L'Hér ex Aiton (Geraniaceae) were related to the force necessary to penetrate the epidermis of the tissue; they could not penetrate tissues that required more than 0.35 N (Constant et al., 1996). On the leaf mid-rib, which was easily penetrated by the bug across its length, the eggs were restricted to sites that were wide enough to encapsulate the egg (Constant et al., 1996). Often, areas of the plant with higher trichome densities are avoided by ovipositing females (Esselbaugh, 1946), although the opposite pattern was observed in *L. hesperus* (Miridae) in cotton (Benedict et al., 1983).

4.2.2. Chemical cues in distinguishing preferred oviposition sites on plants

Plant chemistry may also be involved in deciding where to lay an egg on a plant. Lundgren et al. (2009b) found that reproductive *Orius insidiosus* (Anthocoridae) did not use infochemicals in locating oviposition plants over long distances. In contrast, Dwumfour (1992) found that *A. nemorum* (Anthocoridae) was attracted to volatiles from a number of plant species, and this could very well be associated with finding preferred plants for oviposition. It is likely that infochemicals are involved as proximate cues in identifying the suitability of oviposition sites on a plant (Panizzi et al., 2004), although this has been poorly studied for predaceous species. Recent work has shown that oviposition by two species of primarily herbivorous Heteroptera change the chemical profile of a host plant (Frati et al., 2009). What is particularly striking is that one of these bugs that elicits a chemical response, *Murgantia histrionica* (Hahn) (Pentatomidae), lays its egg on the surface of the plant, and oviposition does not damage the plant (Conti et al., 2008). The implications of plants emitting chemistry that may solicit natural enemies of eggs of predatory Heteroptera is worthy of future research.

4.2.3. Prey-based cues for oviposition

Some species lay their eggs near prey resources, although observations of this tendency tend to be fairly anecdotal. Several anthocorids oviposited near several prey populations, and oviposition by each generation of the predator tracked the available prey species as they changed over the season (Anderson, 1962b; Saulich and Musolin, 2009). *Anthocoris gallarum-ulmi* (Anthocoridae) tracked the populations of their gall-forming aphid prey as they left their galls on elms and established onto the roots of red currant and gooseberry (Saulich and Musolin, 2009). Isenhour and Yeagan

(1982) described the dispersion of eggs of *Orius insidiosus*, *Nabis roseipennis*, and *N. americanoferus* on soybean plants, and attribute their distribution to where primary prey species (thrips and lepidopteran eggs for the anthocorid and nabids, respectively) reside on the plants. Other work has shown that reproductive females use chemical cues from prey species as attractants (Dwumfour, 1992) and to elicit oviposition (Ferkovich and Shapiro, 2007). Thus, it seems likely that prey availability has a role to play in eliciting oviposition, but the current data is unclear whether this is a sufficient cue on its own.

4.2.4. Offspring performance on plants preferred for oviposition

Females usually prefer to lay their eggs on plants that maximize the performance of their offspring. Coll (1996) found that survival of 1st instars of *Orius insidiosus* (Anthocoridae) differed substantially among four different plants, and he hypothesized that females preferred to lay eggs upon plants of high quality for their omnivorous young. Lundgren et al. (2008) pursued this question further and were able to statistically illustrate the relationship between a female's oviposition preference among certain plants and the survival of her offspring on those plants. Similarly, females of *Dicyphus hesperus* Knight (Miridae) preferred to lay their eggs on *Verbascum thapsus* L. (Scrophulariaceae) under choice conditions, and this plant was the most suitable for her offspring (Sanchez et al., 2004). Indeed, it was the only plant species that some of the nymphs could complete development upon in the absence of prey. It is also commonly observed that nymphs prefer to reside on regions of the plant where their mothers preferred to lay eggs (Sands, 1957; Rhainds and English-Loeb, 2003). In addition to survival, nymphal host plant resulting from their mother's oviposition choice may also affect other aspects of their fitness (Miller, 2008; Miller and Emlen, 2010). The suitability of a host plant for her progeny is dynamic over a growing season (Shintani, 2009), and predatory bugs shift their preferences accordingly. On water-stressed plants, *Orius insidiosus* (Anthocoridae) changes its oviposition behavior to lay on structures that are less prone to desiccation and with higher available nitrogen content (Seagraves et al., 2011). Given the strong implications of oviposition preference for the reproductive success of female predatory bugs, one would expect that maternal experience with areas of high quality for her nymphs to influence her oviposition choice. When this has been studied in Heteroptera, prior experience with high-quality prey patches did indeed influence a female's residency time and oviposition rate (Nakashima and Hirose, 2003), but this was not found to influence female oviposition behavior in an herbivorous species (Groot et al., 2003). While the data strongly supports that females oviposit at sites of high nutritional quality for their offspring, it is not clear whether they are choosing these sites because they are easier to oviposit into, or are somehow assessing the nutritional quality of these plants for their progeny.

Another hypothesis supported by the literature is that the relative quality of oviposition sites is influenced to some degree by competitive interactions and intraguild predation among predatory heteropterans. The first system that lends support to this hypothesis involves the oviposition preferences of anthocorids and nabids on soybeans when presented plants with and without their competitors. When reared on soybeans without other insects present, *N. roseipennis* (Nabidae) lays eggs throughout the top 80% of soybean plants (Pfannenstiel and Yeagan, 1998), and *Orius insidiosus* (Anthocoridae) displays no preferences for particular nodes throughout a plant (Lundgren and Fergen, 2006). In contrast, under field conditions when both of these species are present together, *Orius insidiosus* prefers to oviposit on the top portions of the plant and *N. roseipennis* restricts its oviposition to the mid-section of the plants (Isenhour and Yeagan, 1982). On apple and pear leaves, *A. nemorum* (Anthocoridae) lays their eggs near leaf

margins on the upper side of damaged leaves, whereas the congener *A. nemoralis* prefers the leaf vein on the undersides of healthy leaves (Sisgaard, 2004). Similarly, *Nabis* spp. lay their eggs on the larger, non-basal and main stems of alfalfa plants, whereas *Lygus* spp. preferred the primary stems, larger branches, and floral parts of the plant (Graham and Jackson, 1982). Finally, Benedict et al. (1983) found that *L. hesperus* (Miridae) prefers to lay their eggs on pilose cotton varieties with numerous trichomes over more glabrous cotton varieties. Although these pilose plants inhibited nymphal development, there were significantly more nymphs found on these lines under field conditions. Although Benedict et al. (1983) did not study this directly, other work has shown that some species oviposit on plants with more trichomes to avoid intraguild predation (Griffen and Yeargan, 2002; Seagraves and Yeargan, 2006). Related to the importance of intraguild interactions, overcrowding in mass rearing operations often affects the reproductive performance of a female (Chu, 1969; Ambrose, 1999; Bueno et al., 2006; Luo et al., 2010). The hypothesis that oviposition preferences are influenced by competitive intraguild interactions merits more directed experimentation in the future.

4.2.5. The relative contributions of plants and prey to oviposition by predatory Heteroptera

The availability and quality of nutritional resources for her progeny weigh heavily on a mother's decision on where and when to oviposit. Given the fact that nearly all predatory Heteroptera are best described as omnivores (Lundgren, 2009), the relative importance of plant- and prey-based resources is a central question that requires attention. Although the data on this topic is sparse, it appears that two general strategies seem likely for habitat generalists and specialists.

For habitat generalists, plant-based cues seem to over-ride prey-based cues as oviposition elicitors, although this is strongly influenced by the quality and availability of these two resources. Seagraves and Lundgren (2010) showed that *Orius insidiosus* (Anthcoridae) preferred to lay eggs on green bean over soybean, and they preferred to lay eggs on green beans with prey than on green beans without prey. What was most telling is that females still preferred green beans, even when the soybean plants were subsidized with prey. *A. nemorum* (Anthcoridae) prefers to lay their eggs on barley plants when both barley and pear leaves are subsidized with prey; when only the pear leaves are subsidized with prey, there was no preference (Herard and Chen, 1985). Sanchez et al. (2004) found that *Dicyphus hesperus* (Miridae) also preferred to lay eggs on host plants of highest quality, although their plant choice among high-quality plants was more influenced by prey availability than was seen in *O. insidiosus*. Finally, plant preferences of reproductive *Geocoris punctipes* (Geocoridae) were not influenced by prey availability (Naranjo and Stimac, 1987), but within a plant, this species' eggs were strongly correlated with prey dispersion (Torres and Ruberson, 2006). All of this work suggests that prey availability is important, but plant quality is often the first factor considered by ovipositing females. Neonate nymphs of many omnivorous arthropods tend to be relatively phytophagous compared to older stages (McPherson, 1982), and plant quality may be a more predictable resource for mothers to assess for their progeny.

Although they are undoubtedly omnivorous to some degree, oviposition by habitat specialists tends to be more closely tied to prey populations than habitat generalists (but there is currently very little research on this topic). Evans (1982b) performed an excellent study on the reproductive ecology of two pentatomids, one generalist feeder (*P. maculiventris*) and one species that specializes on soft-bodied beetle larvae (*Perillus circumcinctus* Stål) in response to the availability *Trirhabda* (Chrysomelidae) larvae on goldenrod. Reproduction by the specialist was closely tied to the prey populations, whereas there was a lag in the response of *P.*

maculiventris populations. Thus, it is entirely conceivable that habitat specialists like *Perillus circumcinctus*, *A. gallarum-ulmi* and *A. sarothamni* lay their eggs on their host plants with predictable prey resources, the data remain unconvincing that prey resources are an over-riding motivation for more habitat generalists.

4.3. Behavior associated with oviposition in predatory Heteroptera

4.3.1. Sensory selection of a suitable oviposition site

The two organs most involved in selecting a suitable oviposition site are the mouthparts and the ovipositor. In egg-inserting bugs, sensillae on the mouthparts are important in selecting a suitable oviposition site. In *L. lineolaris* (Miridae), the sensillae on the tip of the labium distinguish between preferred and non-preferred cotton varieties for oviposition (Avé et al., 1978; Hatfield and Frazier, 1980). Romani et al. (2005) found that the Type 1 sensillae trichodea (which are chemosensory and mechanosensory) on the stylet tip were likely involved in oviposition site selection in *Lygus rugulipennis* (Miridae). Blocking gustatory sensillae with zinc sulfate did not affect oviposition behavior, whereas ablating the stylet tip affected their oviposition behavior. In anthcorids and mirids, the female will probe the plant tissue with her mouthparts prior to inserting her ovipositor, and a short feeding bout may also ensue (Ferran et al., 1996; Romani et al., 2005; Lundgren et al., 2008). The antennae are also very active during this probing procedure (Hill, 1957; Chu, 1969). In contrast to egg-inserting species, surface-layers appear to select their oviposition sites using their ovipositors (Eyles, 1963; He and Wang, 2000). This was cruelly confirmed by Conti et al. (2008) in *Murgantia histrionica* (Pentatomidae), when females displayed no changes to their oviposition patterns after having their mouthparts removed.

4.3.2. Oviposition process

It should come as no surprise that egg-inserters and surface-layers differ substantially in their oviposition behavior, largely due to the underlying differences in the mechanics inherent in the two processes underlying oviposition. Davey (1997) describes the hormonal process that initiates the act of oviposition for two species. In *Iphita limbata* Stål (Pyrrhocoridae), injections of mature eggs, hemolymph and neurosecretory cells from the pars intercerebralis from ovipositing females into conspecifics can induce them to lay eggs. The eggs secrete a hormone that stimulates the pars intercerebralis to produce neurosecretory hormone that induces the oviducts to contract and the egg to move into the common oviduct and out through the ovipositor. A similar process is likely experienced by *Rhodnius prolixus* (a hematophagous reduviid). Obviously, the physiological mechanisms that influence this behavior remain to be fully understood for predatory Heteroptera.

The process of oviposition has been fairly well sequenced for a number of species that insert their eggs into plant material or the soil. In some cases, the ovipositor is inserted directly into the hole made by the mouthparts when the female is probing for an oviposition site (Ferran et al., 1996; Romani et al., 2005), but this may not be a ubiquitous trait. Most species bend their abdomen and position their legs in a characteristic pattern during this process in order to more easily insert their ovipositor into the substrate (Liquido and Nishida, 1985; Ferran et al., 1996; He and Wang, 2000). Essentially, the legs serve as an anchor, and grip the substrate tightly in order to gain more leverage (Liquido and Nishida, 1985; He and Wang, 2000). In *Nabis alternatus* (Nabidae), the abdomen is raised to facilitate the insertion of the ovipositor (Richards and Harper, 1978). Liquido and Nishida (1985) describe that *Cyrtorhinus lividipennis* (Miridae) required slight up-and-down lacerating movements of their ovipositor in order to insert it into the leaf tissue. After the ovipositor is inserted, approximately 33% of *M. caliginosus* (Miridae) females abandon the oviposition process, suggesting that the

ovipositor may have some sensory capabilities that can assess the quality of the oviposition site (Ferran et al., 1996). In the herbivore *N. huttoni* (Lygaeidae), the ovipositor is wiggled from side to side in order for the egg to enter the shaft (Eyles, 1963). The egg is visible externally as a bulge in the ovipositor as it is slowly inserted, cephalic side up, into the plant tissue (Lundgren et al., 2008). The process of inserting the egg can be accompanied by pulsing motions of the abdomen, or a raising of the head (Eyles, 1963; He and Wang, 2000; Lundgren et al., 2008). A shaking motion of the abdomen has been observed after the ovipositor is removed from the substrate (Chu, 1969), and a female may retain her bent abdomen if she intends to lay eggs in close succession (Liquidó and Nishida, 1985). The eggs are usually inserted such that only the operculum is visible externally on the plant (Fig. 2) (Conti et al., 2000), and the eggs may be perpendicular or parallel with the stem or leaf vein selected for oviposition (Anderson, 1962a; Sanford, 1964; Richards and Harper, 1978; Conti et al., 2000). Although egg-inserters typically lay solitary eggs, some species of egg-inserters lay eggs gregariously (Sanford, 1964; Pfannenstiel and Yeagan, 1998; Conti et al., 2000). The act of inserting the egg may or may not damage the surrounding plant tissues. For example, *Anthocoris antevolens* White (Anthocoridae) damages leaf cells during the oviposition process (Anderson, 1962a) and *Elatophilus nigricornis* (Zetterstedt) (Anthocoridae) makes a slit in the stem tissue where it inserts its eggs (Sands, 1957), whereas *Acompocoris pygmaeus* (Fallén) (Anthocoridae) uses the ovipositor to separate the epidermal cells without causing cellular disruption (Sands, 1957). It is often the case that eggs leave an externally visible lump surrounding the oviposition site (Sanford, 1964; Conti et al., 2000). The entire process of ovipositing a single egg lasts for less than 2 min (Hill, 1957; Chu, 1969; Richards and Harper, 1978).

Surface layers usually oviposit clutches of eggs, often in distinct patterns. Pentatomids and some other pentatomorphans lay their eggs in 1–3 distinct but adjacent rows (Javahery, 1994; Silva and Panizzi, 2007; Dzerefos et al., 2009). The tight and precise arrangement of egg clutches in pentatomids is created when the female lays two eggs touching one another, and then repeatedly deposits the subsequent eggs in the recess between two existing eggs (Esselbaugh, 1946). Typically, pentatomids lay approximately 25 eggs per clutch, although this varies substantially (Silva and Panizzi, 2007). Not all surface-layers produce such neatly arranged clutches. Reduviids and phymatids lay their clutches in tight but imprecise clutches, and some lay eggs individually (Southwood, 1956). Based on observations of 114 species, Ambrose (1999) categorized five approaches to oviposition in reduviids. These were species that lay (1) single clusters glued to each other and the substrate, (2) clutches glued only to the substrate (either basally or longitudinally), (3) solitary eggs glued to the substrate, (4) eggs glued to fresh frass, and (5) eggs loosely strewn about. The clutches of *Agriosphodrus dohrni* (Signoret) (Reduviidae) are laid beginning at the perimeter of the egg mass, working into the center, which produces oblique rows of eggs (Luo et al., 2010). Other groups even lay their eggs atop one another (Cheng and Pitman, 2002).

4.3.3. Accessory gland secretions

Accessory gland secretions are particularly instrumental in the oviposition process of surface-layers. Each egg is affixed to the substrate and to each other using glues produced by the accessory glands (Esselbaugh, 1946; Southwood, 1956; Javahery, 1994; Luo et al., 2010). In most groups, the cement is kept free from the operculum or pseudoperculum, presumably to allow the hatching nymphs to escape (Esselbaugh, 1946; Southwood, 1956). After *Nezera viridula* L. (Pentatomidae) lays an egg, she touches it with her hind tarsi, presumably to insure that the glue seals the egg to the substrate (Panizzi, 2006). In addition to gluing the eggs to the surface, the accessory gland secretions act as an additional

protective covering against physical stresses and in maintaining water homeostasis (Ambrose, 1999). In some reduviids, the female secretes so much cement onto the egg mass that it resembles an ootheca (Luo et al., 2010). Secretions of the accessory glands are also involved in the embryonic orientations within the eggs of a clutch. In a wonderful series of experiments, Lockwood and Story (1986) showed that an ethanol extractable chemical in the glue used by at least 10 species of pentatomids (and possibly belastomatids) to affix the eggs to one another made the embryos orient toward the center of the clutch. Embryonic orientation appears to be important in aggregating the newly hatched nymphs upon the clutch during the first stadium. It is notable that the eggs of the only predatory pentatomid observed in Lockwood and Story's study, *P. maculiventris*, did not display this embryonic orientation. Finally, the accessory gland secretions may contain vertically transmitted symbiotic microbes, as is observed in pentatomids (Southwood, 1956; Prado et al., 2006; Prado and Almeida, 2009).

4.3.4. Parental guarding behavior

Various groups of Heteroptera are known to guard their brood after the females have oviposited, and predatory taxa are no exception. Eggs of most species are abandoned by their mothers, but occasionally the male will stand guard over the developing eggs (McPherson, 1982). Reduviids and some of the aquatic and semi-aquatic groups are particularly noticeable in this regard (Smith, 1976; Jahnke et al., 2006; Luo et al., 2010). In reduviids, both males and females are recorded as tending broods, but it differs among species. In *Rhinocoris tristis* (Reduviidae), the males guard the broods against parasitoids, and females will actually add eggs to the broods that males are guarding (Gilbert and Manica, 2009). Belastomatids are well known for their paternal care of the eggs, which are laid directly onto the back of the father. The males aerates the eggs, chooses favorable microclimates for their development, and keeps oxygenated water flowing over them through a process called "brood pumping" (Smith, 1976; Munguía-Steyer et al., 2008). Thus, the presumption is that eggs that are guarded by a parent experience higher survival, such that the benefits of guarding may overcome the risks for the parent of sitting atop an exposed clutch of eggs (Smith, 1976; García-González et al., 2005; Munguía-Steyer et al., 2008; Dzerefos et al., 2009; Heard et al., 2009; Ogorzalek and Trochimczuk, 2009).

Another behavior that is worth additional attention is the guarding of preferred oviposition sites by females. Given the discerning behavior entailed in site selection by ovipositing females, it is likely that high quality oviposition sites for a species are limited within a local habitat; particularly for species that insert their eggs into plant tissues. Thus, it may benefit a parent to guard these sites from competitors. Groenteman et al. (2006) described just such a behavior in *O. albidipennis* (Anthocoridae). *Orius* spp. are known to reside on very specific parts of the plant (Shields and Watson, 1980; Groenteman et al., 2006). On cotton leaves, *O. albidipennis* females rest directly where the leaf meets the plant, and mated females are often successful in maintaining their station against invading conspecifics, particularly when the nitrogen content of the leaves are enriched. This preferred location is also where *O. albidipennis* eggs are most successful; they experience a hatch rate that is at least twice as high as eggs laid anywhere else on the plant. Whether or not females of other predatory species defend preferred oviposition sites certainly merits further investigation.

5. Conclusions

The reproductive ecology of predatory Heteroptera is a dynamic and inter-related series of processes and events that inter-relate to

drive the population growth rates of these economically important insects. Although the diversity of physiology and life history strategies displayed by this guild of insects is profound, examining the extensive literature on this topic reveals some general and underlying themes to the reproductive ecology in predatory Heteroptera. Three of these themes presented in this paper are summarized below.

- (1) Physiology, especially of the female and the egg, drives the reproductive ecology of a species. Everything from the potential fecundity of a female, to the site she selects for oviposition is driven by her physiology. Likewise, the egg's physiology dictates where an egg will survive and where it will die, and is intimately coupled to the environment in which an insect chooses to live.
- (2) At least three dynamic parameters come to bear on the reproductive success and rate of population increase of a species: rate of maturation, realized fecundity, and reproductive diapause. These parameters fluctuate widely in when and where they will occur within and among species, driven largely by the physiological status of the female (e.g., mating status, female age and size, and her nutritional status) and the environmental conditions (e.g., temperature, photoperiod, and water availability) in which she and her eggs live. Also, natural enemies (pathogens, predators, and parasitoids) bear strongly on the reproductive ecology of a species by influencing the rate of population increase and the behaviors involved in reproduction.
- (3) Once a female is reproductively fit, a hierarchy of events must occur before an egg is deposited on or in a preferred oviposition site. First, a female must find a suitable habitat for oviposition, this process being particularly important for habitat specialists. Once a habitat is found, the female must locate a suitable plant or substrate for oviposition. This process may involve chemical or morphological cues present on the various oviposition surfaces, and it appears that proximate cues are most useful for distinguishing suitable from unsuitable substrates. Finally, a suitable microsite is located, again using proximate cues. Cimicomorphan females assess microsites primarily using their mouthparts, and pentatomorphans relay more on their ovipositor.

Understanding the reproductive ecology of predatory bugs, and how a particular species fits on the continuum of behaviors presented in this review, undoubtedly improves our ability to use predatory bugs in biological control programs. Mass production of heteropterans for augmentative biological control programs is strongly tied to providing females with suitable oviposition substrates. Ensuring that suitable conditions for reproduction are present in the field is key to conserving endemic and released predators within a cropping environment (e.g., availability of food, mates, and overwintering sites, and providing preferred oviposition substrates). Finally, pest management programs involving host plant resistance and insecticide applications can be employed more efficiently integrated with biological control when the reproductive ecology of generalist predators is better understood (e.g., providing spatial and temporal refugia from pest suppression to generalist predators; using chemistries with fewer direct effects on natural enemies). It is my hope that understanding the natural history of generalist predators, such as is presented here, will form the basis for more reliable and biologically intensive pest management solutions.

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