CHAPTER SEVENTEEN

Utetheisa ornatrix (Erebidae, Arctiinae)

A Case Study of Sexual Selection

VIKRAM K. IYENGAR and WILLIAM E. CONNER

Pyrrolizidine Alkaloids: Chemical Defense and Links to Large Size

Utetheisa ornatrix, also known as the rattlebox moth, is a brightly colored erebid moth that relies on chemistry for both defense and communication, and the complex reproductive strategies of both sexes have made it a model system for studying sexual selection. *U. ornatrix* (henceforth referred to as *Utetheisa*) ranges in the Americas from the Rocky Mountains to the Atlantic coast, and from North Carolina to the northern parts of South America (Pease 1968), and can be reliably found in the dry, scrub habitat near the Archbold Biological Station in central Florida. As a larva, *Utetheisa* feeds on plants of the genus *Crotalaria* (family Fabaceae), which contain poisonous pyrrolizidine alkaloids (PAs) that play a fundamental role in the life of both sexes (Eisner and Meinwald 2003). Larvae store PAs systemically, retaining them through metamorphosis into the adult stage. At mating, the male transfers up to 11% of his body mass in a spermatophore containing sperm, nutrients, and PAs (LaMunyon and Eisner 1994). The female transmits PAs to the eggs, using not only some of the PAs she herself sequestered, but also PAs that she receives from the male via the spermatophore at mating (Dussourd et al. 1988). As a result of having PAs in their bodies, all life stages of *Utetheisa* are protected against natural enemies, the adults and larvae against spiders (Eisner and Eisner 1991) and the eggs against ants (Hare and Eisner 1993), chrysopid larvae (Eisner et al. 2000), coccinellid beetles (Dussourd et al. 1988), and parasitoid wasps (Bezzerides 2004).

PAs are potent phagostimulants, and the presence of these compounds in their diet causes larvae to invest more time feeding, thereby growing more quickly than those on diet without PAs (del Campo et al. 2005). These data are also supported by the fact that PAs and adult body size are strongly correlated in *Utetheisa* (Conner et al. 1990). In other words, feeding on PAs during the larval period is, to some degree, responsible for the attainment of large size, which has important reproductive consequences for both sexes.

Courtship and the Role of Pheromones

The female sex attractant of *Utetheisa* is a blend of long-chained polyenes (Conner et al. 1980; Huang et al. 1983; Jain et al. 1983; Choi et al. 2007; Lim et al. 2007). The female pheromone is released through the rhythmic exposure of tubular glands and triggers the upwind flight of males at a distance (Conner et al. 1980). One of the most intriguing aspects of the female's reproductive behavior is that they respond to the pheromone of nearby female conspecifics and release more rigorously, forming "female pheromone choruses" (Lim and Greenfield 2007; Lim et al. 2007). Although there are many interesting and unexplored areas of research regarding the female pheromone, this case study will focus on *Utetheisa* as a model system for understanding the evolution of male pheromones through female mate choice.

Once in close proximity of a female, the male releases a male courtship pheromone, hydroxydanaidal (HD), that he derives chemically from the acquired PAs (figure 17.1). The chemical is more volatile than PAs, and is aired by the male from two brush-like structures (coremata) that he everts near the antennae of the female (Conner et al. 1981). Females are capable of distinguishing between males differing by less than 2 micrograms of HD, and use this pheromone as the sole criterion of choice (Iyengar et al. 2001). Mate choice mediated

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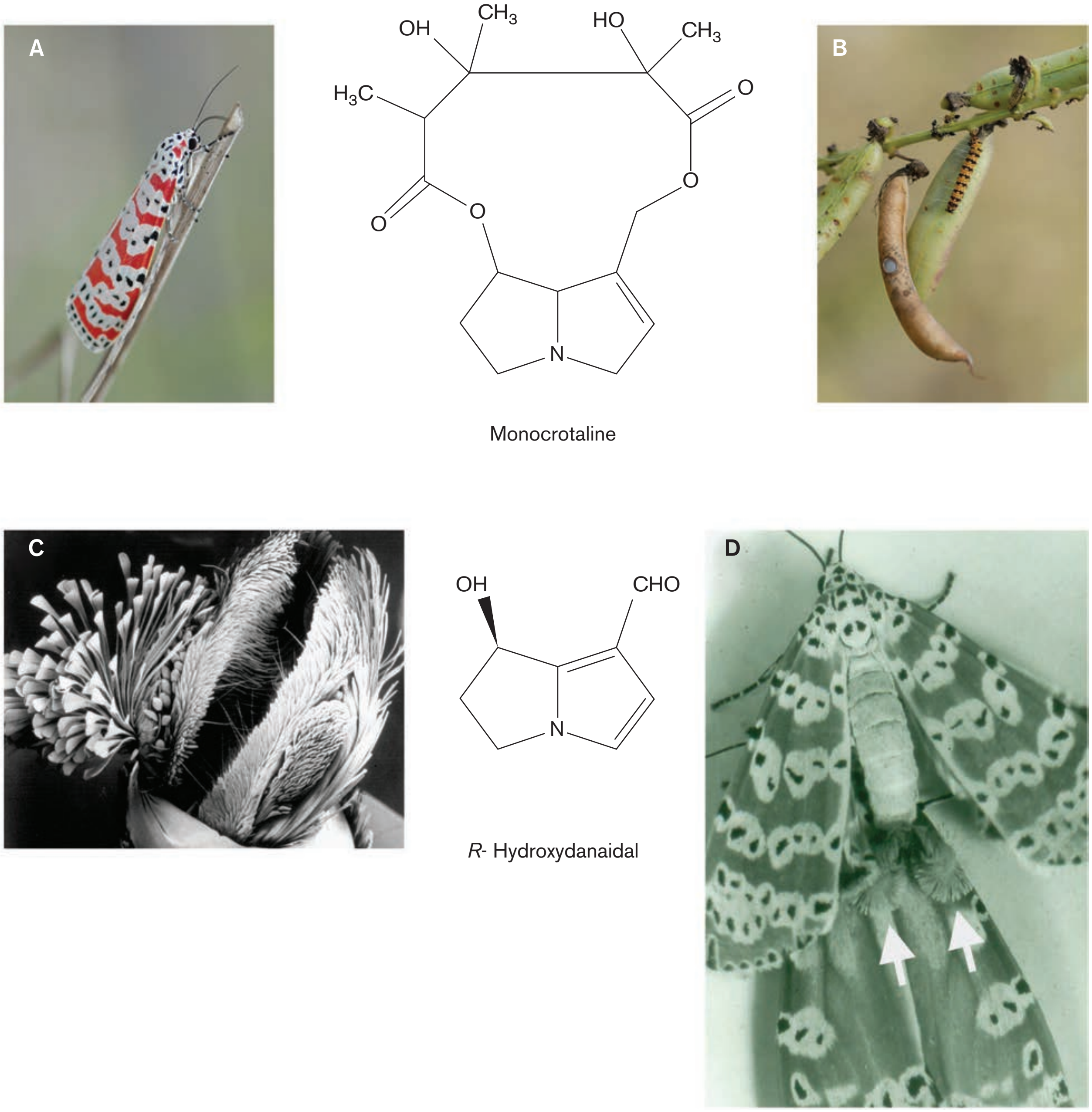

FIGURE 17.1 *Utetheisa ornatrix*: (A) Adult photographed at the Archbold Biological Station; (B) larva resting on the seed pod of *Crotalaria mucronata*, a pyrrolizidine alkaloid-containing hostplant; (C) scanning electron micrograph of the partially exposed genital coremata of a male; (D) corematal eversion captured in courtship (arrows highlight coremata). Chemical structures: (top) monocrotaline, an example of a pyrrolizidine alkaloid; (bottom) *R*-hydroxydanaidal, the male courtship pheromone.

by HD has been observed in laboratory tests, in which males with different amounts of the pheromone were offered simultaneously to females for comparative assessment (Iyengar and Eisner 1999b), and in field experiments, in which males approached females sequentially and were therefore subjected to independent assessment (Conner et al. 1981). Although PA-free (and therefore HD-free) males were not entirely rejected in these experiments, they were significantly less successful than PA-containing males. Females failed to differentiate between males of different size or PA content if these males lacked HD, but they expressed a preference for males bearing HD, even when these were size matched and PA free (Iyengar et al. 2001). Thus, HD appears to be the only criterion on which the female bases her decision to mate.

Benefits to Female Precopulatory Mate Choice

The fitness advantages that females derive from mating with multiple males are broadly classified as direct or indirect benefits. Direct (phenotypic) benefits are the result of nongenetic quantities that have a positive impact on the survivorship and offspring production of the female such as enhanced paternal care (Davies 1992), the transmission of antipredator defensive chemicals (González et al. 1999), and the acquisition of nutrient-rich nuptial gifts (Thornhill and Alcock 1983; Gwynne 1984). Indirect (genetic) benefits are those that are experienced in the next generation in the form of increased offspring survivorship ("good genes") and mating success of sons ("sexy sons," Andersson 1994). In *Utetheisa*, females gain multiple benefits through mate choice based on the male's courtship pheromone. Laboratory studies demonstrated that females mate preferentially with males that contain higher amounts of HD and, by doing so, they also mate with males possessing larger quantities of four correlated attributes: body mass, spermatophore mass, PAs transferred in the spermatophore, and systemic content of PAs (derived from the larval diet; Conner et al. 1990; Dussourd et al. 1991). Therefore, females would derive both direct phenotypic and indirect genetic benefits by choosing males based on the amount of pheromone. By selecting an HD-rich male, females would ensure receipt of a large alkaloidal gift and consequently eggs that were better protected from predators (direct benefit; Dussourd et al. 1988), a large nutrient gift that could be used to increase fecundity by as much as 15% per mating (direct benefit; LaMunyon 1997), and genes that encode for large body size (indirect benefit; Iyengar and Eisner 1999a). Because body size is heritable, females mating with males with higher levels of HD have larger sons that are more successful in courtship (sexy sons) and larger daughters that lay more eggs (good genes; Iyengar and Eisner 1999b). The cumulative effect of both direct and indirect benefits is substantial: a female given a choice between males differing by 10% in body mass will have an estimated 25% more grandchildren by mating with the larger male (Iyengar and Eisner 1999b). The strong selection for large males in *Utetheisa* may account for why in this species, contrary to the norm for Lepidoptera (Opler and Krizek 1984), males are larger than females (LaMunyon and Eisner 1993). Interestingly, given that females profit from both genetic and nongenetic components of the male's spermatophore, females do not appear to compete for males (but see Lim and Greenfield 2007) and males do not obviously exhibit mate choice even though it would benefit them to do so (Iyengar and Eisner 2004).

The relative importance of direct phenotypic and indirect genetic benefits in the evolution of female mate choice has received considerable attention (e.g., Kirkpatrick and Barton 1997). Despite this, it is not clear whether direct or indirect selection drives female choice in *Utetheisa*. Because earlier work showed that male HD titers are correlated positively with both systemic PA content and the amount of PAs that the male transmits to the female as a gift, it was thought that females might use male HD titer as a parameter for gauging male "reproductive value" (Dussourd et al. 1991). Furthermore, because PA content also correlated with male mass (as well as the mass of the spermatophore transferred), it was hypothesized that, through assessment of male HD titer and therefore the amount released during courtship, a female could evaluate male size (Conner et al. 1990; Iyengar and Eisner 1999a). Because body size is a heritable trait with known fitness consequences (Iyengar and Eisner 1999a, 1999b), it was hypothesized that female *Utetheisa* could use pheromone titer to evaluate the phenotypic and genetic quality of individual males.

This early work described the relationship between male quality and female choice in *Utetheisa*, in virgin moths. A field study at the Archbold Biological Station in Florida revealed that while male body mass, spermatophore mass, PA transferred in the spermatophore, and systemic PA content were all positively correlated, corematal HD content was not correlated with any of these factors (Bezzerides et al. 2005). Based on their apparent age (wing wear) and our knowledge of female mating frequency, it is likely that most of these field males were not virgins. A subsequent study attempted to reconcile the lab data on virgin males and the field data by determining whether the male pheromonal (HD) titer changes over an individual's lifetime. Male HD titer was observed to remain unchanged despite the loss of PAs and body mass with each spermatophore transfer (Kelly et al. 2012). Thus, females are choosing males based on an honest signal (HD) that represents the total amount of PAs acquired by the larva, a representation of the ability to compete for access to PA-rich seeds (likely a genetically based, heritable trait), rather than the amount of PAs transferred at mating (a phenotypic quantity). While females receive direct benefits with every mating (indeed, all males transfer *some* PA and nutrient in each spermatophore), these recent results suggest that indirect genetic benefits (and the larval acquisition of PAs) are an important evolutionary force that plays a role in driving sexual selection in *Utetheisa*.

Female Promiscuity and Postcopulatory Sperm Selection

A fundamental tenet of sexual selection has been that males maximize their reproductive success by mating as often as possible, whereas females maximize their fitness by mating selectively with one or a few mates of high quality (Williams 1966; Trivers 1972; Parker 1979). Given that one mating often provides sufficient sperm to fertilize a female's entire complement of eggs, the costs of multiple mating for a female often outweigh the benefits that she may accrue by being promiscuous (Andersson 1994). For example, in many insect species, accessory substances passed from the male to the female at mating can have numerous negative effects on female fitness (e.g., increased risk of disease transmission and energetic and opportunity costs incurred as a consequence of courtship and copulation; Thornhill and Alcock 1983; Watson et al. 1998). Despite the costs of multiple mating in females, the advent of more accurate and accessible means to assess paternity has revealed that females of many species are more promiscuous than previously thought (Birkhead and Møller 1998; Arnqvist and Nilsson 2000). In many cases where females mate multiply, researchers have found evidence that sperm from the highest quality mate is used preferentially; this postcopulatory selection leaves open the possibility that females can accrue direct benefits from multiple males while having offspring with the highest genetic quality (Birkhead and Møller 1995; Keller and Reeve 1995; Eberhard 1996; Slatyer et al. 2011).

Utetheisa females are highly promiscuous. Female mating incidence is readily established by counting the number of colla (tubular remnants of spermatophores) in the bursa (spermatophore receptacle) of females (LaMunyon and Eisner 1993). Based on such counts, previous investigators had reported mating frequencies of, on average, 4–5 per female *Utetheisa* in nature (Pease 1968). More recent field data showed colla counts to average 11 per female, and to range upward to 22 per female (Iyengar et al. 2001). These are among the highest mating frequencies recorded in Lepidoptera. Furthermore, paternity is biased among twice-mated *Utetheisa* females, and progeny are sired almost exclusively by the larger of the two males (LaMunyon and Eisner 1993). Follow-up studies (in which large males were induced to produce small spermatophores) revealed that it is not body size per se that determines paternity, but instead the relative size of the male's spermatophore that dictates the sperm used to fertilize the eggs (LaMunyon and Eisner 1994). In many males, spermatophore size is an accurate indicator of male size; thus, a female may use stretch receptors in the bursa to indirectly gauge male size and quality (Sugawara 1979).

Currently, it is unknown whether biased paternity results from cryptic female choice or sperm competition. Cryptic female choice has been demonstrated in many organisms (Eberhard 1996), and there is evidence that female *Utetheisa* control the mechanism by which one set of sperm is favored over another. LaMunyon and Eisner (1993) found that, in 70% of twice-mated females, the larger male sired *all* of the offspring. Because both males were virgins with spermatophores presumably containing some sperm, this result suggests that siring success is not proportional to the quantity of sperm transferred. When females are anesthetized to inactivate their muscles, the normal routing of sperm is inhibited because sperm never reach the spermatheca, the usual storage destination (LaMunyon and Eisner 1993). Finally, the reproductive system of female *Utetheisa* is a complex labyrinth of ducts and chambers, which leaves open the potential for sophisticated manipulation of the contents of the spermatophore (Engelmann 1970). Despite this evidence for female control, it cannot be ruled out that sperm competition (Birkhead and Møller 1998) or seminal products may bias paternity (Wolfner 1997). *Utetheisa* males, like those of most lepidopterans, possess two types of sperm (nucleated eupyrene and anucleated apyrene sperm). The presence of nonfertilizing sperm in the male ejaculate of species with promiscuous females has led many to speculate that these apyrene sperm function in postcopulatory sperm competition (Swallow and Wilkinson 2002; Curril and LaMunyon 2006). While it remains unknown precisely how the various components of the system operate, there appear to be mechanisms in place that allow *Utetheisa* females to profit directly from each partner while having the mate of highest quality fertilize the majority of her eggs. In fact, PAs from at least three different males can be found in a single egg, thus confirming a female's ability to pool resources from multiple matings to benefit offspring belonging to one sire (Bezzerides and Eisner 2002).

Utetheisa and the Sexy-Sperm Hypothesis

Female promiscuity is particularly prevalent in insects in which females receive nuptial gifts containing nutrients and other chemicals that increase egg production or offspring survival (Choe and Crespi 1997; Vahed 1998). Numerous explanations based on genetic rather than phenotypic benefits to females also have been offered to explain female promiscuity (Kokko et al. 2003). For example, multiply-mating females may obtain indirect genetic benefits by increasing their odds of finding a mate of superior genetic quality (Yasui 1998; Jennions and Petrie 2000). Alternatively, Halliday and Arnold (1987) suggested that selection for extreme male promiscuity may drive female promiscuity nonadaptively through pleiotropic gene action.

Keller and Reeve (1995) proposed another hypothesis for the evolution of female promiscuity that has received limited empirical attention. They hypothesize that female multiple mating and male sperm competition can coevolve in a runaway, or Fisherian, process (the sexually selected sperm, or "sexy-sperm" hypothesis). It has recently been argued theoretically that ZZ/ZW genetic systems, such as those found in lepidopterans and birds, are especially conducive to Fisherian sexual selection when female preference genes lie on the Z chromosome (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004). *Utetheisa* females gain nutrients, chemical protection, and higher-quality offspring through promiscuity, but the possibility that they also gain sons with more-competitive sperm, in accordance with the sexy-sperm hypothesis, has not been addressed. The sexy-sperm hypothesis involves selection generated by female choice favoring males with competitive sperm and should be promoted by Z-linkage of female preferences in *Utetheisa* (Iyengar et al. 2002). A recent study found that, although the genes for male promiscuity are inherited autosomally, the underlying genes responsible for female promiscuity are Z-linked (Iyengar and Reeve 2010). These results demonstrate a genetic pattern consistent with the sexy-sperm hypothesis, and experiments are underway to test whether increased opportunities for multiple mating will increase the sperm competitiveness of the sons resulting from such matings.

Summary

Sexual selection is an important area of behavioral ecology that explains competitive interactions that occur in both precopulatory (e.g., exaggerated male traits used as armaments to fight other males or ornaments to attract females) and postcopulatory contexts (e.g., sperm competition and cryptic female choice). *Utetheisa ornatrix* is a moth where males use larvally acquired defensive chemicals to produce a short-range pheromone used by females to assess male quality during courtship. By choosing males based on this pheromone, females receive a substantial spermatophore whose contents provide both direct phenotypic benefits (via increased nutrients and defensive PAs) and indirect genetic benefits (via genes for larger size). Given that reproduction and defense are inexorably linked via this pheromone, *U. ornatrix* is a model organism for studying all aspects of sexual selection, and there continue to be many exciting new avenues to explore regarding the reproductive strategies of both sexes in this moth.

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