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THE EVOLUTION OF INSECT MATING STRUCTURES THROUGH SEXUAL SELECTION

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ABSTRACT

Mating structures are of interest to a wide range of biologists because, in many taxa, mating structures are incredibly diverse and range widely in elaboration even between closely related species. As a result of this diversity, mating structures have been useful in species identification. Historically, the evolution of diverse mating structures has been attributed to post-zygotic selection for pre-zygotic isolation to avoid production of hybrid offspring. More recently, sexual selection has been proposed as an alternative explanation for the rapid diversification of mating structures. Mating structures could diversify between populations through sexual selection if sexual selection acted differently on mating structures in different populations. Eberhard (1985) wrote a comprehensive book explaining how sexual selection could result in the diversification of mating structures and providing examples to support the hypothesis, but none of the examples were experimental tests of the hypothesis. Since 1985, a few studies have experimentally tested this hypothesis. However, there have been no empirical studies that connect intraspecific selection with interspecific diversification. In this paper, I review the reproductive isolation and sexual selection hypotheses and two recent experimental tests of the sexual selection hypothesis. Then, I provide a description of a system that may allow one to establish a connection between sexual selection on mating structures within a species and diversification of mating structures between species.

Key Words: genitalia, diversification, sexual selection, *Melanoplus*

RESUMEN

Las estructuras de apareamiento son de interés de una amplia variedad de biólogos por que, en muchos taxa, las estructuras de apareamiento son increíblemente diversas y se extiende ampliamente en elaboración aun entre especies estrechamente relacionadas. Como resultado de esta diversidad, las estructuras de apareamiento han sido útiles en la identificación de especies. Históricamente, la evolución de las estructuras de apareamiento diversas ha sido atribuida a la selección poscigótico para el aislamiento precigótico para evitar la producción de descendientes híbridos. Más recientemente, la selección sexual ha sido propuesta como una explicación alternativa para la diversificación rápida de las estructuras de apareamiento. Las estructuras de apareamiento puede diversificar entre poblaciones por medio de la selección sexual si la selección sexual actúa diferentemente en las estructuras de apareamiento en poblaciones diferentes. Eberhard (1985) escribió un libro comprehensivo explicando como la selección sexual puede resultar en la diversificación de las estructuras de apareamiento y proveyendo ejemplares para apoyar su hipótesis, pero ninguno de los ejemplares fueron pruebas experimentales de la hipótesis. Desde 1985, unos pocos estudios han probados experimentalmente esta hipótesis. No obstante, no han habido estudios empíricos que relacionan la selección intraspecifica con la diversificación interspecifica. En este papel, examino las hipótesis del aislamiento reproductivo y la selección sexual y dos pruebas experimentales recientes de la hipótesis de la selección sexual. Después, proveo una descripción de un sistema que puede permitir establecer una conexión entre la selección sexual de las estructuras sexuales dentro de una especie y la diversificación de las estructuras de apareamiento entre especies.

Morphological structures involved in coupling, and in transferring and receiving sperm have long been of interest to taxonomists because of their utility in distinguishing between species (e.g., Hubbell 1932; Kennedy 1919). These structures (hereafter called "mating structures") are also of interest to evolutionary biologists for two reasons (e.g., Alexander & Otte 1967; Arnqvist 1998; Eberhard 1985; Tatsuta & Akimoto 2000). First, they are much more complex in appearance than would

seem necessary for mating. For example, in the damselfly genus *Argia*, male genitalia vary from rather simple structures to extremely complex structures (Fig. 1). It seems unlikely that the difficulty of transferring sperm would differ enough between species in this genus to account for the differences in complexity in genitalia. Second, mating structures show much more rapid diversification than structures that are not involved in mating. This is again exemplified by the diversity

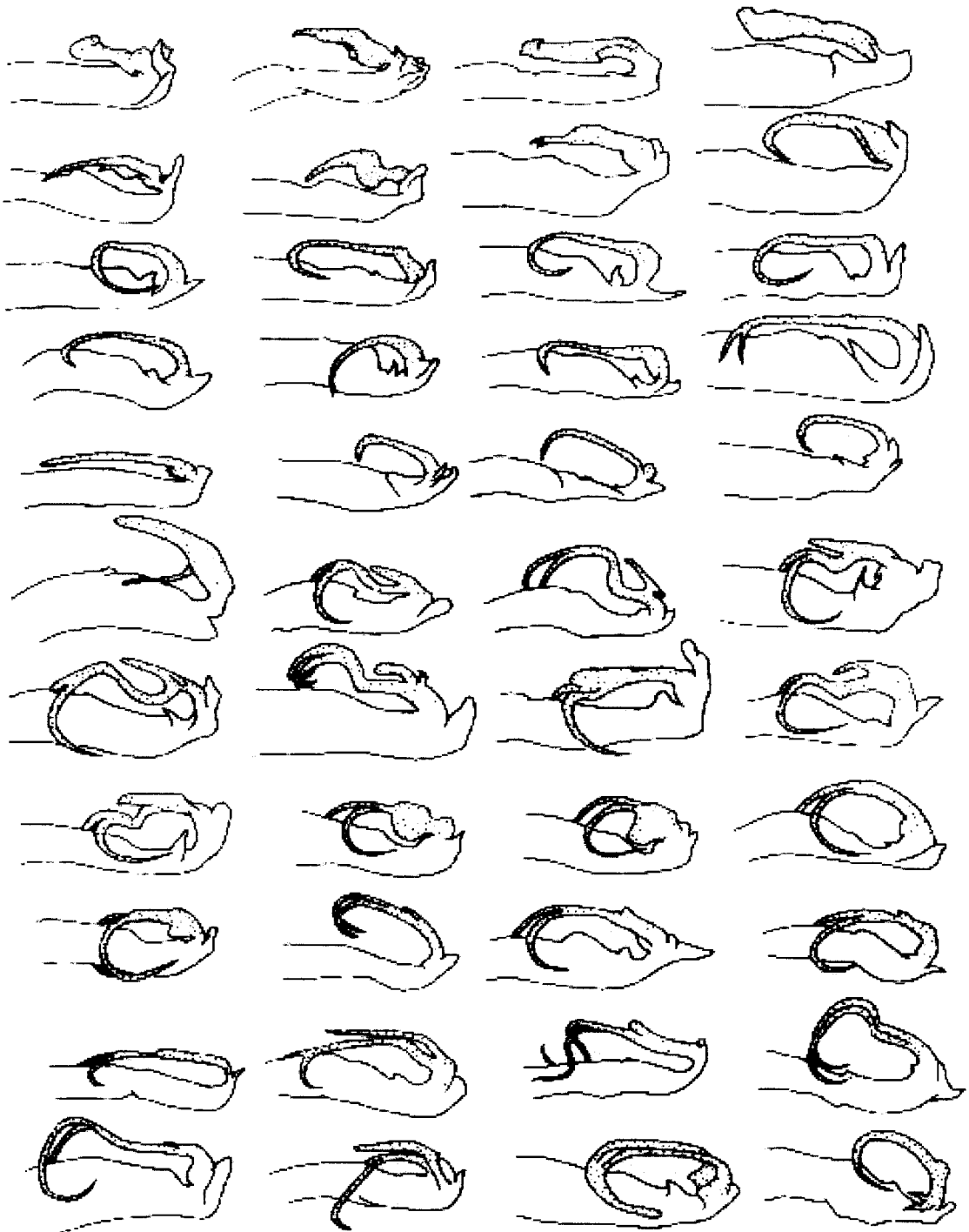


Fig. 1. Diversity of male genitalia in the damselfly genus *Argia*. Figure from Eberhard 1985, reprinted with permission of author and courtesy of Harvard University Press.

of forms of genitalia within the genus, *Argia* (Kennedy 1919; Fig. 1). Similar diversification occurs in female structures that receive and store sperm (e.g., grasshoppers: Slifer 1943; water strid-

ers, *Gerris*: Andersen 1993; Fig. 2). Further, we also see this diversification in other structures that are involved in matings such as modified antennae and legs that males use to grasp females

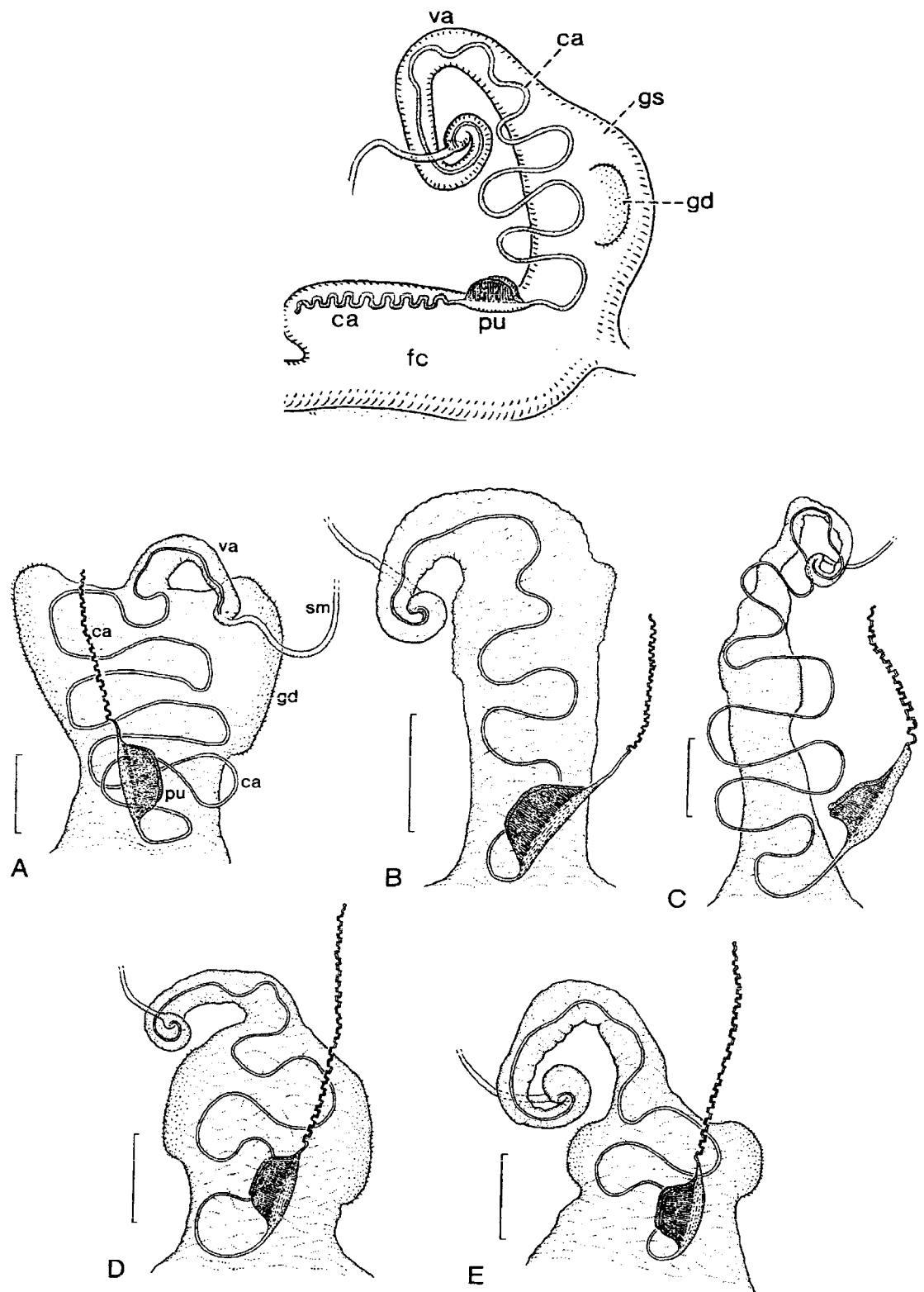


Fig. 2. Diversity of female structures that receive and store sperm in the water strider genus *Gerris*. Drawings from Andersen 1993, reprinted courtesy of the canadian Journal of Zoology.

during copulation in some water strider species. This diversification is seen across many taxonomic groups (Eberhard 1985). Two main hypotheses have been proposed to explain the diversification of genitalia: the reproductive isolation hypothesis and the sexual selection hypothesis.

Reproductive Isolation Hypothesis

Historically, diversification of mating structures has been attributed to selection for prezygotic isolating mechanisms that prevent hybridization. According to this “reproductive isolation” hypothesis (a.k.a. “lock-and-key”), there is strong selection on females to avoid mating with heterospecific males. As a result, females evolve complicated reproductive structures that allow them to discriminate between conspecific and heterospecific males and to avoid heterospecific fertilizations. The occurrence of this process with each speciation event would result in a pattern of rapid diversification of genitalia across closely related species.

The reproductive isolation hypothesis has two main predictions. First, if the diversification and elaboration of mating structures results from selection for reproductive isolation, there should be species-specific fits of male and female mating structures. Second, there should be more diversification of mating structures in sympatry than in allopatry. Certain systems are consistent with these predictions (Eberhard 1985). However, there are many systems for which we do not see a species-specific fit between male and female mating structures; in these species, female structures do not prevent intromission by males of other species (Eberhard 1985; Shapiro & Porter 1989). This finding alone is not sufficient to reject the reproductive isolation hypothesis because it is possible that (1) reproductive isolation is achieved not through a mechanical fit but through a sensory fit such that the male reproductive parts stimulate females in a species-specific manner or (2) the genitalia no longer serve as reproductive isolating mechanisms because other mechanisms have evolved (e.g., behavioral).

Data from many taxa also do not support the second prediction of the reproductive isolation hypothesis. In several cases, rapid diversification of mating structures appears to have occurred in allopatry. There are patterns of extreme diversification of mating structures of species that are geographically isolated from any morphologically similar species. For example, certain species of the homopteran genus *Oliarus* appear to have evolved separately on different islands of the Galapagos (Fig. 3). The male intromittent organs of species on different islands have diverged substantially (Eberhard 1985; Fennah 1967). In sum, there are many cases of apparent rapid diversification of mating structures that the reproductive isolation hypothesis cannot explain.

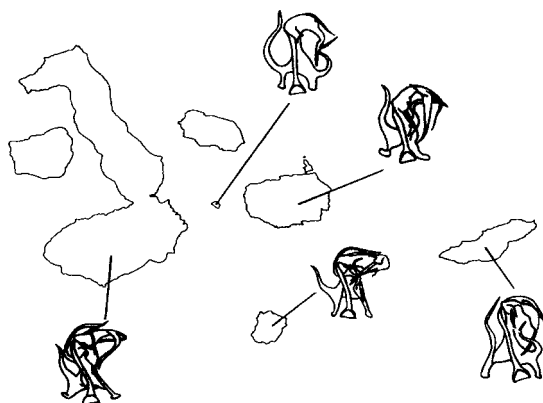


Fig. 3. Male genitalia of species of the homopteran genus *Oliarus* found on different islands of the Galapagos. Figure from Eberhard 1985, reprinted with permission of author and courtesy of Harvard University Press. Genitalia drawings from Fennah 1967, reprinted courtesy of the California Academy of Sciences.

Sexual Selection Hypothesis

An alternative to the reproductive isolation hypothesis is that the diversification of mating structures is a result of sexual selection. Sexual selection results from differential access to mates based on differences in phenotypic traits. However, in the last twenty years, it has become abundantly clear that sexual selection does not end once coupling has begun. Within the female reproductive tract, there are battles between sperm of different males and differential use of sperm by females (Birkhead & Moller 1998; Eberhard 1996). Sexual selection could act on mating structures if differences in the shape or size of these structures resulted in differential coupling and fertilization success (Lloyd 1979; Short 1979). The sexual selection hypothesis is that sexual selection acting on mating structures differently in different populations could result in diversification of mating structures between populations.

There are three mechanisms by which sexual selection can act, and all have been invoked in explaining the evolution of elaborate mating structures. First, sexual selection could act on mating structures through mate choice. Male mating structures may evolve through cryptic female choice in which females preferentially use sperm from males based on characteristics of the male structures. Selection could also act on females, favoring those that have structures that enable them to be more selective amongst males.

Second, sexual selection could act on mating structures through intrasexual competition. For example, selection could act if certain characteristics of male reproductive structures made them better able to deliver sperm or remove or otherwise compete with the sperm of other males.

Third, sexual selection could act on mating structures through intersexual conflict over fertilization. If male quality varies, then females should be selected to choose sperm of high quality males. Males should be selected to overcome the female choice mechanisms and to manipulate female behavior to their advantage (Gavrilets et al. 2001; Holland & Rice 1999; Rice 1996) and selection should act on females to avoid this manipulation (at least to some degree; Alexander et al. 1997; Cordero & Eberhard 2003) leading to an intersexual arms race involving the mating structures of males and females.

Diversification of mating structures between populations through sexual selection is most likely to occur through female choice because female choice can act on arbitrary traits (Andersson 1994). Advances in the study of the evolution of mating structures through sexual selection have taken two forms: investigations of the form and function of mating structures (e.g., Arnqvist 1998; Arnqvist & Thornhill 1998; Eberhard 1992, 2001; Eberhard & Pereira 1993; Fritz & Turner, 2002; Robinson & Novak 1997; Waage 1979) and experimental tests of selection acting on these structures (e.g., Arnqvist and Danielsson 1999; Arnqvist et al. 1997; Cordoba-Aguilar 1999).

Studies of the Form and Function of Mating Structures

Investigations into the form and function of male and female mating structures support the hypothesis that sexual selection is acting on mating structures. For example, in Waage's (1979) classic work on jewelwinged damselflies, *Calopteryx maculata*, he concluded that the intricate structures of the damselfly penis were used not only to transfer sperm to females but also to remove sperm of other males from the female reproductive tract. Waage (1979) came to this conclusion based on four lines of evidence. 1. Females who had previously mated had more sperm in their reproductive tract before and after a second mating than when mating was interrupted. 2. When copulating pairs were dissected (after being killed), male genitalia were found in the female sperm storage organs. 3. Males have backward-pointing spines on the parts of their genitalia that reach the sperm storage organs. 4. Clumps of sperm were found on the male genitalia after the male withdrew from the female. Together, these results suggest that selection could be acting on the size and shape of male genitalia in *Calopteryx*. Subsequent studies suggest that similar processes occur in other odonate species.

More recently, investigations into the form and function of female reproductive structures have supported the cryptic female choice hypothesis for the diversification and elaboration of mating structures. Mechanisms have been found by which females could control the use of sperm (Eberhard

1996). This appears to be the case in the Caribbean fruit fly, *Anastrepha suspensa*. In this species, females have multiple spermathecae and store different amounts of sperm in each spermatheca (Fig. 4). Females have thin spermathecal ducts leading to the bursa copulatrix. Each of the spermathecae has a separate valve that could potentially be used by females to control the storage and release of sperm. These data suggest that female *A. suspensa* have the ability to discriminate between the sperm of different males by controlling the storage and release of the sperm. Whether they use this ability has not been established.

These studies of form and function of mating structures are important for understanding how selection might act on these structures, but they are not actual tests of the sexual selection hypothesis. To demonstrate sexual selection, one must show that differences in the mating structures result in differential access to gametes. Very few studies have actually tested this. In fact, in the insect literature, I am aware of only four studies that actually test for differential fertilization success based on differences in mating structures, although there are other studies that relate differences in mating structures to differences in access to mates (e.g., Arnqvist et al. 1997). I will review two recent studies that test for sexual selection on mating structures.

Case Study I: *Gerris lateralis*

The first case is a recent study by Arnqvist and Danielsson (1999) on the water strider, *Gerris lateralis*. They studied the effect of variation in reproductive and non-reproductive structures on

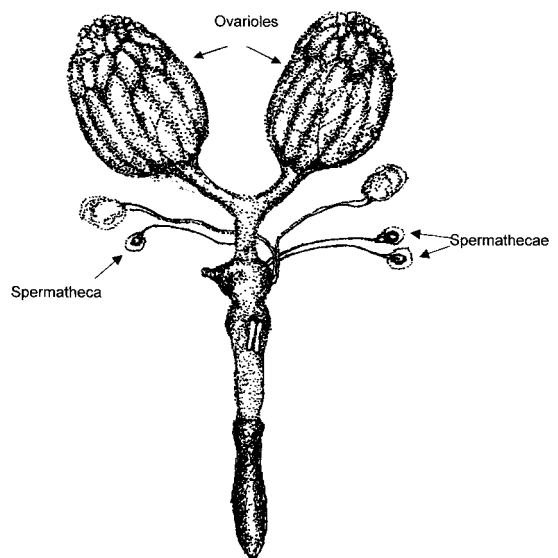


Fig. 4. Female reproductive structures of *Anastrepha suspensa*. Drawing by A. Fritz, printed with permission.

sperm precedence of the first and second males to mate with a female. There was evidence for sexual selection acting on sclerites that are found in the distal portion of the aedeagus. Although the function of these sclerites is not known, they appear to play a role in the placement of the aedeagus within the female reproductive tract and/or stimulation of the female.

Arnqvist and Danielsson (1999) found that the shape of the lateral sclerites of the first male to mate and the dorsal and ventral sclerites of the second male to mate affect sperm precedence. In addition, the degree of the effect of the ventral sclerite of the second male on sperm precedence depended on the size of the female. Together, these results suggest that selection acts on male mating structures in *G. lateralis* and that the strength of selection depends on the distribution of female phenotypes in the population. However, two questions remain unanswered about the selection process. First, it is unclear whether selection is acting directly or indirectly on the sclerites. It is possible that selection is actually acting on a trait that is correlated with the shape of the sclerites and not on the sclerites themselves. The authors controlled for many possible correlates, but, without manipulating the structures and randomly assigning males to treatment groups with differently shaped structures, it is difficult to infer causal relationships. Second, the mechanism by which selection is acting is also still unclear. It could be that (1) the shape of the sclerites allow males to position their own sperm or the sperm of other males in such a way that they have an advantage or (2) females use sperm of certain males preferentially depending on the shape of their sclerites.

Case Study 2: *Calopteryx haemorrhoidalis*

A study of damselfly reproduction provides more evidence of selection acting directly on a mating structure. This study is on a species of calopterygid damselflies, the same group in which Waage (1979) found sperm removal by males. Cordoba-Aguilar (1999) found patterns of sperm storage in *Calopteryx haemorrhoidalis* similar to those that Waage (1979) found in *C. maculata*, suggesting that sperm removal was also occurring in *C. haemorrhoidalis*. However, in *C. haemorrhoidalis*, the male genitalia could not get into the spermatheca, ruling out the possibility of direct sperm removal by males. Instead, Cordoba-Aguilar (1999) proposed that males stimulate females to eject sperm. Females have two sclerotized plates in their reproductive tract each bearing sensilla. When eggs pass by these plates, the plates are distorted and this distortion sends a stimulus through an abdominal ganglion to the sperm storage organs. The sperm storage organs respond by ejecting sperm for fertilization. Dur-

ing copulation, the male genitalia distort these plates in a manner similar to that of eggs passing through. Females with more sensilla store less sperm when their copulations are interrupted than females with fewer sensilla.

Cordoba-Aguilar predicted that males with wider genitalia would stimulate the sensilla more and stimulate the females to eject more sperm. He tested this prediction experimentally by simulating copulations using genitalia that he had removed from males. He used only the portion of the genitalia that normally makes contact with the plates to control for the effect of any correlated characters and to ensure that no sperm was removed directly by the male genitalia. Females mated with males with wider genitalia stored less sperm after simulated mating than females mated with males with narrower genitalia. However, the mechanism of sperm ejection is still poorly understood. It is very difficult to distinguish whether this is a case of female choice, male-male competition, or sexual conflict.

Connecting Intraspecific Selection with Interspecific Diversification

These two case studies are among the first to demonstrate sexual selection on mating structures. However, no studies have yet connected selection on mating structures within a species to diversification of mating structures between species. A group of grasshoppers found in Florida offers an excellent opportunity to study this connection (Fig. 5). These are the brachypterous (short-winged) species of the genus *Melanoplus* (Capinera et al. 1999; Deyrup 1996; Hubbell 1932, 1984; Squitier et al. 1998). In Florida, most of these species are found only in sandhill and scrub habitat. Because much of this habitat occurs in patches in Florida (Myers 1990; White 1970), some of the species are effectively isolated from other similar species (Fig. 6). This group is



Fig. 5. *Melanoplus ordwaye* pair in copula at Gold-head Branch State Park, FL.

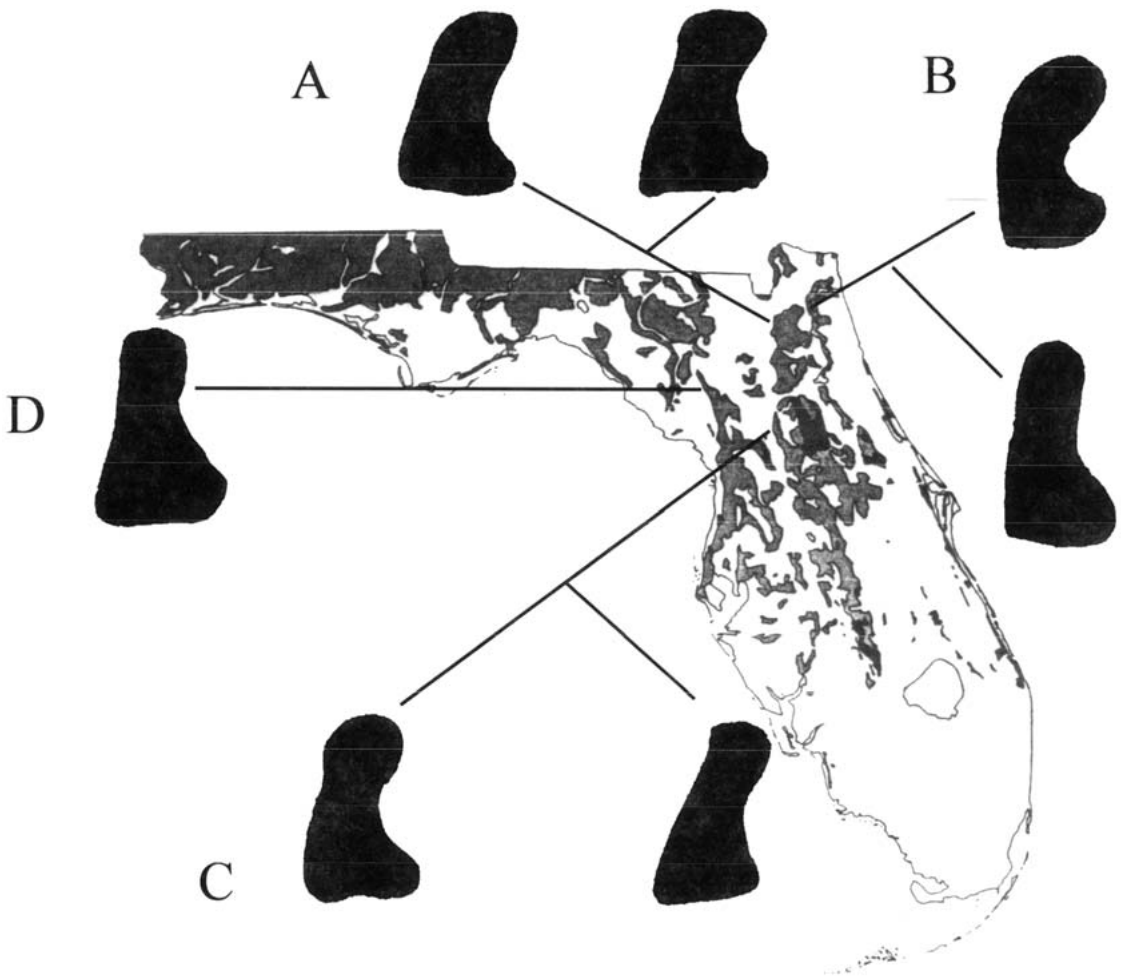


Fig. 6. Cerci of male *Melanoplus rotundipennis* from four sites in Florida. Map from Myers & Ewel 1990, reprinted courtesy of University Press of Florida. A. Goldhead Branch State Park; B. Welaka State Forest; C. Ocala National Forest; D. University of Florida's Thomas Farm (Gilchrist Co.).

characterized by extraordinary diversification of both internal and external male mating structures. For example, the cerci of different species form what Lloyd (1979) predicted as "a veritable Swiss Army Knife of gadgetry" (Fig. 7). The internal genitalia are similarly complex and diverse.

In addition to the interspecific variation in mating structures, there is also much intraspecific variation. For example, the cerci of *Melanoplus rotundipennis* vary both within and between populations. Figure 6 shows cerci from four populations of *M. rotundipennis*. The cerci differ both in curvature and in the width of the head relative to the rest of the cercus.

During copulation, the cerci appear to be used by males to gain access to the genital chambers of females (Fig. 8). The cerci squeeze against a flap that lies flat against the female's ventral surface, just below her ovipositor blades. This flap, called

the egg guide, encloses the genital chamber, which is attached to the spermathecal tube. During coupling, the male's cerci appear to pinch either side of the egg guide (pers. obs.). Pressure on the sides of the egg guide results in the egg guide popping open, exposing the genital chamber. Sexual selection could act on the shape and size of the cerci through female choice in which females mate only with males whose cerci fit into the grooves of their egg guides (Eberhard 1998).

The shape of the cerci differ between populations of *M. rotundipennis* (Fig. 6). This variation suggests that selection could be acting differently in different populations. One could test this hypothesis in *M. rotundipennis* because it is possible to manipulate the shape and size of cerci (e.g., Krieger & Krieger-Loibl 1958), thus, removing the effect of correlated traits on reproductive success. It is possible to manipulate the shape and size of



Fig. 7. "Veritable Swiss Army Knife" of cerci of different species of brachypterous grasshoppers of the genus *Melanoplus* found in Florida. Drawings of cerci from Capinera et al. 2001, with permission of author.

cerci by cutting them with microscissors. A similar method was used to test for sexual selection on male genitalia in the beetle, *Chelymophra alternans* (Rodriguez 1995). In this species, males with longer genitalic structures (called "flagella") sire more offspring. This pattern could indicate direct selection on flagellum length or indirect selection

on a correlated trait. Rodriguez distinguished between these possibilities by manipulating the length of males' flagella. Males with longer manipulated flagella sired more offspring, demonstrating direct selection on flagellum length. By using this method in *M. rotundipennis*, one could test whether and how cerci size or shape affected male reproductive success. Cerci size or shape could affect male reproductive success in a number of ways including increasing a male's sperm precedence or the female's oviposition rate or decreasing the likelihood that the female will remate (Eberhard 1996; Simmons 2001). Demonstration of sexual selection for different sized or shaped cerci in different populations would provide a connection between sexual selection on mating structures within a species and diversification of mating structures between species.

In conclusion, recent studies have established that sexual selection is acting on male mating structures. However, more work is needed in three main areas for us to have a better understanding of the evolution of mating structures through sexual selection. 1. We need to investigate and attempt to distinguish the processes by which sexual selection is acting on mating structures. As exemplified by Cordoba-Aguilar's (1999) research on *C. haemorrhoidalis*, it is often difficult to distinguish whether sexual selection on mating structures is a result of female choice, male competition, or intersexual conflict. More than one of these pro-

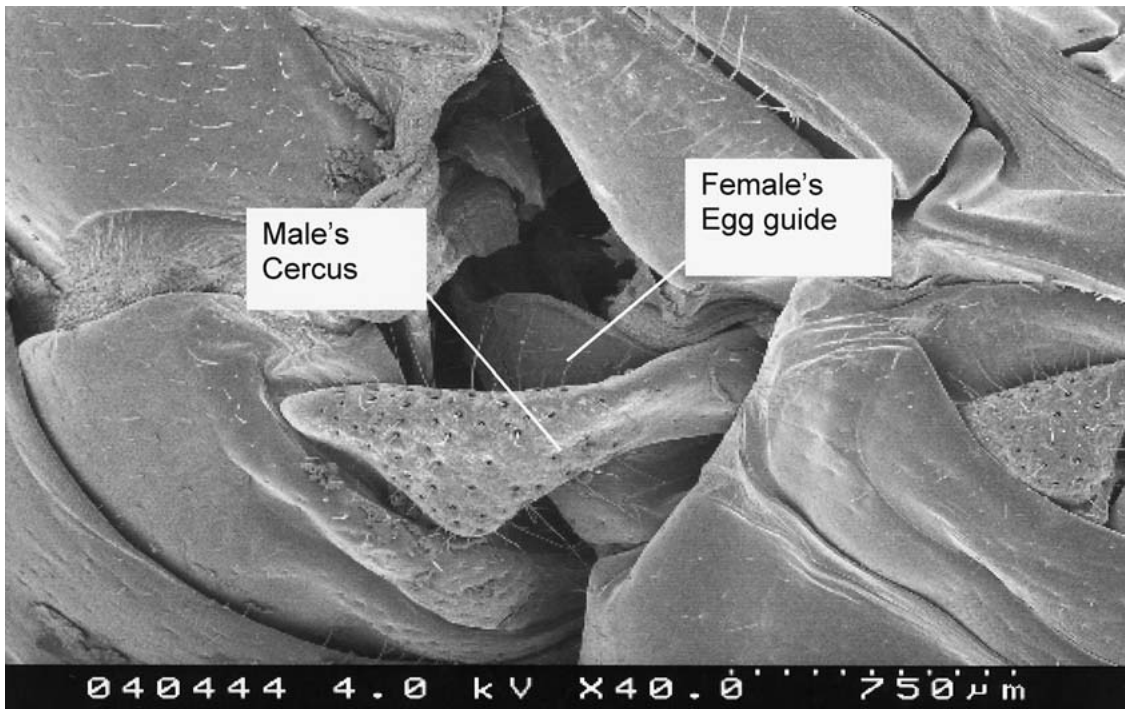


Fig. 8. SEM photo of external mating structures of *M. rotundipennis* pair in copula.

cesses could be acting simultaneously. We can understand sexual selection on mating structures more thoroughly by determining which of these processes are occurring. 2. We need to study the form and function of female mating structures and how selection acts on these structures. Female mating structures are a part of the selective environment in which male mating structures evolve, and vice versa. Understanding the biology of female mating structures will allow us to understand the sensory and physical environment in which male mating structures evolve. 3. We need to connect the process of intraspecific sexual selection on mating structures with interspecific diversification of mating structures. Current research on sexual selection on mating structures is focused predominantly on intraspecific processes. We must conduct studies across populations of the same species and closely related species to extrapolate how intraspecific sexual selection can result in interspecific diversification.

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