Chapter 11
Sexual Conflict in Water Striders, Dragonflies and Diving Beetles

Adolfo Cordero-Rivera and Anais Rivas-Torres

Abstract The field of sexual selection has been historically dominated by a stereotyped view of the sexual roles, with competing males and selective females, but in recent decades there has been a paradigm switch, with the emergence and dominance of the concept of sexual conflict. Put simply, there is sexual conflict when the optimum value for a trait (or a group of traits) is different for females and males. Although the recent literature mainly considers sexual conflict as a process separate from the other well-known processes in the field of postcopulatory sexual selection (sperm competition and cryptic female choice), our approach is that sexual conflict is the consequence of several pressures related to natural and sexual selection, and not a process by itself. Therefore, here we consider sexual conflict as a part of a continuum of sexual selection mechanisms. We concentrate on the effects of sexual conflict on reproductive behaviour of three groups of aquatic insects, whose habitats differ markedly, water striders, odonates and diving beetles, but also include some examples of studies addressing sexual conflict in other groups of aquatic insects. Our hypothesis is that the dimensional structure of the habitat will affect the intensity of sexual conflict over mating rate, copulation duration and postcopulatory guarding. There is abundant evidence and comprehensive reviews of the conflict over mating rates in water striders, odonates and, to a lesser degree, diving beetles. The bi-dimensionality of the water surface allows an easy monopolisation of females by males in this microhabitat, and water striders conform to this rule, so that the commonest mating system is characterised by strong conflicts and struggles before and after copulation. For animals like odonates, which are fast fliers and can use diverse terrestrial microhabitats, the opportunities for males to force females to copulate are certainly limited. In the case of diving beetles, the situation seems more favourable for the females, as they could control male approaches by hiding easily in the vegetation, or even in the case of extreme male density they could fly away and move to a different water body. The sexual conflict over mating duration is also intense in water striders, and also relevant in the other reviewed groups. In the field of postcopulatory conflicts, odonates have offered the best examples of male

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adaptations and female counter-adaptations, which are even more elaborated when studying the evolution of genitalia. We end by summarising our main conclusions and propose some ideas for future work. We stress that a comprehensive understanding of sexual conflicts in animals requires the study of both male and female anatomies, as well as their behaviours, avoiding assumptions or gender stereotypes, which have historically biased research to a male-view approach.

Keywords Behaviour · Equity · Cryptic female choice · Sperm competition

11.1 What Is Sexual Conflict

Observing a pair of animals contributing to the rearing of the next generation may seem at first sight a beautiful example of cooperation for a common goal. However, as many other widespread layman misconceptions about animal behaviour, the two members of a pair cooperate but are at the same time in permanent conflict (Arnqvist and Rowe 2005). This is especially strong in species with high parental investment, where both partners will have more to gain than to lose if "convincing" the other progenitor to invest more in the offspring. Sexual selection will therefore favour cheating the partner. This "sexual conflict" is only one of the many evolutionary conflicts of interests that can be found in all levels of biological complexity (Queller and Strassmann 2018).

George C. Williams was the first to use the term "sexual conflict" in his book "Adaptation and Natural Selection" (Williams 1966, p. 184), and although it received some attention the dominant view at that time was cooperation between males and females. After some years of silent, the concept of sexual conflict was brought to life again thanks to the chapter on "Parental Investment and Sexual Selection" by Trivers (1972).

In 1983, as a second-year biology student, the first author was "gently obliged" by his genetics professor to read a recent book (at that moment) with the curious title "The Selfish Gene" (Dawkins 1976). This book, that has sold more than a million copies, clearly proposed the idea of conflicts between genes as one of the main forces in evolution. There is a chapter entitled "The Battle of the Sexes", where the idea of sexual conflict is introduced, using these terms:

> "As a convenient approximation, we can once again assume that each individual body is a selfish machine, trying to do the best for all its genes. The best policy for such a selfish machine will often be one thing if it is male, and quite a different thing if it is female."

However, the credit for popularising the concept of sexual conflict among evolutionary biologists is for Geoff Parker, who in 1970 published a review of mating behaviour in insects, and defined the term "sperm competition". He introduced the idea that intrasexual selection between ejaculates continues after mating, inside the female (Parker 1970), and a few years after studied the evolutionary consequences of the conflict between the sexes (Parker 1979). Parker (2006) defined the term as

> "[…] a conflict between the evolutionary interests of individuals of the two sexes".

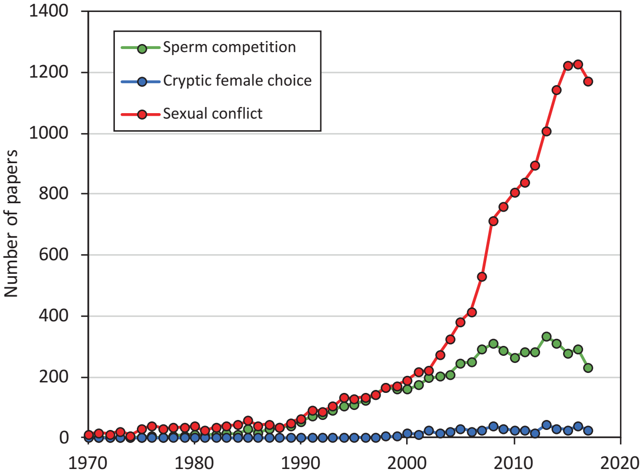

Fig. 11.1 The diffusion of the idea of sexual conflict is an example of a paradigm switch in evolutionary ecology. The figure shows the trends in the number of papers that cite each concept in their title or abstract since 1970 to 2017. Note that "cryptic female choice" does not appear in the titles of papers until 1995. Source: Web of Sciences, accessed October 2018

The picture was completed when the female perspective was also explicitly considered in models of sexual selection, and was denominated "cryptic female choice", because it was not apparent to an observer (Thornhill 1983; Eberhard 1996). Put it simply, there is sexual conflict when the optimum value for a trait (or a group of traits) is different for females and males. The "trait" can also be different for both sexes. The recent literature tends to use the term "sexual conflict" (Fig. 11.1), as a process separate from the other well-known processes in the field of postcopulatory sexual selection (sperm competition and cryptic female choice), but sexual conflict is in fact the consequence of several pressures related to natural and sexual selection (Cordero Rivera and Córdoba-Aguilar 2016), and not a process by itself (Shuker 2014). Therefore we here consider sexual conflict as a part of a continuum of sexual selection mechanisms (Simmons 2014). Some have argued that sexual conflict is so intrinsically linked to sexual selection, that both terms can be synonymous or that sexual selection is better described by the term "sex-dependent selection" (Carranza 2009). The important question for us is that sexual conflict can occur before, during and/or after mating, and therefore it can affect almost all the behavioural repertories of males and females related to reproduction. Sexual conflict can even occur in monogamous species (for instance for mating rate), while sexual selection will be weak.

Although sexual conflict can be obvious in animals with parental care, particularly vertebrates, the first conceptual and experimental studies were mainly inspired by insects, where parental care is extremely rare (Machado and Trumbo 2018). If parents die before the offspring hatches, as it occurs in many insects, parental care cannot evolve. Insects are therefore good models to study conflicts over mating rate and postcopulatory conflicts over fertilisation. For a general review of what is known about sexual conflict in animals see Arnqvist and Rowe (2005).

11.2 The Ecology of Sexual Conflict in Aquatic Insects

We here concentrate on the effects of sexual conflict on reproductive behaviour of three groups of aquatic insects, whose habitats differ markedly, water striders, odonates and diving beetles, but also include some examples of studies addressing sexual conflict in other groups of aquatic insects. Our hypothesis is that the dimensional structure of the habitat will affect the intensity of sexual conflict over mating rate, copulation duration and postcopulatory guarding. There is ample evidence for the relevance of local ecological settings in the evolution of sexual conflict (Perry and Rowe 2018).

Water striders have been at the core of sexual conflict studies over mating rate, due to the prolific studies of Locke Rowe and Göran Arnqvist, who pioneered the field (e.g. Rowe et al. 1994). Water striders live in a world essentially bi-dimensional, on the surface of rivers, ponds, lakes and even the sea (Fig. 11.2). This fact conditions the ability of females to avoid unwanted male mating attempts, and likely is a factor contributing to the extreme adaptations exhibited by some species. For a review of their ecology and behaviour see Spence and Anderson (1994).

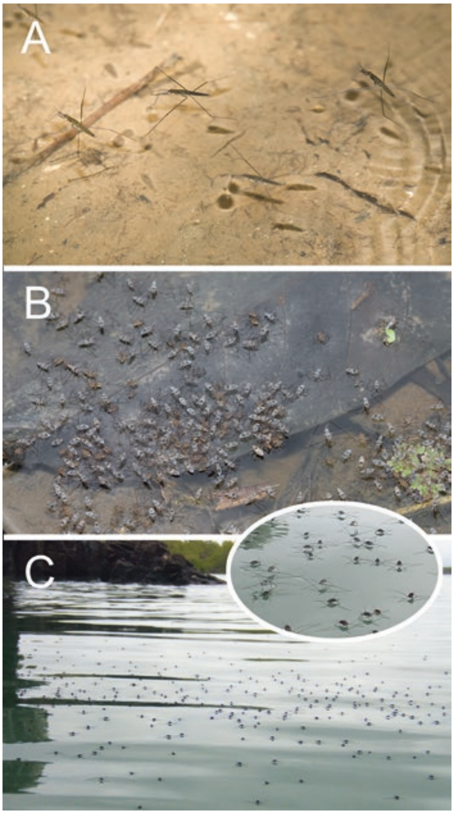

Fig. 11.2 The bi-dimensionality of the water surface, and the high densities of many populations of water striders around the world, conditions the ability of females to avoid unwanted matings, and therefore sexual conflict over mating rate is usually very high. (**a**) A group of *Aquarius najas* in an Italian stream; (**b**) an aggregation of water striders and veliids (likely *Microvelia*) in a pond in the National Park Pacaya-Samiria in Peru; (**c**) an aggregation ("flotilla") of *Halobates robustus* in the coast of Santa Cruz island (Galapagos), consisting of males, with a detail in the insert. Pictures by ACR

The second group that we will review is totally different, in the sense that the adults live in a complex tri-dimensional world, are highly mobile and are fast flyers: the odonates. Since the early studies of postcopulatory sexual selection, damselflies and dragonflies have been a textbook example for sperm competition, particularly after the clever experiments of Jonathan Waage (1979) showing that the male intromittent organ can be used to remove sperm from rival males before insemination (Cordero-Rivera and Córdoba-Aguilar 2010). This fact conditioned for long time our view of odonate mating behaviour, but recent evidence has shown the relevance of other mechanisms apart from sperm competition (Córdoba-Aguilar and Cordero-Rivera 2008).

Finally, we review the literature on reproductive behaviour and sexual conflict in a group of aquatic insects whose adults live in the water, but also have the ability to fly, the diving beetles (the family Dytiscidae), and therefore have a multidimensional world available: the aquatic and the aerial habitats. We predict that this multidimensional space will increase the ability of females to escape from males and therefore this fact will diminish the intensity of sexual selection and particularly of sexual conflict.

11.2.1 Sexual Conflict Over Mating Rate

There is ample evidence that the optimum number of matings is different for males and females. The common pattern is the so-called Bateman's principle that states that male reproductive success increases in a direct way with the number of matings achieved (i.e. males are limited by the number of females they mate with), whereas in females the limitation is the amount of energy and time available for egg production and maturation (i.e. females are limited by resources and less by the number of mates) (Bateman 1948). This asymmetry predicts that males will be more indiscriminate and try to maximise the number of matings, whereas females are predicted to be more selective and maximise mate quality and resources. Some studies have shown that increasing the number of matings over the optimum can be negative for females (Arnqvist and Nilsson 2000). Therefore, there is sexual conflict over the number of matings.

If the optimum number of matings is different for males and females, then another prediction of sexual conflict theory is that selection would favour the evolution of adaptations in males that allow them to hold females and even force copulation (a diverse array of grasping appendages—see Fig. 11.6—but also behavioural adaptations) (Clutton and Parker 1995). The same hypothesis predicts the evolution of mechanisms in females to avoid being grasped by males or to make this extremely difficult or even dangerous. For instance, females can evolve anti-grasping mechanisms (like in *Gerris*; Arnqvist and Rowe 2002). Sexual cannibalism (Fig. 11.3b) could also be a way for females to solve the conflict, and at the same time get extra resources for future reproduction (Schneider 2014).

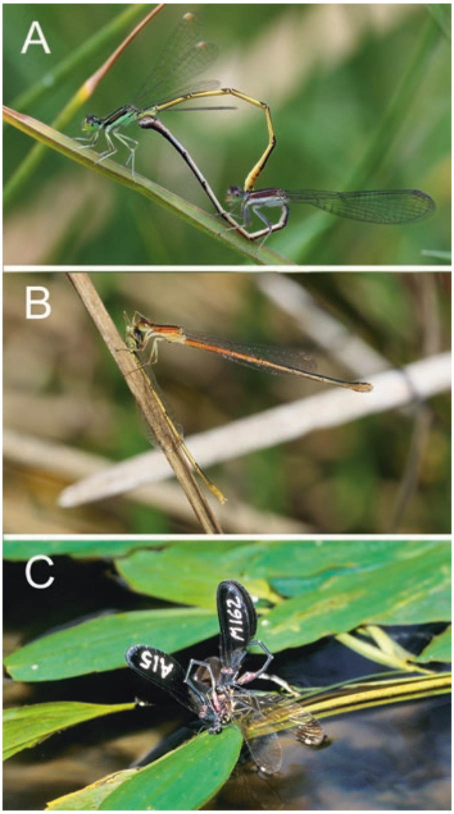

Fig. 11.3 Odonates are fast fliers and live in a complex tri-dimensional habitat. Female odonates have to collaborate to mate (like in **a**, *Ischnura hastata* at the Galapagos). Sexual conflict over mating rate and mating duration can be very intense, and sometimes females show sexual cannibalism (**b**, a female *I. hastata* cannibalising a mature male; Zarabanda, Cuba). Males cannot force copulations under normal densities, but can harass females until a convenience polyandry is the best of a bad job for them (**c**, an ovipositing female of *Calopteryx haemorrhoidalis* being taken forcibly in tandem by two males; Pontecorvo, Italy). Pictures by ACR

The bi-dimensionality of the water surface allows an easy monopolisation of females by males in this microhabitat, and water striders conform to this rule, so that the commonest mating system is characterised by strong conflicts and struggles before and after copulation (type I sensu Arnqvist 1997). For example, in *Gerris buenoi* females are frequently harassed by males in search of mating, and the only way to escape for females is to fight with the male (pre-mating struggles; Fig. 11.4a), which has the negative effect of increasing predation rate by backswimmers (Notonectidae) (Rowe 1994). In fact, the mating frequency of females in *Aquarius remigis* is positively related to male density (Lauer et al. 1996). Mating is specially costly for females, because they have to carry the males on their back for long periods of time (Fig. 11.4b, c), decreasing their skating efficiency (Rowe et al. 1994), and likely increasing predation. A review of 15 species of the genus *Gerris* indicates that conflict over mating rate is widespread in the group, with species where males apparently have gained control over mating rate, and others where females retain a relative advantage (Rowe and Arnqvist 2002). When harassment rate is experimentally increased, females reduce their resistance and therefore mating rates increase (Fig. 11.5), a fact that suggests that this mating system can be characterised as “convenience polyandry” (Rowe 1992). However, water striders can exhibit also

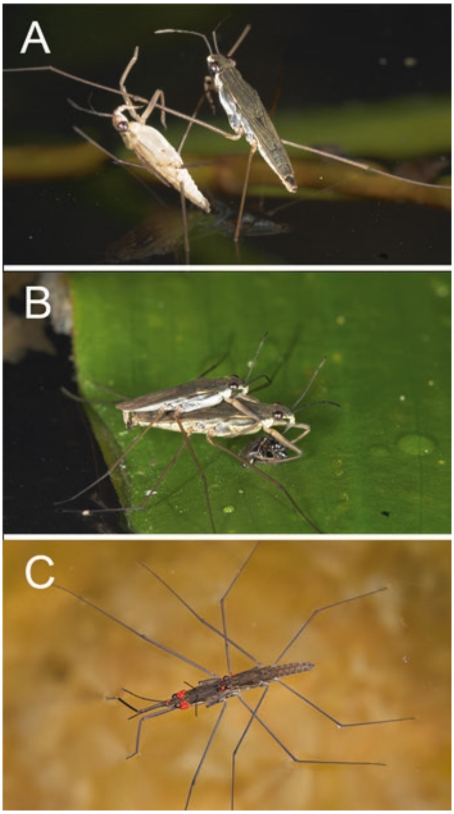

Fig. 11.4 Sexual conflict over mating rate in water striders is evident by pre- and postcopulatory mating struggles. (**a**) Struggle between two *Gerris* individuals; (**b**) copulation (*Gerris* sp., Pontecorvo, Italy) can be brief or very long, and in many species males remain in the back of females for hours, days or even weeks, increasing predation risk, like this couple of *Aquarius najas*, heavily parasitised by water mites (**c**; Tarragona, Spain). Pictures by ACR

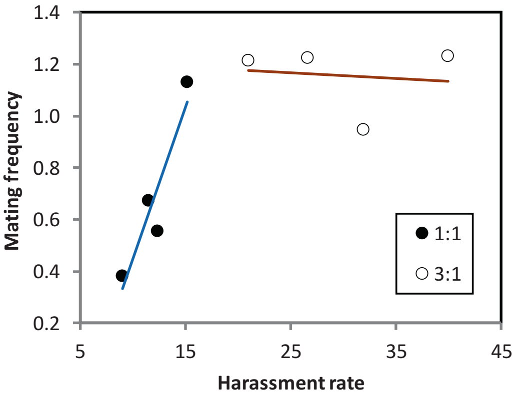

Fig. 11.5 The effect of harassment rate of male *Gerris buenoi* over female mating frequency, at two different sex ratios. Harassment was measured as the number of male attempts to copulate with females per single female hour. Lines represent regressions. Source: modified from Rowe (1992)

a second mating system, with little apparent conflict (type II sensu Arnqvist 1997). In the commonest case, males have apparently "won" the battle for controlling mating rate, but in the type II mating system males have become territorial and court females, so that females have higher control over mating rates (Arnqvist 1997).

The above discussion can be extended to other groups of aquatic insects that live on the water surface, like Mesoveliidae, Veliidae and Hydrometridae (Heteroptera). However, very little research has been done using these other families as models. Searching for sexual conflict and the family name in the Web of Sciences gives no papers for Mesoveliidae and Hydrometridae and only two papers for Veliidae. One of such studies for the subfamily Microveliinae found several examples of putative grasping and anti-grasping adaptations, suggesting that they have evolved due to sexual conflict over mating rate (Cassis et al. 2018). Some Veliidae show males that remain for long periods over their females (Polhemus 1974), a situation paralleling a common behaviour in water striders, which is known to generate costs on females (see above). There is even one case where females have evolved a gland on their dorsal surface that produces a secretion used by males to feed, a clear example of a counter-adaptation of females to reduce kleptoparasitism by their mates, which remain on the back of females for long periods of time (Arnqvist et al. 2006).

For animals like odonates, which are fast fliers and can use diverse terrestrial microhabitats, the opportunities for males to force females to copulate are certainly limited. Female odonates have to blend up their abdomen and cooperate with the male for a successful copulation (Figs. 11.3a and 11.8a). This has led some authors to assume that female odonates cannot be forced to mate (e.g. Fincke 1997). This view is probably true in most ecological settings. However, males have evolved the ability to concentrate in places that females have to visit to lay their eggs, monopolising the area; that is, they behave as territorial (Baker 1983). Under these circumstances, males can be so insistent as to force copulation (Fig. 11.3c), again in a case of "convenience polyandry" (Cordero 1999; Cordero and Andrés 2002).

The odonates are also particular because males have a secondary genitalia, and therefore both individuals contact in two body regions to mate. The typical pattern is for males to search for females either actively or waiting at the shore of the water bodies. When a female is found, the male tries to grasp her in tandem, using his anal appendages (Cordero-Rivera 2002), and at this moment conflict over mating rate can be intense. Females can avoid being grasped by escape flights, by refusal displays (Utzeri 1988) or by visiting the water bodies when males are absent (Cordero-Rivera et al. 1999). Once grasped, they can also refuse to bring the abdomen in contact with male genitalia, even if males can be insistent (Cordero et al. 1992). In *Phylolestes ethelae*, and endemic species of the mountains of the island of Hispaniola, males commonly grasp females in tandem during the morning, and remain in this position until the night, when they mate and release the female (ACR unpubl. obs.). This is probably the longest precopulatory tandem in the order. In general, however, the tri-dimensional habitat of adult odonates allows females to have greater control over their mating rate. In an extreme case, females of some species have been observed practising sexual cannibalism (Cordero 1992), which is the most dramatic (for the male) way of solving the conflict (Fig. 11.3b). On the other hand, the existence of conflict over mating rate seems to explain the widespread occurrence of female colour polymorphism in odonates (Cordero et al. 1998; Fincke 2004), a topic out of the scope of this chapter (for a review see Van Gossum et al. 2008).

Males of odonates are selected to be efficient in grasping females in tandem, and the structure, size and orientation of their anal appendages seem the result of conflict over mating rate, particularly among the Gomphidae, a family whose males have conspicuous forceps as anal appendages (Fig. 11.6). However, the only experimental study that has addressed this question did not find any pattern of hyperallometry in the grasping apparatus of five species, a prediction from the sexual conflict hypothesis (Córdoba-Aguilar et al. 2015). This topic needs to be studied in a large number of species, and in a phylogenetic context. Other possible ways for males to control mating frequency derive from ethological adaptations. For example, males could search for newly emerged females and force mating, because these females cannot refuse or escape with efficiency. This has been observed in *Ischnura aurora*, whose New Zealand populations consist of males that mate with teneral females (Rowe 1978).

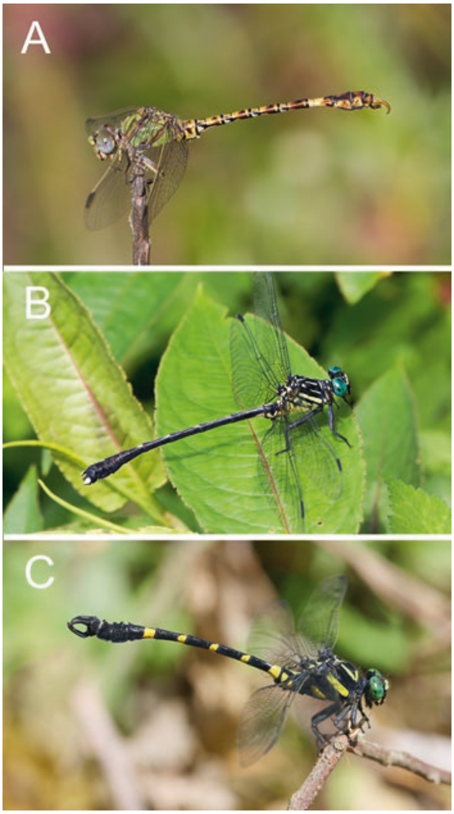

Fig. 11.6 Sexual conflict over mating rates may select for complex and strong "grasping devices" in males, and for "anti-grasping devices" in females. Among the odonates, the family Gomphidae shows the most elaborated anal appendages, whose function as potential sexual conflict adaptations merits further study. (**a**) Male of *Paragomphus genei* (Cáceres, Spain); (**b**) male of *Leptogomphus intermedius* (Nankunshan, China); and (**c**) male of *Lamelligomphus annakarlorum* (Yunnan, China). Pictures by ACR

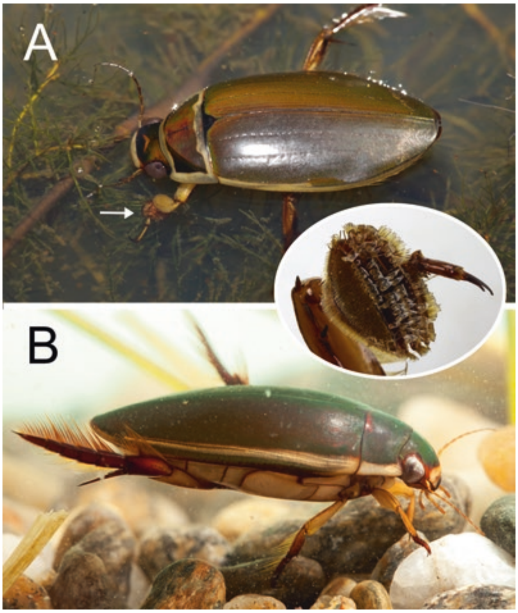

Fig. 11.7 Sexual conflict is evident in the sexually dimorphic forelegs of dytiscid beetles. (**a**) Male of *Dytiscus* in a pond. The arrow indicates the enlarged foreleg, used as a grasping device during mating, and a detail of the adhesive setae of a male *Cybister* (ventral view; the size of the sucker is 2.4 × 3.3 mm). (**b**) Lateral view of a female *Cybister*. Note the absence of modifications in the forelegs. Pictures by ACR

In the case of diving beetles, the situation seems more favourable for the females, as they could control male approaches by hiding easily in the vegetation, or even in the case of extreme male density they could fly away and move to a different water body. Apparently, in some species, there is intense conflict for mating rates, because grasping and anti-grasping mechanisms have been found (Miller 2003). Although little or no courtship behaviour is known, it seems that males could perform acoustic and chemical signals to attract and detect females. Diving beetles produce chemicals for defence and it could be that males also use their chemical senses to detect or attract females (Dettner and Schwinger 1980). In some species, males use stridulatory devices to produce acoustic signals to attract receptive females (Miller and Bergsten 2014).

From the scarce evidence available, we can say that the Dytiscidae show three phases during their reproduction, some divided into subphases. The first phase would be divided into attachment and female resistance, the second in copulation and postcopulatory guarding (see below in the next sections), and finally the release phase, end of copula (Cleavall 2009). In this section, we are concerned with the first phase, attachment and female resistance. These two subphases are the result of the arms war derived from sexual conflict. The males develop sucker-shaped adhesive setae on the pro-tarsomeres, principally (Fig. 11.7). These setae vary in density, number or size, and this fact is not random; the complexity of these sucker setae will go hand in hand with the mechanisms of resistance that the females possess, and these go from modifications of the cuticular surface of the pronotum and the elytra, by dense punctuations, striations or furrows (Miller 2003). In fact, it is possible to establish a parallel classification joining the adaptations of the setae in the males and the surface of the elytra in the females. Sucker setae with three large and smaller cups are related to dense and large punctures on the surface of females' elytra, and furrows on females' elytra co-evolved with setae that have three medium and minute cups or one large and two medium cups (Miller and Bergsten 2014).

11.2.2 Sexual Conflict Over Mating Duration

During copulation, the ability of the pair to move, fly and escape from predators is evidently reduced, and these are only part of the costs of mating (see Daly 1978). Therefore, if there is sexual conflict for copulation duration, the prediction is that both sexes will be continuously under antagonistic coevolution.

Natural selection should favour brief copulations, enough to complete insemination, but sexual selection often favours the opposite. From a natural selection perspective, copulation should be efficient in sperm transfer, and should be completed as soon as possible. However, when copulatory processes are studied in detail, often we discover that insemination occurs at the end of copulation, after several minutes (Cordero-Rivera and Zhang 2018), or even hours (Andrés and Cordero-Rivera 2000). Prolonged copulations can be the result of sperm competition, cryptic female choice or both (Andrés and Cordero-Rivera 2000). In the case of water striders, copulation duration can be highly variable among species. In most cases, copulations are brief, between 5 and 20 min (Arnqvist 1997). In the American water strider *Aquarius remigis*, it lasts for 2–3 h in the laboratory, and insemination occurs at the end (Campbell and Fairbairn 2001). In *A. remigis*, copulations lasting less than 15 min did not produce any viable egg, suggesting that no sperm was transferred during that period of time, whereas "once sperm transfer began, however, virtually the entire sperm load was delivered instantaneously to the female" (Rubenstein 1989). Surprisingly, the European *Aquarius najas* (see Fig. 11.4c) mates for only 1–4 min, but males remain over their mates for weeks (Sattler 1957). It is clear that insemination can be completed in a brief copulation, and the experimental evidence in water striders indicates that copulation duration has high relevance for paternity (Arnqvist and Danielsson 1999).

Some odonates are known for their long copulations (even 7 h; Fig. 11.8) which may be a way for males to guard their mates while still in copula, acting as a living mating plug (Cordero 1990). However, long copulations can be costly for both partners, and conflict is expected. Copulatory processes in odonates are well studied. Copulation starts with a stage I, very variable in duration, which is employed by the male to remove rivals' sperm from the sperm storage organs of the female, and only the last phase is employed for insemination (stage II) (Cordero-Rivera and Córdoba-Aguilar 2010). The damselfly *Ischnura graellsii* mates during the afternoon, and males of this species have apparently evolved the ability to retain their females in copula until the end of reproductive activity (Fig. 11.8), so that females are forced to lay their eggs the day after, at noon (Cordero 1989). Interestingly, its sister species, *Ischnura elegans*, usually mates early in the morning, also for several hours,

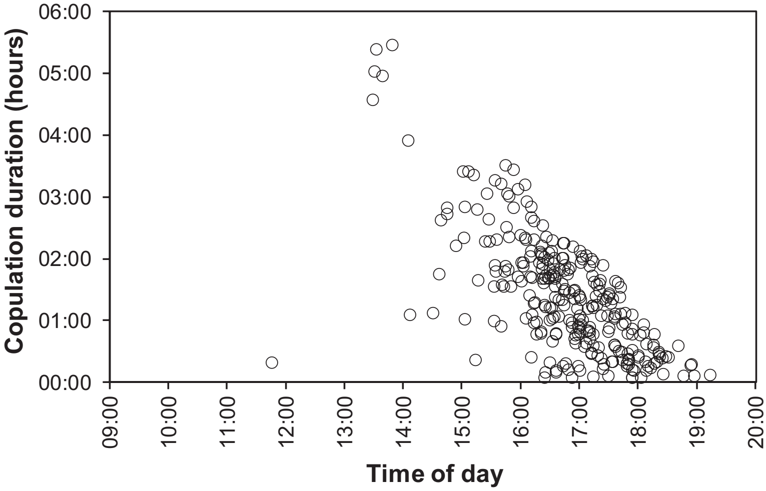

Fig. 11.8 The relationship between time of day and copulation duration in a high-density population of the damselfly *Ischnura graellsii* at Cangas (Spain). Copulation duration ($N = 282$) was estimated as the time between the first and the last observation of marked mating pairs, and in most cases is therefore an underestimation of the whole copulation duration. Note that there is a limit to copulation duration, which in this case coincides with the end of reproductive activity. In this species males control copulation duration, and females are released too late, and therefore are forced to lay eggs the day after. The maximum density of ovipositing females occurs between 12 and 14 h. Source: unpublished data from Cordero-Rivera and Egido Pérez (1998)

and ends copulations by noon, seemingly the best moment for females to lay eggs (Miller 1987a). These two species exemplify contrasting solutions to the same problem by closely related species, by means of interspecific ethodiversity (Cordero-Rivera 2017a). As a by-result, this time separation between the activity of both species contributes also to minimise hybridisation when they are sympatric (Sánchez-Guillén et al. 2014).

Copulation duration has been investigated in detail in many species of odonates, and has been classified as short (less than 1 min), medium (1–5 min) and long (more than 5 min to several hours) (Corbet 1962). The fact that very brief copulations are as effective as copulations that last for hours clearly indicates that copulation duration in many species is not optimised by natural selection. Postcopulatory sexual selection affects copulation duration in odonates, by means of sperm competition and cryptic female choice mechanisms, which usually determine sexual conflict (reviewed by Córdoba-Aguilar and Cordero-Rivera 2008). Sexual selection also affects copulation duration by its interaction with territorial behaviour, and as a consequence territorial species of odonates copulate on average for shorter times than non-territorial ones (Córdoba-Aguilar et al. 2009).

Experimental manipulations in damselflies have shown that copulation duration is under male control (Miller 1987a). Males have sensilla in their genital ligula and are able to detect female mating status, prolonging copulation with mated females compared to virgin females (Andrés and Cordero-Rivera 2000; Uhía and

Cordero-Rivera 2005). Only the pre-insemination phase of copulation is prolonged, suggesting that this is the result of postcopulatory sexual selection (cryptic female choice) rather than natural selection (Andrés and Cordero-Rivera 2000). Previous studies have concluded that the source of conflict is the sperm stored in the spermatheca (Cordero-Rivera et al. 2004), the organ used by females for long-term storage of sperm (see below).

In diving beetles, as we mentioned above, their mating behaviour includes three phases, and in this section we are interested in the second phase, copulation and the transfer of the spermatophore. Copula durations range from 1 to 10 min in species such as *Thermonectus nigrofasciatus* and *Rhantus binotatus* (Cleavall 2009). In contrast, in *Dytiscus alaskanus* copulation varies between 5.4 and 8.3 h (Aiken 1992). In other species, the only information available includes the complete duration of the mating, which includes the three phases discussed above. In this case, a mating event duration would last between 4 and 45 min in species of the genera *Agabus*, *Colymbetes*, *Acilius* and *Rhantus* (Cleavall 2009). Due to the large duration of the mating event, especially in the Dysticinae subfamily, it could be that the females have evolved to a smaller size and thus avoid the risk to be drowned by the male, since these would be able to breathe directly from the water (Madsen 2012) and discard asphyxiation by the male as a coercive strategy.

11.2.3 Postcopulatory Sexual Conflicts

There is a large variation in the association between males and females after copulation. In a classic paper, Parker (1970) showed that the competition between males continues after copulation, by battles between the ejaculates inside the female, a process he named “sperm competition”. He also showed that many postcopulatory behaviours of males could be interpreted as adaptations to reduce sperm competition. In fact, postcopulatory associations between the male and the female are widespread in the insects (Alcock 1994).

Again, if costs and benefits are taken into account, the fact that males remain in close contact with the females, grasping them or in the females’ back, is likely to be costly for females (Figs. 11.3a, 11.4b, c), who probably would benefit by ending the association immediately after copulation. However, in some circumstances, the presence of the male could be beneficial for the female, if the male helps in finding suitable oviposition sites (Byers and Eason 2009), defends the female from the interference of other males (e.g. type II mating of Gerridae, sensu Arnqvist 1997) or helps to detect predators. The duration of postcopulatory associations can be therefore a matter of sexual conflict, and it has been shown to be highly variable among and inside species (Alcock 1994).

As occurred with mating rate, the dimensionality of the habitat can theoretically affect the outcome of this conflict. Many water striders (Gerridae), but also other insects of the water surface, are typical examples of males kleptoparasiting their females, by remaining over their backs for weeks, feeding on the prey that the female has secured. To dislodge their mates, females of water striders use vigorous struggles (Fig. 11.4a), which in some species invariably dislodge the male, but in others do not (Arnqvist 1997). These struggles are clear indicators of conflict over (post)mating duration, but are a risky behaviour: predators are five times more successful capturing struggling pairs compared to single individuals (Rowe 1994). On the other hand, the costs related to carrying the males are likely to be density dependent, because, at high density, other males will try to mount the females if they are successful in dislodging the first male. In fact, in *A. remigis* it has been found that paired females can be more efficient in foraging (85% of efficiency) compared to lone females (32%) precisely because they receive less disturbance by mate-searching males (Wilcox 1984).

In the case of odonates, there is a large variation in the extent of male-female associations after copulation. In a classical paper, Waage (1984) argued that most postcopulatory behaviours could easily be interpreted in the context of sperm competition theory, but also included a cautionary note about other possible functions of postcopulatory mate associations. For instance, males in tandem sometimes adopt a vertical position, which could allow them a better vision over the oviposition substrates and help in detecting potential predators. In this case, both individuals would benefit from the behaviour. The possible behavioural alternatives were recently reviewed as an example of the concept of ethodiversity (Cordero-Rivera 2017a), and are here presented in Table 11.1.

One example of a female behaviour which could be related to cryptic female choice due to sexual conflict is the ejection of sperm after some copulations, provided that the sperm ejected belongs to the last male to copulate with her (Fig. 11.9). This has not been demonstrated with genetic markers, and is a priority for future research. However, the fact that in the laboratory, where female mating history is controlled, females sometimes eject sperm after their first mating agrees with a sexual conflict interpretation via cryptic female choice. The presence and duration of postcopulatory tandem have been associated to male density and disturbance (e.g. Utzeri and Ercoli 2004), and understood as an example of male adaptation to reduce sperm competition. In agreement with this, in some species, males show plasticity in this behaviour, remaining in tandem after copula when rivals' density is high but switching to non-contact guarding at low density (Latty 2006).

The mode of oviposition, including site selection and duration, can also be a source of sexual conflict (Table 11.1). There is apparently a trend from females that are never guarded by males, to others that always lay their eggs in tandem, and this trend seems related to the intensity of male disturbance. In the Libellulidae, the level of male harassment affects female oviposition behaviour, but inconsistently among species (Koch 2006), and there is no evidence for a special female strategy to cope with male disturbance. Perhaps the most extreme case of female behaviour apparently evolved to avoid the negative effects of male disturbance in underwater oviposition (Fig. 11.10), a behaviour which is the rule in some *Enallagma* species (Fincke 1986). If this behaviour has the function to reduce sexual conflict, the expectation is that females would submerge more often at higher male densities. To our knowledge this topic has not been experimentally addressed. However, females

Table 11.1 Alternative behaviours after copulation in the Odonata, with representative examples

Behaviour	Alternative	Example	Reference
Postcopulatory sperm ejection	Never	*Hemiphlebia mirabilis*	Cordero-Rivera (2016)
	Occasional	*Ischnura graellsii*	Pers. obs.
	Common, almost immediately after copulation	*Enallagma praevarum*	Córdoba-Aguilar (2006)
Postcopulatory tandem duration	Absent	*Pseudolestes mirabilis*	Cordero-Rivera and Zhang (2018)
	Short (<1 min)	*Ischnura graellsii*	Cordero (1989)
	Medium (1–10 min)	*Sympetrum internum*	Latty (2006)
	Long (>10 min)	*Lestes virens*	Utzeri and Ercoli (2004)
Postcopulatory courtship	Absent	*Ischnura graellsii*	Cordero (1989)
	Depending on male strategy	*Diastatops obscura*	Bañuelos Irusta and Araújo (2007)
	Common, almost always after copulation	*Calopteryx haemorrhoidalis*	Córdoba-Aguilar (2000)
Oviposition mode	Female alone, not guarded	*Anax imperator*	Corbet (1957)
	Female alone, non-contact guarding	*Calopteryx maculata*	Alcock (1979)
	In tandem	*Lestes sponsa*	Stoks et al. (1997)
	Male and female submerge	*Pseudagrion pilidorsum*	Matsubara and Hironaka (2005)
	Submerged, male guarding out of water	*Hetaerina vulnerata*	Alcock (1982)

Some alternatives are clearly more favourable for males' interests (e.g. prolonged postcopulatory tandem), and others for females (e.g. sperm ejection), suggesting that postcopulatory sexual conflict is common in the order

of some species do submerge to oviposit, even at very low male density, or in the complete absence of males, like parthenogenetic females of *Ischnura hastata* at the Azores (Fig. 11.10b, c; Lorenzo-Carballa et al. 2009). Furthermore, in some species both the male and the female submerge to oviposit (e.g. Matsubara and Hironaka 2005). It seems therefore premature to interpret that underwater oviposition is a result of postcopulatory sexual conflicts. Alternative explanations are to avoid the risk of eggs drying due to changing water levels, or even to escape from egg parasitoids (Santolamazza et al. 2011).

In diving beetles, there is a high complexity in the female reproductive tract and a diverse array of sperm morphology (Miller and Bergsten 2014). As expected by sexual conflict theories, both the modifications of the reproductive tract and the great variety of morphology in the sperm seem to have evolved due to an arms race. Therefore, for the female these modifications of the tract would allow long-term sperm storage and then make a selection of sperm, and consequently a high control over paternity (i.e. cryptic female choice). The common disposition of the

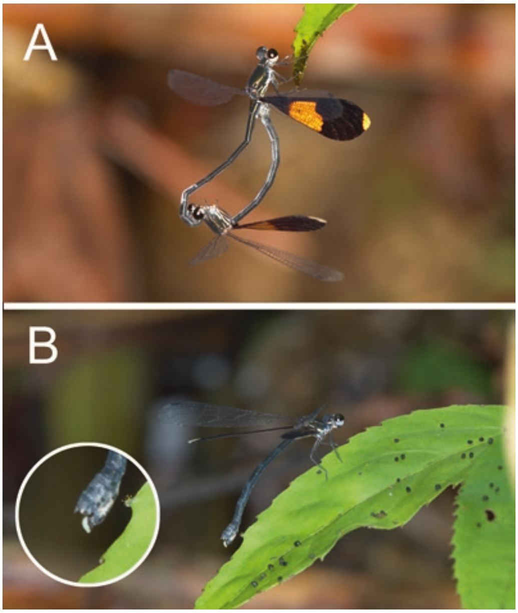

Fig. 11.9 Postcopulatory sexual conflicts can be subtle, like the ejection of sperm after copulation. In odonates this behaviour is known in several species and can be labelled as "cryptic female choice" (Córdoba-Aguilar 2006). (**a**) The figure shows a mating pair of *Pseudolestes mirabilis* (Hainan, China), and (**b**) the female perched after copulation, ejecting sperm (see detail in the insert). Source: Cordero-Rivera and Zhang (2018). Pictures by ACR

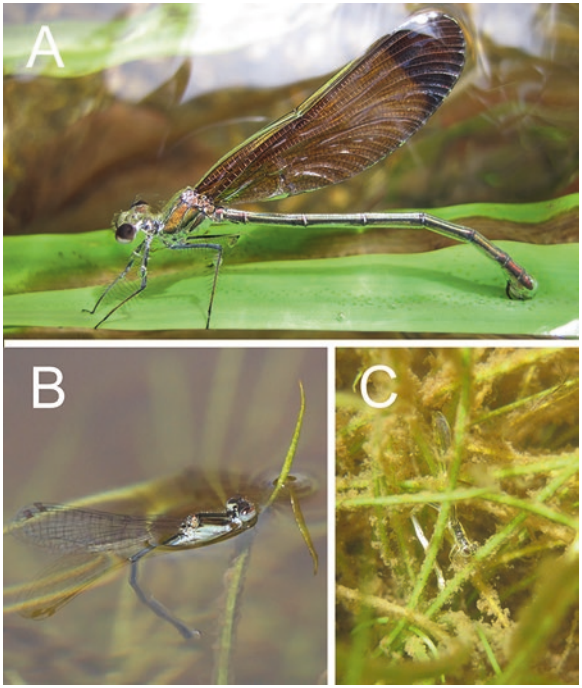

Fig. 11.10 Male disturbance is a source of conflict after copulation, if females are accessible to mate-searching males during oviposition. Underwater oviposition (**a**; *Calopteryx haemorrhoidalis* from Pontevedra, Spain) could be a female adaptation to cope with unwanted male mating attempts, but other explanations, not related to sexual conflict, are also possible. For instance, parthenogenetic females of *Ischnura hastata* from the Azores islands frequently oviposit underwater, in the absence of males (**b** and **c**), although sometimes are harassed by males of *Ischnura pumilio*

reproductive tract is in loop with two genital openings (Heberdey 1931). One of the openings receives the spermatophore and is named *bursa copulatrix*. From this bursa, a spermathecal duct leads to the spermatheca and from this a fertilisation duct to the vagina near the oviduct (see Miller and Bergsten 2014). Therefore, we are facing a decoupling between the site of fertilisation and oviposition, allowing the female this cryptic choice. Miller (2001) was the first to establish a Dytiscidae female internal genital morphology classification, based principally on the number of genital openings, “Amphizoid type” and “Hydroporine type” with two genital openings, and “Dytiscinae type” with a single genital opening. Therefore, the main differences between Dytiscidae subfamilies, Hydroporinae and Dytiscinae, might be associated with the importance that pre-insemination or post-insemination systems would acquire, the latter being the most complex in the Hydroporinae subfamily, both in females and males, as we will see below.

Then, as mentioned above, the diving beetles are within an arms race and therefore females seem to counteract the sperm competition mechanisms by their cryptic female choice abilities. These adaptations are reflected in both the external and internal genitalia of the male. In external genitalia several species have spines or sawlike structures (Sharp and Muir 1912). On the other hand, it has been found conjugation (Higginson and Pitnick 2011) and/or heteromorphism on sperm morphology (Higginson et al. 2012a). Dytiscidae diving beetles have different degrees of conjugation (i.e. two or more spermatozoa physically unite for transport in a female reproductive tract): simple conjugation (two sperm heads unite), medium conjugation (aggregation of multiple sperm heads) and complex conjugation or “rouleaux”. However, in some cases sperm is found solely too, named as singleton (Higginson et al. 2012b). Apart from co-occurrence with conjugation, diving beetles also show sperm heteromorphism (i.e. the simultaneous production of more than one type of sperm) that is manifested by head shape and sperm length (Higginson et al. 2012a), which in other organisms is associated to sperm competition mechanisms (for a review, see Cordero Rivera and Córdoba-Aguilar 2016).

In addition to the adaptations concerning the internal and external genitalia of both sexes, it has been found that some *Dytiscus* species produce a mating plug in the apex of the female abdomen (Aiken 1992) that remains attached to the female during long periods after fertilisation, a strategy that is believed to be used in male-male competition for paternity.

11.2.4 Sexual Conflict and Genitalia

The change in paradigm that occurred in sexual selection studies in the last decades (Fig. 11.1) was in fact initiated when the relationship between animal genitalia and sexual selection became evident, with the pioneering work by William Eberhard (1985). The recent review of the field has found extensive support for the sexual selection hypothesis as the main driver of genital evolution (Leonard and Córdoba-Aguilar 2010). However, the relative importance of sperm competition and cryptic female choice, and the associated sexual conflicts, remains controversial, and particularly understudied in vertebrates (Brennan and Prum 2015).

One prediction from the sexual conflict hypothesis is that it leads to sexually antagonistic co-evolution at the genital level, where each sex is selected to advance control over mating and fertilisation, and as a consequence there is a co-evolutionary arms race (Brennan and Prum 2015).

The relationship between sexual conflict and genital evolution has been reviewed recently in insects (Simmons 2014), and in-depth discussions exist for several taxa, including water striders (Arnqvist 1997), odonates (Córdoba-Aguilar et al. 2003; Cordero-Rivera and Córdoba-Aguilar 2010) and water beetles (Miller and Bergsten 2014). Therefore, here we concentrate in a few clear examples, and suggestions for future experiments.

Distinguishing between hypotheses of genitalic sexual selection is extremely difficult, due to the interactions between males and females and the fact that the same prediction can be derived from different hypotheses, like sexually antagonistic co-evolution and cryptic female choice (Eberhard 2010). In the context of this review, the most relevant pattern is the diversity and rate of evolution of genitalia when compared with other traits. Genitalia evolves much faster (Eberhard 1985), and this needs an explanation. In the Gerridae several studies have shown that genitalia is under sexual selection, and that the form of particular male sclerites is related to fertilisation success, easily interpreted as the result of variable ability among males in sperm competition, mediated by female phenotype (i.e. cryptic female choice) (Arnqvist and Danielsson 1999). There is also evidence that genitalia may evolve by sexually antagonistic co-evolution (Perry et al. 2017).

In the odonates, there is good knowledge of functional morphology of copulation, especially after the work of Peter Miller (1987a, b). The form of the genital ligula is characterised by the presence of apical and lateral lobes and horns, and by a variable amount of backwards-oriented spines, which are used to trap and remove sperm from the previous mates of the female (reviewed by Córdoba-Aguilar and Cordero-Rivera 2008; Cordero-Rivera and Córdoba-Aguilar 2010). These spines in the intromittent organ could also function as copulatory weapons, known in other insects (Reinhardt et al. 2014), and merit further study. If during copulation males damage the internal genitalia of females, there could be an arms race and sexually antagonistic co-evolution.

In the European genus *Calopteryx*, common in rivers and streams (Fig. 11.3c), this sexual conflict over control of sperm reserves can be experimentally studied by using "hand-pairing" (Opphenheimer and Waage 1987), a technique which allows obtaining even interspecific matings. If females co-evolve with conspecific males at the genital level, heterospecific males should have an advantage when interspecific matings occur because females will show less resistance to them than to conspecific males. This is what Cordero-Rivera (2017b) found when *Calopteryx haemorrhoidalis* and *C. splendens* were hand-paired, and it is the first experimental evidence in odonates for such a sexually antagonistic co-evolution in the genitalia (Fig. 11.11).

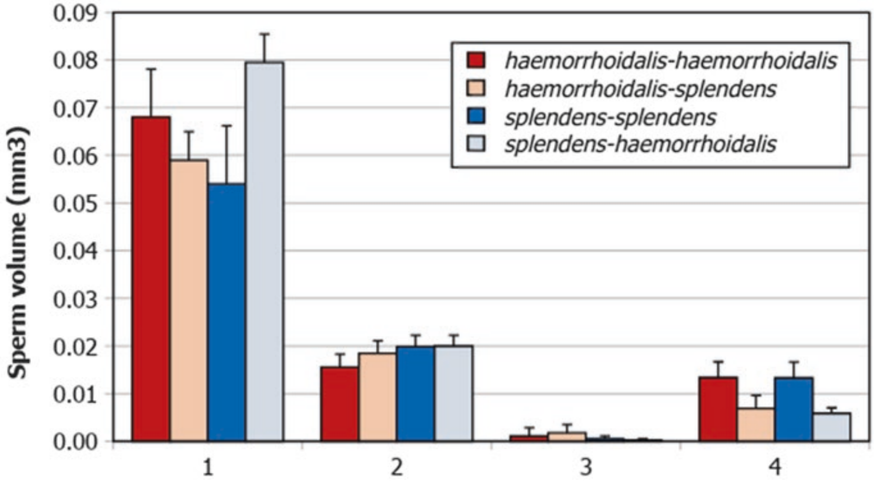

Fig. 11.11 The volume of sperm in the *bursa copulatrix* and spermatheca of double-mated females after conspecific and heterospecific matings (postcopula treatment; the male species is indicated first in the legend), compared to the volume stored by females mated to a conspecific male and then to a conspecific or heterospecific male, but interrupted after 60 movements of stage I, before insemination. The volume of sperm in the *bursa* was reduced by 98–100% in all cases. The volume of the spermatheca in intraspecific matings was reduced by 14% in *Calopteryx haemorrhoidalis* and by 26% in *C. splendens*. In contrast, volume reduction was 63–69% in heterospecific matings. These results indicate that females have more control over spermathecal sperm when mating with a conspecific male (i.e. there is sexually antagonistic co-evolution). Source: Cordero-Rivera (2017b)

11.3 Conclusions and Suggestions for Future Work

Our review of the literature about three groups of aquatic insects is consistent with our working hypothesis about the dimensionality of the habitat as a modulator of male ability to control reproductive decisions. The existence of complex grasping apparatus in some species suggests that sexual conflict is behind the evolution of these characters. We propose that, in the odonates, the family Gomphidae is a priority for future work, given their elaborated male anal appendages (Fig. 11.6). Unfortunately, the study of gomphid behaviour is lagging behind other odonate families, probably because they are rarely seen in mating. In diving beetles, some subfamilies are more affected by the modifications that derive from the pre-copula phase (i.e. Cybistrinae and Dytiscinae), others from the post-copula phase (i.e. Hydroporinae) and other subfamilies that are at a morphological and behavioural intermediate point (Miller and Bergsten 2014). Thanks to this fact, the Dytiscidae beetle family gives us the opportunity to study the sexual conflict and its gradient, in the different phases of sexual behaviour. However, nearly all the phases of reproductive behaviour, and particularly of copulation in this group, require further investigations (Miller and Bergsten 2014).

Other aquatic insects are promising for future work in this field. For instance, in the water bugs of the family Nepidae, male genitalia has a pair of parameres with a hook (Keffer 2004), and we hypothesise that these could have evolved as adaptations to grasp females for copulation. In the Megaloptera, there is good evidence for a trade-off between elaborated weapons and size of nuptial gifts (Liu et al. 2015), and they are another group worth studying from a sexual conflict perspective. The whirling beetles (Gyrinidae) live, as water striders, on the water surface, and are also constrained to a bi-dimensional habitat (although they can also dive). Sexual selection can therefore be intense, at least on some organs (e.g. Fairn et al. 2007). More studies of morphological and ethological adaptations that can be used by males to try to monopolise females and also a detailed analysis of female counter-adaptations are needed to obtain a balanced view of conflict resolution (Ah-King et al. 2014).

In relation to copulation duration, we have good information from the Gerridae and many families of odonates, but for diving beetles information is scarce. Morphological studies have been completed in many genera, but without an ethological perspective the picture is clearly incomplete. The possibility that sexual conflict over mating duration has selected for smaller body size in females, allowing them to breathe directly from the water (Madsen 2012), is a suggestion for future investigations. It must be noted that this hypothesis predicts that females should be smaller at increasing intensity of sexual conflict over mating duration. Species with very long copulations (Aiken 1992) are particularly interesting in this context. Other aquatic insects, like Corixidae, Notonectidae and Aphelocheiridae, some of which obtain the oxygen from the water, should also be studied to detect sexual conflicts.

In some species, sexual conflict has apparently resulted in the evolution of aggressive copulation by males, whose intromittent organ has evolved as a wounding device, resulting in extreme sexual conflict (Reinhardt et al. 2014). The genital ligula in male odonates has a diverse form and commonly is covered by spines, which are thought to be devices to trap and remove rivals' sperm (Córdoba-Aguilar et al. 2003). However, its function as wounding devices has to be studied, and the same can be applied to other aquatic insects (i.e. the aedeagus of *Dytiscus*; see Guignot 1933). Although not an aquatic taxon, the genus *Neotrogla* (Psocodea: Prionoglarididae) from Brazilian caves is an excellent model of study because it shows reversed genitalia, with female penis, male vagina and females that mount males and that control copulations that may last for 40–70 h (Yoshizawa et al. 2014), likely resulting in extreme sexual conflict. The ecological pressures that are behind the evolution of this sex-role reversal might also apply to other taxa.

The field of postcopulatory sexual conflicts, derived from sperm competition and cryptic female choice mechanisms, is another priority for future research. It is known that some odonate females eject sperm after copulation (Fig. 11.9), but this behaviour is so cryptic that probably it is much more common than previously thought. A comprehensive review of this behaviour is needed, and an experimental approach with genetic markers is an absolute priority to know if this behaviour is a consequence of sperm competition (the sperm ejected is the amount removed by the last copulating male; e.g. Lindeboom 1998) or is cryptic female choice in action (Córdoba-Aguilar 2006). Furthermore, do Gerridae females or diving beetles eject sperm after copulation? We could not find any reference to this behaviour in the surveyed literature.

The behaviour of males and females after copulation can also be affected by sexual conflict. We have discussed the strategy of underwater oviposition in female odonates, and the same could be applicable to insects of the water surface. Gerridae females sometimes lay eggs underwater. Is this behaviour related to male disturbance, as expected from sexual conflicts? Or other natural selection pressures, like avoiding egg parasites (e.g. Amano et al. 2008), or the presence of a helping male in tandem (Hirayama and Kasuya 2008), are more relevant? In diving beetles, there is evidence for arms races between male and female genitalia (Miller and Bergsten 2014), and the existence of mating plugs (Aiken 1992) seems easily interpretable as an example of a male adaptation to control fertilisation, which can generate a sexual conflict. If so, mating plugs should be more common in species with high-density populations, where the encounter rate between sexes is high.

The study on sexual selection, sexual conflict and mating behaviour, among others, was based on beliefs and stereotypes that are far from a feminist vision (i.e. equality). Since Darwin proposed that females were timid per se, that idea further fuelled a male-centred stereotype, which even today persists in many minds both in men and women (Ah-King et al. 2014). The influential work of Darwin was used as a justification by contemporary researchers to maintain stereotyped thinking about female behaviour, to such an extent that they came to question the mental abilities of females to choose their mates (Milam 2010). Like the snake that bites its own tail, the assumption that the role of the female in sexual selection or in sexual conflict is merely the one of a secondary protagonist, or not even that, but as a simple spectator leads to the belief that it is difficult to study female genitalia. But that belief loses all its validity with the modern technologies, or just with an unbiased review of the taxonomic literature (e.g. Eberhard 2006). In fact, there are no biological reasons for this lack of studies of female genitalia and behaviour, and the bias does not depend on the gender of the investigator (Ah-King et al. 2014).

We conclude that a comprehensive understanding of sexual conflicts in animals requires the study of both male and female anatomies, as well as their behaviours, avoiding previous assumptions, or stereotypes. Conflict appears when two individuals are involved, a conclusion that a priori seems obvious, since the same word conflict implies two or more individuals, so it does not make sense to study only one part. A balanced study of this field requires a more egalitarian approach, i.e. a feminist view of the science (Ah-King et al. 2014).

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