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Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives

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Evolução e Ecologia de Calopterygidae (Zygoptera: Odonata): Conhecimento Atual e Perspectivas de Pesquisa

RESUMO - Neste artigo revisamos estudos sobre evolução e ecologia da família Calopterygidae. Os adultos são reconhecidos pelas asas pigmentadas e comportamento territorial. Três gêneros têm sido bem estudados: *Hetaerina, Calopteryx* e *Mnais*. As larvas desenvolvem-se em ambientes aquáticos e a seleção opera principalmente nesse período, resultando em indivíduos de grande massa muscular. Os adultos levam alguns dias para se tornarem sexualmente maduros e durante esse período alimentam-se extensivamente acumulando as reservas de gordura que consumirão para voar e produzir ovos. Entretanto, gregarinas parasitas podem consumir essas reservas. Os machos utilizam duas estratégias de acasalamento que podem ser determinadas geneticamente (*Mnais*) ou ambientalmente (*Calopteryx* e *Hetaerina*): territorialidade e não-territorialidade. No gênero *Mnais* as estratégias comportamentais parecem ser balanceadas de acordo com sua adaptabilidade ao longo do tempo. Os machos de*Calopteryx*, *Mnais* e *Phaon* realizam corte pré-cópula, comportamento ausente em *Hetaerina*. A pigmentação das asas dos machos parece sinalizar às fêmeas, durante a corte, algum nível de resistência imunológica a parasitas. Durante a cópula os machos retiram o esperma armazenado em cópulas anteriores pelas fêmeas. Há grande variação na habilidade e nos tipos de mecanismos para a retirada do esperma, assim como na morfologia genital de ambos sexos. Tal variação pode resultar de co-evolução entre os sexos direcionada a controlar o esperma armazenado. Após a cópula os machos defendem as fêmeas evitando que elas copulem com outros machos. Nessa revisão sugerimos aspectos a serem estudados nessa família.

PALAVRAS-CHAVE: Reserva de gordura, pigmentação alar, capacidade imune, coevolução de genitália

ABSTRACT - We review the studies of evolution and ecology in the Calopterygidae. Adults are easily distinguished for their pigmented wings and territorial behaviour. Three genera have been well studied: *Hetaerina, Calopteryx* and *Mnais*. Larvae develop in riverine aquatic environments. Selection operates at this stage to produce large muscle mass for adults. The adult spends some days until sexually ready. During this time, it feeds extensively to produce muscle fat for egg production and flight. However, gregarine parasites may ingest the fat reserves. Males may use two mating tactics or strategies that may be genetically (*Mnais*) or environmentally (*Calopteryx* and*Hetaerina*) determined: territoriality and nonterritoriality. In *Mnais*, these strategies appear balanced in fitness terms. Males of *Calopteryx*, *Mnais* and *Phaon* show a precopulatory courtship that is not the case for *Hetaerina*. Male wing pigmentation seems to signal how good the male is to deal immunologically with parasites to females during the male courtship. During copulation, males displace the sperm the female has stored in the storage organs from previous matings. There is an enormous variation in male sperm displacement mechanisms and ability, and in genitalic morphology in both sexes. This variation possibly results from a coevolutionary game between the sexes to control stored sperm. After copulation, males guard females apparently to avoid that other males take the female in copulation. Our review suggests sources for research in this family.

KEY WORDS: Fat reserve, wing pigmentation, immune ability, genitalic coevolution

Odonates have been used as models in the study of ecology, evolution and behaviour since the 1950's (for a review see Corbet 1999). A number of hypotheses have been tested using them which is due to their practical characteristics: a) a relatively large body size; b) easy for manipulation both in the field and in the laboratory (which is not necessarily the case for Calopterygidae); and c) faithfulness of adults to the reproductive sites. For these reasons, it is not surprising that significant advances in pragmatical issues such as mark-recapture studies, mating systems, alternative mating strategies, sperm competition, immunocompetence, foraging competition, male and female polymorphism have been achieved using odonates.

Within odonates, one of the families that have been most intensively studied, especially at the adult stage, is Calopterygidae. We have very good data on the European representatives of this family, and their biology has been recently reviewed (Rüppell *et al.* 2005). The family is widely distributed in all continents, excepting Australia and New Zealand, inhabiting rivers and streams (Silsby 2000). Possibly their only limit is low temperatures. In this paper we summarize the results of different studies of calopterygid evolution and ecology and suggest possible aims for future research. After introducing generalities on Calopterygidae, we have used a "life cycle" outline and as such we have divided this review in three instances: pre-, syn and post-reproductive pressures.

Generalities of Calopterygidae

This family is composed of three subfamilies: Caliphaeinae (the clearwings), Calopteryginae (demoiselles), and Hetaerininae (the rubyspots mainly). Most calopterygid males can be distinguished by the absence of pterostigmae while females have white spots named pseudostigmae instead of pterostigmae. Both sexes have strikingly iridescent metallic body colors (particularly at young and not too old stages) with some species bearing unique male wing pigmentation patterns (see Silsby 2000). It is a well-distributed family both in temperate and tropical habitats and males are very active in sunny conditions. It has 16 genera with approximately 161 species. Our knowledge of the evolution and ecology of these animals comes, unfortunately, mainly from only three genera – *Hetaerina*, *Calopteryx* and *Mnais* (Fig. 1a-d) – and, therefore, a few species (possibly not more than 16).

The Larval and Adult Pre-Reproductive Stage

Similar to other odonates (see Corbet 1999), the calopterygids spend some time as aquatic larvae. Very little is known as for how long this stage lasts. Given that calopterygids occupy places that go from temperate climates

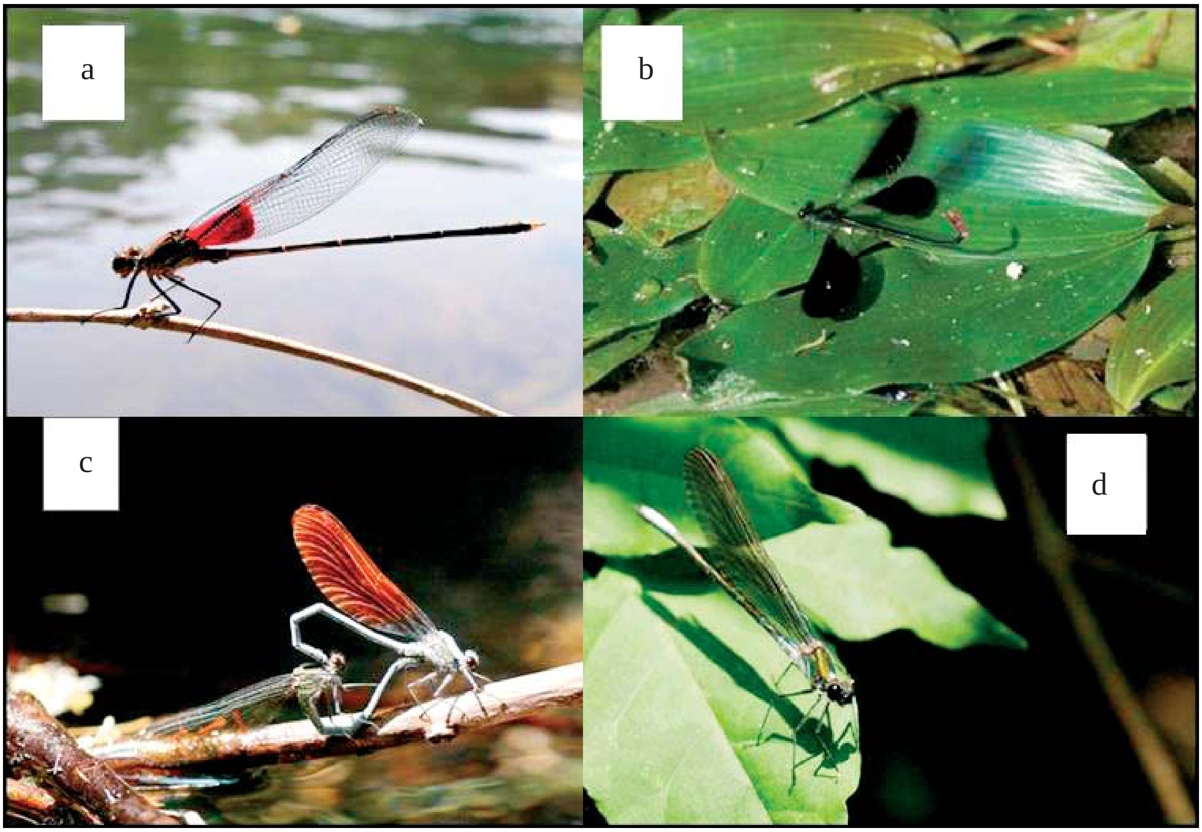

Fig. 1. *H. americana* male (a), a *C haemorrhoidalis* male displaying his wings over *Potamogeton* on the river bank in the absence of current (b), *M. pruinosa* orange (territorial) male in copula (c), *M. pruinosa* hyaline (nonterritorial) male (d).

with marked seasonality to tropical climates with supposed constant conditions, there must be considerable inter-specific variation in the larval period duration. This topic needs to be investigated further.

There should also be intra-specific differences considering those temperate species in which some individuals are likely to develop and emerge in the same season while others enter in diapause to emerge until the following year. For instance, in *C. haemorrhoidalis*, samples obtained during five consecutive years from a permanent stream in the Sierra Morena Mountains, southern Spain, are consistent with the population being mainly univoltine, a few individuals being semivoltine, and the life cycle being predominantly of the summer-species type (Ferreras Romero*et al.* 2000).

Current studies in other odonates have uncovered a great array of life history strategies that allow animals to deal with seasonal changes (e.g. Mikolajewski *et al.* 2005, Dmitriew & Rowe 2005, Suhling *et al.* 2005). These studies indicated, for example, that larval duration changes adaptively in relation to biotic and abiotic factors so that the animals can survive, grow and reproduce successfully. Although multivoltinism has not been documented in calopterygids as a response to environmental opportunities, the fact is that most calopterygids studied are from temperate regions where multivoltinism is less likely to occur as the reproductive season is very short (Corbet 1999). The few records of calopterygid larval ecology found that there is intense selection for large flight muscle mass that is heavily affected by diet (Plaistow & Siva-Jothy 1999). Diet also affected fat reserves at emergence and accelerated development reducing body size but not larval survival (Plaistow & Siva-Jothy 1999). How larvae compete to accrue these advantages remain to be investigated.

Previous to finish the larval stage, the animal stops feeding and takes some days to get ready for the final moult (Corbet 1999). Following emergence, the animal has very little fat (e.g. Marden & Waage 1990, Plaistow & Siva-Jothy 1996), which will be extremely important for reproductive activities (Plaistow & Siva-Jothy 1996, 1999). It has a pale aspect, a weak flight and both the exoskeleton and wings have not hardened yet. At this stage, also called teneral, and in the following days the adult calopterygid devotes its time to feeding mainly (Kirkton & Schultz 2001).

Similar to other odonates, calopterygids are easy prey to any visual predator (Corbet 1999). Teneral calopterygids feed on small prey (usually no larger than their mouth parts) such as Chironomidae and Culicidae (Higashi *et al.* 1979). The length of the teneral stage has been estimated to last between one to two weeks, depending on the species and population (Table 1). The function of this period is to complete sexual maturation in both sexes and this includes

Table 1. Estimates of maturation, survival and maximum longevity in calopterygids.

Species	Maturation (in days)	Daily survival rate		Maximum longevity (in days)		Reference
		Males	Females	Males	Females	
C. aequabilis	5.1	0.77 ± 0.7	0.7 ± 1.053	32	22	Conrad & Herman 1990
C. atrata		0.63[1]	0.67[1]	28	34	Miyakawa 1982
C. cornelia				52	40	Suzuki & Tamaishi 1981
C. haemorrhoidalis	10			29		Heymer 1972
	9	0.91 ± 0.120	0.92 ± 0.140	40	21	Cordero 1989
		0.94 ± 0.047	0.89 ± 0.032	43	30	
		0.84 ± 0.035	0.86 ± 0.047			Cordero 1999
		0.94	0.94			Beukema 2002
C. japonica	11	0.60[1]	0.65[1]	26	32	Muyakawa 1982
	5	0.82 ± 0.09	0.93 ± 0.02	> two weeks	> two weeks	Watanabe *et al.* 1998
		0.87 ± 0.06	0.87 ± 0.05			
C. maculata	11			37[2]		Waage 1972, 1973
C. splendens	1-4					Buchholtz 1955
C. virgo		0.86 ± 0.046	0.95 ± 0.077	36	24	Cordero 1989
	1-3			41		Klötzi 1971
C. xanthostoma		0.66 ± 0.176	0.89 ± 0.223			Cordero 1989
H. cruentata	15-18[3] 12[4]	0.98				Córdoba-Aguilar 1993, 1994
M. nawai				53	41	Suzuki &Tamaishi 1981
M. pruinosa	10	0.94				Higashi 1976, 1982
		0.94-0.95	0.96			Nomakuchi *et al.* 1988
				60		Tsubaki *et al.* 1997

the acquisition of the adult color, mass and fat reserves. In odonates, most fat is deposited in the thorax in males that is more similarly distributed between thorax and abdomen in females (Anholt*et al.* 1991). This disparity is likely to have an adaptive explanation for two functions that are differently used in both sexes: males require fat for flying (which is the activity to which they devote most energy) while females may divert some of this to egg manufacturing (Anholt *et al.* 1991). It would be interesting to test this with experimental manipulations in calopterygids in which there is intense selection for heavy and fat males (Plaistow & Siva-Jothy 1996, 1998) compared to nonterritorial odonate species. For example, it would be interesting to see how males and females allocate fat resources under severe food shortage conditions. Also, since it would be expected selection to minimize the time as teneral (to have more time to be devoted to reproduction), it would be interesting to see whether the intra- and inter-specific differences observed in the duration of this stage are due to weather conditions which may reduce feeding opportunities or warming of the body (Corbet 1999) or to biotic pressures that result also in time differences. The male polymorphism observed in some *Mnais* species, with territorial and non-territorial males, makes this genus especially appropriate for such an investigation.

One heavy pressure factor in this last respect is gregarine (Protozoa) parasites (Fig. 2a). These are intestinal parasites that get attached to and aggregate in the posterior gut region of the adult calopterygid where they develop and reproduce by using the odonate's ingested food (Åbro 1971, 1974; Siva-Jothy & Plaistow 1999). Studies in several *Calopteryx* species have shown that gregarines are a major selective factor causing a considerable negative impact on male and female adult fitness (e.g. Åbro 1987, 1990; Siva-Jothy & Plaistow 1999). Gregarines affect longevity and survival mainly (Córdoba-Aguilar 2002a, Córdoba-Aguilar *et al*. 2003a). Adult calopterygid life-span is about one month (Table 1), but there are no studies that test the effect of gregarines on longevity. Furthermore, it is not known which proximate factors gregarines affect. Some possibilities, which are not mutually excluding, are: a) that the damselfly starves as the ingested food is used by the parasite (Åbro 1987, 1990); b) that the mode of gregarine attachment to the intestine may allow the entry of infective agents (such as bacteria and fungi) to the rest of the damselfly body (Åbro 1987, 1990); c) that an excess of resources are devoted to immune defense instead of other functions (Siva-Jothy 2000, Córdoba-Aguilar 2002). These three possibilities may cause a delay in the teneral period as the damselfly may need a longer time to reach sexual maturity. Given, however, the role of fat body in dealing immunologically with parasites (e.g. Hoffman & Reichhart 1997), there are different situations a damselfly may face in terms of development according to a gregarine infection. In these different situations animals should allocate resources as predicted by life history theory (e.g. Williams 1966, Roff 1982, Stearns 1992) and parasite attack (Sasaki & Godfray 1999, Fellowes & Godfray 2000,

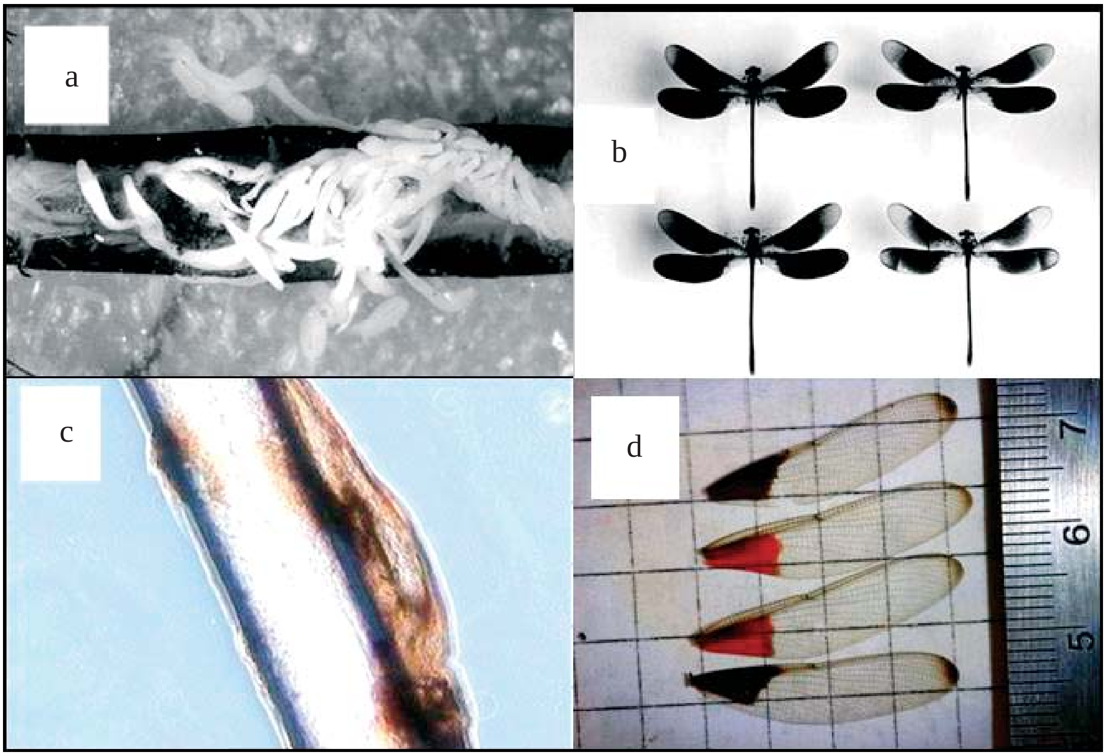

Fig. 2. A dissected *Calopteryx* abdomen showing gregarine parasites as enlarged structures (a), wing pigmentation variation in *C. haemorrhoidalis* males (b), a nylon implant that was inserted in the abdomen of a *H. americana* male, covered with melanine (c), wing pigmentation in *H. titia* (d).

Joop & Rolff 2004). In the absence of parasites, it would be expected that the animal devote its resources to reach sexual maturity in a short time. Consequently, survival will be high as the resources are entirely devoted to non-immune functions and are not sequestered by the parasite either. The time spent as teneral, however, will increase if the possibility and actual gregarine infection increases either. This would occur as an outcome of allocating more resources to immunity and food resources being used by the gregarines. In this case, a negative relationship between parasite number and survival will be detected. In an extreme situation of heavier parasite infection, there would be a point at which the cost of immune defence may be so high that the host avoids any further investment to immune defence and allocates what is possible to reach sexual maturity and increase survival. Probably, the animal would live less but will still have time to reach sexual maturity. Obviously, these different situations assume that food access is similar under any situation. These have not been tested. The only related source of evidence indicates that the enzyme phenoloxidase which is directly linked to immune ability in insects, was positively selected in a year in which gregarine load was very high in a *Calopteryx xanthostoma* Charpentier population (Rolff & Siva-Jothy 2004).

Of the most conspicuous changes that calopterygids go through during the teneral stage is the color acquisition for wings, thorax and abdomen. In males, the animal gets a metallic appearance in the thorax and abdomen as well as pigmented wings. It is not known how long the animal takes to finish deposition of body and wing color. The wings of *C. xanthostoma* and *C. haemorrhoidalis* Vander Linden acquire their full coloration after 5 and 10 days respectively (Dumont 1972, Heymer 1973) which in *Calopteryx atrata* Selysand *C. splendens* Harris is achieved in a few hours (Sugimura 1993 in Corbet 1999; and Dumont 1972, respectively). However, given the evidence of the effect of diet on pigmentation (Hooper *et al.* 1999, Fitzstephens & Getty 2000), there is the need of more studies as, surely, there must be inter-individual variation in this parameter. It is likely that the rate at which wing pigmentation is deposited may be affected by gregarine burden in *Calopteryx* since the immune response used for dealing with these parasites is based on the melanine protein (Siva-Jothy 2000), which is actually the same protein used for wing pigmentation (Hooper *et al.* 1999).

There is great color pattern variation among and within (also between and within sexes) calopterygid species (Silsby 2000; Figs. 1a-d). In *Calopteryx*, for example, wings appear as darkened patterns covering most wing surface in some species (Fig. 1b) while in *Hetaerina*, wings have a basal red spot which do not cover more than 40% of the wing (Fig. 1a) except for *Hetaerina titia* Drury, Johnson 1963; Fig. 2d). In *Mnais*, one male morph has orange-pigmented wings while the other male morph has clear wings (Hooper *et al*. 1999; Figs. 1c-d). In *Phaon iridipennis* Burmeister, both sexes have hyaline wings (Miller 1985). Very little is known about the pigment products that are involved in the calopterygid colors. Studies in *Mnais* indicate that wing color is caused by melanine (Hooper *et al*. 1999). In *Calopteryx maculata* Palisot de Beauvois, the lamellae that compose the epicuticle are more compressed and show a short wavelength reflectance in young males compared to old ones (Fitzstephens & Getty 2000). This indicates that color tends to become less intense (at least to the human eye) with age. This change correlates with fat stores as was experimentally found by Fitzstephens and Getty (2000) by varying diet. This suggests a possible physiological relationship between the lamellae responsible of color and diet. Related to this, in *Mnais pruinosa costalis* Selys, males provided with a rich diet maintained high levels of pigmentation intensity compared to males with a poor diet (Hooper *et al*. 1999). As for the amount of pigmentation, frequently, however, it is found that males differ in how much of this is deposited on their wings (Fig. 2b). Males may have small spots devoid of pigmentation on their wings (Siva-Jothy 1999, Rantala *et al.*2000). This variable does not change with age (Córdoba-Aguilar 2002a). These two aspects of pigmentation - area and color intensity - may reflect different aspects of the animal condition. Possibly, body color intensity reflects the immediate condition such as how much it has been ingested (also see Fitzstephens & Getty 2000). In this way, how much fat stored has been acquired in the adult stage may be signaled by the body color. On the other hand, the quantity of wing pigmentation may partly reflect how much food has been obtained during the larval stage given that deposition of pigment starts taking place immediately after the adult emergence (Córdoba-Aguilar 1993) so that resources from the larval stage may be needed for pigment elaboration (Siva-Jothy 1999, 2000).

Color differentiation with age is more striking in males than females. In fact, sexually active males look less similar to the teneral stage compared to sexually active females to their teneral stages. Interestingly, in *C. haemorrhoidalis*, teneral males start with wing pigmentation patterns very similar to fully mature females (A. Córdoba-Aguilar, unpub. data). These patterns are difficult to explain. One possibility is that males resemble females to reduce aggressive response by territorial conspecific males (for a similar explanation between*Calopteryx* species see De Marchi 1990).

The Reproductive Period

Alternative Mate Securing Behaviors by Males

Once mature, males go to reproductive places to try to mate. Calopterygid reproductive places are usually riverine sites with some submerged vegetation. Females, on the other hand, also go to these places presumably only when they have eggs to lay. Daily survival rate of adults oscillates between 0.85 and 0.95 in most species (Table 1), which means that their expected longevity is 6-19 days. Most of the time, males are highly territorial and defend river spaces that must (e.g. *Calopteryx*; Waage 1973) or must not have plant substrates for oviposition (e.g. *Hetaerina*, A. Córdoba-Aguilar, unpub. data). However, not all males are able to obtain a territory. Some of the factors known to affect territory acquisition are the following: the amount of muscle mass and fat reserves to be allocated to it (Marden & Waage 1990, Plaistow & Siva-Jothy 1996, Koskimäki *et al*. 2004, Contreras-Garduño *et al*. in press), and the availability of riverine sites which depends on the number of competing males (Pajunen 1966). It is for the latter reason that in the beginning of the reproductive season is common to find no competition and restricted aggression which become more intense as the season progresses or density increases (Pajunen 1966; Cordero Rivera & Andrés 2002).

Studies in Calopterygidae, except for *Mnais* (Tsubaki 2003), have repeatedly shown that territorial and nonterritorial behaviors are conditional mating tactics (*sensu* Gross 1996). For example, Forsyth and Montgomerie (1987) described how *C. maculata* males decline in their ability to hold a territory after 20 days and after this period, males abandon territories and wander on the reproductive sites trying to obtain a mate. Studies in the same and in closely related species have also suggested that this nonterritorial option is "the best of a bad job" alternative which is adopted when the condition of the animal does not suffice to defend a place (Forsyth & Montgomerie 1987). As mentioned before, fat reserves play a role here and those males, which have not accrued enough fat resources, will not be able to defend a place (Marden & Waage 1990, Plaistow & Siva-Jothy 1996, Koskimäki *et al*. 2004, Contreras-Garduño *et al*. in press). This nonterritorial tactic has been occasionally mentioned to take two additional forms, sneaking and wandering, such as in *Mnais pruinosa costalis*Selys(Watanabe & Taguchi 1990) and *Hetaerina cruentata* Rambur (Córdoba-Aguilar 1995). In the former, nonterritorial males consistently stay in the same places while in the latter, males cross many territories and do not show any sort of fidelity. Waage (1972) suggested that nonterritorial males are more likely to migrate to other locations, which deserves exploration to understand dispersal and migrant patterns in odonates. Previous works in calopterygids made no clear distinction between these two tactics and in general described those animals that are not able to defend a territory as nonterritorial (e.g. Pajunen 1966; Waage 1972, 1973, 1979a; Grether 1996a, 1996b; Plaistow & Siva-Jothy 1996). These two nonterritorial options should be studied in more detail as they may reflect differences in male condition that can be affected by age (e.g. "wanderer" males being older and less likely to face an attack by the territorial male than "sneaker" males; Watanabe & Taguchi 1990). The nonterritorial tactic, however, will usually not be good enough as that of the territorial. For example, it was shown that the mating success of territorial males may be a thousand times higher than that of a nonterritorial (Plaistow & Siva-Jothy 1996, for a similar although less extreme trend see Forsyth & Montgomerie 1987 and Córdoba-Aguilar 1995). The essential reason for this is that females mate with territorial males mainly (Waage 1973, 1979a, Plaistow & Siva-Jothy 1996, Córdoba-Aguilar 2000). Nevertheless, under extreme high population density, territorial defense becomes so expensive that non-territorial males might have similar reproductive success (Cordero 1999, Cordero Rivera & Andrés 2002).

Mating tactics may also have a genetic basis in some calopterygid species. In *Mnais* species, males appear in two morphologically and behavioral, genetically-based different morphs (Tsubaki 2003; Figs. 1c-d). The nonterritorial form has hyaline wings and a smaller size than the territorial morph that has pigmented wings (Siva-Jothy & Tsubaki 1989a, b: Watanabe & Taguchi 1990). The genetic polymorphism of *Mnais* seems explained by an autosomal, single locus, two alleles with complete dominance (Tsubaki 2003). Studies in these species have shown that the hyaline, nonterritorial morph lives longer (Tsubaki *et al*. 1997, Tsubaki & Hooper 2004, however, see Nomakuchi *et al*. 1988 who did not find differences between morphs) and never establishes a territory (Watanabe & Taguchi 1990) except when there are no other territorial males (Nomakuchi *et al*. 1984). Females in this system mate preferentially with territorial males but since nonterritorial males have a larger sperm displacement ability (see section of Copulatory Processes below), they are able to fertilise more eggs as they can transfer more sperm to the female (Siva-Jothy & Tsubaki 1989a). Territorial males produce more muscle than nonterritorial males at the time of maturation (after the teneral stage) (Plaistow & Tsubaki 2000). There is a descend with age of fat reserves in territorial males which, however, keeps steady in nonterritorial males (Plaistow & Tsubaki 2000) which is due to the fact that territorial males fight much more frequently than nonterritorial ones (Nomakuchi *et al*. 1984). The difference in longevity is possibly a consequence of gregarine pressure (Tsubaki & Hooper 2004), the cost of producing the wing pigmentation in territorial males (Hooper *et al*. 1999) and/or the energy devoted to contests (Nomakuchi *et al*. 1984, Watanabe & Taguchi 1990, Tsubaki *et al*. 1997). The estimates of lifetime reproductive success indicate that both morphs achieve a similar fertilization success that explains the effectiveness and the maintenance of the nonterritorial alternative (Tsubaki *et al*. 1997). It is interesting that the male dimorphism evolved apparently just once in this family and, in fact, it is only found in the Megapodagrionidae (González-Soriano & Córdoba-Aguilar, 2003, 2005) and Coenagrionidae (genus*Megalagrion*) (Polhemus & Asquith 1996).

Territory Acquisition

As implied before, fat reserves play a tremendous role in male territorial success. Territorial disputes in calopterygids may be of short or large duration (Waage 1988a, Córdoba-Aguilar 2000). In the short level dispute, a territorial male simply follows an intruder that does not fight back but leaves instead (e.g. Waage 1973, Marden & Rollins 1994, Córdoba-Aguilar 2000). These encounters usually start with the intruder male invading the owner male's territory and do not take more than a few seconds (e.g. Waage 1988a, Córdoba-Aguilar 2000) in which it is usually the resident male who wins the contest (e.g. Waage 1973; Córdoba-Aguilar 1995, 2000; Lefevre & Muehter 2004). In the large duration encounters, the intruder male does not leave and, instead, also chases the owner male (Johnson 1962a, Waage 1988a, Marden & Waage 1990, Marden & Rollins 1994, Plaistow & Siva-Jothy 1996, Córdoba-Aguilar 2000, Thompson

2000). This mutual chasing can be seen as ascending and descending, circular trajectories of variable radii on the territory in dispute and also on those that are close to it (Waage 1973, Córdoba-Aguilar 2000). These encounters stop at times when both males perch on the vegetation but, in general, may take several hours (Waage 1973, Córdoba-Aguilar 2000, Koskimäki *et al*. 2004). These encounters are more likely to result in the resident eviction of the territorial male (e.g. Marden & Waage 1990, Marden & Rollins 1994, Plaistow & Siva-Jothy 1996, Córdoba-Aguilar 2000). It will be expected that if a male will engage in a fight, a sort of assessment of the opponent should occur to avoid unnecessary fights. However, no supporting evidence has been found for this idea and, actually, contests were interpreted as wars of attrition where males fight until exhaustion (Marden & Waage 1990, Marden & Rollins 1994). The winners of these fights are those males with more fat (Marden & Waage 1990, Plaistow & Siva-Jothy 1996).

Recent evidence, however, has indicated that body pigmentation in *C. maculata* may serve to communicate fat reserves (Fitzstephens & Getty 2000). Some additional supporting evidence comes from *Hetaerina americana*Fabricius in which territorial males with an experimentally increased amount of wing pigmentation could stay more days in the defended territory and, in general, survived longer (Grether 1996a). This suggests that opponent males may assess the pigment enlarged male and avoid fighting. In *C. haemorrhoidalis*, males with more pigmentation were more likely to defend a territory (Córdoba-Aguilar 2002a). Some more experimentation is necessary here to see the role of pigmentation in reliably signaling male condition (as fat) and whether this can be communicated during contests. Related to this, Koskimäki *et al.* (2004) suggested that males may use pigmentation to assess immune ability. However, it does not seem clear why males should need this information for. Actually, a positive correlation between fat reserves and immune ability has been found in *H. americana*, which suggests that it is more logical to assume that if there is some information that is being communicated between contestant males, it should be fat for which immune ability appears indirectly correlated (Contreras-Garduño *et al*. in press).

Grether (1996b) found evidence that body size and wing pigmentation were selected via male-male competition in*H. americana*. Interestingly, sexual selection on body size was only significant in nonterritorial males but not in territorial males, possibly because nonterritorial individuals were better at subduing females during the clasping, pre-tandem stage (Grether 1999a). This result is somehow compatible with other studies in *H. cruentata* and *C. splendens* in which there was no size difference between territorial and nonterritorial males (Córdoba-Aguilar 1995, Hilfert-Rüppell2004). However, body size can be selected via survival as different studies have corroborated (Grether 1999b, Córdoba-Aguilar 2002) and the explanation for this may be that a large size can allow more fat resources to be stored as a study in *C. xanthostoma* has documented (Plaistwo & Siva-Jothy 1999). Interestingly, one potential constraint for body size may be forest structure as documented by Taylor and Merriam (1995) in which large *C. maculata* males were more likely to be found in open than in forest habitats, presumably due to the flight problems to maneuver in the forest habitats.

Pre-Copulatory Events

There is variation among calopterygid genera in the behaviour shown previous to copulation. In *Hetaerina*, for example, females arrive to the reproductive sites and are taken by males without any apparent courtship (Johnson 1963, Weichsel 1985). In *Phaon*, males hover over females before copulation (Miller 1985, Miller & Miller 1988). In *Calopteryx*, *Neurobasis*, *Vestalis* and *Mnais* however, only territorial males perform an elaborated courtship that consists (with some interspecific variation) in showing the forewings to the perched female while the hindwings sustain the animal (Pajunen 1966; Heymer 1973; Waage 1973, 1988b; Kumar & Prasad 1977; Higashi 1981; Miyakawa 1982; Nomakuchi *et al*. 1984;Conrad & Herman 1987; Plaistow 1997; Thompson, 2000; Rüppell *et al*. 2005). This behaviour is carried out for a few seconds and has been called wing display (sensu Waage 1973). The wing display is performed particularly when the female moves but at other times, the male remains close and perched. At occasions, a female may fly directly to the aquatic substrate that is then followed by the male (e.g. Gibbons & Pain 1992, Córdoba-Aguilar 2000). If she gets close to the river surface, he allows himself to be taken by the current for a few centimeters, floating with his abdomen (but not the tip which is curved upwards) and thorax making contact with the water and spreading their wings in front of the female (seeFig. 2b; Córdoba-Aguilar 2000). All these behaviours differ mainly in degree among *Calopteryx* species (Meek & Herman 1990).

Both these behaviors and the wing pigmentation patterns have been interpreted as adaptive in a female choice context in *Calopteryx*. In *C. splendens xanthostoma* and *C. haemorrhoidalis*, the amount of pigmentation correlates inversely with gregarine number (Siva-Jothy 2000, Córdoba-Aguilar 2002a). Experimental evidence suggests that males with more pigmentation are more resistant to gregarine infections (Siva-Jothy 2000, Tsubaki & Hooper 2004; for gregarines see Fig. 2a; for wing pigmentation variation see Fig. 2b) and, in general, have higher immune abilities (Rantala *et al*. 2000, Siva-Jothy 2000; see Fig. 2b for immune defense). Interestingly, females are more likely to mate when the male has more pigmentation (Siva-Jothy 1999, Córdoba-Aguilar *et al*. 2003a). Especially for the wing display, researchers have concluded that males may use their pigmentation patterns to communicate their resistance to gregarine infection (Rantala *et al*. 2000, Siva-Jothy 2000, Córdoba-Aguilar 2002a). It has not been investigated whether there is a genetical basis for the assumed resistance but the pigmentation seems to reflect the ability to cope with parasites as the pigmentation is made of melanine (Hooper *et al*. 1999), the same protein used to encapsulate large pathogens (such as gregarines) during immune defense (Siva-Jothy 2000; see Fig. 2c for melanine-based immune defence). In this way, a male with more pigmentation may communicate that he has a good ability to successfully fight back parasites (Siva-Jothy 1999, 2000; Rantala *et al*. 2000; Córdoba-Aguilar 2002a). Furthermore, the fact that melanine is made of an essential aminoacid, phenylalanine, suggest that only those animals able to gather more nutrients may be better able to cope with infections and develop more wing pigmentation (Hooper *et al*. 1999). Paradoxically, a study in which the strength of selection in pigmentation and phenoloxidase (a key immune enzyme) was measured, found that only the enzyme, but not the pigmentation, was positively related (Rolff & Siva-Jothy 2004).

As for the cross display, also an adaptive explanation has been offered. In *C. splendens*, females not only chose to mate with those males that had more pigmentation but also with males that were able to defend a place with a particular river flow rate (Gibbons & Pain 1992, Siva-Jothy *et al*. 1995) and with oviposition plant substrates (Waage 1978, Gibbons & Pain 1992). Some experiments showed that at a particular river flow rate, the probability of fungi infection in the eggs was less likely (Siva-Jothy *et al*. 1995). The cross display may indicate in this case how fast the flow was so that the female may get another piece of information revealing site quality (Gibbons & Pain 1992, Siva-Jothy *et al*. 1995). This, however, was not found in other calopterygids such as *C. haemorrhoidalis* in which females mate independently of this variable and only chose males with more pigmentation (Córdoba-Aguilar *et al*. 2003a). Furthermore, in some populations of *C. haemorrhoidalis*, males perform this display over floating vegetation, where flow rate is absent (A. Cordero Rivera, unpublished). That the site is important for the female is not the case in *Hetaerina* in which males and females go away from the male's territory to mate and lay eggs (A. Córdoba-Aguilar, unpub. data). Although it happens that males defend territories with oviposition substrates, when these are removed, males still stay in the territories and females do not change their visit rate to those territories with removed substrates (Alcock 1987)

Wing pigmentation, however, does not seem to be favored by females in *Hetaerina* at least not in the pre-copulatory instance (Grether 1996a). As mentioned before, males in these species grab females as soon as they happen to fly on the male's territory (Weichsel 1985). Interestingly, gregarine parasites are common in *Calopteryx*but only rare in *Hetaerina* (A. Córdoba-Aguilar, unpub. data). An explanation for this is that the dark *Calopteryx*pigment evolved to communicate the male ability to deal with parasites. In fact, *Hetaerina* appears more basal in the Calopterygidae phylogeny than *Calopteryx* (Misof *et al*. 2000; Dumont *et al.* 2005 Fig. 3). This suggests that, possibly, female choice arose once the gregarine infection became a selective pressure that was communicated by males via the black pigmentation. This hypothesis can be tested comparatively by looking at the courtship behavior and gregarine occurrence in the Calopterygidae. One interesting species related to this situation is *H. titia*. This species is one of the few of this genus with gregarines which shows both black and red coloration (e.g. Johnson 1963; Fig. 2d). It would be appealing if male behavior in this species resembles that of *Calopteryx*although some evidence suggests this is not the case (Johnson 1963).

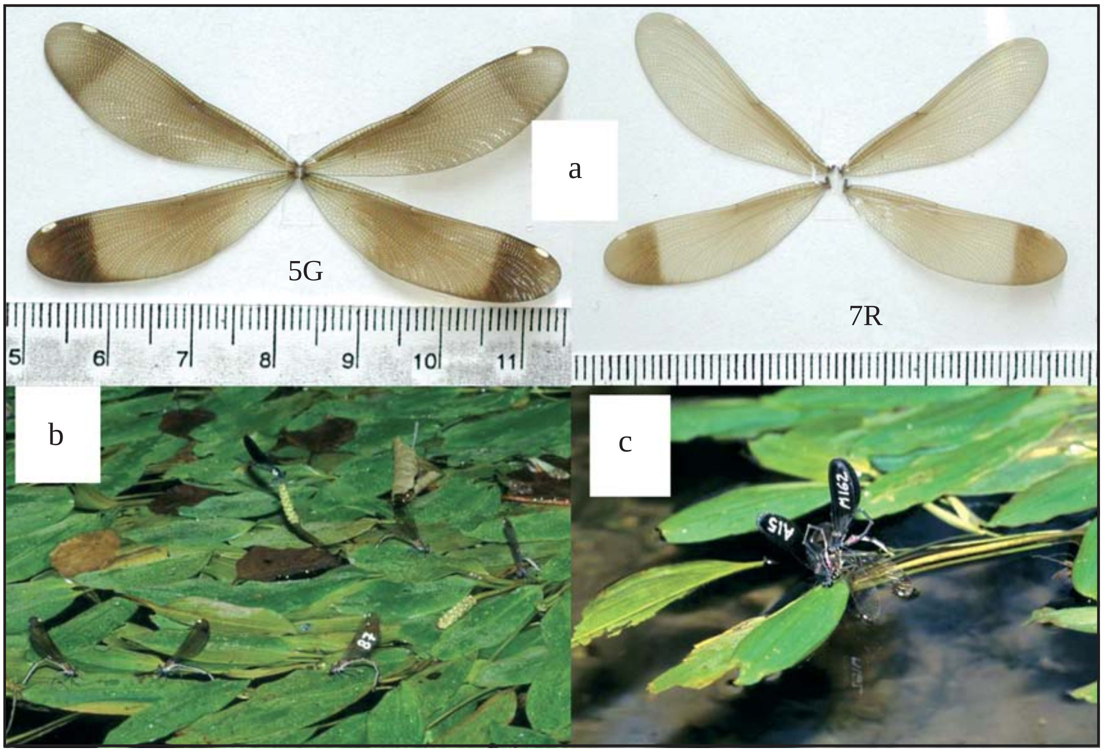

Fig. 3. Female wing pigmentation variation in two *C. haemorrhoidalis* females (a), *C. haemorrhoidalis* females attracted to an oviposition spot defended by a male landing on a *Potamogeton* stick (b), a *C. haemorrhoidalis* females forcibly taken by a conspecific male (c).

One of the questions that remains to be answered is what the constraints are for wing pigmentation. One of the possible explanations is that there is an environmental component underlying pigment production. Experimental results indicate that diet may affect the amount of pigmentation so that this trait is affected by a restricted food regime (Hooper *et al*. 1999). A second possibility is that an enlarged pigmentation may make prey capture more difficult as the prey may detect the damselfly's attack and proceed to escape (Grether & Grey 1996). A third hypothesis is that a lack of recognition of interspecific patterns may induce interspecific male aggression. This is supported by observations of male aggressive behaviour between *C. splendens* and *C. virgo* L. (Tynkkynen *et al*. 2004). In this case, *C. virgo* males were more aggressive against those *C. splendens* males with enlarged wing pigmentation patterns causing negative selection on the wing pigmentation on the latter species (Tynkkynen *et al*. 2004, 2005). Interestingly, when *C. virgo* males were less abundant, *C. splendens* were more likely to survive longer (Tynkkynen *et al*. 2005). This interspecific aggression pressure seems so intense that may cause pervasive negative selection on pigmentation expression causing character displacement (Tynkkynen *et al*. 2005). This idea seems unlikely to be generalised for other species such as *Hetaerina* in which most species share very similar wing pigmentation patterns and also live in sympatry (at occasions more than four species live in the same place; C. Anderson, unpublished data). The last hypothesis for the wing pigmentation patterns in Calopterygidae is to avoid interspecific matings (Waage 1975, 1979b). Some results have actually supported this in *C. maculata* and *C. aequabilis* Say in which both males and females appear wing pigmented. In sympatry areas, females of both species tended to be more different than in allopatry and males mated preferentially with conspecific females. This agrees with the reproductive character displacement hypothesis (Waage 1975, 1979b) but strangely it is males that are able to discriminate (Waage 1975, Beukema 2004). Recent evidence suggests that this example is a case of displacement of sexual signals and their associate preference in fully reproductively isolated taxa upon secondary contact (S. P. Mullen and J. A. Andrés, pers. comm. 2005). Similar results were corroborated in *C. haemorrhoidalis* in which males discriminated between conspecific and heterospecific females on the basis of wing coloration (Beukema 2004). All these hypotheses of constraints in male pigmentation elaboration are not mutually excluding.

Very little is known of calopterygid female mating patterns (however see Nomakuchi 1988, Córdoba-Aguilar *et al*. 2003a). This is not surprising in odonates as there has been an emphasis in describing and explaining male reproductive traits mainly, likely due to higher male site fidelity. What is known is that females appear not to mate indiscriminately (e.g. Waage 1973, Siva-Jothy 1999, Córdoba-Aguilar 2000) except when male densities are extremely large (e.g. Cordero 1999) in which it has been admitted that females mate according to a convenience mating polyandry to reduce costs due to male sexual harassment (Cordero Rivera & Andrés 2002).

Some recent evidence was described in *C. haemorrhoidalis* where mating patterns of a large set of females were monitored (Córdoba-Aguilar *et al*. 2003a). It was found that females mate from two to seven times during their lives and that this number and the male phenotypes females mated with were apparently affected by the gregarine burden of females. Females with a large gregarine burden were less choosy (spent less time to accept to mate when being courted) and mated fewer times compared to females with few or no parasites. This indicates that females may take decisions (or be forced to take them) in relation to their condition. Probably, females in good condition have more time to inspect males, mate with more and do so with highly pigmented males (Córdoba-Aguilar *et al*. 2003a). Besides, these females were observed to carry out more stealing-a-guard (SAG) oviposition where oviposition is not preceded by copulation in the male's territory. In *C. splendens xanthostoma*, it has been shown that during this oviposition type, females use spermathecal sperm (Siva-Jothy & Hooper 1996) where sperm from different males has been accumulated so that the offspring comes from different males (Siva-Jothy & Hooper 1995). *C. haemorrhoidalis* females in bad condition, however, carried out fewer SAG ovipositions and, instead, carried out more mated-and-guarded (MAG) oviposition in which oviposition is preceded with a copulation with the owner of the territory (Córdoba-Aguilar *et al*. 2003a). In *C. splendens xanthostoma*, these MAG events resulted in last-male fertilisation success from the recent mate (Siva-Jothy & Hooper 1996). The results in *C. haemorrhoidalis* need to be confirmed in other species as well as their evolutionary implications. According to this, it seems that there are benefits of mating multiply and incur in oviposition events in which genetic diversity is secured for the eggs (Siva-Jothy & Hooper 1995). We need to investigate what these benefits are. Additionally, *C. haemorrhoidalis* females showed wing pigmentation patterns which were also negatively related with their gregarine burden but positively with the number of eggs produced (Córdoba-Aguilar*et al*. 2003a; Fig. 3a). Interestingly, females with more pigmentation were guarded for longer periods by the mating male. The explanation is that males may evaluate female's reproductive value by using female pigmentation (Córdoba-Aguilar *et al*. 2003a).

Females are not only attracted to male phenotypic traits. Females of some *Calopteryx* species may also pay attention to territory quality defined as the amount of substrates where they can lay eggs. Work in *Calopteryx maculata* and *C. amata* Hagen (but not in *C. aequabilis*) has indicated that females may prefer to mate with those males that defend places with more oviposition vegetation substrate (Meek & Herman 1991). This preference can be extended also to places where river flow rate is relatively high as eggs can survive better, because fungal infections on eggs are less likely (Siva-Jothy *et al*. 1995). Males presumably detect the quality of the territory as they defend places with more vegetation (Alcock 1987, Waage 1987, Meek & Herman 1991). It is not clear, however, if males do detect the amount of oviposition substrate or the number of females that are attracted to a place. Actually, the memory ability of males seem to fail at large densities as shown by Alcock (1979) in *C. maculata* whose males in low density conditions tended not to pair with females they have paired with. In *C. haemorrhoidalis*, males are also apparently unable to recognize previous matings, and defend mates and non-mates (Cordero 1989). The memory ability was suggested nevertheless by Hooper (1995). This author discusses the possibility that the apparent recognition by males may be actually provided by signals emitted by the recently mated female persuading male's behavior. Males are attracted to species-specific characters, and, in the case of female *C. haemorrhoidalis* wing pigmentation seems to be of primary importance (Beukema 2004). Curiously, however, *C. virgo* and *C. splendens* males do not seem to be able to recognize each other to the extent that interspecific aggression occurs which reduces survival on *C. splendens* males (Tynkkynen *et al.* 2004, 2005).

Females can also be attracted to particular sites if other females are already ovipositing (Alcock 1987, Waage 1987; Fig. 3b). This may be a way for females to assess indirectly the oviposition site. An assessment of oviposition substrates was documented by Hooper and Siva-Jothy (1997) but in terms of male interference: *C. xanthostoma* females took a series of distinctive flights, called flybys, finally copulating on those places with less male interference. Assessment of potential male harassment is adaptive as, although not documented, the energetic costs for females can be potentially high. In *C. haemorrhoidalis*, for example, high population densities induce males to skip courtship and force females to mate (Cordero 1999) even when these do not have any eggs to lay (Cordero Rivera & Andrés 2002). Under these circumstances, females could not finish oviposition as they were interrupted continuously by males (Cordero 1999).

Forced matings have only rarely been documented with the exception of *C. splendens* (Hilfert & Rüppell 1997, Rüppell *et al*. 2005) and *C. haemorrhoidalis* (Cordero 1999, Cordero Rivera & Andrés, 2002; Fig. 3c) under extreme population densities. Under these circumstances high male density may make economically impossible to defend a territory (Cordero 1999).

Copulatory Processes

Perhaps the animal group where different aspects of the copulatory processes are best known is the Calopterygidae. Similar to what occurs in other odonates, the male copulatory organ is not close to the organ where sperm is produced. Males, previous to copulation, have to transfer their sperm from the ninth abdominal segment to the second and third segments where the intromittent organs are present. Due to this reason, these animals adopt a curious copulatory wheel (Fig. 1c) where the female mesostigmal plates, located between the head and thorax, are grabbed by the male anal appendices located at the end of the abdomen. At occasions, the male bites the female when he is grabbing her (Alcock 1983).

Copulation takes place in two stages (Miller & Miller 1981). In the first stage, the male uses his intromittent organ to displace the sperm the female has stored from previous copulation (Waage 1979c, Córdoba-Aguilar *et al*. 2003b). In doing this, the male increases his chances of fertilization success by eliminating the sperm of other males, therefore avoiding the risk of sperm competition (the competition between the sperm of two or more males for the fertilization of a set of ova; Parker 1970). After this sperm displacement stage, the male then transfers his own sperm to the female.

Copulation lasts on average 1.5-4 minutes in all species so far studied (Table 2), the stage I (sperm displacement) covering most of the time. It is remarkable that in such brief matings males are able to displace almost all sperm from the female storage organs in clear contrast with other species, that mate during several hours (Córdoba-Aguilar *et al*. 2003b). Both the morphology and function of the calopterygid genitalia are closely related to the displacement function although they are not as diverse as in other odonate species (Córdoba-Aguilar *et al*. 2003b).

In the calopterygid species studied, the penis head has a rhomboid form (Fig. 4a) with two distal horns that are covered with pointing spines (Córdoba-Aguilar 2003a; Fig. 4b). In *Hetaerina*, the horns are wide (A. Córdoba-Aguilar, unpub. data) while in *Calopteryx* the horns are narrow (Adams & Herman 1991). In *Mnais*, the horns are even narrower (Córdoba-Aguilar 2003b). Females have two sperm storage organs: the bursa copulatrix and the spermatheca (Fig. 4c). Both sites are connected with a small tube. The bursa has a spherical form that is uniform in the three genera and stores less sperm than the spermatheca (Córdoba-Aguilar 2003a). There are morphological differences in the spermatheca across genera. In *Hetaerina*, the spermatheca is a small spherical elongation much smaller than the bursa. In *Calopteryx* and *Mnais*, the spermatheca has two elongated, narrowed ducts that, along with the connected duct to the bursa, produce a T form (Siva-Jothy & Hooper 1995; Córdoba-Aguilar 2003a, b). In *Mnais* the spermatheca is extremely small compared to the bursa (Hayashi & Tsuchiya 2005). Curiously, in two cases out of 200 examined individuals, two *C. haemorrohoidalis* females were found with one spermatheca rather than two (Córdero Rivera *et al*. 2004).

Two sperm displacement mechanisms have been described in this family: a) removal in which the rivals' sperm is displaced mechanically (Waage 1979c, Miller 1987); and, b) sensory stimulation in which the sperm is ejected by the female due to spermathecal muscular contractions induced by the male sensory stimulation (Córdoba-Aguilar 1999a, 2000). During removal, the penis horns enter the spermatheca. The spines on the horns remove the sperm masses and withdraw them to the outside (Waage 1979c, Miller 1987). During stimulation, the medial part of the aedeagus (the structure that holds the penis head), moves deforming two vaginal plates with embedded mechanoreceptor sensilla (Córdoba-Aguilar 1999a; Fig. 4d). These sensilla coordinate the muscles that surround the spermatheca and induce, once stimulated, spermathecal sperm ejection. This process is similar to that used during fertilization as the egg induces the same stimulus to be fertilized (Miller 1987).

One of the most interesting lines in the study of Calopterygidae is precisely that of sperm displacement mechanisms. Although bursal sperm is invariably displaced,

Table 2. Copulation duration and the possible factors affecting it in calopterygids.

Species	Locality	Copulation duration ± SE (N) min	Factors affecting copula duration	Reference
C. atrata	Japan	1.28 (range 0.52-2.62)		Miyakawa 1982
C. cornelia	Japan	4.23 (range 3.83-4.63)		Miyakawa 1982
C. dimidiata	USA	2.40 (range 1.93-3.80)		Waage (in Miyakawa 1982)
C. h. asturica	Spain	2.48 ± 0.24 (12)		Cordero 1989
	Spain	2.79 ± 1.11 (27)		Córdoba-Aguilar 1999b
C. h. haemorrhoidalis	Italy	2.23 ± 1.08 (118)	Temperature (-); Time of day (-)	Cordero 1999
	Italy	1.85 ± 0.09 (73) (courtship) 1.66±0.11 (40) (forced)	Temperature (-); Density (+); type of mating	Cordero & Andrés 2002
C. japonica	Japan	Range 0.83-1.67		Aida 1974
	Japan	1.73 (range 0.93-3.05)		Miyakawa 1982
C. maculata	Northern USA	1.68 (range 0.50-5.00)		Waage 1973
	Central USA	1.72 (range 0.67-4.28)		Waage 1973
	Southern USA	5.00 (little variation)		Johnson 1962
C. splendens	Germany	1.50 (range 0.83-2.50)		Buchholtz 1951
	Asia minor	0.52		Buchholtz 1955
	Europe	2.00-3.00		Roberts 1958
	Italy	2.88 ± 0.57		A. Cordero unpublished
	Oker, Germany	2.00 ± 0.01 (65) (with courtship) 2.18 ± 0.03 (35) (no courtship) 7.23 ± 0.12 (27) (at roosting site)	Temperature (-) and type of mating	Rüppell *et al.* 2005; Hilfert-Rüppell, 2004
	La Chapellete, France	1.83 ± 0.07 (8) (with courtship) 1.87 ± 0.05 (17) (no courtship) 3.55 ± 0.12 (8) (at roosting site)	Temperature (-) and type of mating	Rüppell *et al.* 2005; Hilfert-Rüppell, 2004
C. virgo	Europe	2.00-5.00		Roberts 1958
H. cruentata	Veracruz, Mexico	2.50 (range 2.25-3.45) (28)	Density	A. Córdoba-Aguilar unpublished
H. vulnerata	Arizona, USA	3.82 ± 0.28		Alcock 1982
M. pruinosa costalis	Japan	1.16 ± 0.07 (34) (inside territory) 1.76 ± 0.14 (32) (outside territory)	Location	Watanabe & Taguchi 1990
M. p. pruinosa	Japan	2.45 ± 0.13 (65) (opportunistic males) 1.28 ± 0.001 (199) (territorial males) 0.91 ± 0.06 (9) (sneaky males)	Type of male strategy	Siva-Jothy & Tsubaki 1989
Phaon iridipennis	Kenya	1.47 ± 0.65 (21)		Miller & Miller 1988
Vestalis amabilis	Brunei	2.07 (range 1.75-2.75)		Thompson 2000

there is variation within and among species in the occurrence and the mechanisms used for spermathecal sperm displacement (Córdoba-Aguilar *et al.* 2003b). For example, there is spermathecal sperm displacement in *C. maculata*, *C. aequabilis*, *C. h. haemorrhoidalis*, *C. haemorrhoidalis asturica* Ocharan, *C. splendens*, *C.*

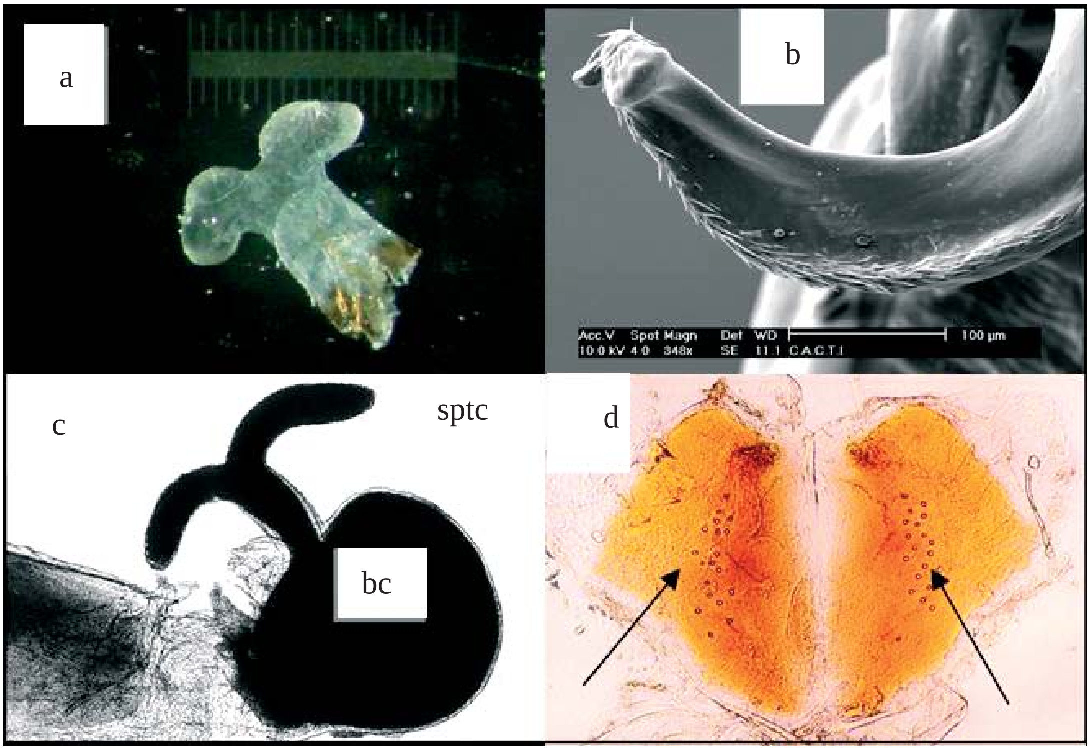

Fig. 4. *H. americana* penis showing the two distal horns (a), a close inspection to the spines emerging from a *C. haemorrhoidalis* lateral penis horn (b), female sperm storage organs: bc: bursa copulatrix, sptc: spermatheca (c), sensilla (indicated by pointing arrows) on the two vaginal plates of a *C. haemorrhoidalis* female (d).

virgo and *Mnais pruinosa* Selys which is not the case for *C. xanthostoma* and *H. cruentata* (Córdoba-Aguilar 2003b). There is a morphometrical correlation in both male and female genitalia related to these differences: in those species in which males remove spermathecal sperm, the penis horns are narrower than the spermathecal ducts while the contrary occurs for species in which males are unable to remove spermathecal sperm. These differences allow or impede the entry of the horns. The exception to this pattern is *C. haemorrhoidalis asturica* in which males stimulate, rather than remove, to displace spermathecal sperm. In this case, there is spermathecal sperm displacement but the horns are wider than the spermathecal ducts (Córdoba-Aguilar 1999a).

Recent detailed research has revealed that different populations can also differ in their ability to displace spermathecal sperm (Cordero Rivera *et al*. 2004). This is the case of *C. virgo* and *C. splendens* as indicated by horn-spermathecal ducts morphometrical differences. In some populations the horns are wider than the spermathecal ducts and the contrary pattern also occurs. We believe that probably the different populations are evolving distinct mechanisms, which would eventually produce different species in the same way we observe them today (Cordero Rivera *et al*. 2004). Possibly, both sexes are coevolving at the level of genital form and function and this coevolution takes place within each population. If this is true, this means that post-copulatory sexual selection is promoting species divergence (for a similar rationale but for wing pigmentation see Svensson *et al*. 2004). The evidence is still scarce but some experiments in *C. h. asturica* have provided support to this. In this species, males use a sensory stimulation mechanism. Possibly males were prevented from entering the spermathecal ducts via a reduction of these structures (Córdoba-Aguilar 1999a). When females of *C. splendens*, *C. virgo* and *H. cruentata*, whose males do not use a sensory stimulation mechanism, were stimulated with a *C. haemorrhoidalis* aedeagus, they ejected sperm (Córdoba-Aguilar 2002b). This suggests that males of those other species are not able to stimulate despite the fact that their females are able to be stimulated and eject sperm. This bias was "exploited" in *C. haemorrhoidalis* (Córdoba-Aguilar 2002b, 2005). The mechanism of this bias lies on the widened aedeagus (much wider than in the other calopterygids) and the vaginal sensilla. Interestingly, and still compatible with the coevolution idea, *C. h. asturica* females have fewer mechanoreceptor sensilla than other calopterygids (Córdoba-Aguilar 2003b, 2005). This reduced number possibly evolved to make the ejection less intense. To test this, an experiment was carried out and was found that the sperm ejected by *C. splendens*females was much higher than in *C. haemorrhoidalis* when using the same *C. haemorrhoidalis* aedeagus (Córdoba-Aguilar 2005). This evidence indicates that, possibly, once the stimulation ability evolved, females "responded" by reducing the number of sensilla, and that this was translated in less sperm ejected.

There are more questions related to this game of genital differences. In *C. haemorrhoidalis* for example, it is common to find that the distribution of sensilla on the vaginal plates is very patchily distributed, apparently different from the rest of Calopterygidae, where females have a more aggregated sensillum distribution on the center of the plates (A. Córdoba-Aguilar, unpub. data). One explanation for this is that this distribution makes stimulation harder impeding that the aedeagus could reach all the sensilla. There is some evidence that the sensilla may control certain regions of the spermatheca (Córdoba-Aguilar & Siva-Jothy, 2004) so that this explanation may have a sound basis.

Another interesting research avenue is the inter-specific size differences in spermathecal storing capacity. In those species in which spermathecal sperm displacement takes place, the spermatheca appears smaller than in those species in which sperm is not displaced (Hayashi & Tsuchiya 2005). It is not known what the explanation is for this difference but it would suppose that there must be a benefit for storing sperm in the spermatheca which explains why in those species in which spermathecal sperm is not displaced, the spermatheca is larger. In this context, it is remarkable that males of many species of odonates from different families are able to detect the presence of sperm inside the female (Uhía & Cordero Rivera 2005). Laboratory experiments showed that copulation duration with mated females was almost twice as long as with virgins but only in species with spermatheca. These results suggest that even in odonates, where sperm removal is widespread, females have retained control over sperm reserves in their spermatheca(e), and males prolong copulation with mated females to elicit rival sperm ejection and/or to induce females to use their sperm in fertilization (Uhía & Cordero Rivera 2005). The only study that has demonstrated a benefit of using spermathecal sperm comes from *C. xanthostoma* where females use spermathecal sperm during SAG ovipositions events. MAG females, however, use bursal sperm which comes from the recent guarding mate (Siva-Jothy & Hooper 1995, 1996). Since there is not spermathecal sperm displacement in this species (Siva-Jothy & Hooper 1995), sperm in the spermatheca becomes more and more diverse with an increasing number of copulations (Siva-Jothy & Hooper 1995). Not surprisingly, SAG females' progeny is more genetically diverse (comes from different fathers) while MAG females' offspring has only one father.

Interestingly, Hayashi and Tsuchiya (2005) has just found evidence that spermathecal sperm viability differs depending on whether the spermathecal sperm is displaced by the male or not. In *C. amata*, spermathecal sperm is not displaced which is not the case of *M. pruinosa*. In the former case, sperm survive much better than in the latter case (Hayashi & Tsuchiya 2005). This result opens a new line of research as for why females would not be "interested" in storing and maintaining sperm that is being displaced during each mating and how the evolution of sperm displacement mechanisms have affected female physiology in terms of having a machinery to keep sperm alive (a machinery that is possibly costly to maintain).

An interesting research line is that of copulation duration. In some species, duration is affected by temperature, time of day, type of mating (forced or non forced copulation), location and/or male mating strategy (Table 2). The role of the first four variables in sperm displacement have not been explored which is not the case for male mating strategy in which is known that nonterritorial males spend longer in copula and displace more rival sperm (Siva-Jothy & Tsubaki 1989a). This is perhaps the significance that should be looked for with the other variables affecting copula duration. This is especially the case for whether matings were forced or non-forced in which perhaps males with forced matings displaced less sperm as they copulated for less than courting males (Cordero & Andrés 2002).

The answer as for why females and males show so many inter- and intra-specific differences is not easy. Our hypothesis is that there is a conflict of interests where males' adaptations to displace sperm go against females' interest to store sperm (Córdoba-Aguilar *et al*. 2003b). In a recent review, we postulated the possible benefits females accrue (Córdoba-Aguilar *et al*. 2003b). It seems that the two possible benefits are the genetic diversity mentioned before and good genes benefits mating with males that are resistant to parasite infections and good sperm "displacers". For the first case, females would gain in terms of having genetically variable offspring with possible genes that confer advantages during unknown environmental events (Siva-Jothy 2000). For the second, females would select for some particular males with high sperm displacement ability which would male offspring similarly able (Córdoba-Aguilar 1999a; for a similar rationale but in another damselfly family see Andrés & Cordero Rivera 2000). These hypotheses are not necessarily mutually excluding and need experimental work.

Some paternity analyses have uncovered that there is variation in male fertilization success. Although the first eggs laid are fertilized by the last male (Siva-Jothy & Tsubaki 1989a, Hooper & Siva-Jothy 1996), if the female continues, the fertilization is less biased (Siva-Jothy & Tsubaki 1989a) which means that the sperm of different males mix with each other. Of course, not always a mixing process will be observed as in some species, sperm displacement patterns are of almost 100% (e.g. Waage 1979c). However, that females may have the potential to bias paternity has been shown in *C. xanthostoma* (Siva-Jothy & Hooper 1995, 1996). The means by which this can be done include the differential storage sites (spermatheca or the bursa) (Siva-Jothy & Hooper 1996) or the musculature surrounding each sperm storage organ which may allow differential exit of sperm during their route to the egg (Córdoba-Aguilar 2003a).

Post-Copulatory Processes

The interaction between female and male still continues after copulation and this is one aspect that has not been studied in entire detail in calopterygids. One event, which until recently has received little attention, is that females may have the opportunity to manipulate the male's sperm. One way they can do this is by ejecting the sperm and cleaning it from the ovipositor that can be seen after copulation. Sperm ejection after copulation has been, in fact, documented in other odonates that have been interpreted as a way by which females can filter males after copulation (e.g. *Paraphlebia quinta* Calvert, González-Soriano & Córdoba-Aguilar 2004). Lindeboom (1998) carried out some experiments with *C. splendens* virgins and found that after the first pairing, the ejected sperm was that present in the vaginal duct. Lindeboom's explanation is that if the female does not eject that sperm, the duct may get obstructed and impede the exit of the egg. This natural selection explanation however, needs to be confirmed with non-virgin females. Observations in a number of odonates, including calopterygids such as *C. haemorrhoidalis*, *H. americana* and *H. cruentata*, indicate that females also eject sperm after copulation (A. Cordero Rivera and A. Córdoba-Aguilar, unpub. data). Also virgin females of other species like*Ischnura graellsii* Rambur sometimes eject sperm in laboratory-controlled matings (A. Cordero Rivera, unpub. data). Actually, recent evidence suggests that this behaviour may be sexually selected and that females may use it as means to bias paternity in Zygoptera and Anisoptera (Córdoba-Aguilar in press).

After copulation, the female goes to the oviposition sites to start looking for a place to lay eggs. Males accompany females, which is particularly the case for territorial males. The apparent function of this male behaviour is to impede other males from sexually harassing the female. However, this does not explain why in some species of *Calopteryx*, males still perform the cross display (Higashi 1981, Miyakawa 1982, Waage 1988b, Meek & Herman 1990, Córdoba-Aguilar 2000) when it is supposed that the male was already evaluated by the female previous to copulation. At least in these species, there are other possible explanations for this. One of these is that it may serve as a form of courtship (Córdoba-Aguilar 2000). Evidence in other insects indeed suggests that post-copulatory courtship occur in which males are still persuading the female to use the courting male's sperm (Eberhard 1996). This has not been investigated in calopterygids in which a clear prediction would be that males performing the post-copulatory behaviour will get a higher fertilization success. Waage (1978) found that *C. maculata* females oviposited for longer when guarded by the male than when the male was not present. It would be interesting to see how male fertilization varies depending on the male's cross display.

In *Hetaerina*, the male does not release the female after copulation but keeps her grabbed. Unlike other calopterygids, *Hetaerina* couples leave their defended space to find places for oviposition (A. Córdoba-Aguilar, unpub. data). This induces flying chases by other males that try to grab the female on the couple's way to those places. Interestingly, oviposition sites are sometimes defended by males although it does not seem relevant for female visit and mating rate (Alcock 1987). If the site is not important at all, this can be a real lek system in which only males directly are "assessed" with no material benefits for females (at least not to be evaluated previous to copulation). In this way, the territories are just the arena for male exhibition and female detection.

There is interspecific variation in whether or not the male submerges with the female when she is laying eggs. In some species, males only perch close to the female when she is laying eggs. Under extreme male density, males switch to contact guarding, by perching on the tip of females' wings (Cordero 1999). It is not known how long the male remains with the and why. Studies in *C. haemorrhoidalis asturica* have indicated that the time the female is guarded depends on how many eggs she is carrying which is signaled by the female pigmentation (Córdoba-Aguilar *et al*. 2003a). However, females of other species do not show pigmented wings.

Concluding Remarks

We summarized the calopterygid biology but it is clear that still much is to be known. Special emphasis should be given to species in tropical areas from which very little is known. Larval work needs extensive research especially considering that at this stage animals should get as much resources as possible in order to survive and pair successfully. Our understanding of pre-copulatory sexual selection in *Calopteryx* and *Mnais* is fairly good but more work has to be done with the other genera, including *Hetaerina*. We have no data on the reproductive behaviour of several large genera, like *Mnesarete*, *Neurobasis*, *Sapho* or *Umma* and only one species of *Vestalis*(representing about 60 species). Genital work is still generating new ideas as still many species have to be studied to see their functional and morphological aspects. New work can be done by testing whether really sexual selection is driving genital evolution causing species divergence. Finally, post-copulatory events have received very little attention although they may still affect male and female fitness. Much research is therefore expected in this fascinating damselfly family.

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