



## Female reproductive decisions and parasite burden in a calopterygid damselfly (Insecta: Odonata)

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There is currently a gap in sexual selection theory about how much the environment drives female mating decisions. We present field data that suggest that female sexual behaviour in the damselfly *Calopteryx haemorrhoidalis* is influenced by parasite burden. Male wing pigmentation in *Calopteryx* is a sexually selected trait that signals a male's ability to cope with eugregarine parasites (an intestinal parasite that feeds on the adult's ingested food). Because adult *C. haemorrhoidalis* females also show wing pigmentation, we examined whether this trait is similarly influenced by parasite burden and whether it may signal the female's reproductive value. Male *C. haemorrhoidalis* defend riverine substrates that females use for oviposition. After copulation and during oviposition, females are guarded by the copulating male against intruder males. Alternatively, females may avoid mating and 'steal' an oviposition site within a male's territory. In the present study, we found that the amount of female wing pigmentation was negatively correlated with the number of eugregarines present. Females with more parasites produced fewer eggs, survived fewer days, spent less time during courtship, 'inspected' fewer males before mating, had a lower mating success, were guarded for less time during oviposition and engaged in fewer 'stealing' events during oviposition. The reduced egg production and survival of heavily infected females may result from eugregarine depletion of the females' consumed food reserves. Thus, to offset reduced longevity, heavily infected females may accept a mating more rapidly and mate with fewer males. 'Stealing' behaviour may be related to the female's differential use of sperm from some males, particularly high-quality males. Interestingly, males that mated with low-pigmented females showed greater variance in wing pigmentation than did males that mated with high-pigmented females. Possibly, female wing pigmentation may signal a female's reproductive value, which provides females with longer mate-guarding episodes and reduced interference from intruder males. This study points out one possible constraint, intestine parasites, that females may face during mating decisions. Because females in bad condition mate with males in both good and bad condition, this constraint may be pervasive enough to weaken the intensity of selection for a male sexually selected trait, wing pigmentation, and help to maintain its variation in phenotypic expression.

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Sexual selection, the competition for mates (Darwin 1871), has been extensively corroborated with different sources of evidence. One of the most important caveats, however, has been what maintains variation in the expression of sexually selected traits (Andersson 1994). One hypothesis suggests that variation may be maintained by condition-dependent selection: only those males in good condition will develop more elaborate

ornamental traits (Andersson 1994). A subset of this hypothesis proposes that the action of parasites may be one selective agent (Hamilton & Zuk 1982; Folstad & Karter 1992).

Although the effect of parasites on male ornament expression has been documented in different species (reviewed by Loye & Zuk 1991; Andersson 1994), the effect of parasites on females has received less attention. This lack of information can have important consequences for understanding female mating decisions. For example, in a recent paper, López (1999) investigated female mating preferences in the guppy. She demonstrated that parasitized females do not prefer males with more elaborate courting traits. This result has two broad

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implications for sexual selection theory: (1) it shows how sexual selection intensity is weakened due to female condition; and (2) it may help to explain the maintenance of variation in the expression of sexually selected traits (apart from those factors that also help to maintain variation, e.g. condition dependence), because males expressing the traits less intensively still have gains in reproductive success (López 1999).

Current knowledge of sexual selection theory applied to odonate mating systems has placed little emphasis on the opportunity of sexual selection acting before copulation, particularly with regard to female choice (Fincke 1997). Recently, however, some studies have provided important results that are changing this view. More specifically, studies in the Calopterygidae family indicate that male wing pigmentation, a character that is widespread in this family, may influence male-male competition and female choice (Grether 1996a, b; Siva-Jothy 1999; Córdoba-Aguilar 2002a). Male calopterygids defend aquatic substrates (usually submerged plants) that are used by females during oviposition (Corbet 1999). Studies in different species have shown that males with higher pigmentation levels are able to survive and defend territories for longer (Grether 1996a, b; Córdoba-Aguilar 2002a), and are preferred by females (Siva-Jothy 1999).

One explanation of why pigmentation is sexually selected in Odonata lies in its close relationship with eugregarine parasite infection. Eugregarines (Protozoa) are commonly found in diverse odonate habitats and infect both sexes (Åbro 1971, 1974). Parasites are ingested by the adult and develop in the midgut where they reproduce (Åbro 1976). Eugregarines may negatively affect male fitness in two nonexclusive ways: (1) by using the food consumed by the adult, which would affect muscle fat building (Siva-Jothy & Plaistow 1999), a necessary requisite for territory defence (Marden & Waage 1990; Plaistow & Siva-Jothy 1996); and (2) in large numbers, eugregarines might obstruct the gut, breaking it and allowing the invasive action of other infectious agents (such as bacteria and fungi; Åbro 1971, 1974). Given that pigmentation development is constrained by food consumption (Siva-Jothy 2000), eugregarines are likely to suppress pigmentation expression. In line with these arguments, observational (Siva-Jothy 2000; Córdoba-Aguilar 2002a) and experimental (Siva-Jothy 2000) studies have shown a negative correlation between pigmentation and parasite burden. Together, these results suggest that male pigmentation may signal a male's condition to other males and may indicate the male's ability to cope with parasites to females.

Compared with other odonate species, sexual behaviour in Calopterygidae is complex. In *Calopteryx*, territorial males use a conspicuous courtship during which the pigmented wings are shown to the female: the male flies around the female, approaching her repeatedly from behind (Siva-Jothy 1999; Córdoba-Aguilar 2000). Few courting displays lead to mating and therefore most females leave the courting male at some time during the sexual interaction. On the few occasions a female does accept a mate, she lays her eggs in the male's territory and is guarded by him for a variable length of time (Waage

1973; Córdoba-Aguilar 2000). Mate guarding is important for females, because they receive protection from sexual attempts by intruder males (Fincke 1997). This may be especially valuable at high population densities when male harassment is also high (e.g. Cordero 1999). However, mating is not a prerequisite for the use of a male's defended space: females may oviposit in a territory without previously mating with the territorial male (Waage 1973; Siva-Jothy & Hooper 1995; Córdoba-Aguilar 2000). During the latter tactic, a female usually arrives on a male's territory and starts oviposition in areas that are concealed by vegetation, thus 'escaping' the male's attention (*C. haemorrhoidalis*: Córdoba-Aguilar 2000). These two oviposition behaviours have been called mated-and-guarded (MAG) and stealing-a-guard (SAG) tactics (Siva-Jothy & Hooper 1995), respectively.

Calopterygidae males are well known for their ability to displace stored sperm from the female sperm storage organs (bursa copulatrix and spermathecae) during copulation before transferring their own sperm (e.g. *C. maculata*: Waage 1979). Sperm displacement ability is variable across species. For example, in *C. splendens xanthostoma*, males displace most bursal sperm but are not capable of accessing spermathecal sperm (Siva-Jothy & Hooper 1995). Because of this and because females mate multiply (as in most odonates; A. Córdoba-Aguilar, E. Uhía & A. Cordero, unpublished data), the genetic diversity of sperm stored in the spermathecae is higher than that in the bursa in this subspecies. Interestingly, the use of the SAG and MAG oviposition tactics appears to be correlated with the sperm use of each storing site: SAG females tend to use spermathecal sperm and MAG females tend to use bursal sperm (Siva-Jothy & Hooper 1996). Although the adaptive value of such differences remains unclear, one possibility is that females may be able to store sperm from high-quality males and use their sperm reserves accordingly (Siva-Jothy & Hooper 1995, 1996).

Females of a few calopterygid species (e.g. *C. dimidiata*, *C. haemorrhoidalis*: Corbet 1999) also have pigmented wings. Experimental work by Waage (1975) indicates that males may use this trait to avoid copulation with heterospecific females in sympatric zones. Apart from this natural selection explanation, no other attempts have been made to study the functional significance of female wing pigmentation. In *C. haemorrhoidalis* females, as in males, once pigmentation is fixed in the adult, it does not change with age (see Results). Females of this species show striking similarities to females of *C. s. xanthostoma*: (1) they use MAG and SAG tactics (Córdoba-Aguilar 2000); and (2) because bursal sperm is completely displaced but spermathecal sperm is not (Córdoba-Aguilar 1999, 2002b), multiple mating is likely to promote higher genetic diversity in the spermathecae than in the bursa. Our preliminary results indicated that the expression of female pigmentation is negatively correlated with parasite burden (see Results). Assuming that the effect of parasites on female fitness may be considerable (as it seems to be for males; Córdoba-Aguilar 2002a), we made a series of predictions in relation to the females' reproductive history. We tested these predictions using data that had been previously obtained in the field. We

predicted that females with reduced pigmentation would have reduced survival and lowered egg production. If such correlates were found, we also predicted that these females would invest less time during courtship before mating and would also have reduced mating success. As a consequence of the detrimental effect of parasites, females with more parasites may not be as selective as females with few or no parasites. We therefore predicted that females in good condition would not only mate with high-quality males but would also show reduced variance in wing pigmentation relative to their mates, compared with females in bad condition. Because mating less probably decreases genetic diversity of the spermathecal sperm stores, we also predicted that low-pigmented females would engage in fewer SAG events (because females mainly use spermathecal sperm during these events). Finally, and as a tentative explanation of the benefit for females of advertising their pigmentation, we examined the relation between wing pigmentation and the duration of male mate-guarding behaviour during MAG oviposition. We predicted that highly pigmented females would be guarded for longer than low-pigmented females.

## METHODS

We studied *C. haemorrhoidalis* females near Pontevedra, Spain from May to September 1996 and June to July 1998. The study site was a narrow (range 0.40–1.5 m), shallow (ca. 0.40 m) stream about 200 m long. It had some physical barriers at the extremes (a large concrete tunnel at one end and dense vegetation at the other end), which were likely to prevent damselflies from dispersing.

We captured damselfly females weekly for marking once sexual activities had finished (1800–1900 hours Eastern Standard Time). Each female was marked by writing an individual number (using indelible ink) on the right forewing. After 7–10 days, and at the end of daily sexual activities, we recaptured marked females and photographed their four wings using the settings described in Córdoba-Aguilar (2002a). Wing pigmentation is normally fixed in *C. haemorrhoidalis* within 7–10 days (indicating that individuals are sexually mature, and in the case of females, when they visit oviposition sites for the first time; unpublished data). Females were released on the same day.

In June–July 1998, we marked another set of females and followed them to investigate whether pigmentation intensity remained constant with age. We marked 63 young females (as judged by their 'clear' wings and relatively 'shiny' body appearance; Johnson 1973) at the study site and photographed their wings. After 10–12 days, we recaptured 34 of these females and rephotographed their wings. We then compared wing pigmentation on both dates. Considering that females may live as long as 20 days as adults (see Results), the time elapsed between marking and recapture allowed us to investigate an effect, if any, of age on pigmentation.

We obtained a broad indication of survival from daily censuses of all females present on the study site and

the surrounding area (approximate distance from the stream: 500 m). However, given that dispersion cannot be excluded, these data should be taken only as an approximate measure of survival.

To record data on sexual activities, we followed females closely each time they arrived at males' territories. We recorded the following aspects of female behaviour: (1) number of males that courted each female before copulation; (2) the time it took males to court the visiting females; (3) the identity of those males that females visited and/or mated with (i.e. most of the males at the study site had been marked and photographed previously and their wing pigmentation patterns were known: Córdoba-Aguilar 2002a); (4) whether a female engaged in a MAG or, if she avoided copulation, a SAG oviposition; and (5) the duration of postcopula guarding by males.

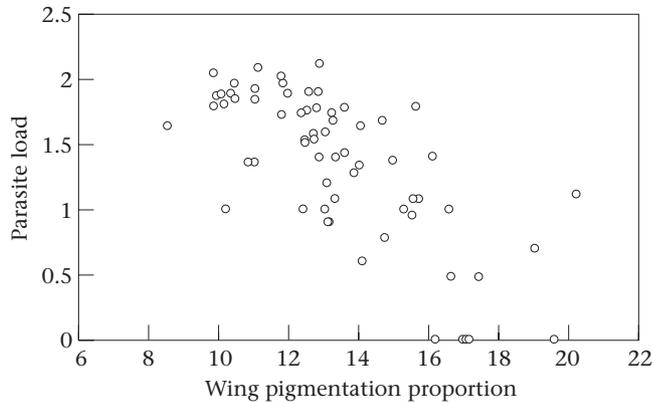
## Quantifying Parasite Burden, Egg Load and Wing Pigmentation

At the end of the reproductive season in 1996, we obtained a sample of 56 unmarked females. These were middle-aged females (as judged by their body condition: dark body colour and dusty appearance of the last abdominal segments due to past ovipositions; Johnson 1973) that were captured before they started oviposition (i.e. they had mature eggs). These individuals were used for parasite, egg and wing pigmentation quantification.

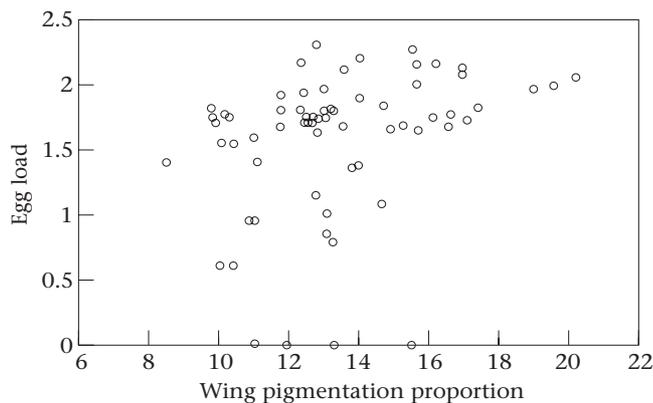
We counted parasites by cutting the head off of each female and pulling the last abdominal segment until the gut was completely removed. We dissected the gut longitudinally in water and counted the number of parasites attached to the gut wall. We counted eggs by opening the entire abdomen.

We measured wing pigmentation by obtaining a photograph of the wings using a digital camera. Photographs were taken at a constant distance, stored in a computer and examined using the Scion Image for Windows software. We then measured the relative percentage of dark areas of the four wings. Using this measure, we avoided any bias caused by size (for example, larger individuals having larger pigmented areas). Male wing pigmentation was taken from the data set generated from previous studies in this species (Córdoba-Aguilar 2002a).

We also used this female sample to examine the correlation between wing pigmentation, parasite burden and egg number. In these correlates, we also included body size, because it may be related to egg number. We measured body size from the apex of the wing to the nodus of the anterior, right wing (Maibach 1985, 1986). Because our preliminary results indicated that only wing pigmentation, but not body size, predicts parasite burden (more pigmentation, fewer parasites) and egg number (more pigmentation, more eggs), we used pigmentation level as a cue for female condition (parasite level) and reproductive value (number of eggs produced) to examine the predictions outlined above using the behavioural data obtained from marked females in the same reproductive season.



**Figure 1.** Parasite burden of females in relation to their proportion of wing pigmentation.



**Figure 2.** Number of eggs produced by females in relation to their proportion of wing pigmentation.

Egg and parasite data were transformed using the formula  $\log(x+1)$  to fulfil the assumptions needed for the use of parametrical tests. Mean  $\pm$  SD are provided unless stated otherwise.

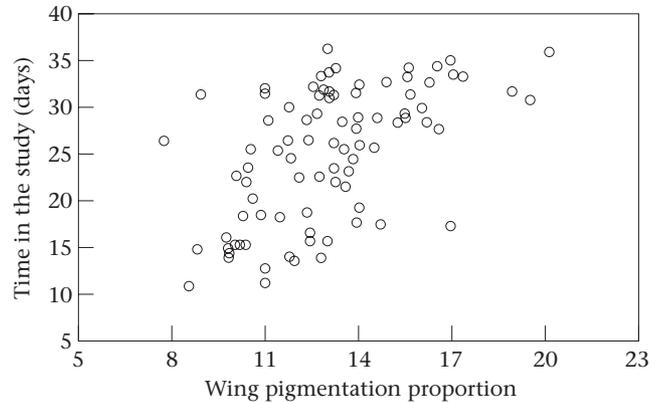
## RESULTS

### Age, Parasite Burden, Egg Load, Wing Pigmentation and Body Size

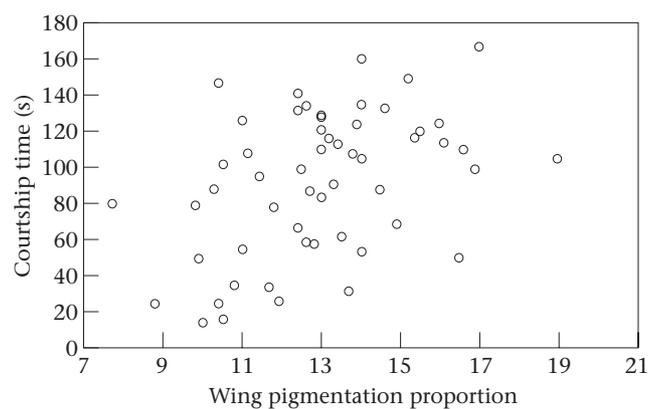
Wing pigmentation did not change with age ( $\bar{X} \pm$  SD: at first photograph:  $18.79 \pm 4.06$ ; at second photograph:  $18.72 \pm 4.15$ ; paired  $t$  test:  $t_{66}=0.71$ ,  $P=0.48$ ). Number of parasites was related to wing pigmentation (Pearson correlation:  $r_{63} = -0.72$ ,  $P < 0.0001$ ; Fig. 1) but not to body size ( $r_{63}=0.19$ , NS). Similarly, egg load was related to wing pigmentation ( $r_{63}=0.3$ ,  $P < 0.01$ ; Fig. 2) but not to body size ( $r_{63} = -0.16$ , NS).

### Pigmentation and Number of Days in the Study Site

Wing pigmentation of females was positively related to how long they stayed in the site ( $r_{85}=0.42$ ,  $P < 0.01$ ; Fig. 3).



**Figure 3.** Number of days that females were found in the study site in relation to their proportion of wing pigmentation.

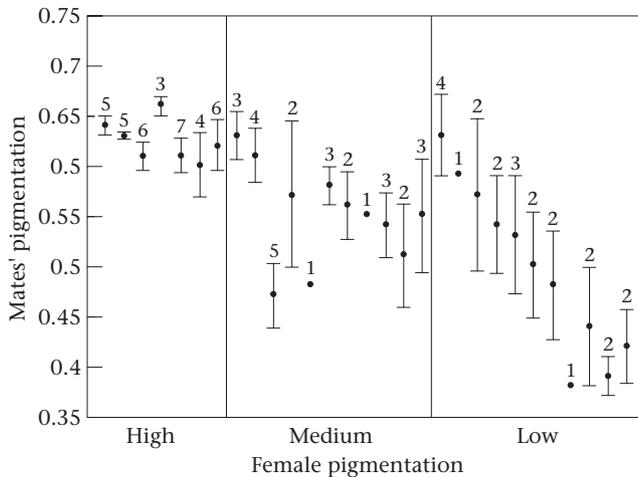


**Figure 4.** Courtship duration (in s) received by females in relation to their proportion of wing pigmentation.

### Pigmentation and Mating and Oviposition Decisions

Wing pigmentation was positively correlated with courtship duration (events that led to copulation;  $r_{53}=0.45$ ,  $P < 0.01$ ; Fig. 4). There was a significant positive relationship between a female's proportion of wing pigmentation and the number of males that courted her during a visit to the reproductive site before she accepted a mating ( $r_{33}=0.81$ ,  $P < 0.01$ ). Wing pigmentation of females was directly related to mating success: the higher the pigmentation, the higher the mating success ( $r_{27}=0.66$ ,  $P < 0.001$ ; Fig. 5). To investigate whether mating decisions (in terms of mates' pigmentation) was affected by female condition (as signalled by pigmentation), we used the copulatory events of those females that had been previously courted and arbitrarily divided them into three groups according to their relative proportions of wing pigmentation (low, medium and high; see Fig. 5). Highly pigmented females showed less variance in wing pigmentation relative to the males they mated with than did medium- and low-pigmented females (Bartlett's test:  $B=20.09$ ,  $P < 0.0001$ ; Fig. 5).

Although nearly all females appeared to use both MAG and SAG tactics at least once in their lives (4 of 29 females used only the MAG tactic), highly pigmented females



**Figure 5.** Proportion of female wing pigmentation and the pigmentation level ( $\bar{X} \pm SE$ ) of their mates. Females were divided into three groups according to their degree of wing pigmentation (low, medium and high). Number of males each female mated with is given above each bar.

were more likely to use both tactics (MAG:  $r_{27}=0.66$ ,  $P<0.01$ ; SAG:  $r_{27}=0.53$ ,  $P<0.01$ ).

Guarding time was positively correlated with female pigmentation in MAG females ( $r_{13}=0.57$ ,  $P<0.05$ ).

## DISCUSSION

Much attention has been recently paid to the evolutionary effect of parasites on sexual selection (Andersson 1994). In line with this research avenue, several sources of evidence indicate that eugregarine parasites may play a decisive role in male calopterygid reproductive biology (Siva-Jothy & Plaistow 1999; Siva-Jothy 1999, 2000; Córdoba-Aguilar 2002a). These sources indicate that the expression of male traits might be signalling the male's ability to cope with eugregarines during male–male competition and female choice. Our results in *C. haemorrhoidalis* suggest that females may also be affected but in different ways. Eugregarines may influence: (1) a female's 'survival' (i.e. days in study site) and egg production; (2) mating decisions; and (3) oviposition tactics, which may be related to fertilization decisions.

Females infected with fewer parasites stayed in the study site longer and produced more eggs. This 'survival effect' result would be expected considering what is known about the parasite effect on males. In this species, males with fewer parasites survive longer (Córdoba-Aguilar 2002a; but see Hecker et al. 2002). Given this similarity, some explanations about the proximal effects of parasites may be generalized for both sexes. Soon after emergence but prior to sexual maturity, adults feed abundantly in order to accumulate fat reserves (Corbet 1999). During this period, however, adults also become susceptible to eugregarine parasites (Åbro 1971, 1974; Siva-Jothy & Plaistow 1999). Because eugregarines feed on the adult damselfly's consumed food (Siva-Jothy & Plaistow 1999), the general effect for both sexes would be a reduction in body fat accumulation. For males, fat is

relevant for territorial defence (Marden & Waage 1990; Plaistow & Siva-Jothy 1996); for females, fat may be more important for egg production. Supporting evidence for this effect was found by Anholt et al. (1991), whose results indicate that mass gain is differentially allocated in both sexes in Odonata during maturity: females similarly allocate fat to both the thoracic (where flying muscle is located) and abdominal (where eggs are produced) regions and males allocate more fat to the thoracic region. Our results suggest that, similar to males, the general effect of parasites on females would be on fat accumulation but, unlike males, the effect will be expressed in terms of egg production. Another more extreme effect of parasites may be that, when found in large numbers, they may break the gut wall and allow other parasites to infect the body (Åbro 1971, 1974). This second effect would be the same for both sexes: it would decrease survival. Our results are in agreement with this effect in females.

Parasite burden was related to female mating history. Females with fewer parasites were courted for longer, visited more males, had a higher mating success and mated with highly pigmented males. These results cannot be explained on the basis that males were selectively discriminating females: because the daily number of matings a male obtains rarely exceeds more than one (Córdoba-Aguilar 2002a), males should court and mate with any receptive female. Similar to other studies in different species (Poulin 1994; Poulin & Vickery 1996; López 1999), we believe that female condition drives female mating decisions. If the costs of mate sampling are considerable, a female should become less choosy (Real 1990). This might be the case if females are condition-stressed (López 1999). Calopterygid females inspect different territories before accepting a male, particularly *C. haemorrhoidalis* females (Córdoba-Aguilar 2000). Because of the high costs of eugregarine infection on survival, infected females should invest less time during courtship and mate less often. Moreover, if they invest less time, then the 'strength' of their preference should be weakened, and they should accept nearly any male to ensure fertilization. This may explain why low-pigmented females' mates showed a high variance in pigmentation, because low-pigmented females were less selective than were highly pigmented females.

Why do less parasitized females mate more often, choose more pigmented males and engage in more SAG oviposition events? Females in this species retain some stored spermathecal sperm, but bursal sperm is emptied during male copulatory sperm displacement (Córdoba-Aguilar 1999, 2002b). Research in the closely related species *C. splendens xanthostoma*, indicates that, given that males are not able to displace the sperm stored in the spermatheca, females have a higher genetic diversity in this sperm storage organ compared with that of the bursa (Siva-Jothy & Hooper 1995). Furthermore, females are able to use their sperm stores differentially, depending on the situation: during MAG oviposition, they use the sperm of the last male, and during SAG oviposition, they use spermathecal sperm (Siva-Jothy & Hooper 1996). There is no a priori reason why this should not apply to *C. haemorrhoidalis*. If females of this species are able to

use their sperm differentially during oviposition events, mating multiply and with highly pigmented males would provide them not only with sperm from the best-quality males (e.g. individuals able to successfully cope with parasites) but with the opportunity to use it accordingly. This would explain why multiply mated females tended to engage in more SAG ovipositions events, because they would have accumulated more sperm in the spermathecae from different high-quality males.

We advanced the hypothesis that one benefit females may receive for expressing their pigmentation is that they may be guarded for longer. Cordero (1999) found that at high densities of a *C. haemorrhoidalis* Italian population, females were highly harassed and were an easy 'target' of many intruder males. One extreme but common consequence of this was that some females died during male mating attempts (A. Cordero, personal communication). In fact, high densities are also frequent during mid-reproductive season (July) in our Spanish population (unpublished data). Under such conditions it may benefit females to advertise their reproductive value (in the form of more mature eggs to be laid). Siva-Jothy (1999) and Córdoba-Aguilar (2002a) have suggested that one benefit females may obtain during mate choice is to be granted with a good resource holder that can provide effective guarding. This might be the case for *C. haemorrhoidalis* females.

Another possibility we cannot discard is that instead of assessing female wing pigmentation, males may assess female weight to obtain information about their mates' reproductive value. Males could assess female weight during carrying episodes between perch sites, which take place while the pair is in-tandem before, during and after copulation. This possibility could be tested by experimentally varying female pigmentation intensity and weight.

Unlike other species in which females gain clear benefits of signalling their reproductive potential through the expression of male-like ornamental traits (e.g. Møller 1994), female wing pigmentation in *C. haemorrhoidalis* does not appear to be a sexually selected trait. This is because it is unlikely that males choose their mates in this system. Another explanation for the pigmentation is that males may use it as a cue for avoiding heterospecific pairing. Despite Waage's (1975) evidence that female pigmentation may be functioning as a reproductive isolation character in other *Calopteryx* species, this hypothesis does not apply to *C. haemorrhoidalis*. The habitats used by this species are so particular that other *Calopteryx* species are rarely found (Cordero 1989; personal observation). Although we occasionally found *C. virgo* and *C. xanthostoma* at our study site, both of these species were present at very low densities (unpublished data).

Finally, we admit that our interpretation of the correlates found in the present study precluded a nonadaptive alternative explanation, and therefore, that the female condition signalling hypothesis may not be the only explanation for such correlates. One hypothesis is that the expression of pigmentation has nothing to do with condition signalling in females, but is an unavoidable and unique consequence of the indirect effect of parasites on pigmentation deposition (as judged from previous

studies in calopterygids; Siva-Jothy 2000; Córdoba-Aguilar 2002a) and egg load. To elucidate this, future research should be directed to experimentally examining pigmentation expression and egg production under variable levels of eugregarine infection. Also, female pigmentation intensity should be manipulated and male postcopulatory guarding time recorded to determine whether the positive correlation we found still holds.

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