



Conflict resolution in the Odonata: implications for understanding female mating patterns and female choice

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Predictions of mating patterns in animals have focused on males and how they compete for fertilizations by controlling females. With reference to the Odonata, a taxon in which mating requires cooperation of the female, the active role that females play in mating decisions is often ignored, leading to the premature conclusion that male coercion of females is common. A critical review of the outcome of sexual conflict among odonates leads me to alternative explanations of female mating patterns that need to be refuted before concluding that males coerce matings. Because Anisoptera males have greater control over tandem formation, they have a greater potential for coercion than Zygoptera males. However, Anisoptera females may simply be willing to remate more often if they receive insufficient sperm to fertilize an entire egg clutch. Contrary to prior assumptions, in both suborders, male defence of oviposition sites does not preclude females from choosing among sites or among males. I find that the evolution of non-aggressive sexual signals by males is a reliable indication that sexual conflict has been resolved in favour of female interests. Although I predict that the benefits to females of choice of male phenotype should rarely exceed the cost of such discrimination in Odonata, female choice is most likely to evolve in territorial species whose males must endure high physiological stress in order to mate, and when site quality is not a reliable predictor of the genetic quality of a potential mate.

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INTRODUCTION

Paradigms explaining mating behaviours have traditionally emphasized male control over females and male-male competition for fertilizations (e.g. Thornhill & Alcock, 1983; Waage, 1984a; Ridley, 1990). For example, Emlen & Oring (1977) hypothesized that sexual selection on males increases as males are increasingly able to monopolize females and/or critical resources. This paradigm addresses only male fitness and male mating patterns; female choice is not even considered as a source of variance in male reproductive success. Despite increasing documentation that females of many species exercise considerable control over reproductive decisions (reviewed by Andersson, 1994), and indications from genetic models that mate choice is feasible (e.g. Kirkpatrick, 1982; Pomiankowski, 1988; Price, Schluter & Heckman, 1993), we lack a predictive paradigm for female mating patterns (see also Bradbury & Andersson, 1987).

Several hypotheses proposed to explain female mating patterns assume that sexual conflict over mating is resolved in favour of male fitness at the cost of female fitness. I refer to such hypotheses as being 'male-biased'. For example, 'rape' (Parker, 1970, 1979) or 'convenience polyandry' (Rowe, 1992; see also Walker, 1980; Thornhill & Alcock, 1983; Halliday & Arnold, 1987) is a form of male coercion; the female loses fitness at the expense of the male who stands to gain fitness from the mating. Convenience polyandry is thought to evolve if males persist in harassing females for a longer time than the average copula duration. Then, the reasoning goes, a female should 'give in' and mate. Otherwise she wastes more time by resisting than she would by mating (Parker, 1979). This reasoning assumes that time loss is of greater consequence to females than to males. In convenience polyandry, mate guarding must limit the number of times a female could be coerced. Otherwise, excessive time loss and/or damage incurred by mating repeatedly should favour females that resist.

Mate guarding that serves to protect a male's sperm investment from rival males (reviewed by Alcock, 1994) is often considered a benefit to females that selects for multiple matings (e.g. Thornhill & Alcock, 1983; Waage, 1984a). However, such guarding would not *initially* select for remating by females, even if, once multiple mating evolved for some other reason, it increases a female's reproductive efficiency (e.g. Waage, 1978; Tsubaki, Siva-Jothy & Ono, 1994).

'Material benefit polyandry' (Thornhill & Alcock, 1983) is another implicitly male-biased hypothesis when it refers to females that exchange matings for resources that are controlled by territorial males (e.g. Waage, 1984a; Ridley, 1990; Conrad & Pritchard, 1992). Such an exchange is simply another form of male coercion if a female's choice is either to mate with the controlling male or forego successful reproduction. More likely however, a female that already carries sperm could reject the territory owner. She could still lay eggs when the territorial male is absent, or use another site. In that case we would expect a male to advertise what he offers in exchange for a mating, and his behaviour would best be described as *enticement*, rather than coercion. The female has greater control over the outcome, and is free to accept or reject the male. Nevertheless, as in coercion, her resulting fitness may be less than it would be in *the absence of male control*. Finally, if there is little or no fitness cost to a female of refusing a potential mate, then a male's advertisement is more akin to *solicitation* or *courtship*. If a male offers a superior larval habitat and/or superior genes,

then both the male and female may benefit from mating (e.g. Tsubaki *et al.*, 1994).

A major hindrance in distinguishing among the above possibilities is the paucity of data on the fitness consequences to females of resisting male mating attempts. Nevertheless, we can gain insights into the causal factors underlying female behaviour by analysing mating patterns and the resolution of sexual conflict of interests. I use the comparative data available for odonates to consider conflict resolution from a female, as well as male, perspective. My findings are relevant to insects generally, and suggest that females derive natural selection benefits from mating multiply, even though such benefits may depend on the mode of sexual selection on males.

POTENTIAL FOR FEMALE ODONATES TO INFLUENCE MATING DECISIONS

Because their reproduction is easily observed under field conditions, the Odonata have provided a wealth of data on long-term reproductive behaviour, particularly of males, which are often more localized than females (reviewed by Corbet, 1962; Bick, 1972; Waage, 1984a; Fincke, Waage & Koenig, 1997). Hereafter, 'dragonfly' refers to species of the suborder Anisoptera and 'damselfly' to species of the suborder Zygoptera. In both suborders, male mating patterns range from mate searching to long-term defence of oviposition sites. The mechanisms of male-male competition for mates and sperm competition in particular, are well understood (Waage, 1984a). Females store sperm in a sac-like bursa and one or two smaller spermathecae, using sperm from the bursa to fertilize eggs as they are laid. Males of both Anisoptera and Zygoptera typically displace or reposition the sperm of previous mates (Waage, 1979a, 1984a; Siva-Jothy, 1984, 1987; Miller, 1990, 1991a), resulting in the final mate fertilizing most if not all of the eggs laid shortly after mating (Fincke, 1984a; McVey & Smittle, 1984; Wolf *et al.*, 1989; Hadrys *et al.*, 1993). Males appear to exercise considerable control over the termination of tandem pairing and of copula. They can remain in tandem with ovipositing females and/or vary copula duration to maximize their fertilization success. Because sperm precedence of the last mate may decrease with time (e.g. McVey & Smittle, 1984), some males increase copula duration if it is unlikely that a female will oviposit immediately afterwards (Ueda, 1979; Siva-Jothy, 1987, Siva-Jothy & Tsubaki, 1989a,b; Wolf *et al.*, 1989; Fincke, 1992).

Several features of female mating behaviour suggest that although a male maximizes his opportunity for fertilization success, he may not often do so at the expense of a female's fitness. First, the unique mating morphology of the Odonata makes it impossible for a male to copulate without cooperation of the female. Before a male can mate, he must take a female in tandem by grabbing her pronotum with his anal appendages. Once in tandem and after a male has transferred sperm to his penis vesicle on his second abdominal segment, a female must raise her abdomen to permit the male to engage his genitalia.

Secondly, female monogamy, apparently a derived condition, constrains sperm competition in males. The penis morphology of *Ischnura* for example, is characteristic of species that can remove a rival's sperm (Waage, 1984a). Nevertheless, several *Ischnura* species typically mate only once per lifetime. They reject males with a wing signal and oviposit above water, unguarded by mates. A female *Ischnura verticalis*

typically receives enough sperm from a single mating to fertilize all of the eggs she ever produces (> 1500 , Grieve, 1937; Fincke, 1987).

Thirdly, cooperation between the sexes in communicating sexual intentions is common. Most females are receptive to mating only on days when they have mature eggs to lay, and become unreceptive after laying an egg clutch (Fincke, 1986a). I use 'receptive female' to designate one carrying mature eggs, that may or may not be willing to mate, depending on the costs and benefits to her of doing so. An 'unreceptive female' lacks mature eggs and *invariably* resists mating. As summarized in Table 1, females use their location, behaviour, and specialized signals to indicate their willingness to mate and to avoid unwanted male attention. Whereas it should always pay for a male to heed the rejection signals of an unreceptive female that hasn't yet matured eggs, males also heed a female's rejection signal after she has completed laying on a given day. Then, there is little chance that a male's sperm would fertilize eggs in her later clutches. If such females are taken in tandem at the water, they signal and/or actively resist males and are released in a matter of minutes (Kaiser, 1985; Fincke, 1986a; Forbes & Teather, 1994). Male respect of these female signals argues against coercion because the male fails to persist, even though *a female's presence at the oviposition site indicates that she might be receptive*. When females ultimately control the outcome of the interaction, male cooperation should minimize time and energetic losses to both sexes (see also Gorb, 1992).

It is often assumed that harassment of females by mate-searching males is the cost that selects for females to mate multiply. However, although male harassment directed towards ovipositing tandem pairs is costly to females and may even kill them (Robertson, 1985; Ruppell & Hadrys, 1988; Hadrys *et al.*, 1993; Fincke, 1994a), fitness costs of harassment to *solo* females is not well documented (e.g. Forbes, 1991). In species whose males search for females, pairs often form in feeding areas away from the body of water where oviposition occurs, but harassment is not known to occur there (Fincke, 1982; Michiels & Dhondt, 1991). In territorial species in which females do not remain in tandem during oviposition, harassment by males may

TABLE 1. Indicators of female condition and willingness to mate in odonates

RECEPTIVE AND WILLING	REFERENCES
Location	Siva-Jothy & Tsubaki, 1989b
Developmental body colorations	Kaiser, 1985; Fincke, 1987, Langenback, 1993; Robinson & Jordan, 1996
Perching near male	Oppenheimer, 1987; Robertson, 1982; Moodie, 1995
Conspicuous flight	Kaiser, 1985; Michiels, 1989
Wing signal	Fincke, 1987; Waage, 1984b
UNRECEPTIVE AND/OR UNWILLING TO MATE	
Hiding, remaining motionless	Jacobs, 1955; Pajunen, 1966; Ubukata, 1984; Kaiser, 1985
Wing signal	Bick 1966; Robertson 1982; Utzeri, Falchetti & Carchini 1983; Fincke, 1987; Martens & Refeldt, 1989; Gorb, 1992
Abdomen curl	Utzeri, 1988
Dislodging male with forelegs	Ruppell, 1989a; Koenig, 1991
Resisting flight	Bick & Bick, 1963
Holding perch	Fincke, 1986a; Oppenheimer & Waage, 1987
Shaking	Forbes & Teather, 1994

decrease oviposition efficiency (e.g. Ubkata, 1984; Waage, 1987), but how often females remate to avoid such harassment is unclear.

Finally, if male coercion were common, we should expect females to often mate multiple times per egg clutch, but this is the exception rather than the rule. The literature on male competition emphasizes the *maximum* number of matings per individuals (e.g. Waage, 1979b, 1984a; Ridley, 1990). In many published studies in which females were followed over time, authors rarely reported the mean number of times females mated per clutch. I obtained unpublished data from such studies by personal communication with the authors. When means were not known but females were not seen to remate or did so only rarely, I assigned a mean of 1.0 (*I. elegans*, *I. ramburi*, *I. verticalis*, *M. coeruleus*, *C. elisa*). I also noted whether or not a species was territorial and had pigmented wings. Of the 22 species in 17 genera surveyed, females of only 4 (18%) typically mated more than once (Table 2). As shown in Table 3, the maximum number of matings significantly differed among the three reproductive categories ($F_{2,19} = 6.4$, $P < 0.01$, females; $F_{2,10} = 5.2$, $P < 0.03$, males, 1-way ANOVA). The mean number of matings did not significantly differ among categories, though the trend was in a similar direction. More accurate estimates of the frequency of multiple matings, particularly for species whose females are difficult to follow under field conditions, could be achieved by using microsatellite DNA analysis to identify the 'paternity' of sperm that a female carries.

ALTERNATIVES TO MALE-BIASED HYPOTHESES

Ironically, despite the above indications that females wield considerable influence over mating decisions, several authors have suggested, implicitly or explicitly, that male coercion of matings is widespread in this insect order (e.g. Waage, 1984a; Ridley, 1990; Koenig, 1991; Conrad & Pritchard, 1992). This conclusion is premature at best. Coercion is a justifiable conclusion only if: (1) control of oviposition sites by territorial males effectively precludes females from using such sites without mating with the territory owner; (2) males that manage to take receptive but unwilling females in tandem are successful in fertilizing their eggs; (3) harassment of a solo female carries more of a fitness cost to the female than to the male; females that don't resist are more fit than those that do.

Determining whether any of the above conditions is true has important implications for our understanding of reproductive behaviour. In the odonate literature for example, explanations based primarily on the male's perspective have been proposed for the evolution of courtship displays, female colour polymorphisms and female mate choice, summarized in Table 4(a). At best, such hypotheses are incomplete. For example, Waage (1975, 1979c) suggested that in *Calopteryx* species, premating displays function in reproductive isolation, by allowing males to correctly select conspecifics as mates. He found that the sexually dimorphic wing patterns of *Calopteryx aequabilis* differed more in sympatry than allopatry, and that males were less likely to display to a pinned, sympatric heterospecific female than to an allopatric one. However, because male wing pattern in the absence of a behavioral display was sufficient to cue species identity to a female (Buchholtz, 1951), premating displays by *Calopteryx* males beg additional explanation (see also Corbet, 1962).

At worst, failure to consider the female perspective is misleading. For example, Hinnekint (1987) predicted that the female colour morphs found in mate-searching

damselflies such as *Enallagma* and *Ischnura*, are maintained by density-dependent selection. He reasoned that females coloured like males are less likely to be recognized by males as potential mates. Thus, at low density they risk not mating at all, but at high density they enjoy reduced male harassment, and mate less often than females coloured differently from males. In this scenario, females are viewed as passive objects of a male's attention. However, long-term data on mating frequency of marked individuals in four species suggest that female morphs are equally successful in attracting and avoiding males. No differences between morphs were found in mating or oviposition rates (Thompson, 1987, 1989; Fincke 1994a,b; Forbes, 1994; for a different conclusion, see Robertson, 1985; Cordero, 1992).

TABLE 2. Mean mating rate (and ranges) or best estimates available, for mated males and females on a given day. Terr.: resource defence; Pig.: wing pigmentation; *unpublished data from cited study

	Terr.	Pig.	Female	Male	Source
ZYGOPTERA					
<i>Coenagrion puella</i>	no	no	1.0 (1-2)	- (1-3)	Thompson*, 1987
<i>Enallagma boreale</i>	no	no	1.7 (1-4)	- (1-3)	Fincke, 1994
<i>Enallagma hageni</i>	no	no	1.1 (1-2)	1.1 (1-4)	Fincke, 1982
<i>Ischnura elegans</i>	no	no	1.0	-	Paar & Palmer, 1971; Cordero Santolamazza & Utzeri, unpubl.
<i>Ischnura graellsii</i>	no	no	1.0	1.0	Cordero*, 1992, 1995
<i>Ischnura ramburi</i>	no	no	1.0	-	Robertson*, 1985
<i>Ischnura verticalis</i>	no	no	1.0	1.0	Fincke, 1987
<i>Calopteryx maculata</i>	yes	yes	2.0 (1-5)	4.7 (1-9)	Waage, 1979b
<i>Calopteryx splendens xanthostoma</i>	yes	yes	1.0 (1-4)	1.5 (1-12)	Siva-Jothy* <i>et al.</i> , 1995
<i>Megaloprepus coerulatus</i>	yes	yes	1.0 (1-2)	1.0 (1-2)	Fincke*, 1992
<i>Mnais pruinosa pruinosa</i>	yes	yes	1.0 (1-5)	2.0	Siva-Jothy* & Tsubaki, 1989
<i>Platycypha caligata</i>	yes	yes	often >1 (1-5)	-	Robertson 1982
ANISOPTERA					
<i>Celithemis elisa</i>	no	no	1.0 (1-2)	-	Waage, 1986a
<i>Sympetrum danae</i>	no	no	1.1 (1-3)	1.5 (1-6)	Michiels, 1989
<i>Crocothemis erythraea</i>	yes	no	1.5 1.8 (1-7)	- 1.2 (1-5)	Rehfeldt, 1991 Siva-Jothy* 1984
<i>Nanophya pygmaea</i>	yes	no	1.0 (1-3)	1.0 (1-6)	Tsubaki, Siva-Jothy* & Ono 1994
<i>Orthetrum cancellatum</i>	yes	no	1.0 (1-2)	1.0	Siva-Jothy*, 1987a
<i>Pachydiplax longipennis</i>	yes	no	1.0 (1-2)	-	Dunham*, 1993
<i>Erythemis simplicicollis</i>	yes	yes	2.0 (1-7)	-	Waage 1986a
<i>Leucorrhinia intacta</i>	yes	yes	often >1 (1-7)	-	Wolf <i>et al.</i> , 1989
<i>Libellula luctuosa</i>	yes	yes	1.0 (1-2)	-	Moore*, 1990
<i>Plathymis lydia</i>	yes	yes	1.0 (1-5)	2.6 (1-14)	Koenig*, 1991

TABLE 3. Summary of daily mating rates of mated individuals as a function of reproductive class. Number of species used to generate each mean is in parentheses

Reproductive class		Females		Males	
Territorial?	Wing pigmentation?	Mean	Maximum	Mean	Maximum
No	No	1.1 (9)	1.8 (9)	1.1 (5)	2.7 (7)
Yes	No	1.2 (4)	3.5 (4)	1.1 (3)	5.5 (2)
Yes	Yes	1.4 (8)	4.7 (9)	2.4 (5)	9.3 (4)

Indeed, for none of the *Ischnura* listed in Table 2 were females seen to naturally mate more than once per day, and with the possible exception of *I. ramburi* (see Waage, 1986b), they typically mated no more than twice per lifetime. Conrad & Pritchard (1992) implicitly contradict Hinnekint's prediction by proposing that females of mate-searching species are the most 'free' to exercise mate choice. This prediction is not based on a consideration of female behaviour, but rather on the assumption that territorial males can coerce matings by controlling reproductive resources. On logical grounds, both of the hypotheses cannot be correct; I find little evidence for either.

In what follows, I analyse conflict resolution between males and females. My results counter the above male-biased assumptions, and lead to the alternative hypotheses in Table 4(b) that are in need of testing. The point of these examples is to illustrate how contrasting hypotheses of reproductive behaviour arise, depending on which sex is assumed to have relatively greater control over mating decisions. My analysis below suggests females commonly have considerable control, and that many females mate multiply because they derive direct benefits by doing so.

TABLE 4. Alternative hypotheses arising from male (a) and female (b) perspectives of three phenomena relevant to female mating patterns in Odonata

	REFERENCE
1. PREMATING DISPLAYS:	
(a) Courtship functions in reproductive isolation. Males discriminate among females.	Waage, 1979c
(b) Females use displays to assess male quality.	herein
2. FEMALE COLOUR POLYMORPHISMS:	
(a) Female mating frequency depends on the ability of males to recognize females as potential mates.	Robertson, 1985; Hinnekint, 1987; Cordero, 1992
(b) Female morphs are equally successful in attracting or rejecting males.	herein
3. FEMALE CHOICE	
(a) Female mate choice is least likely to evolve in territorial species because females are not 'free' to exercise choice.	Conrad & Pritchard, 1992
(b) Females are rarely coerced. Female choice of sires is most likely in territorial species whose males are under high physical stress.	herein

POTENTIAL PHYLOGENETIC EFFECTS ON CONFLICT RESOLUTION

In odonates, phylogeny potentially influences the outcome of sexual conflict. Suborders, families, and/or genera differ in: (1) the ease with which males can grab females; (2) the accessibility of ovipositing females; (3) the amount of sperm relative to a female's clutch size, that is transferred in a single copulation; and (4) the cues used by females to discriminate among potential mates.

For example, female Anisopterans appear vulnerable to being coerced into mating. Because an Anisopteran cannot hold its wings together over the thorax, a perched female may be relatively easy for a male to grab. Male dragonflies also readily take flying females in tandem (Rehfeldt, 1989). Anisopterans that insert eggs into plant stems do not avoid males by submerging; their outstretched wings would make manoeuvring underwater difficult. Submerged oviposition apparently offers no advantage to many dragonfly females that can quickly oviposit thousands of eggs on the water surface (e.g. Corbet, 1962; McVey & Smittle, 1984).

Alternatively, anisopteran females may be more willing to remate because they are at greater risk of sperm limitation. This may be particularly true for species with large clutches that copulate for only seconds. In Zygopterans, risk of sperm limitation appears to be lower because even the shortest copulations occur for at least a few minutes, and clutch sizes are typically less than a few hundred (e.g. Corbet, 1962, 1980; Waage, 1984a).

Coercion appears to be more difficult for a Zygopteran male because a female must usually perch before he can 'walk' down her wings and achieve tandem (Conrad & Herman, 1987; but see Alcock, 1982). Furthermore, some females in the Zygopteran families Coenagrionidae and Calopterygidae submerge to insert their eggs into plant stems, thus limiting the ability of males to further interact with them. In territorial *Calopteryx dimidiata* whose females submerge, males stopped displaying to females after a rejection display. In *C. maculata*, females rarely submerge, and some males persisted in displaying even after being rejected initially (Waage, 1984b). Submerged oviposition is unlikely to have evolved primarily as a means to avoid unwanted male attention. It protects eggs from drying (Corbet, 1962; Fincke, 1986a) but also increases a female's risk of drowning and being eaten by aquatic predators (Fincke, 1986a). Coenagrionids that typically submerge do so regardless of the operational sex ratio at the water (Fincke, 1982, 1986a) although in *Calopteryx* with variable oviposition behaviour, submergence may be correlated with male density (e.g. Pajunen, 1966).

Among zygopterans, cues that stimulate a female to copulate are known to differ. Consequently, coercion may potentially be easier for some males, once an unwilling female is taken in tandem. Females that use visual cues to discriminate among mates prior to tandem may mate automatically, once in tandem (Corbet, 1962). Males in the Calopterygidae family have sexually dimorphic, species-specific wing patterns (Bucholtz, 1951; Heymer, 1973; Waage, 1975), and females can discriminate against conspecifics coloured to resemble congeneric males (Bucholtz, 1951). However, if forced into a heterospecific tandem by hand-pairing, a female *Calopteryx* usually copulates if her legs are free of the substrate (Oppenheimer & Waage, 1987). In contrast, some clear-winged coenagrionids reject heterospecific males during tandem formation. They are cued by tactile stimuli made by a male's species-specific anal appendages in contact with the female's pronotum (Robertson & Paterson, 1982;

Tennessen, 1982). In such species, copula does not automatically follow tandem formation as discussed below.

CONFLICT RESOLUTION, MALE SIGNALS AND LIMITS TO COERCION

Whereas a male should persist in trying to mate with a reluctant female if he can influence the outcome in his favour, a female should resist such attempts if the mating does not provide her a greater fitness advantage than if she did not mate. To what extent do male odonates that ignore a female's rejection signal, increase their fitness at the expense of female fitness?

Even though territorial males defend resources critical to females, their ability to coerce matings appears limited. Females often leave sites without mating (Waage, 1973; Robertson, 1982; Fincke, 1992). Moreover, by ovipositing in the presence of a male's mate, a female can use defended sites without mating and without being harassed by the territory owner (Waage, 1979b; Conrad & Herman, 1987; Koenig, 1991; Tsubaki *et al.*, 1994). Such exploitation is possible because males apparently cannot not recognize individual females (but see Hooper, 1995) and simultaneously guard mates and non-mates. Extreme exploitation occurs in the damselfly, *Platycypha caliqata* (Martens & Rehfeldt, 1989; Rehfeldt, 1989). Even though males controlled all available oviposition sites, by synchronizing the timing of ovipositions, 89% of the females oviposited without mating with territory owners beforehand. Thus, contrary to the prediction made by Conrad & Pritchard (Table 4), females of territorial species are free to choose mates independently of oviposition sites, a necessary requirement for active mate choice.

A second way a male might coerce an unwilling female is to persist in disturbing her until she mates with him. The success of male persistence depends on (1) his probability of losing a territory or additional matings by persisting (Waage, 1979b) and (2) the ability of the female to resist. Oppenheimer (1991) cleverly demonstrated a potential for coercion in the zygoptera *Calopteryx maculata* by hand-pairing males with 'resisting' females whose abdomens were artificially stiffened. Although males persisted in tandem with such females for more than three times the average copula duration, it was a relatively short time (311 ± 38 sec), as expected of a species whose territory owners risk losing a territory to an intruder. However, under natural conditions when a *C. maculata* male succeeded in taking an unwilling female in tandem without displaying to her beforehand, she usually resisted him by holding onto her perch until he released her (Oppenheimer & Waage, 1987). Although territorial males sometimes persisted in displaying to a female after receiving a rejection signal, they were successful in mating only a third of the time, and their fertilization success was unknown (Waage, 1984b). Moreover, if a female that gave a rejection signal was subsequently mated by hand-pairing her to the male, she typically left his territory without laying eggs (Oppenheimer, 1991). Oppenheimer suggested that premating displays allowed males to solicit information from potential mates. Males that ignored the information received were unlikely to gain fertilizations. Surprisingly however, she concluded that behavioural displays in *C. maculata* did not function in female choice, because once in tandem, females mated indiscriminately, whether or not they were courted beforehand.

I interpret the data on *Calopteryx* somewhat differently, because *Calopteryx* is a genus in which females are capable of visually discriminating among males before

permitting tandem formation. Thus, I find Oppenheimer's results consistent with female choice. At the very least, the behaviour of territorial male *C. maculata* displaying at a territory suggests enticement rather than coercion. There is no benefit to a coercing male of signalling any specific information to the female. Indeed, he might do better by concealing his intention to forcibly take her in tandem. Territorial *Calopteryx* have not been seen to forcibly take females in tandem (Waage, 1973; Conrad & Herman, 1987). Thus, a *C. maculata* male that achieves tandem by persisting in displaying does so by advertising what he offers, either an oviposition site, or, his physical condition (i.e. his genes). The energetic costs of the complex displays in *Calopteryx* likely prevent males from falsely advertising their physical condition (see Ruppell, 1989b).

Although the displays of many territorial males signal the location of oviposition sites to females (Corbet, 1962; Waage, 1973; Miller, 1991b; Fincke, 1992; Gibbons & Pain, 1992; Tsubaki *et al.*, 1994), *C. maculata* is unusual in that males perform one display at oviposition sites where pair formation begins, and a different display (usually on the bank) before the female is taken in tandem and copulates. Some males without territories gain matings after courting females on the bank, in which case the female locates oviposition sites alone (Waage, 1973, 1984b). Thus, a female *C. maculata* is free to assess oviposition site and male quality independently, and may leave after either male display.

Male coercion is uncommon in other damselflies as well. Territorial male *Megalopteryx coerulatus*, with widely dispersed territories in tree fall gaps, rarely encounter more than a single receptive female or male interloper on any given day. After detecting a female, a male typically displays over the water-filled tree hole. Females can avoid tandem by evasive flight, and often leave without mating, returning later to oviposit when the male is gone (Fincke, 1992). Unlike most odonates, a male *M. coerulatus* in tandem with a female can chase the rare intruder. Thus, territorial males could afford to persist in trying to copulate with unwilling, tandem females without much risk, but they typically do not do so. Occasionally males achieve tandem with an unwilling female after first knocking her to the ground, but in that case, females may resist copula as long as the male persists before he gives up (e.g. 1.5 h, Fincke, 1984b). Although males will sometimes display to females in small light gaps that lack oviposition sites, females inevitably leave without mating. If tethered, a female is unable to resist tandem formation and often will copulate. However, often she does not lay eggs afterwards (Fincke, unpublished data), reminiscent of hand-paired *C. maculata* females.

In mate-searching damselflies (*Amphiagrion*, *Anomalagrion*, *Enallagma*, *Ischnura*) and a few territorial ones (*Argia*, *Hetaerina*), males solicit information from potential males about their willingness to mate *after* they achieve tandem (Robertson & Tennessen, 1984). A male jerks on the female's pronotum and transfers sperm to his penis vesicle only after a female responds to his solicitation by touching, but not engaging, his genitalia. If she ignores his signal, he releases her in a fraction of the time of an average copula duration, and thus conserves his sperm (e.g. Fincke, 1986a).

In the three examples above, a male's use of a specialized, non-aggressive signal (i.e. display or solicitation of genital touching) would have been sufficient evidence for us to determine that coercion did not occur (see also Ridley, 1990). In Anisoptera, genital touching is not known, and premating displays are rare. However, because many dragonflies have fast flight and elusive pairing habits, subtle solicitation behaviour by males, or rejection behaviour of females may not be readily observed

(e.g. Ruppell, 1989a). Before assuming that remating by females results from male coercion, it is critical to show that females mating multiple times per day derive no benefit by doing so.

BENEFITS TO FEMALES OF MATING MULTIPLY

If females aren't coerced, what might they gain from mating multiply? Odonate females are not known to obtain nutritional benefits or increased fecundity from remating (reviewed by Ridley, 1990). They more likely gain: (1) sperm to complete the fertilization of a clutch; (2) survival protection by guarding males; (3) access to superior larval habitats, or (4) access to superior genes. Note that mate guarding from conspecific males is not considered here because it becomes a benefit only after multiple mating has evolved for some other reason.

Because females store sperm, their risk of sperm shortage depends on the time over which sperm remain viable, and the degree to which males are sperm limited. Insurance against insufficient or inviable sperm may best explain why most females seem willing to mate once per clutch. Because females that arrive at oviposition sites often carry some sperm before they mate again, it is commonly assumed that females are not sperm limited (e.g. Waage, 1984a). However, it is not known if they carry enough sperm to completely fertilize a clutch. Inviability of sperm is not uncommon in other insects (reviewed by Ridley, 1988) and needs to be examined for odonates. Additionally, competition among males for fertilizations can exacerbate a female's risk of sperm limitation. Male fertilization success may sometimes be sperm limited or limited by the demands of territorial defense (Wolf *et al.*, 1989). In three dragonflies that mate for only seconds, copula duration decreased as male mating frequency increased (Jacobs, 1955; Michiels, 1992). In both suborders, territorial males often copulate for a shorter time than satellite males, apparently to reduce their risk of losing their territory to intruders (e.g. Siva-Jothy, 1987a; Fincke, 1992). Physiological limits to mating frequency (Waage, 1979b; Fincke, 1986a; Hooper, 1995) further support the idea that fertilization success in males may sometimes be sperm limited.

In some Anisoptera, females are more likely to remate when male density is high (Wolf *et al.*, 1989; Koenig, 1991; Rehfeldt, 1991), suggesting that males coerce matings. However, without knowing the sperm loads of the remating females, this trend is equally consistent with the hypothesis that at high male density, females are more at risk of receiving insufficient sperm because copulation duration is also shorter. Females of two *Orthetrum* species with large clutches and short copula durations were found to suffer temporary sperm shortages (Miller & Miller, 1989). In the dragonfly, *Crocothemis erythraea*, males reposition sperm of previous mates and multiple matings increases the number of sperm a female carries (Siva-Jothy, 1984). In some sperm-removing Zygoptera and Anisoptera on the other hand, the morphology of a female's spermatheca may prevent a male from removing all of the sperm of a previous mate (Waage, 1984a; Siva-Jothy & Tsubaki, 1989a), decreasing to some extent, the risk of sperm depletion resulting from male sperm competition.

Experiments using virgin females are critical to determine if females always receive enough sperm to fertilize an entire clutch, particularly in the Anisoptera. For example, in sperm competition experiments on three different species, a male's

paternity in a clutch that was immediately laid by his non-virgin mate, dropped as copula duration decreased or was shortened artificially (Wolf *et al.*, 1989; Michiels, 1992; Hadrys *et al.*, 1993). Had virgin females been used, they might have suffered infertility as the result of very short copula durations. This conclusion assumes that in the original experiment, copula duration was correlated with the quantity of sperm transferred rather than with the quantity of a rival's sperm that was displaced, as Michiels (1992) concluded. Similarly, the finding that a male's paternity decreases with successive clutches laid by his mate (McVey & Smittle, 1984; Hadrys *et al.*, 1993), may indicate that a single sperm load is insufficient to fertilize all of a female's eggs, or simply that, as time passes, a male's sperm mixes with rival sperm.

One known natural selection benefit of remating in some Zygopteran with submerged oviposition is survival protection by males from drowning. Between bouts of underwater egg laying on a given day, a *Enallagma hageni* female accepts copula with any male seizing her. By so doing, she gains his vigilance and subsequent rescue service should she fail to clear the air-water interface upon surfacing. When she has completed egg laying however, a female refuses to copulate with any male taking her in tandem. Thus, a female that resurfaces unsuccessfully from her last bout of laying that day, exploits any male that pulls her from the water. Her lack of eggs becomes evident to him only after the rescue, when she resists his attempts at copula (Fincke, 1986a). Similarly, survival protection from frog predators is a possible benefit of remating for *Sympetrum danae* in which the few rematings observed were associated with second oviposition bouts (Michiels & Dhondt, 1989, 1990).

Finally, a female might remate if she assesses a second site or potential sire to be superior relative to her first choice ('mating with assurance', Waage, 1984a). Females of a few territorial species with pigmented wings, actively reject males, and typically mate twice during oviposition (Table 2). Unfortunately, no study of a territorial species to date has followed marked females long enough to determine the fitness consequences of mating more than once per clutch. In some dragonflies and damselflies, defended sites differ in quality as larval habitats and females are known to differentiate among sites (Wolf & Waltz, 1988; Fincke, 1992; Tsubaki *et al.*, 1994; Siva-Jothy, Gibbons & Pain, 1995). However, there is no evidence that females must remate in order to gain access to such sites, even though males might entice them to do so. In the dragonfly *Libellula luctuosa*, most of the matings over two years consistently occurred at the same three sites (Moore, 1989), suggesting that females discriminated among sites. At high male density, females visited fewer territories and oviposited for shorter durations, as expected if they were minimizing the risks of male harassment during oviposition. Nevertheless, because nearly all of the observed females mated only once (Moore, pers. comm.), females did not remate as the result of harassment, nor to improve their choice of either site or sire.

A PHYSIOLOGICAL MODEL OF FEMALE MATE CHOICE

Even though most odonate females may have the freedom to choose among sires, there may rarely be any selective advantage in doing so. Widespread male-male competition, coupled with conspicuous female behaviour that tends to promote competition (e.g. Kaiser, 1985; Michiels, 1989), should often weed out poor performing males prior to females mating with them. In addition, any genetic benefit of mate choice may not offset the time and risks involved in assessing male quality

(see Pomiankowski, 1987). Odonate breeding sites are typically exposed areas, where predator risks may be greater than in feeding areas (e.g. Rehfeldt, 1990, 1992; Convey, 1992; Forbes, 1994). Thus, although we would always expect females to discriminate against heterospecifics and dysfunctional conspecific males, the threshold of genetic quality of sires above which females face diminishing returns by discriminating, may generally be low.

Is there any reason to suspect that the genetic benefits per time invested in discriminating among sires is greater for some females than for others? I predict that such benefits/cost should be greatest in species or populations whose males face considerable physiological challenges to reproduce. In non-territorial species, whose males search for females, such challenges appear to be low relative to the stress endured by territorial males. In mate-searching species, longevity is typically the best predictor of male mating success but survivorship is largely stochastic (Banks & Thompson, 1985; Fincke, 1986b; Michiels & Dhondt, 1991). Variance in male mating success is relatively low (reviewed by Fincke *et al.*, 1997). Females are typically larger than males, and some males actually lose mass between emergence and sexual maturation (Anholt, Marden & Jenkins, 1991). Consistent with my above prediction, females of non-territorial species rarely mate more than once per reproductive bout (Table 2). When they do, as in *Enallagma*, female acceptance of additional mates depends on whether or not they have eggs to lay, rather than on male phenotype.

In a territorial species on the other hand, flight endurance and manoeuvrability is often at a premium. Hence the impact of a deleterious mutation on male performance should be greater than in a mate-searching species. Variance in male reproductive success tends to be highest in territorial species (Fincke *et al.*, 1997). Sexual size dimorphism in territorial odonates is low or male-biased. These males also gain more mass than females during maturation (Anholt *et al.*, 1991), suggesting that large male size carries a greater selective advantage compared with mate-searching species. Patrol and fighting flight required to hold a territory, and the display flight of some territorial males appear to be more expensive energetically than the forward flight with low acceleration used by mate-searching males (Fried & May, 1983; Vogt & Heinrich, 1983; Singer, 1987; Marden, 1989; Ruppell, 1989b, Ruppell & Fincke, 1989; May, 1991; Watanabe, 1991). Territorial male *Calopteryx* require large fat stores to successfully win prolonged fights and are often near their physiological limit (Marden, 1989; Marden & Waage, 1990). These and other territorial males must forage throughout their lives to maintain or restore energy levels (Dunham, 1993; Fried & May, 1983). Furthermore, within a single species whose males exhibit both territorial and non-territorial tactics, shifts from the former to the latter occur either at old age and/or low energy stores (Forsyth & Montgomerie, 1987; Waltz, 1982; Waltz & Wolf, 1993). In *Mnais* damselflies, the territorial male morphs conserve much needed energy by thermoregulating more efficiently than non-territorial morphs (Watanabe, 1991; Watanabe & Taguchi, 1990).

Despite the greater potential benefits of choice in territorial species, if the quality of an oviposition site is a reliable predictor of the genetic quality of the male defending it, then females indirectly gain superior sires simply by mating only with males at high quality sites (i.e. 'passive mate choice', Thornhill & Alcock, 1983). Furthermore, if environmental effects on male phenotype were greater than effects resulting from genetic variation underlying those traits, then any advantage of direct female choice would be constrained.

EVIDENCE FOR FEMALE CHOICE OF MALES IN THE ODONATA

In the territorial damselfly, *Megaloprepus coerulatus* (Pseudostigmatidae), current data suggests females indirectly choose large males by mating only at defended oviposition sites (Fincke, 1992). Females readily mate with small satellite males that occasionally frequent defended tree holes. This species has very low population density and environmental effects on male phenotype are high. Male body size, a reliable predictor of territorial and mating success, increases with the volume of the tree hole larval habitat (Fincke, 1992). In this species, both the costs and benefits to females of discriminating among sires appears to be low for much of the season.

Territorial residency may not always be a reliable indication of male quality if high density or stochastic factors affects a male's ability to consistently control sites, or affects which sites are the most favourable for females (e.g. Waage, 1987). In the above mentioned *M. coerulatus* for example, when tree holes first fill at the onset of wet season, small males are as likely as larger males to initially hold a territory (Fincke, 1992). Then, assuming there is genetic variance for male size, females might benefit from discriminating among males on the basis of phenotype. Distinguishing between choice of site versus choice of sire is best done by noting the mating choices of females over time, when phenotypically variable males sequentially control the same oviposition areas.

In territorial odonates, one possible cue to male quality independent from site quality is sexually dimorphic pigmentation. Sexually dimorphic wing patterns are found in territorial species of the zygopteran families Calopterygidae, Pseudostigmatidae and Chlorocyphidae, and in the anisopteran families Libellulidae and Aeshnidae (Walker, 1953; d'Aguilar, Dommanget & Prechac, 1986; Dunkle, 1989; Watson, Theischinger & Abbey, 1991). Consistent with my physiological model of female choice, of the 13 territorial species I surveyed, 9 have pigmented wings (Table 2). This latter group also has the highest female mating rates (Table 3). Some Libellulidae and Chlorocyphidae also have strikingly dimorphic abdominal pigmentation, and males in the latter family also have expanded, coloured tibia that they display to males and females (Robertson, 1982; Orr 1996). In a survey of 11 chlorocyphids, Orr (1996) found that females rejected heterospecifics, but also often rejected courting conspecifics. Experimental manipulation of sexually dimorphic characters could determine if such traits are preferred by females. For example, in the chlorocyphid, *Platycypha caligata*, Jennions (1995) artificially blackened the white tibia of males. Complete elimination of the signal decreased a male's presence at the mating site, suggesting the white tibia functioned in male-male interactions. However, because natural signal size was correlated with copula duration and the number of matings a male obtained, female choice of a correlated trait could not be ruled out. Similarly, Grether (1996) artificially increased the red area of the wing in male *Hetaerina americana* (Calopterygidae). Males subsequently enjoyed greater mating success, which resulted from their increased territorial holding ability rather than from female preference of the trait. Thus, for both species, discrimination among sites may be sufficient to insure that a female mates with a high quality sire.

In the libellulid *Plathemis lydia* which has sexually dimorphic wings, Koenig (1991) concluded that females were not exercising mate choice. He found no consistent difference between mated and unmated males with respect to size, age or mass, even though the latter two characters were good predictors of male success in alternative years. Males that were most successful at mating were also the most active, and

consequently were also the ones most often rejected by females. Unfortunately, variation in male pigmentation was not measured.

The best evidence to date for direct female choice in an odonate is provided by Moore's (1990) study of mating success in *Libellula luctuosa* (Anisoptera). He studied the same territory sites over two successive seasons. Males were rarely seen for more than a day, but among males successful in holding a given territory, mating success was correlated with the width of the brown and white wing pigments.

Female choice of male phenotype is most likely to evolve in territorial species with premating displays, such as those in the genera *Calopteryx* and *Platycypha*. In these species, population densities are often sufficiently high to make defence physiologically stressful. The sexually dimorphic males perform complex displays prior to tandem formation, providing females with both the time and visual display to assess the condition of potential mates. Interestingly, recent work suggests that female *C. splendens xanthostoma* prefer to mate with males with uniformly dark wing pigments (Hooper, 1994). Because Anisopteran females may have less control over mating decisions, it may not be surprising that premating displays occur only rarely in this taxon (Jacobs, 1955; Corbet, 1962; Miller, 1991b).

CONCLUSIONS

In many insects females are often thought to remate to minimize time lost by resisting harassing males (e.g. Parker, 1970; Anderson, 1994; Rowe *et al.*, 1994). For odonates, this assumption is not well-supported by data on female mating rates nor by my analysis of intersexual conflict resolution. Indeed, the most costly conflicts in odonates occur between a mated pair and other males rather than between a male and a solo female. The considerable control females have over the resolution of sexual conflicts of interests is clearest in cases where males exhibit non-aggressive sexual signalling. Many females are able to exploit male services, even when mates control critical reproductive resources.

Thus, the absence of female mate choice, especially in Zygoptera, is unlikely explained by an inability of females to exercise choice. Rather, the benefits/costs of mate choice appear to be low in the Odonata. In my physiologically-based model of female choice, the relative benefit of mate choice for females depends on the type of male-male competition that evolves. It is thus an extension of the Emlen & Oring (1977) paradigm. Female mate choice is most likely to be found in insects with non-aggressive male signalling and whose males are subjected to high physiological stress, such as territorial odonates that court females, or orthoptera that must call to attract females (reviewed by Gwynne & Morris, 1983). In highly visual insects, costly pigmentation may cue females to variation in male quality as it does in some vertebrates (reviewed by Andersson, 1994). Measuring the effect on male mating success, of variation in male pigmentation and in the vigour of premating displays, is a critical first step in assessing the possibility of female mate choice in odonates and other similar insects.

Because the resolution of sexual conflict is a dynamic process undoubtedly affected by ecological and social conditions, the relative control females have over mating is likely to vary among populations. Determining the cause of the variation that exists in female mating frequency both between and within species, remains a challenge for future research. Long-term data on mating patterns of marked females are required

to determine the extent to which females vary in their need for benefits acquired by mating, or in their ability to resist male harassment (see Gowaty, 1992).

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