

The Evolution of

Mating Systems in Insects and Arachnids

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3 • Natural and sexual selection components of odonate mating patterns

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ABSTRACT

Traditionally, students of odonate reproductive behavior have focussed on how males compete for access to mates and fertilizations. This tendency has yielded considerable information on male reproductive strategies and on the proximate and ultimate mechanisms involved in male-male competition, but has left numerous gaps in our knowledge of other aspects of odonate mating systems.

We review relevant aspects of odonate biology and examine the extent to which current data on mating patterns support predictions arising from sexual selection theory. Although long-term studies offer some such support, they also indicate that natural selection for longevity and stochastic factors such as weather play critical roles in influencing reproductive success. Relatively little of the variance in male reproductive success in odonates has been traced to variance in male phenotype.

We emphasize the role of females as determinants of odonate mating patterns and discuss sexual conflicts of interest over mating, fertilization, and oviposition decisions. Finally, we explore ways in which natural selection underlies female mating decisions and how larval and adult ecology interact to influence adult reproductive behavior.

INTRODUCTION

The study of mating systems is the study of the behavioral, physiological, and ecological factors that underlie predictable patterns of male and female interactions during reproduction. Much of the literature on mating systems emphasizes male-male competition and its effects on male morphology and behavior. However, fertilization success of males cannot be explained solely by pre- and post-copulatory interactions of males or their gametes (see Alexander *et al.*, this volume). There are at least three reasons for this in odonates.

First, the unique copulation process in odonates requires cooperation on the part of a female. Males may be able to take a female in tandem (grasp the female's head

or prothorax with specialized anal appendages), but she must bend her abdomen to engage the male's penis. Second, sperm competition does not take place in a neutral arena; it occurs within females. Males invade this arena by removing sperm of prior mates as part of copulation (Waage 1979a, 1986a; Siva-Jothy 1987a). If females are able to differentially use the sperm from individual males, then male copulatory behavior or mating order alone would not be sufficient to determine paternity. Third, females can negate whatever males accomplish through sperm removal and replacement simply by leaving a male's territory and mating with another male before ovipositing any eggs. These three factors demonstrate that the role of females in odonate mating systems goes well beyond simply being a limiting factor in male reproductive competition.

RELEVANT ODONATE BIOLOGY

Odonates are well suited for interspecific comparisons, field studies, and enclosure studies. They show considerable variation in reproductive behavior within and among species. Adults are often relatively easy to catch, making it easy to quantify their behavior and perform long-term studies on marked individuals. Because their lives are divided into three distinct stages, selection pressures on different life-history episodes can be studied.

The larval stage of odonates lasts from several months to several years, during which time they are aquatic predators. They emerge from this stage as winged, visually oriented predators and enter a period (lasting a few days to several weeks) of feeding and sexual maturation called the teneral stage, usually, but not always, away from oviposition areas. Adult reproductive lifespans range from days to months. Females mature batches of eggs and usually spend the time between reproductive episodes away from the water.

Odonates are one of the taxa for which the mechanisms and associated morphology for sperm competition have been most clearly identified (Siva-Jothy 1984, 1987a;

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Fincke 1984a, 1986a; Miller 1990, 1991a). Copulation involves a two-stage transfer of sperm, first within the male from the penis to the secondary storage vesicle and then to the female using copulatory apparatuses that are homologous to other insect reproductive organs. The male penis consequently is used for two distinct functions: to transfer sperm to a female's storage organs and to remove or displace sperm from these organs. The success of these behaviors results in considerable sperm precedence by males that are the last to mate with females prior to oviposition (Fincke 1984a; McVey and Smittle 1984; Wolf *et al.* 1989; Michiels 1992; Hadrys *et al.* 1993).

Because males may mature faster than females and are usually able to mate daily whereas females often require at least several days to mature eggs, operational sex ratios for most species are male-biased. Male agonistic behavior takes the form of chases and ritualized fights and attempts to displace males in tandem with females. Competition among males for fertilizations is common and often fierce, resulting in a diverse array of mate-guarding behaviors (Waage 1979b, 1984a; Sherman 1983; Tsubaki *et al.* 1994) and alternative mate-finding tactics (Waltz 1982; Fincke 1985, 1992a; Forsyth and Montgomerie 1987; Waltz and Wolf 1988, 1993). Shifts from one tactic to another are typically conditional on age, energy stores, and habitat structure or density, but may also be phenotypically fixed as has been shown in *Mnais* damselflies (Watanabe and Taguchi 1990; Watanabe 1991; Nomakuchi 1992).

Odonates include two major groups, the damselflies (suborder Zygoptera) and dragonflies (suborder Anisoptera). These groups show many intriguing patterns of convergent and divergent evolution in morphology and behavior. For example, zygopterans copulate for a minimum of 1–2 min and oviposit into plant tissues, whereas anisopteran copulations may be as short as a few seconds and most females deposit eggs directly onto the water surface. Males of both taxa use the penis to remove or displace sperm. However, the morphologically more complex anisopteran penis is homologous to the temporary sperm-holding vesicle in Zygoptera, whereas the zygopteran penis with its sperm-removal morphology is homologous to a supporting member of the anisopteran copulatory complex (Waage 1984a). Interestingly, the families with the most complex courtship and territorial behavior (Calopterygidae, Pseudostigmatidae and Libellulidae) are quite remote phylogenetically and very different morphologically, suggesting that mating behavior is plastic and may be subject to relatively few phylogenetic constraints. Information on

phylogenetic patterns of male sperm competition and mate guarding can be found in Waage (1984a, 1986a).

THE CLASSIFICATION OF ODONATE MATING SYSTEMS

Odonate reproductive behavior can be organized according to a variety of variables. Although varying widely in emphasis, most such classifications are organized around the continuum of resource monopolization proposed by Emlen and Oring (1977). The basic premise is that the distribution and abundance of either oviposition sites, females, or both determines the degree and type of competition for matings that is profitable for males. As oviposition areas used by females become too large or widely dispersed for an individual male to monopolize, or as females become more synchronous in receptivity, searching for mates becomes more profitable for males than localized defense of encounter sites. Where oviposition sites are smaller relative to a male's patrol flight ability and more spatially clumped, and as females become more asynchronous in receptivity, defense of oviposition sites becomes more profitable. Between these two extremes, males should control female encounter sites if females are found at such sites more predictably than at oviposition areas. If females oviposit immediately after mating, males that compete by mate-searching should remain in tandem following mating until their mates oviposit in order to avoid losing their sperm investment. In contrast, an oviposition site that attracts many females should be more valuable to a territorial male than any given mate. Therefore, territorial males generally use non-contact guarding of females to ensure paternity, a behavior that offers greater opportunity to chase intruders from oviposition sites they control.

Several predictions emerge concerning the expected strength of sexual selection in different odonate mating systems. For example, because fewer males can monopolize sites than can monopolize females themselves, competition among males for mates and sexual dimorphism in traits functioning in male-male competition should increase from mate-searching systems to those in which males defend oviposition sites. Sexual selection on males should increase with increasing asynchrony in female receptivity since this offers males more opportunity to monopolize multiple mates. Finally, because the operational sex ratio of odonates tends to increase with population density (Fincke 1994a), male-male competition should also increase with density.

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None the less, the expected overall strength of sexual selection in different mating systems is unclear. Female mate choice, to the extent that it occurs, may increase in tandem with male–male competition, leading to strong sexual selection in species with male resource defense. Alternatively, female choice of males may be greatest where males do not control oviposition sites, encounters between the sexes are fairly frequent, and consequently male–male competition is relatively weak (Conrad and Pritchard 1992). If this is true, the strength of female choice and male–male competition oppose each other and there should be moderate sexual selection across all levels of male resource monopolization.

Although much is known concerning the factors influencing the mating patterns of adult odonates, the role of at least one prominent feature of their life history – larval ecology – has thus far been neglected (Buskirk and Sherman 1985). For example, three species of tropical pseudostigmatid damselflies overlap in their use of tree-hole oviposition sites in Panama, but males of only the largest species, *Megaloprepus coerulatus*, defend this resource (Fincke 1984b). Based on the Emlen and Oring (1977) paradigm, all three species should be territorial since tree holes are limiting and easily defendable. The solution to this paradox appears to be interspecific larval competition that prohibits territoriality from being profitable for the two smaller *Mecistogaster* species (Fincke 1992b). Although male *Mecistogaster* stand to gain as many matings as do *Megaloprepus coerulatus* by defending large holes in tree-fall gaps, survivorship of *Mecistogaster* larvae is rarely greater than one per hole. Thus, although males of both genera are capable of defending the oviposition site, the pay-off of tree-hole defense differs between the two taxa, not in the number of matings obtained, but in the number of offspring produced.

SEXUAL SELECTION

Evidence from odonate mating patterns

Many aspects of odonate biology suggest strong sexual selection. They exhibit a wide variety of mating patterns from female monogamy (Rowe 1978; Fincke 1987) to mate-searching and territorial polygyny. Many species are sexually dimorphic. Males in some species fight for access to mates through defense of territories. Finally, males often compete for fertilizations by sperm competition and pre- and postcopulatory guarding (Waage 1984a). These features

render odonates well suited to testing sexual selection theory, even though none provides unambiguous evidence of ongoing sexual selection.

Color and size dimorphism illustrate this problem. Most odonate males and females differ in coloration and patterns of the thorax and abdomen, which in some species functions in sexual recognition (Corbet 1962; Moodie 1995). However, if males and females generally occupy different foraging habitats, natural selection may explain much of the observed sexual dimorphism in body coloration (Hafrenik and Garrison 1986). Males of a few species have distinct wing patterns or color patches on the body that are displayed during courtship. Although wing dimorphisms may have a sexual selection function in male–male competition or female choice, most of the evidence to date suggests that they aid in species or sexual recognition rather than in sexual selection (Buchholtz 1951; Waage 1975, 1979c; Fincke 1984b; De Marchi 1990).

Similarly, most odonates exhibit sexual size dimorphism, with females typically being slightly larger than males (Anholt *et al.* 1991). Since larger females can usually carry more eggs than smaller females, this suggests that natural selection on females to increase clutch size has been greater than sexual selection favoring large males. Male-biased size dimorphism is rare in odonates, and in only a few species has size been shown to increase mating efficiency (see below).

Nor is variation in mating success sufficient evidence for sexual selection. If success at defending territories or accumulating matings over time is mostly due to foraging success or predator avoidance, and if much of that success is due to the timing of weather events during maturation or adulthood, then reproductive success will primarily be due to a combination of natural selection and chance (Fincke 1986a; Koenig and Albano 1986; Michiels and Dhondt 1991a).

Finally, although the widespread occurrence of sperm removal and postcopulatory guarding in odonates provides unambiguous evidence for sexual selection in the past, these behaviors are not sufficient to demonstrate current sexual selection. For that, one must be able to detect and correlate variation in sperm displacement or guarding duration with fertilization success among individual males.

Evidence from long-term studies

Does the opportunity for sexual selection vary with the ability of males to monopolize resources or females, as

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Table 3-1. *Studies of lifetime reproductive success in odonates*

Species	References
<i>Zygoptera</i> (damselflies)	
<i>Enallagma hageni</i>	Fincke 1982, 1986a, 1988
<i>E. boreale</i>	Anholt 1991; Fincke 1994a
<i>Coenagrion puella</i>	Banks and Thompson 1985, 1987; Thompson 1987, 1989, 1990; Harvey and Walsh 1993
<i>Ischnura gemina</i>	
<i>I. graellsii</i>	Hafernik and Garrison 1986
<i>Argia chelata</i>	Cordero 1992a Hamilton and Montgomerie 1989
<i>Anisoptera</i> (dragonflies)	
<i>Erythemis simplicicollis</i>	McVey 1988
<i>Libellula luctuosa</i>	Moore 1989, 1990
<i>Plathemis lydia</i>	Koenig and Albano 1987
<i>Nannophya pygmaea</i>	Tsubaki and Ono 1987
<i>Sympetrum rubicundulum</i>	Van Buskirk 1987
<i>Sympetrum danae</i>	Michiels and Dhondt 1991a ^a

^a Enclosure study.

predicted by Emlen and Oring (1977)? Because daily variation in male mating success is typically much higher than variation over the lifetime of individuals (Fincke 1982, 1988; Banks and Thompson 1985; Koenig and Albano 1987; McVey 1988), studies of lifetime reproductive success are best used to answer this question. Odonates have provided fertile ground for measuring lifetime reproductive success with at least 12 species, evenly divided between damselflies and dragonflies, studied to date (Table 3-1).

An index of the relative opportunity for sexual selection relative to natural selection can be obtained by partitioning total variance in lifetime reproductive (LRS) or mating (LMS) success (Arnold and Wade 1984a,b). For example, lifetime mating success (LMS) can be partitioned into variance in lifespan (days alive), mating efficiency (mates per day), and female reproduction (eggs fertilized per mating). Of these three episodes, only mating efficiency is likely to primarily represent sexual selection, and thus the proportion of the total variance in LRS accounted for by variation in mating efficiency provides an estimate of the relative importance of sexual selection.

Unfortunately, quantifying and partitioning variance in reproductive success entails numerous pitfalls (Sutherland 1985, 1987; Koenig and Albano 1986; Wade 1987; Grafen 1988). First, because most odonates have mechanisms for sperm competition, mating success may not reflect fertilization

success. Second, sampling must be unbiased. This is particularly important for intersexual comparisons, because differential dispersal or other ecological dissimilarities can result in sex-related differences in reproductive success that are easily misconstrued as being due to sexual selection. Even within members of a sex, demographic parameters may vary significantly within a season, and thus the apparent importance of sexual selection may depend on what part of the breeding season is sampled (Fincke 1988).

Third, natural and sexual selection are not easy to separate, especially if male behavior affects both mating success and offspring survivorship (Fincke 1992a). Dividing up behaviors influencing fitness into ever finer episodes can help distinguish components representing natural and sexual selection and thus alleviate this problem, but at the cost of increasing the total proportion of variance attributable to covariance components that are themselves difficult to interpret. For example, Koenig and Albano (1987) found the most important component of the opportunity for selection in male *Plathemis lydia* was lifespan, explaining 27% of the total variance in LRS. However, they partitioned the remaining variance into multiple episodes, many of which entailed aspects of male mating efficiency such as visits per day and matings per hour. Consequently, covariance components represented 52% of the total variance, making the results difficult to interpret and compare with other studies.

Despite these difficulties, some trends predicted by sexual selection are qualitatively supported by long-term studies on odonates. For example, the majority of lifetime studies of odonates show greater variance in lifetime mating (LMS) or reproductive success (LRS) for males than females, consistent with odonates having polygamous mating systems (Waage 1984a; Conrad and Pritchard 1992). However, there are several exceptions.

In the territorial dragonfly *Erythemis simplicicollis*, the proportion of total variance in male LRS due to sexual selection was high, but the total variance in male LRS was slightly less than that of female LRS (McVey 1988). Similarly, variance in mating success among males and females did not differ between male and female *Ischnura gemina* (Hafernik and Garrison 1986), although the total selection on males was slightly higher than that on females. This species is particularly interesting because its mating pattern is closer to serial monogamy than to polygyny. Males are not territorial and spend a long time *in copula* and tandem mate-guarding, obtaining on average only one mating every four days. This suggests that male copulatory and

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postcopulatory behavior may constrain sexual selection on males.

Studies partitioning variance in LMS or LRS into episodes of selection on lifespan and mating efficiency support the prediction that the importance of sexual relative to natural selection increases across species as males are better able to monopolize reproductive resources. For example, male mating efficiency accounted for 61% of the variance in male LRS in the territorial *Erythemis simplicicollis* (McVey 1988) compared with only 39% of male LRS in the non-territorial *Enallagma hageni* (Fincke 1988). Similarly, although variance in lifespan accounted for only about a quarter of the total variance in male LRS in territorial *Plathemis lydia* (Koenig and Albano 1987), it accounted for 78% of the variance in LMS in *Coenagrion puella* (Banks and Thompson 1985), a species in which males compete by mate-searching and remain with females during oviposition. Although these comparisons are promising, more lifetime studies are needed on understudied odonates including gomphids, aeshnids, and species breeding in streams and in the tropics.

In summary, the numerous long-term studies of odonates offer at least weak support for the hypothesis that sexual selection on males increases as the ability of males to monopolize fertilizations increases. These studies are considerably more consistent on two other scores. First, they unambiguously demonstrate that survivorship is an important predictor of reproductive success for males and females regardless of the male mating pattern (Fincke 1982, 1986a, 1988; Banks and Thompson 1985; Koenig and Albano 1987; Tsubaki and Ono 1987; McVey 1988; Hamilton and Montgomerie 1989; Michiels and Dhondt 1991a; Cordero 1992a; Harvey and Walsh 1993). Second, they indicate that weather is a major constraint on sexual selection in odonates, with much of the variance in male and female reproductive success being explained by environmental conditions such as the number of sunny days occurring over an adult's lifetime (Thompson 1990; Tsubaki and Ono 1987). Indeed, Michiels and Dhondt (1991a) accurately estimated *Sympetrum danae* lifetime reproductive success by using only the lifetime number of sunny days along with the mean number of matings or ovipositions observed per sunny day.

Role of size and mass in male reproductive success

Even in the absence of any heritable phenotypic differences among males, the male-biased operational sex ratios that

are typical of most odonate populations and the limited number of favored oviposition sites in territorial species would alone result in considerable variation in male mating success. To the extent that the opportunity for sexual selection is realized, we expect reproductively successful males to differ from unsuccessful ones. Although heritability of traits has only been studied in a few odonates (Fincke 1988; Cordero 1992b), we assume that phenotypic differences among males generally reflect genetic differences.

Body size and mass are the most commonly studied phenotypic trait in adult odonates. Although correlated, there is an important distinction between these characters. 'Size' refers to the length or area of a body part, which in insects does not change after emergence as an adult. In contrast, mass may vary over the lifespan of an adult.

There are several ways in which correlating either of these traits with reproductive success can be misleading. First, body size of emerging adults typically decreases over a reproductive season (Banks and Thompson 1985; Tsubaki and Ono 1987; Fincke 1988; Michiels and Dhondt 1989), indicating the need to control for date of emergence when determining the effect of male size on reproductive success. Similarly, because the mass of an individual can change, it is important to weigh individuals at comparable stages of their lives; for example, all females should be measured either when gravid or after oviposition. Second, if dispersal is size- or age-dependent (Anholt 1990; Michiels and Dhondt 1991b), a false relationship between size and survivorship might be found. Third, we know little about how selection for size acts on females and even less about how it acts on larvae, whose growth determines adult size. The result of these difficulties is that it is often hard to interpret selection on size or mass in odonates unless large samples sizes are available and extraordinary care is taken in acquiring the data. Even then, the difficulties in dividing episodes of selection means that interpretations are often ambiguous.

Given these problems, it is a challenge to test even the most basic predictions of sexual selection theory using comparative data. An attempt to do so using data from eleven studies is summarized in Table 3-2.

Prediction 1: size should be a better predictor of male mating efficiency in species with male-biased compared with female-biased size dimorphism
 Three of four (75%) populations in which size dimorphism was male-biased yielded evidence for sexual selection

Table 3-2.
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Species
<i>Coenagrion</i>
<i>Enallagma</i>
<i>E. boreale</i>
<i>Pyrrhosoma</i>
<i>Megaloptera</i>
<i>Libellula</i>
<i>Orthetrum</i>
<i>Pachydiplax</i>
<i>Plathemis</i>
<i>Sympetrum</i>
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Table 3-2. Relationship between size dimorphism, resource defense polygamy, and selection on male mating efficiency with respect to size in odonates

Species	Larger sex	Exhibits resource defense?	Selection on size relative to mating efficiency	Reference
<i>Coenagrion puella</i>	Females	No	Smaller more successful	Banks and Thompson 1985
<i>Enallagma hageni</i>	Females	No	Stabilizing	Fincke 1988
<i>E. boreale</i>	Females	No	Smaller more successful	Anholt 1991
<i>Pyrrosoma nymphula</i>	Females	No	Not detected	Gribbin and Thompson 1991
<i>Megalopterus coeruleus</i>	Males	Yes	Mated males larger	Fincke 1992a
<i>Libellula luctuosa</i>	Males	Yes	Mated males larger	Moore 1990
<i>Orthetrum chrysostigma</i>	Males	Yes	Mated males larger	Miller 1983
<i>Pachydiplax longipennis</i>	Males	Yes	Not detected	Dunham 1993 ^a
<i>Plathemis lydia</i>	Females	Yes	Not detected	Koenig and Albano 1987
<i>Sympetrum rubicundulum</i>	Females	Yes	Not detected	Van Buskirk 1987
<i>S. danae</i>	Females	No	Mated males larger	Michiels and Dhondt 1991 ^a

^a Enclosure study.

acting via male size compared to one of seven (14%) populations in which size dimorphism was female-biased (Fisher exact test, $p = 0.085$). Excluding the two enclosure studies listed in Table 3-2, the count becomes three of three (100%) male-biased versus zero of six (0%) female-biased populations yielding evidence for sexual selection acting via male size ($p = 0.011$). This difference remains significant even if the two studies of *Enallagma*, both of which yielded similar results, are combined ($p = 0.018$).

Prediction 2: selection favoring large males should be more likely to occur in species exhibiting resource defense polygamy

Evidence for this prediction includes the extensive comparative analysis by Anholt *et al.* (1991) demonstrating that there is less female-biased size dimorphism in species exhibiting resource defense. Using the studies summarized in Table 3-2, three of six populations with resource defense (50%) show evidence for sexual selection acting via male size compared with one of five (20%) that do not. Considering only field studies, the count is three of five versus zero of four. This difference is not significant (Fisher exact test, $p = 0.12$), although the trend is in the expected direction.

These results are at best preliminary: besides the problems in measuring selection already discussed, patterns of resource defense within a population can differ according to ecological conditions. However, the results at least

suggest that selection studies in odonates generally support basic predictions of sexual selection theory, despite the numerous difficulties inherent in such comparisons.

One potential reason why the relationship between large size and male success in contest competition is not clearer is that large size may counter the advantages territorial males gain from competitive flight maneuvers and endurance during territorial fights. The result would in some cases be stabilizing selection on size, as found by Moore (1990) among mated males of the territorial *Libellula luctuosa*. This possibility is also suggested by studies demonstrating the importance of factors related to energy reserves and flight capability as opposed to size or mass *per se*. Marden (1989), for example, found that male *Plathemis lydia* with high flight-muscle mass to body mass ratios experienced greater short-term mating success; Marden and Waage (1990) found that fat reserves of male *Calopteryx maculata* correlated with their ability to win territorial contests and thus presumably influenced their reproductive success.

These studies are significant given the importance of energetically expensive flight for patrolling, fighting, courtship, and other activities related for territorial defense (Fried and May 1983; Vogt and Heinrich 1983; Singer 1987; Ruppell 1989a; Marden and Waage 1990; May 1991). Energy reserves may even play a role in determining the alternative mating tactics chosen by males, as suggested by the observation that shifts from territorial to

non-territorial behavior occur in old age or when energy stores are low (Waltz 1982; Forsyth and Montgomerie 1987; Waltz and Wolf 1988, 1993).

We suggest four areas of research that should provide a more balanced view of size and mass in relation to odonate mating patterns. (1) Does selection on size or mass differ for males and females in the same population? (2) Is selection on size or mass the same relative to both survivorship and mating efficiency? (3) What are the exact mechanisms that cause size to be related to survival or mating success? (4) What factors during larval development and the teneral stage affect adult size and mass? Selection relative to size or mass may relate to multiple stages of the life cycle rather than just to adult survival and reproduction.

COURTSHIP AND SEXUAL CONFLICT

Male-female interactions and reproductive conflicts

Much of the literature on odonate mating patterns has focussed on males, with females often ignored or considered as passive partners. As a result, the process of odonate reproduction is often considered to end with mating. However, the inability of males to force females to mate, combined with the fact that many females may be able to fertilize all of their eggs with stored sperm from a single mating (Grieve 1937; Fincke 1987), opens the door for females to exert considerable control over reproductive patterns and for sexual conflict over when, where, and with whom to mate. For example, female *Ischnura verticalis*, in which a single mating supplies enough sperm to fertilize her eggs for life, rarely remate despite frequent encounters with receptive males (Fincke 1987). Although the male's penis morphology suggests that sperm removal by males could occur (Waage 1984a), female monogamy constrains the potential for sperm competition in this system.

Given that female odonates cannot be forced to mate and mating is often costly in terms of time, why do most female odonates mate multiply? This question can be viewed from two complementary perspectives.

First, females may remate in order to gain direct benefits through increased quality or quantity of sperm, nuptial gifts, increased access to high-quality oviposition sites, or some form of male protection (Walker 1980; Waage 1984a; Fincke 1986b). There is little evidence that females remate in order to insure against inviable sperm, to obtain superior male genotypes, or to obtain resources in the form of

nuptial gifts. However, despite sperm storage, females may not always obtain sufficient sperm to last throughout their lifetime in a single mating, at least when copulations are extremely short or are interrupted, as occurs frequently in anisoptera. Thus, females may sometimes remate in order to replenish diminishing sperm stores (Fincke 1987; Miller and Miller 1989). More important is almost certainly access to high-quality oviposition sites (Fincke 1992a; Siva-Jothy *et al.* 1996; Tsubaki *et al.* 1996). Male protection of females against drowning also occurs in at least one species, *Enallagma hageni*, where females oviposit under water and guarding males help females that get stuck resurfacing, thereby decreasing the mortality risk of oviposition (Fincke 1986b). If females benefit from remating by acquiring access to better oviposition sites or better sires, males are likely to gain by advertising the quality of their territories or their own physical or genetic quality so as to 'entice' females to mate with them.

Alternatively, a female may gain nothing from remating other than minimizing the cost of harassment by a persistent male. To the extent that males ignore female rejection signals, males can be considered to be trying to 'coerce' unwilling females into mating. Mating in order to minimize harassment may be widespread in odonates (Waage 1979b, 1984a; Koenig 1991; but see Fincke 1997), and is considered in detail in the following section.

Avoidance of male harassment

Male harassment of females while either ovipositing or searching for an oviposition site may considerably reduce oviposition efficiency. For example, *Erythemis simplicicollis* copulate for 19 s and undisturbed ovipositions average 39 s. However, in areas of high male density, oviposition duration averaged 112 s for females copulating once and ranged up to 780 s for a female who mated seven times and finally left the water, apparently without ever completing oviposition (Waage 1986b). Increased time at oviposition sites increases the risk of predation to females (Convey 1992; Rehfeldt 1992). In extreme cases, male harassment can even injure or kill females in tandem with males (Rüppell and Hadrys 1988).

It is therefore not surprising that females avoid harassment from mate-searching males in a variety of ways. Many oviposit at times and in places where males are rare or absent (Corbet 1962; Koenig 1991). Some female Zygoptera submerge to oviposit, a behavior that serves several functions (Corbet 1962) including avoiding males, who

cannot interfere (1986b). Female water oviposition without first (1989). Similar guarding behavior by females with Koenig 1991).

Yet another male harassment behavior or both. The abdominal cavity is distinct from andromorphs (1975). Andromorphs mate if they mates (Robert may be higher of not mating (1987). Intere frequent in s density ones.

Although that andromorphs or the (Cordero 1992) tive success. (1989; Fincke 1989; Fincke 1989) differences between survivorship, or are in the majority as maintained as male. Recent evidence is modified by

Female rejection

A potentially important mechanism is for females to repel males. These are effective, and both sexes are of being eaten (Cordero 1992). In some species may be (Moodie 1995) (Waage 1984b) *verticalis*, female

cannot interfere as long as a female is under water (Fincke 1986b). Female *Platycypha caligata* synchronize their above-water oviposition, permitting them to use a male's territory without first mating with the owner (Martens and Rehfeldt 1989). Similarly, females of several species parasitize the guarding behavior of territorial males attending other females with which the males are mated (Waage 1979b; Koenig 1991).

Yet another mechanism by which females may avoid male harassment is to mimic males in coloration or behavior or both. In many coenagrionids, the thorax and ventral abdominal color of some females, called heteromorphs, is distinct from that of males whereas other females, called andromorphs, are male-like in body coloration (Johnson 1975). Andromorphs may avoid unwanted attention from males if they are less likely to be recognized as potential mates (Robertson 1985). The costs to andromorph females may be higher predation rates (Robertson 1985) or the risk of not mating at all when male density is low (Hinneking 1987). Interestingly, andromorphs appear to be more frequent in some high-density populations than in low-density ones (Forbes *et al.* 1995).

Although plausible, few data support the hypothesis that andromorphs benefit by lessened harassment from males or that fitness correlates differ between morphs (Cordero 1992a; but see Fincke 1994b). Lifetime reproductive success studies of three coenagrionids (Thompson 1989; Fincke 1994a) indicated no statistically significant differences between female morphs in mating frequency, survivorship, or the number of eggs laid. When andromorphs are in the majority, they are actually more likely to be recognized as mates than are heteromorphs (Forbes 1991a). Recent evidence indicates that mate recognition by males is modified by their past experience (Moodie 1995).

Female rejection signals and male reactions

A potentially more efficient means of avoiding male harassment is for females to signal their willingness to mate and to repel males with refusal displays. If such cues or displays are effective, they can minimize time and energy losses to both sexes and, at least in some *Ishnura* spp., the possibility of being eaten by an unreceptive female (Robertson 1985; Cordero 1992c; Fincke 1994a). Willingness to mate in some species may involve actively seeking males (Kaiser 1985; Moodie 1995) or giving a characteristic wing display (Waage 1984b; Fincke 1987). In *Aeschna cyanea* and *Ischnura verticalis*, female developmental color changes correlate

with receptivity and males are differentially found in areas where there are many females that have recently attained sexual maturity (Kaiser 1985; Fincke 1987). However, males have not as yet been shown to respond differentially to this color cue.

Females of many species indicate their unwillingness to mate by directly resisting (Bick and Bick 1963) and dislodging males following capture (Rüppell 1989b), holding onto perches (Fincke 1986b; Oppenheimer and Waage 1987), 'shaking' (Forbes *et al.* 1995), or curling their abdomen and spreading their wings (Fincke 1987; Utzeri 1988; Gorb 1992). Females typically give such displays following oviposition, and males that take such females in tandem release them relatively quickly (Kaiser 1985; Fincke 1986b).

To what extent are females that have sufficient sperm able to repel males? In general, it benefits a male to ignore a female's rejection signal whenever she has eggs to lay as long as the cost of influencing her mating decision in his favor is less than the benefits of success. The likelihood that this will be the case is in turn influenced by female oviposition behavior, particularly submerged oviposition, which decreases male control over sites and thus the degree to which he can gain matings by harassing ovipositing non-mates.

Consider *Calopteryx maculata* and *C. dimidiata*, two broadly sympatric congeners that share male-defended oviposition sites (Waage 1980, 1984b, 1988). *Calopteryx maculata* females oviposit at the water surface and depend on male guarding for prolonged oviposition and often on mating with the resident male for access to oviposition sites. In contrast, *C. dimidiata* females oviposit only while submerged, increasing the possibility that a female can oviposit without mating with the territory owner. Correlated with this difference, *C. dimidiata* males stop courting when females give refusal displays whereas *C. maculata* males ignore refusal displays and persist in courting, successfully copulating with the female 30% of the time (Waage 1984b).

Conflict of interest between the sexes does not end once a female is taken in tandem. Females can refuse to mate whereas males can persist in holding females. This can result in tandem pairs remaining intact for extended periods of time without successfully mating. For example, male *Megalopterus coeruleus* have been observed to hold unwilling females in tandem, ultimately failing to mate, for 1.5 h (Fincke 1984b) (Fig. 3-2). Experimentally, this has been demonstrated in *Calopteryx maculata* by hand-pairing males with females made 'unwilling' by experimentally

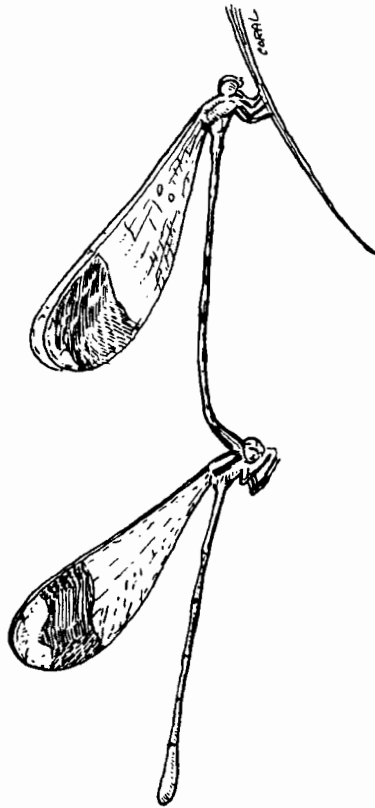


Fig. 3-1. *Megaloprepus coerulatus*: the female may resist mating once in tandem by remaining rigid in response to a male 'jerking' on her pronotum.

stiffening their abdomens. Pairs remained in tandem for up to 5 min, over three times the length of normal copulation (Oppenheimer 1991).

From the male's point of view, the costs of such a war of attrition include the risk of wasting sperm prematurely transferred to their secondary genitalia, losing additional matings, or even losing their territory (Waage 1979b). The potential benefit is that females unable to dislodge males and seeking to maximize oviposition efficiency may ultimately save time and energy by copulating. However, the extent to which males successfully obtain fertilizations by outlasting females otherwise unwilling to mate is unknown.

Courtship displays: a role in female choice?

Courtship displays are found in a variety of odonates, including damselflies in the Calopterygidae, Chlorocyphidae,

Coenagrionidae, Eupacidae, Hemiphlebidae and Pseustigmatidae, as well as several libellulid dragonflies (Jacobs 1955; Corbet 1962, 1980; Miller 1991a). Courtship displays have traditionally been thought both to aid in species recognition and reproductive isolation (natural selection function) and to provide females with information about the quality of potential mates (sexual selection function).

Although species and sex recognition in odonates is generally believed to be based on visual recognition of color, shape, and behavior, the importance of such cues probably depends at least in part on mechanical isolation mechanisms. For example, some species of damselflies that lack courtship and are similar in color and morphology avoid interspecific pairings by mechanical incompatibility, whereas species with courtship and associated differences in wing and body coloration often use species-specific differences in morphology used in tandem formation and copulation (Waage 1975; Tennesen 1982; Robertson and Paterson 1982). Cases of the latter include sympatric *Calopteryx* species that have similar anal appendages and genitalia and that form interspecific tandems when hand-paired (Oppenheimer 1991). Species isolation would seem to be a likely function of courtship in these species (Waage 1975). However, courtship in species such as *Calopteryx* that are highly territorial and mate frequently could, in addition, provide females with the time and information needed for them to assess the quality and condition of potential mates.

Unfortunately, although female mate choice based on courtship cues seems possible, demonstrating its existence in odonates has proved surprisingly difficult. Female reproductive decisions in at least two detailed studies on *Calopteryx maculata* were consistent with choice based on territory quality or minimizing time spent at the water and failed to unequivocally demonstrate female mate choice based on male courtship or appearance (Oppenheimer 1991; Fitzstephens 1994). However, recent experimental work by Hooper (1994) and M. Siva-Juarez (unpublished data) on *Calopteryx splendens* indicates that males that obtain copulations have significantly darker and more homogeneous wing spots and perform more courtship displays than males that fail to mate, after holding territory quality and male wing length constant.

These findings offer the first positive evidence in odonates for active female mate choice based at least in part on courtship displays and suggests that, although similar examples may be more common than currently thought. Good candidates for additional studies

mal species with courtship where male display may be with male quality, females have the time and opportunity to assess male quality, and the physiological changes of territoriality place a premium on females seeking genetically high-quality mates. A promising way to proceed would be to carefully monitor the reaction of naive virgin and non-virgin females to artificially modified secondary sexual characteristics of males displayed during courtship.

Regardless of the role that courtship plays in female mate choice, it clearly provides males with information helping them to determine their mating and reproductive options. For example, rejection displays from courted *Calopteryx maculata* females indicates that copulation is possible but that the female is unlikely to subsequently oviposit, diminishing the male's opportunity for fertilizations (Oppenheimer 1991). A similar interaction occurs in some coenagrionids, where males elicit information about a female's willingness to mate by jerking on her pronotum. Males transfer sperm in preparation for copulation only if the female indicates receptivity by raising her abdomen to tap on his genitalia (Robertson and Tennesen 1984; Fincke 1984b). Males adjust their mating behavior to potential fertilization returns in other ways as well. For example, 'satellite' males pursuing alternative reproductive tactics, at risk that females will remate with a territorial male before oviposition, mate for longer than territory-holders (Siva-Jothy 1987b; Siva-Jothy and Tsubaki 1989a,b; Fincke 1992a).

In summary, refusal and courtship displays in odonates often involve a complex set of interactions and conflicts. Viewing pair formation and courtship as a two-way process in which both males and females acquire information subsequently influencing their behavior may aid us to better understand their roles in odonate reproduction.

THE ROLE OF NATURAL SELECTION IN ODONATE MATING PATTERNS

A general conceptual view of odonate reproductive decisions

Fig. 3-2 presents a conceptual view of the ways in which the factors influencing male and female reproductive decisions may interact (see also Michiels and Dhondt 1991a). Most work on odonate mating patterns relates primarily to the hexagonal boxes representing sexual competition. Relatively unstudied are the factors related to growth and survivorship.

Natural selection underlies the type of mating pattern and potential for sexual selection in at least two major ways. First, factors affecting survivorship, oviposition efficiency, and the quality of oviposition sites may constrain female choice of males. Second, the operational sex ratio, temporal synchrony of females, and spatial distribution of ovipositing females – factors ultimately determining the degree of male–male competition – are affected both by weather and by natural selection on larvae, teneral, and non-reproductive adults. In this section we address female decision-making, arguing that determining the time and location of reproduction may generally be more important to female fitness than choice of mate based on a male's phenotype.

Female mating decisions: what do they choose?

Females control mating by a series of decisions about where, when, and how often to mate and oviposit (Koenig 1991). Choosing which male to mate with, or active female choice, is the only one of these reproductive decisions directly constituting sexual selection.

Ways in which female odonates could exercise active mate choice include (1) refusing to copulate with a particular male, (2) varying the number of fertilized eggs for a given male, (3) choosing to remate before ovipositing, and (4) differentially utilizing sperm of multiple mates. Despite all these possibilities, evidence among odonates for female choice among male phenotypes in a way that might result in sexual selection is lacking (Conrad and Pritchard 1992). Instead, female mating decisions are generally based on natural selection considerations such as maximizing survivorship, oviposition efficiency, and the quality of resources controlled by males (Ubukata 1984; Waage 1987; Wolf and Waltz 1988; Michiels and Dhondt 1990; Martens 1991; Wildermuth and Spinner 1991; Fincke 1992a; Wildermuth 1992, 1993).

In *Plathemis lydia*, females show strong preferences for time and location of oviposition and regularly refuse matings, but do not appear to choose among males on any consistent basis. In fact, 20% of females visiting ponds do not mate at all before oviposition (Koenig 1991), suggesting that many females with sperm stored from prior matings prefer not to mate if they can avoid it. This conclusion is supported by *Cordulia aenea*, in which females prefer to oviposit in areas where interference from males is least (Ubukata 1984), and species like *Calopteryx maculata* (Waage 1979b) and *Platycypha caligata* (Rehfeldt 1989) in which females are able to gain access to oviposition sites and

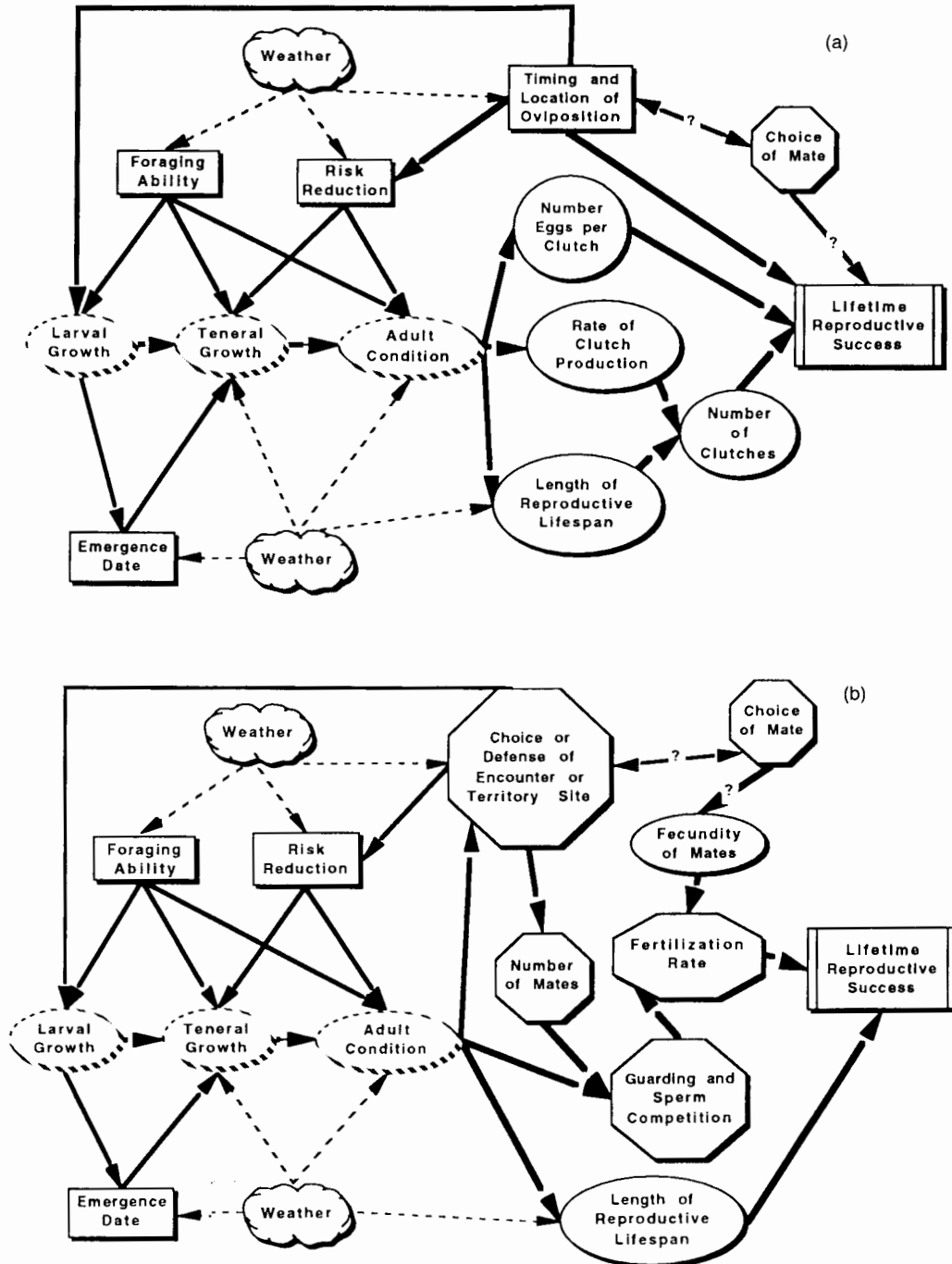


Fig. 3-2. Overview of factors affecting odonate reproductive success for (a) females and (b) males. The thickness of lines indicates the presumed importance of a particular causal factor. Octagons represent behaviors that are the primary focus of mating system classifications based on sexual selection. Other shapes represent additional life history, behavioral, and environmental factors.

male guarding without mating with the resident male. Such parasitism of mate-guarding behavior is facilitated by the tendency for females of some species to be attracted to ovipositing conspecifics (Waage 1979b, 1987; Martens 1989; Moss 1992), a behavior that may allow females to efficiently find and exploit high-quality oviposition sites without mating with the resident male.

In *Enallagma ebrium*, males heavily parasitized by larval water mites are less likely to mate, but this is apparently due to their inability to find mates rather than rejection by females (Forbes 1991b). Heavily parasitized females in this species were also not rejected as mates by males even though they were less fecund than unparasitized females (Forbes and Baker 1991). Given the current interest of the role that parasitism plays in sexual selection, there is clearly plenty of room for additional work along these lines in odonates.

Although female odonates rarely choose directly among males, intense male-male competition for control of resources attractive to females in many species means that females may exercise indirect choice of mates by selecting high-quality, limiting oviposition sites. Female *Megalopterus coeruleus*, for example, mate only at tree-hole oviposition sites defended by large males, but they apparently do not discriminate among males on the basis of size, as indicated by their willingness to mate with small satellite males that take them in tandem at territories defended by larger males (Fincke 1992a).

As in other taxa, differentiating between female choice of oviposition site and female choice of males is difficult. Moore (1990), for example, tried to differentiate the role of these mechanisms in determining sexual dimorphism in *Libellula luctuosa*. Females visited and rejected several males before mating and varied the duration of oviposition following matings. Such behavior is necessary, but not sufficient, for sexual selection by female choice to be occurring. As in *Plathemis lydia*, females could be both rejecting and accepting males arbitrarily with respect to their phenotype (Koenig 1991). An alternative explanation for Moore's (1990) results is that females are choosing among oviposition sites rather than territorial males *per se*. Over a two-year period, for example, three of the 11 territories accounted for 62% of all observed matings (Moore 1989). 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, among males defending a given territory, those with larger wing bands had greater mating

success, suggesting that females might additionally be discriminating among male phenotypes.

Direct female choice of mates should evolve when the benefits of choosing outweigh the costs involved in discriminating among possible mates or mating opportunities. Its apparent rarity in odonates suggests that in general, whom a female mates with may be less important than minimizing the risks associated with oviposition and gaining access to resources controlled by males.

Why choose oviposition sites?

Territorial males, and females of all species, should select oviposition sites favoring larval survivorship and growth (Wolf and Waltz 1988; Michiels and Dhondt 1990). A major assumption of odonate biology is that females use these criteria for choosing oviposition sites. Unfortunately, this is difficult to test with stream or pond species, because larvae disperse away from the oviposition site and development time often exceeds a year. However, several studies that have addressed this assumption suggest that it is valid. *Calopteryx splendens xanthostoma* females prefer sites in areas of high stream flow, where eggs develop faster and have lower mortality than in slower-flowing water (Gibbons and Pain 1992; Siva-Jothy *et al.* 1995). Female *Megalopterus coeruleus* place more eggs in large tree holes, which support a greater number of offspring to emergence, than in small holes, which typically produce only a single adult. Males discover oviposition sites independently of the presence of females, but defend tree holes at sites that predictably attract females only if the holes are also high-quality larval habitats (Fincke 1992a).

Much of the data on oviposition-site choice is also consistent with the hypothesis that, within a given habitat, sites are selected for their proximate value as safe or efficient oviposition sites in addition to their ultimate value as a good place for egg survival and larval growth. Separating these fitness consequences can be difficult. For example, when given a choice among different-sized sites within or between territories, female *Calopteryx maculata* tend to mate and oviposit at larger vegetation clumps independent of the identity of the resident male (Waage 1987; Alcock 1987; Meek and Herman 1991). Females may prefer large sites because they are better places for the development of eggs or larvae. Alternatively, females may have an easier time locating large sites and remain longer at them once they find them, thus maximizing oviposition efficiency (J. K. Waage, personal observations). Testing these

alternatives will require considerably more data on the fate of eggs deposited at different sites and on oviposition safety and efficiency as factors determining the attraction and retention of females at particular sites.

Integrating larval ecology with adult behavior

The interplay between selective pressures during the larval and adult life-history stages represents the largest gap in our understanding of odonate mating patterns, making it impossible to test the basic assumption that successful adult reproductive behavior translates into more or higher-quality offspring. This is unfortunate, because selection at the larval stage is likely to have significant consequences for patterns of adult behavior (Johnson 1991; Fincke 1994c).

For example, interspecific larval competition in tropical guilds of tree-hole-breeding damselflies affects synchrony of emergence and favors differing female and male reproductive strategies among the species (Fincke 1992a,b). In *Megalopterus coeruleus*, selection against the longer developmental time required to produce a large male appears to balance sexual selection favoring large adult males (O. M. Fincke, unpublished manuscript). Similarly, selection for large adults may have resulted in the abnormally high propensity for cannibalism among larvae in this tree-hole-breeding species (Fincke 1994c, 1996). High rates of larval cannibalism may be one factor selecting for an adult male that continues to attract mates to tree holes already saturated with his offspring. Because of cannibalism the number of matings obtained by territorial males – the usual indicator of fitness – is not a good predictor of surviving offspring (Fincke 1992a).

This limitation can now be overcome with molecular fingerprinting techniques that make it possible to measure adult fitness in terms of offspring surviving to emergence and to look for parent-offspring correlations in successful traits or behaviors (see, for example, Hadrys *et al.* 1993). Good candidates for such work would be odonates whose adult and juvenile stages can be studied in large flight cages over small ponds and damselflies whose larval habitats are small and discrete, such as those breeding in tree holes.

SUGGESTIONS FOR FUTURE RESEARCH

Odonates have long fascinated biologists by their obvious and diverse mating behaviors as well as by their mastery

of the aquatic and aerial worlds. Numerous questions and challenges remain for future odonatologists.

First, most studies to date have been done on territorial species and species in which individuals tend to remain fairly localized. Less amenable to study are the more wide-ranging and strong-flying anisopterans such as the Aeshnidae, Cordulegasteridae, Gomphidae, Libellulidae and Petaluridae, which are difficult to capture without harming and tend to leave the area once marked. These families, and tropical ones, represent important gaps in our perspectives on odonate mating patterns and are in need of more study.

Second, long-term studies of marked females that focus on the fitness consequences of mating multiply and of resisting mating attempts by males are critical to understanding how selection on females underlies the evolution of male mating strategies. Third, direct tests of female mate choice by manipulation of male phenotypes are needed to unambiguously assess the relative importance of choice of site versus choice of sire. Fourth, studies measuring fitness in terms of the quality and quantity of surviving larvae would link the complex life history of odonates with their reproductive behavior. Finally, the behavioral diversity of this group combined with modern molecular methods make odonates ripe for phylogenetic analyses of mating and female oviposition patterns.

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LITERATURE CITED

- Alcock, J. 1987. The effects of experimental manipulation of resources on the behavior of two calopterygid damselflies that exhibit resource-defense polygyny. *Can. J. Zool.* 65: 2475–2482.
- Anholt, B. R. 1990. Size-biased dispersal prior to breeding in a damselfly. *Oecologia (Berl.)* 83: 385–387.

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- . 1991. Measuring selection on a population of damselflies with a manipulated phenotype. *Evolution* 45: 1091-1106.
- Anholt, B. R., J. H. Marden, and D. M. Jenkins. 1991. Patterns of mass gain and sexual dimorphism in adult dragonflies (Insecta: Odonata). *Can. J. Zool.* 69: 1156-1163.
- Arnold, S. J. and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709-719.
- . 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38: 720-734.
- Banks, M. J. and D. J. Thompson. 1985. Lifetime mating success in the damselfly *Coenagrion puella*. *Anim. Behav.* 33: 1175-1183.
- . 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *J. Anim. Ecol.* 56: 815-832.
- Bick, G. H. and J. C. Bick. 1963. Behavior and population structure of the damselfly *Enallagma civile* (Hagen) (Odonata: Coenagrionidae). *Southwest. Nat.* 8: 57-84.
- Buchholtz, C. 1951. Untersuchungen an der Libellengattung *Calopteryx* Leach unter besonderer Berücksichtigung ethologischer Fragen. *Z. Tierpsychol.* 8: 273-386.
- Buskirk, R. E., and K. J. Sherman. 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Fla. Entomol.* 68: 39-51.
- Conrad, K. F. and G. Pritchard. 1992. An ecological classification of odonate mating systems: the relative influence of natural, inter- and intra-sexual selection on males. *Biol. J. Linn. Soc.* 45(3): 255-269.
- Convey, P. 1992. Predation risks associated with mating and oviposition for female *Crocothemis erythraea* (Brulle) (Anisoptera: Libellulidae). *Odonatologica* 21: 343-350.
- Corbet, P. S. 1962. *A Biology of Dragonflies*. London: Witherby Ltd.
- . 1980. Biology of odonata. *Annu. Rev. Entomol.* 25: 189-217.
- Cordero, A. 1989. Reproductive behaviour of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 237-244.
- . 1992a. Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *J. Anim. Ecol.* 61: 769-780.
- . 1992b. Morphological variability, female polymorphism and heritability of body length in *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 21: 409-419.
- . 1992c. Sexual cannibalism in the damselfly species *Ischnura graellsii* (Odonata: Coenagrionidae). *Entomol. Gen.* 17: 17-20.
- De Marchi, G. 1990. Precopulatory reproductive isolation and wing colour dimorphism in *Calopteryx splendens* females in southern Italy (Zygoptera: Calopterygidae). *Odonatologica* 19: 243-250.
- Dunham, M. L. 1993. Fighting and territorial behavior in the dragonfly *Pachydiplax longipennis*. Ph.D. dissertation, Brown University.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science (Wash., D.C.)* 197: 215-223.
- Fincke, O. M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol., Sociobiol.* 10: 293-302.
- . 1984a. Sperm competition in the damselfly *Enallagma hageni* (Odonata: Coenagrionidae), and the benefits of multiple matings for males and females. *Behav. Ecol. Sociobiol.* 10: 293-302.
- . 1984b. Giant damselflies in a tropical forest: reproductive biology of *Megaloprepus coerulatus* with notes on *Mecistogaster* (Zygoptera: Pseudostigmatidae). *Adv. Odonatol.* 2: 13-27.
- . 1985. Alternative mate-finding tactics in a non-territorial damselfly (Odonata: Coenagrionidae). *Anim. Behav.* 33: 1124-1137.
- . 1986a. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). *Evolution* 40: 791-803.
- . 1986b. Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females. *Behav. Ecol. Sociobiol.* 18: 405-412.
- . 1987. Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica* 16: 791-803.
- . 1988. Sources of variation in lifetime reproductive success in a nonterritorial damselfly (Odonata: Coenagrionidae). In: *Reproductive Success*. T. H. Clutton-Brock, ed., pp. 24-43. Chicago: University of Chicago Press.
- . 1992a. Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. *Ecology* 73: 449-462.
- . 1992b. Interspecific competition for tree holes: Consequences for mating systems and coexistence in Neotropical damselflies. *Am. Nat.* 139: 80-101.
- . 1994a. Female colour polymorphism in damselflies: failure to reject the null hypothesis. *Anim. Behav.* 47: 1249-1266.
- . 1994b. On the difficulty of detecting density-dependent selection on polymorphic females of the damselfly *Ischnura graellsii*: failure to reject the null. *Evol. Ecol.* 8: 328-329.
- . 1994c. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. *Oecologia (Berl.)* 100: 118-127.
- . 1996. Larval behaviour of a giant damselfly: territoriality or size dependent dominance? *Anim. Behav.*, 51: 77-87.
- . 1997. Conflict resolution in the Odonata: implications for understanding female mating patterns and female choice. *Biol. J. Linn. Soc.*, in press.
- Fitzstephens, D. M. 1994. Color as a reliable signal of fighting ability in male damselflies, *Calopteryx maculata*. Ph.D. dissertation, Michigan State University.
- Forbes, M. R. L. 1991a. Female morphs of the damselfly *Enallagma boreale* Selys (Odonata: Coenagrionidae): a benefit for androchromatypies. *Can. J. Zool.* 69: 1969-1970.
- . 1991b. Ectoparasites and mating success of male *Enallagma ebrium* damselflies (Odonata: Coenagrionidae). *Oikos* 60: 336-342.
- Forbes, M. R. L. and R. L. Baker. 1991. Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen): the importance of ectoparasites. *Oecologia (Berl.)* 86: 335-341.

- Forbes, M. R. L., J. M. L. Richardson and R. L. Baker. 1995. Frequency of female morphs is related to an index of male density in the damselfly *Nehalennia irene* (Hagen). *Ecoscience* 2: 28–33.
- Forsyth, A. and R. D. Montgomerie. 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. *Behav. Ecol. Sociobiol.* 21: 73–81.
- Fried, C. S. and M. L. May. 1983. Energy expenditure and food intake of territorial male *Pachydiplax longipennis* (Odonata: Libellulidae). *Ecol. Entomol.* 8: 283–292.
- Gibbons, D. W. and D. Pain. 1992. The influence of river flow rate on the breeding behaviour of *Calopteryx* damselflies. *J. Anim. Ecol.* 61: 283–289.
- Gorb, S. 1992. An experimental study of the refusal display in the damselfly *Platycnemis pennipes* (Pall.) (Zygoptera: Platycnemididae). *Odonatologica* 21: 299–307.
- Grafen, A. 1988. On the uses of data on lifetime reproductive success. In: *Reproductive Success*. T. H. Clutton-Brock, ed., pp. 472–486. Chicago: University of Chicago Press.
- Gribbin, S. D. and D. J. Thompson. 1991. The effects of size and residency on territorial disputes and short-term mating success in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Anim. Behav.* 41: 689–695.
- Grieve, E. 1937. Studies on the biology of the damselfly *Ischnura verticalis* Say, with notes on certain parasites. *Entomol. Am.* 17: 121–153.
- Hadrys, H., B. Schierwater, S. L. Dellaporta, R. DeSalle and L. W. Buss. 1993. Determination of paternity in dragonflies by random amplified polymorphic DNA fingerprinting. *Molec. Ecol.* 2: 79–88.
- Hafernik, J. E. and R. W. Garrison. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? *Am. Nat.* 128: 353–365.
- Hamilton, L. D. and R. D. Montgomerie. 1989. Population demography and sex ratio in a neotropical damselfly (Odonata: Coenagrionidae) in Costa Rica. *J. Trop. Ecol.* 5: 159–171.
- Harvey, I. F. and K. J. Walsh. 1993. Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Entomol.* 18: 198–202.
- Hinneking, B. O. N. 1987. Population dynamics of *Ischnura elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia* 146: 3–31.
- Hooper, R. 1994. Sexual selection in a damselfly: female perspectives. Ph.D. dissertation, University of Sheffield.
- Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36: 566–586.
- Johnson, C. J. 1975. Polymorphism and natural selection in ischnuran damselflies. *Evol. Theory* 1: 81–90.
- Johnson, D. M. 1991. Behavioral Ecology of Larval Dragonflies and Damselflies. *Trends Ecol. Evol.* 6: 8–13.
- Kaiser, H. 1985. Availability of receptive females at the mating place and mating chances of males in the dragonfly *Aeschna cyanea*. *Behav. Ecol. Sociobiol.* 18: 1–7.
- Koenig, W. D. 1991. Levels of female choice in the white-tailed skimmer *Plathemis lydia* (Odonata: Libellulidae). *Behaviour* 119: 193–224.
- Koenig, W. D. and S. S. Albano. 1986. On the measurement of sexual selection. *Am. Nat.* 127: 403–409.
- . 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer *Plathemis lydia* (Odonata Anisoptera). *Evolution* 41: 22–36.
- Marden, J. H. 1989. Bodybuilding dragonflies: costs and benefits of maximizing flight muscle. *Physiol. Zool.* 62: 505–521.
- Marden, J. H. and J. K. Waage. 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Anim. Behav.* 39: 954–959.
- Martens, A. 1989. Aggregation of tandems in *Coenagrion pulchellum* Van der Linden 1825 during oviposition (Odonata; Coenagrionidae). *Zool. Anz.* 223: 124–128.
- . 1991. Plasticity of mate-guarding and oviposition behaviour in *Zygonyx natalensis* (Martin) (Anisoptera: Libellulidae). *Odonatologica* 20: 293–302.
- Martens, A., and G. Rehfeldt. 1989. Female aggregation in *Platycypha caligata* (Odonata: Chlorocyphidae): a tactic to evade male interference during oviposition. *Anim. Behav.* 38: 369–374.
- May, M. L. 1991. Dragonfly flight – power requirements at high speed and acceleration. *J. Exp. Biol.* 158: 325–342.
- McVey, M. E. 1988. The opportunity for sexual selection in a territorial dragonfly, *Erythemis simplicicollis*. In: *Reproductive Success*. T. H. Clutton-Brock, ed., pp. 44–58. Chicago: University of Chicago Press.
- McVey, M. E. and B. J. Smittle. 1984. Sperm precedence in the dragonfly *Erythemis simplicicollis*. *J. Insect. Physiol.* 30: 619–628.
- Meek, S. B. and T. B. Herman. 1991. The influence of oviposition resources on the dispersion and behaviour of Calopterygid damselflies. *Can. J. Zool.* 69: 835–839.
- Michiels, N. K. 1992. Consequences and adaptive significance of variation in copulation duration in the dragonfly *Sympetrum danae*. *Behav. Ecol. Sociobiol.* 29: 429–435.
- Michiels, N. K. and A. A. Dhondt. 1989. Effects of emergence characteristics on longevity and maturation in the dragonfly *Sympetrum danae* (Anisoptera: Libellulidae). *Hydrobiologia* 17: 149–158.
- . 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). *Anim. Behav.* 40: 668–678.
- . 1991a. Sources of variation in male mating success and female oviposition rate in a nonterritorial dragonfly. *Behav. Ecol. Sociobiol.* 29: 17–25.
- . 1991b. Characteristics of dispersal in sexually mature dragonflies. *Ecol. Entomol.* 16: 449–460.
- Miller, P. L. 1983. The duration of copulation correlates with other aspects of mating behaviour in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12: 227–238.
- . 1990. Mechanisms of sperm removal and sperm transfer in *Orthetrum coerulescens* (Fabricius) (Odonata: Libellulidae). *Physiol. Entomol.* 15: 199–209.
- . 1991a. T. lidiae (C
- . 1991b. I. cius) (A Miller, P. *Orthetrum* time for Moodie, B flies. M Moore, A (Burme and ma
- . 1990. T. the separation. *Ev*
- Moss, S. (Hagen), (Zygot
- Nomakua specific (Zygot
- Oppenhei: *maculata* Ph.D. di
- Oppenhei: *Calopteryx* 291–296
- Rehfeldt, C. *cypha ca* activity
- . 1992. A *Sympetrum* *Sociobiol*
- Robertson in a dam *Behav.* 3
- Robertson and me Coenagr
- Robertson, contact
- Rowe, R. J. mating 1 375–383
- Rüppell, C. oeuvres
- . 1989b. F 18: 391–
- Rüppell, G. male co
- Sekt. Bio*

- the white-tailed (e). *Behaviour* 119:
- measurement of
- and the opportu-
ner *Plathemis lydia*
- ists and benefits of
5–521.
- damselfly territorial
Behav. 39: 954–959.
- enagrion *pulchellum*
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lulidae). *Odonatolo-*
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ctic to evade male
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- quirements at high
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- ence of oviposition
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- s of emergence char-
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biologia 17: 149–158.
- iposition site selec-
onata: Libellulidae).
- success and female
Behav. Ecol. Socio-
- ally mature dragon-
- correlates with other
rystigma (Burmeis-
12: 227–238.
- d sperm transfer in
t: Libellulidae). *Phy-*
- 1991a. The structure and function of the genitalia in the Libellulidae (Odonata). *Zool. J. Linn. Soc.* 102: 43–74.
- 1991b. Pre-tandem courtship in *Palpopleura sexmaculata* (Fabricius) (Anisoptera: Libellulidae). *Not. Odonatol.* 3: 99–101.
- Miller, P. L. and A. K. Miller. 1989. Post-copulatory 'resting' in *Orthetrum coerulescens* (Fabricius) and some other Libellulidae: time for 'sperm handling'? (Anisoptera). *Odonatologica* 18: 33–41.
- Moodie, M. N. 1995. Evolution of female color morphs in damselflies. M.S. thesis, University of Oklahoma, Norman.
- Moore, A. J. 1989. The behavioral ecology of *Libellula luctuosa* (Burmeister) (Odonata: Libellulidae): III. Male Density, OSR, and male and female mating behavior. *Ethology* 80: 120–136.
1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. *Evolution* 44: 315–331.
- Moss, S. P. 1992. Oviposition site selection in *Enallagma civile* (Hagen) and the consequences of aggregating behaviour (Zygoptera: Coenagrionidae). *Odonatologica* 21: 153–164.
- Nomakuchi, S. 1992. Male reproductive polymorphism and form-specific habitat utilization of the damselfly *Mnais pruinosa* (Zygoptera: Calopterygidae). *Ecol. Res.* 7: 87–96.
- Oppenheimer, S. D. 1991. Functions of courtship in *Calopteryx maculata* (Odonata: Calopterygidae): an experimental approach. Ph.D. dissertation, Brown University.
- Oppenheimer, S. D. and J. K. Waage. 1987. Hand-pairing: a new technique for obtaining copulations within and between *Calopteryx* species (Zygoptera: Calopterygidae). *Odonatologica* 16: 291–296.
- Rehfeldt, G. E. 1989. Female arrival at the oviposition site of *Platycypha caligata* (Selys): temporal patterns and relation to male activity (Zygoptera: Chlorocyphidae). *Adv. Odonatol.* 4: 89–94.
1992. Aggregation during oviposition and predation risk in *Sympetrum vulgatum* L. (Odonata: Libellulidae). *Behav. Ecol. Sociobiol.* 30: 317–322.
- Robertson, H. M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* 33: 805–809.
- Robertson, H. M. and H. E. H. Paterson. 1982. Mate recognition and mechanical isolation in *Enallagma* damselflies (Odonata: Coenagrionidae). *Evolution* 36: 234–250.
- Robertson, H. M. and K. J. Tennessen. 1984. Precopulatory genital contact in some Zygoptera. *Odonatologica* 13: 591–595.
- Rowe, R. J. 1978. *Ischnura aurora* (Brauer), a dragonfly with unusual mating behaviour (Zygoptera: Coenagrionidae). *Odonatologica* 7: 375–383.
- Rüppell, G. 1989a. Kinematic analysis of symmetrical flight manoeuvres of Odonata. *J. Exp. Biol.* 144: 13–42.
- 1989b. Fore legs of dragonflies used to repel males. *Odonatologica* 18: 391–396.
- Rüppell, G. and H. Hadrys. 1988. *Anax junius* (Aeshnidae) – Sexual male competition and oviposition behaviour. *Publ. Wiss. Film. Sect. Biol.*, Ser. 20, No. E 2998, pp. 1–12.
- Sherman, K. J. 1983. The adaptive significance of postcopulatory mate guarding in a dragonfly, *Pachydiplax longipennis*. *Anim. Behav.* 31: 1107–1115.
- Singer, F. D. 1987. The behavioral and physiological ecology of dragonflies. Ph.D. dissertation, University of Minnesota.
- Siva-Jothy, M. T. 1984. Sperm competition in the family Libellulidae (Anisoptera) with special reference to *Crocothemis erythrae* (Brulle) and *Orthetrum cancellatum* (L.). *Adv. Odonatol.* 2: 195–207.
- 1987a. The structure and function of the female sperm-storage organs in libellulid dragonflies. *J. Insect. Physiol.* 33: 559–567.
- 1987b. Variation in copulation duration and the resultant degree of sperm removal in *Orthetrum cancellatum* (L.) (Libellulidae: Odonata). *Behav. Ecol. Sociobiol.* 20: 147–151.
- Siva-Jothy, M. T. and Y. Tsubaki. 1989a. Variation in copula duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae) 1. Alternative mate-securing tactics and sperm precedence. *Behav. Ecol. Sociobiol.* 24: 39–45.
- 1989b. Variation in copula duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae) 2. Causal factors. *Behav. Ecol. Sociobiol.* 25: 261–268.
- Siva-Jothy, M. T., D. W. Gibbons and D. Pain. 1995. Female oviposition-site preference and egg hatching success in the damselfly *Calopteryx splendens xanthostoma*. *Behav. Ecol. Sociobiol.* 37: 39–44.
- Sutherland, W. J. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Anim. Behav.* 33: 1349–1352.
1987. Random and deterministic components of variance in mating success. In: *Sexual Selection: Testing the Alternatives*. J. W. Bradbury and M. B. Andersson, eds., pp. 209–220. Chichester: John Wiley & Sons.
- Tennessen, K. J. 1982. Review of reproductive isolating barriers in Odonata. *Adv. Odonatol.* 1: 251–265.
- Thompson, D. J. 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *J. Anim. Ecol.* 56: 815–832.
1989. Lifetime reproductive success in andromorph females of the damselfly *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 209–213.
1990. The effects of survival and weather on lifetime egg production in a model damselfly. *Ecol. Entomol.* 15: 455–462.
- Tsubaki, Y. and T. Ono. 1987. Effects of age and body size on the male territorial system of the dragonfly, *Nannophya pygmaea* Rambur (Odonata: Libellulidae). *Anim. Behav.* 35: 518–525.
- Tsubaki, Y., M. T. Siva-Jothy and T. Ono. 1994. Recopulation and post-copulatory mate guarding increase immediate female reproductive output in the dragonfly *Nannophya pygmaea* Rambur. *Behav. Ecol. Sociobiol.* 35: 219–225.
- Ubukata, H. 1984. Oviposition site selection and avoidance of additional mating by females of the dragonfly *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Res. Popl. Ecol.* 26: 285–301.
- Utzeri, C. 1988. Female 'refusal display' versus male 'threat display' in Zygoptera: is it a case of intraspecific imitation? *Odonatologica* 17: 45–54.

