

FEMALE MONOGAMY IN THE DAMSELFLY *ISCHNURA VERTICALIS* SAY (ZYGOPTERA: COENAGRIONIDAE)

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In contrast to most odon. females which mate repeatedly, females of *I. verticalis* were found to be effectively monogamous, remating only if sperm loads were low enough to cause substantial sterility of egg clutches. A female's colour phase corresponded to her sexual maturation. Virgin and non-virgin females were non-randomly distributed in the field and responded differently to male approaches. Both the penis structure and the behaviour of males during copula suggested that males could displace sperm if given the chance to do so. However, evidence of sperm removal using the volume of sperm storage organs of females interrupted in copula was equivocal. *I. verticalis* females are apparently monogamous because they do not benefit by mating repeatedly and cannot be forced to mate. As predicted for a monoandrous mating system where the potential opportunity for sexual selection on males is relatively low, males showed no overt forms of male-male competition, and were repelled by females giving a wing-flutter display.

INTRODUCTION

The type of male mating behaviour that evolves in a species depends to a large extent on the pattern of sexual receptivity of females. For example, within the Odonata, females typically mate between clutches and often mate repeatedly while ovipositing a single clutch. Such repeated mating by females acts as a selective pressure on males, giving rise to a suite of reproductive behaviours common in many odonates. By effectively shortening the interval between receptive periods in females, multiple matings increase the potential variation in, and

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opportunity for, sexual selection on male reproductive success relative to female monogamy (SUTHERLAND, 1985). In odonates, the male response to an increase in male-male competition for fertilizations has been the evolution of sperm displacement mechanisms (WAAGE, 1984), and mate guarding (e.g. WAAGE, 1979; SHERMAN, 1983; FINCKE, 1986a). Females avoid unnecessary male harassment by visiting the oviposition area only when they are receptive to mating and have eggs to lay, resulting in a male-biased sex ratio at the breeding site (see ref. in CORBET, 1962).

Although much is known about proximal mechanisms that affect female receptivity (cf. ENGELMANN, 1970; MATTHEWS & MATTHEWS, 1978), much less is known about the ultimate factors that are responsible for the evolution of female mating patterns. The adaptive advantages to female odonates of mating repeatedly within the same clutch remain unclear, but because they cannot be forced to mate, it is reasonable to assume that females should remate only if they derive some benefit from it. Such benefits include exchanging fertilizations for: (1) access to oviposition sites controlled by territorial males (WAAGE, 1979a; FINCKE, 1984a) or (2) services offered by males (FINCKE, 1986a). Alternatively, mating in some dragonflies may be very rapid (CORBET, 1962 and ref. therein), making time loss due to remating inconsequential to a female's fitness.

If females incur considerable time loss but no fitness gains by mating repeatedly, one might expect them to be monogamous, either mating only once per lifetime (monoandry; cf. PAGE, 1986), or mating once per egg clutch. Neither serial nor lifetime monogamy has been previously documented in an odonate. Several atypical features of the reproductive behaviour of the damselfly *Ischnura verticalis* suggest that females mate only once. Sex ratios at the breeding site are often female biased, males are not aggressive, and females oviposit alone and unmolested by lone males. Moreover, females repel unwanted males effectively by a wing flutter display (this paper, see also BICK & BICK, 1966). GRIEVE (1937) found that a female *I. verticalis* could fertilize all of the eggs she produced during several successive batches with sperm from only one mating. If monogamy is characteristic of *I. verticalis*, then its biology would provide an important test of predictions about the evolution of odonate mating systems which currently have been based on species whose females mate repeatedly. In this paper I present evidence from field and enclosure studies demonstrating that female *I. verticalis* normally mate only once per lifetime. I discuss the consequences that monogamy may have had on the development of colour changes in females, and on male reproductive behaviour.

MATERIAL AND METHODS

Observations were made during the summers of 1981-1983 on a population of *I. verticalis* that was

localized around Lake Cathleen, a small lake in Emmet County, Michigan, USA. The population was not discrete because marked individuals occasionally dispersed around the lake edges. However, because most of the lake was exposed to wind, oviposition occurred primarily along 200 m of a shallow, protected bay edged with tall grass at the southern end of the lake. The flight season was from late May until the end of August. On 11 days from July 24–Aug. 11, 1981, and on 13 days from July 1–14, 1982, I marked all individuals I saw by writing a number on the wing with an indelible felt-tip pen. Forewing length was measured using calipers. Newly emerged adults were first marked by placing a dot of enamel on the thorax. Those which were later recaptured were then marked with a number on the wing. On each study day, marking and resighting were conducted for a minimum of three hours between 1000 and 1700 hrs, when individuals were active. Within a day of emergence, the thorax and abdomen of females become orange, turning blue in older females. The time required for changes in body colouration was determined by holding newly emerged individuals in an outdoor insectary. To determine if the colour change in females corresponded to sexual maturation, females in both colour phases were dissected and the presence of sperm (in the spermatheca and bursa) and eggs were noted.

Unlike many coenagrionid damselflies which return to ponds or streams only when they are ready to breed, both mature and immature individuals in my study population could be found within 10 m of the lake edge. To determine the distribution of individuals around the pond, I divided the lake edge into 3 zones: (1) the water's edge, which included the oviposition areas of emergent vegetation or nearly submerged algae; (2) a grassy bank about 2.5 m wide adjacent to the shore; and (3) a 5 m-wide sandy edge region beyond the grassy bank, that was sparsely vegetated with milkweed (*Asclepias*) and raspberries which gave way to a pine forest. On each of three days, for 1 hour between 1100 and 1500 hrs, I recorded the sex and colour phase of all individuals entering 3, 1-m² plots in each of the above areas.

I recorded mating frequency of females, and described behavioural interactions between the sexes, by maintaining 32 orange and 13 blue field-collected females in an outdoor insectary (2 x 4.5 x 2 m). At one end I placed a water-filled pan (50 x 20 x 10 cm) into which I secured emergent vegetation of reeds and grasses to serve as oviposition sites. For 2–5 hours on 10 days over a 3-week period, I put 6–10 males in with the above females and sat in the insectary to record their behaviour. All males were removed at the end of each observation period, and fresh males were field-collected every 2 days. Captive adults fed readily on insects collected from sweep-netting the adjacent grassy areas, and on *Drosophila* that were attracted to the rotting fruit hung in the insectary.

During 5, 20-min observation periods in the insectary, I recorded the following responses of orange and blue colour phase females to a male's approach:

(1) Wing flutter display — the female raises her wings and quickly flutters them for a few seconds, while curling her abdomen slightly under (described by BICK & BICK, 1966).

(2) Wing spread — the female spreads her wings widely (there being an angle of about 90° between them) for half a second or more.

(3) No response — the female remains perched.

The male was scored as showing either a positive response (tandem formation, darting at the female in an attempt to form tandem or hovering over the female, which preceded darting at her), or a neutral response (flying away or perching without further interaction).

To determine at what point in the copulation sequence females would accept a second mate, I separated females 5–30 min after the initiation of copulation, and then introduced them to a second male. In order to determine the fertility of eggs from such matings, I allowed the females to oviposit for a day (see below), before dissecting them under a dissecting microscope. I measured the volume of sperm in the spermatheca and bursa by the method described by WAAGE (1979b).

Egg-laying patterns and egg fertility were determined by collecting eggs from mated females and scoring the percentage that hatched. In late afternoon, I put a given female in a cage (10 x 10 x 20 cm) provided with moistened filter paper as an oviposition substrate. In the morning I returned

the female to the insectary to feed, and put any eggs laid (with the filter paper) in a small vial (with screened windows for water flow) which I floated in water (23° C) for about 2 weeks until the eggs hatched. The procedure was repeated daily until the female died. Means are given with \pm s.e.

RESULTS

DEMOGRAPHY

Figure 1 shows the number of individuals marked and resighted, during the study days in 1982. The adult sex ratio was significantly biased towards females in both years (1982 — 449 males: 533 females, $\chi^2 = 7.2$, $df = 1$, $p < 0.01$; 1981 — 126 males: 386 females, $p < 0.01$). In 1982, 56% of the females were marked when still orange, and 32% of the total were resighted after the day of marking. Similarly, 31% of the males marked (11% as tenerals), were resighted after marking. In 1981, only blue females were marked because by the time the study began in the second half of the season, most orange females had already changed to blue. In both years the study covered only a part of the flight season. I thus estimated lifespan from the subset of individuals seen at least 10 days before the study ended. For individuals resighted at least once, the average lifespan was 4.7 ± 0.2 days for females marked in the orange or blue phase ($n = 139$) and 5.8 ± 0.3 days

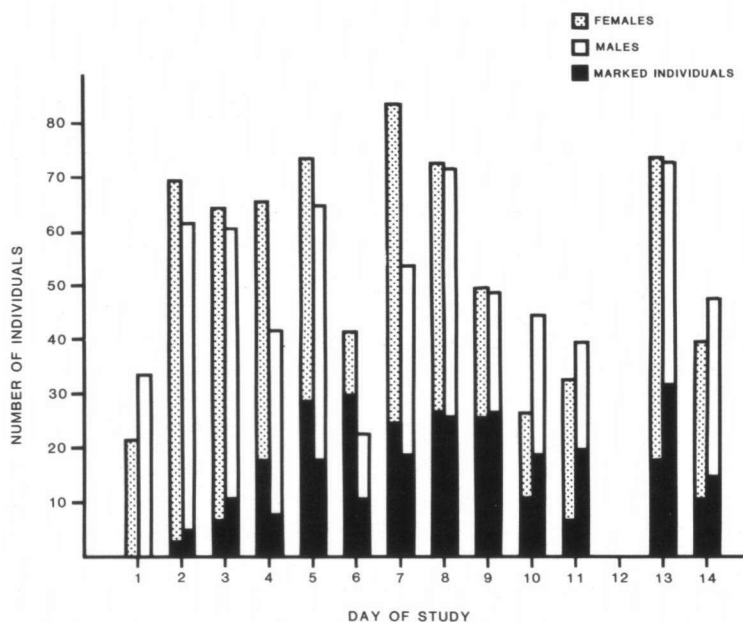


Fig. 1. Mark and resightings of males and females in 1982.

for males ($n=119$) during the first half of the season in 1982. Lifespan of only females marked when blue was not significantly different from that for all females ($\bar{x} = 4.4 \pm 0.4$, $n=41$). During the second half of the season in 1981, the average lifespan was 7.9 ± 0.4 days ($n=138$) for females and 5.3 ± 0.7 days ($n=26$) for males.

Seven of the 10 newly emerged males that were held in cages acquired mature colouration (i.e. green thorax and black abdomen with a blue band at the tip) within 24 hrs and all did so within 48 hrs. In contrast, light orange females, collected at least a day after emergence, required on average 4.5 ± 0.4 days, ($n=20$) to turn blue. Orange females darkened by degrees, with the abdomen and later the thorax turning dark brown ("darkened" females) one to two days before turning blue. In 1982, I found only one andromorphic female (i.e. with male colouration) among the 533 marked (and in 1981, I found none). After three days in the insectary, the abdomen of the andromorph turned completely black while her thorax remained green. Within a week of collection, this female had turned completely blue, and was indistinguishable from mature heteromorphic females.

REPRODUCTIVE BEHAVIOUR

In the 36, and 40 hrs (1981 and 1982 respectively) of field observations (between 1000 and 1720 hrs), I observed only 22 mating pairs (12 in 1981, 10 in 1982).

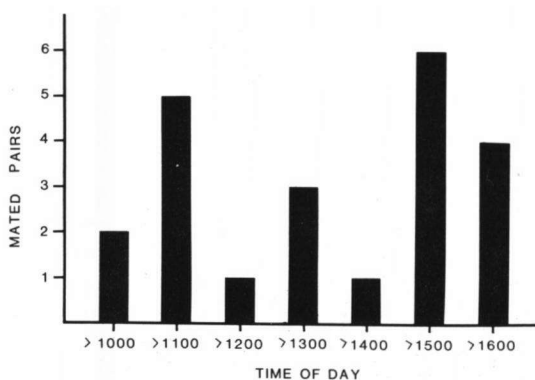


Fig. 2. Time of day during which copulations occurred during 1981 and 1982.

Mating occurred throughout the day (Fig. 2). In the field, no marked individual was seen to mate more than once. All but two of the copulating females were blue; their age from initial marking as a blue female was 1.6 ± 0.3 days. One of the orange females was at least 4 days old whereas the other mated on the day she was marked.

Males did not defend perches, but rather searched for females in the grassy zone around the lakeshore. Males were noticeably unaggressive; they approached other males in what appeared to be an investigatory manner, but thereafter ignored each other. Lone males only rarely approached mated pairs, and never attempted to "take-over" a female from a mating male. It is likely that the tenacity with which females were clasped would

render any such attempts useless. Unlike most damselflies which readily separate when caught in a net, copulating pairs of *I. verticalis* could be held in the hand, numbered, and released without separating.

The behaviour of males just before seizing the female varied somewhat, but a general sequence of events is as follows. If a male hovered around a flying female, she usually turned to face him, hovered, and then perched. I could not discern whether such female behaviour elicited mating attempts by the male, or was merely investigatory. Mature females occasionally ate males (see below), and such behaviour might be a normal response to orientate towards a potential prey item. A male hovering over a perched female usually darted at her unless, when approached, she responded with a wing-flutter display described above. If a female remained perched but did not wing-flutter, a hovering male usually pounced on her. The pair then typically fell to the ground, and if the male was successful in achieving tandem position, copulation occurred. Unresponsive females in tandem occasionally dislocated males by pushing them off with their legs. In the insectary, eleven unresponsive females (1 orange, 6 darkened, and 4 blue) were taken in tandem but failed to raise their abdomens to the male's secondary genitalia. All of these males broke tandem within a few minutes.

Uninterrupted copulation in the insectary lasted 43.5 ± 2.0 min ($n=14$). Typically, a male executed "pumping" motions of his abdomen during the first 12-20 min of copula, after which he depressed his abdomen against that of the female, and then raised it and held it motionless during the last 15-20 min.

After mating, which always occurred on shore, a pair broke, and the male did not associate further with his mate. Because of the high (1.5 m) grass around the lake, it was impossible to follow mated females long after mating. However, all of the females seen to mate in the insectary oviposited either later the same day, or on the subsequent day. Ovipositing females at the lakeshore were most abundant in early to late afternoon. Females always oviposited above water, into floating vegetation, or in exposed vegetation or roots near shore. Ovipositing females that were approached by males typically responded with a wing-flutter display which was usually sufficient to deter males from pouncing on them. It is of note that the only female *I. verticalis* that I saw go under water was one that was continually harassed by a male *Enallagma hageni* that apparently mistook her for a female of his own species. The female remained submerged for about a min.

Ovipositing females usually spent only 5-15 min on a particular stem, and a given female could be found laying eggs on subsequent afternoons. Virgin females that were mated once and then held in oviposition cages laid an average of 363 ± 77 eggs ($n=16$). Seven of these oviposited more than once, on average once every 1.4 days ($n=12$). One female laid a total of 1132 eggs over a span of 6 days.

DISTRIBUTION OF VIRGINS AND MATURE FEMALES AND MALES

Figure 3 shows that the distribution of males, and females in orange and blue colour phases was non-random. Few male *I. verticalis* were found in oviposition areas, which were frequented almost exclusively by blue females. Orange females

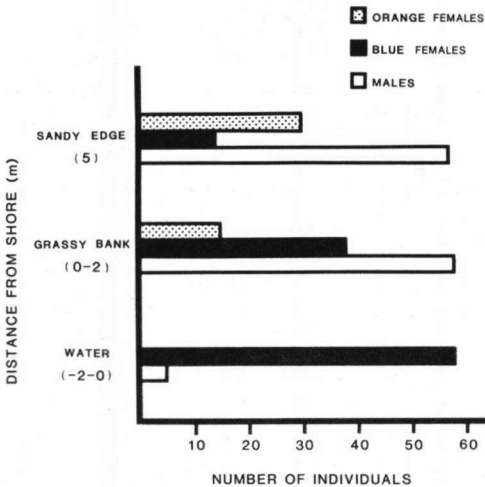


Fig. 3. Distribution of females and males around the pond.

were found mainly in the sandy edge zone where the risk of predation by mature females may be lower. In the insectary, I saw blue females eat 2 orange females and one mature male; mature females in the field often ate newly emerged males and females. The extent of female voracity was clearly shown when I attempted to maintain virgins of *I. verticalis* and *E. hageni* in the same insectary. Within two days, the 14 *E. hageni* females had disappeared, while three blue female *I. verticalis* were seen eating the abdomens which they had neatly snipped off of *E. hageni* females, which

continued to fly about. Males, which were the smaller sex (\bar{x} winglength = 15.9 ± 0.05 mm, $n=211$) were never observed to eat females (\bar{x} winglength = 18.4 ± 0.04 , $n=266$).

As shown in Table I, the blue colour phase of females corresponded with sexual receptivity and egg maturation. All of the light orange-coloured females

Table I

Presence of sperm and eggs in orange and blue female *I. verticalis*. "Mature" eggs refer to those that were ready to be laid; "immature" eggs were not fully developed

Body colour	N	Females with sperm in:		% Virgin Females	Females with:		
		Bursa	Spermatheca		Mature eggs	Immature eggs	No eggs
Orange	16	0	0	100%	1	8	7
Blue	44	30a	38	9%	43	44b	0

a: 6 individuals had sperm in the spermatheca but none in the bursa; only 4 individuals had no detectable sperm.

b: 43 of these also had mature eggs.

were virgins, with none having sperm in the spermatheca or bursa, whereas only 4 of the blue females had not mated. Nearly half of the orange females had not yet matured eggs, in contrast to all of the blue females which carried mature eggs.

FEMALE MONOGAMY

Of the 45 females maintained for 2 weeks in the insectary, none of the 23 females that copulated once did so a second time, despite the fact that they spent an average of 8.7 ± 1.07 days as blue (i.e. sexually mature) adults, and were in the presence of receptive males on average 4.1 ± 0.6 days after their initial copulation.

Table II

Matings by females in the insectary. The day a given female was placed in the insectary was counted as day 1

Colour phase when collected	N	\bar{x} days in insectary	Number alive after 2 weeks	\bar{x} day mated	\bar{x} day on which colour changed
<i>Light orange</i>					
Mated once	19	11.0 ± 1.0	10	4.5 ± 0.5	$3.7 \pm 0.4^*$
Never mated	13	5.3 ± 1.0	0		
<i>Blue</i>					
Mated once	4	8.8 ± 2.6	1	7.8 ± 2.6	
Never mated	9	10.8 ± 1.4	3		

* n = 22, 3 individuals changed colour but did not mate before dying.

Of orange females collected, 78 % lived long enough to develop blue colouration, and 59 % mated before dying, on average 1.6 ± 0.3 days after becoming blue (Tab. II). Nine females mated in the "darkened" stage, just before turning blue. Seven of the unmated females died before becoming mature, and the remaining 6 survived on average 2.3 ± 0.6 days after changing colour. In contrast, few of the females collected when blue mated in the insectary, and 3 of these (75 %) were those whose first copulation in the field was interrupted during capture. Unlike females, males held in the insectary mated repeatedly, up to 3 times on a given day.

BEHAVIOURAL RESPONSES TO MALES

As shown in Table III, blue and orange females responded differently to male approaches. Blue females usually (86 %) reacted to the approach of a male with a wing-flutter display, after which 70 % of the males whose subsequent behaviour was known, left the area, or perched without further attention to the female. In contrast, only 35 % of the orange females actively repelled males (all but two of the interactions were with orange females that were at least 4 days old). Orange females were more likely to remain perched or exhibit the wing spreading display

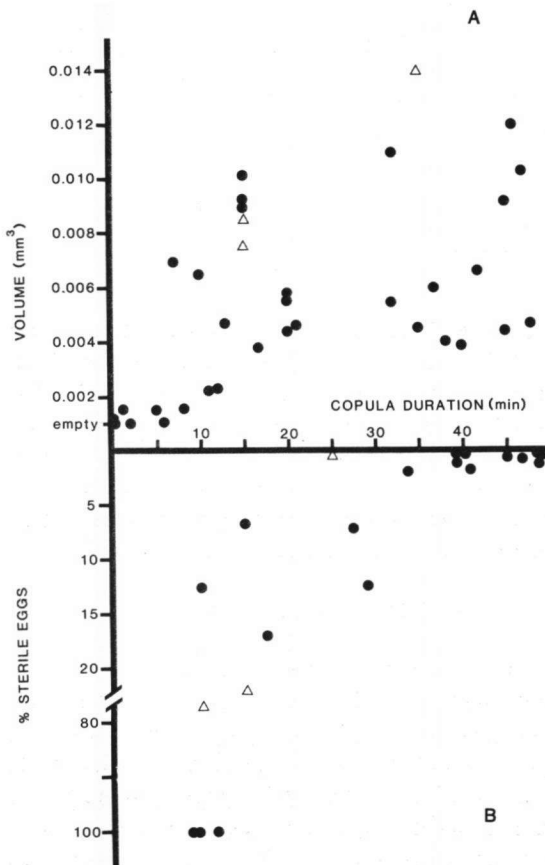
Table III

Behaviour of blue and orange females towards male approaches, and subsequent male response. Subsequent male responses are less than the total female responses because only unambiguous responses by males are reported. Because males did not respond differently with regard to colour phase of the female, male responses were lumped by female response. Positive response includes: tandem, attempted tandem, darting at, or hovering over a female. Neutral response includes: male flying away or perching and subsequently ignoring the female

Female response	Female colour phase		Subsequent male response:	
	Orange	Blue	Positive*	Neutral**
Wing flutter	23	81	17	39
Wing spread	24	2	13	1
No response	18	11	30	0

* tandem, attempted tandem, darting at, or hovering over a female

** male flew away or perched and subsequently ignored female.



than were blue females. These responses elicited mating attempts (e.g. tandem, hovers, or darts at the female) by males 98% of the time.

CONTROL OF REMATING

Females that were separated during copulation remated only if less than a full sperm load was

Fig. 4. (a) Combined sperm volume (bursa and spermatheca) of dissected females. Triangles represent females mating twice [$r = 0.52$, $n = 32$ singly mated females, $p < 0.05$]; — (b) Sterility of eggs as a function of copula duration [$r = -0.56$, $n = 18$ singly mated females, $p < 0.05$]. Females mating for < 10 min did not oviposit; many of the dissected females represented in 4a failed to lay eggs before dying and are thus not represented in 4b.

transferred during the first copulation. Of the 7 virgins that I interrupted after 5 min of copula, 5 (71%) remated with an additional male within the hour, as opposed to only 6 of the 30 (20%) virgins allowed to mate for 10-20 min $\chi^2=7.2$, $df=1$, $P<0.01$). None of the females that were allowed to mate for more than 25 min later remated when given the opportunity ($n=10$ uninterrupted copula; $n=3$ interrupted copula). As seen in Figure 4a, little or no sperm appears to have been transferred during the first 5 min of copula, yet two females mating for less than 10 minutes had high sperm volumes. Two females that I interrupted after 5-10 min of copula, and that subsequently were allowed to remate with second males for 5-10 min (i.e. 15-20 min total copula), had sperm volumes equivalent to females mating with only one male for 15-20 min. This suggests that some sperm was transferred in early copula, and that it was not removed by the second mate.

EGG FERTILITY

The average sterility of the eggs laid by 16 virgins that matured in the insectary and were allowed to mate once (uninterrupted), was 0.04. Sterility in the first egg batches was not significantly different than that for subsequent batches, but the sample was small ($n=12$), and only 2 females laid more than two batches before dying. Egg sterility increased if copula was interrupted before about 30 min (Fig. 4b). No female that mated for only 5 min subsequently laid eggs, and only a few that mated for more than 5 but less than 15 min did so.

DISCUSSION

The paucity of matings observed in the field, coupled with the absence of repeated, full matings by females in both the field and in the insectary, support the hypothesis that females of *I. verticalis* mate only once per lifetime. In the insectary, females oviposited and matured eggs over the 2-week period. The lack of mating was thus not due to a lack of mature eggs to fertilize. Females that I observed remated only if their original copulation was interrupted before 20 min, resulting in less than average sperm load and an increase in egg sterility. I cannot rule out the possibility that very old females will remate if their sperm stores are old or depleted. However, because few females lived longer than 10 days in the field, it seems reasonable to assume that most females are effectively monogamous.

Females of most *Ischnura* oviposit alone and unguarded, but within the genus and within populations, copula duration and the frequency with which remating occurs vary greatly. In England, *I. elegans*, whose copulation duration is comparable to that of *I. verticalis*, mate only rarely (12%) in the field, and hardly ever remate (PARR & PALMER, 1971). Remating in *I. elegans* has been documented to occur in a southern European population of *I. elegans*, which have

long copulations (MILLER, 1987a; cf. also KRIEGER & KRIEGER-LOIBL, 1958). The Australian *I. aurora*, which has relatively short copulations, mates (perhaps for the only time) while still teneral (ROWE, 1978). In contrast, *I. ramburi* females mate for up to 3 hrs, and as often as 4 times on the same day (ROBERTSON, 1985). From these comparisons, it appears that long copulations in *Ischnura* function as a type of contact mate guarding, and that short copulations occur in those species in which mate guarding is unnecessary, because females mate only once or when sperm reserves are low.

Monogamy in *I. verticalis* females appears to be a derived condition because the genitalia of males (a conservative character) indicate they can remove sperm of previous mates. The penis is bifurcated dorsally, and equipped with backwardly oriented spines (pers. obs.; WAAGE, 1984) that serve to remove sperm in related species (e.g. MILLER, 1987b). Males also displayed a pumping movement, characteristic of the sperm removal stage of other coenagrionids (cf. MILLER & MILLER, 1981; FINCKE, 1984). Evidence for sperm removal based on the dissection of females interrupted in copula were equivocal, and the methods used were problematic. Sperm volumes were low for most females interrupted before 10 min of copula, but the few data from twice-mated females indicated that whatever sperm was added in early copula was not removed by a second mate. A more accurate method to quantify sperm loads would be to count sperm (e.g. SIVA-JOTHY, 1984) rather than to measure the volume of sperm storage organs, which fails to detect changes in sperm density. Because I dissected females after allowing them 24 hrs to oviposit, rather than immediately after copula, any change in apparent sperm volume over time would also affect the interpretation of the data. Females that had copulated for more than 20 min could not be induced to remate, and those that would remate had less than normal egg fertility. I was thus unable to use sterile male techniques (e.g. FINCKE, 1984b) to directly measure sperm precedence in *I. verticalis*.

The separation of mature and immature females around the pond was strikingly different from the distribution of most other coenagrionid females, in which both mature and immature individuals avoid male harassment by remaining in areas far from the mating arena (e.g. BICK & BICK, 1963; FINCKE, 1982). Because wing fluttering was effective in repelling unwanted males, unreceptive females were not disturbed by males searching for mates. Rather, both males and immature females may decrease the risk of predation by mature females by staying in the edge areas away from the water (cf. also ROBERTSON, 1985).

Male *I. verticalis* in search of mates may frequent the grassy bank and sandy edge area because that is where they are most likely to encounter a virgin female. Males could potentially use a female's colour as a cue to her receptivity, because females that had darkened, but not yet turned completely blue were often receptive, whereas lighter orange ones were usually unresponsive, and most blue phase females had mated. Blue females that remained in the grassy area during

the afternoon were more likely to be virgins than those ovipositing at the water, which clearly had already mated. Efforts to record male responses to pinned blue and orange females in the field were unsuccessful because of too few interactions. Although I observed few interactions between very young orange females and males in the insectary, males seemed to approach older orange, and blue females randomly with respect to colour, but responded markedly to their subsequent behaviour. Both the wing spreading display and the act of remaining perched apparently signalled receptivity to males because the latter subsequently tried to take the females in tandem. Males persisted if the female reacted favourably, but wasted little effort in pursuing an unwilling female, who might retaliate by treating the male as prey. The orange colour of immature females might allow them to use conspecific cueing to avoid mature females; alternatively, the colour phase might be a neutral trait that is a developmental remnant from ancestral populations in which orange immatures developed into a different adult colour morph (as occurs in *I. elegans*; PARR & PALMER, 1971).

Although colour polymorphisms of mature females are common among coenagrionids (CALVERT, 1915; JOHNSON, 1964; FINCKE, 1982; ROBERTSON, 1985) mature andromorphic females (i.e. those coloured like males) were absent from my study population. ROBERTSON (1985) found that andromorphic female *I. ramburi* mated less frequently than would be expected if mating were random with respect to colour morph of females. He suggested that by mimicking males in body colouration, andromorphs were not recognized as females by males, and thereby avoided harassment by males more effectively than did heteromorphic females. If *I. verticalis* males do use body colouration as a cue to an individual's sex, the lack of andromorphic females in my study population would tentatively support Robertson's hypothesis. Given that females mate only once, having male colouration would be of no benefit to an *I. verticalis* female because males do not persist in attempts to take unreceptive females in tandem. Andromorphic *I. verticalis* in this population with a female-biased sex ratio might be at a disadvantage in attracting a mate if males do not readily recognize them as females. The one andromorph I found was a sexually immature female, which later turned the characteristic blue of a heteromorph. PARR & PALMER (1971, as cited by GARRISON & HAFERNIK, 1981) found both sexually immature and mature andromorphs in *I. elegans*. If the mimicry hypothesis is correct, populations of *I. verticalis* in which sexually mature andromorphic females are abundant should also be those in which multiple matings by females are common.

WALKER (1980) predicted that monogamy should evolve in nonsocial insects if (1) first mates had higher fitness, as might occur in species using ephemeral larval habitats favouring rapid development; (2) females waste considerable time by remating. Alternatively, he suggested that monogamy may be the result of sperm competition, resulting from male derived factors (such as sperm plugs or

hormones) which prevent remating until females have used their sperm to fertilize a clutch. None of the above sufficiently explain monogamy in *I. verticalis*. In odonates, differential fitness among males that is correlated with a heritable trait (which could thus be passed on to a female's offspring) has been documented only once, in *Megaloprepus coerulatus* which exhibits resource defence polygyny (FINCKE, 1984, 1986b). For this species, there is no evidence that the first potential mate encountered is phenotypically more "fit" than subsequent mates (Fincke, unpubl.). Moreover, the larval habitat of *I. verticalis* is not ephemeral, and emergence characteristically occurs over a long span relative to other coenagrionids in the same habitat (pers. obs.). Copulation time in *I. verticalis* is short relative to congeners (KRIEGER & KRIEGER-LOIBL, 1958; ROBERTSON, 1985; MILLER, 1987a) but comparable to many other coenagrionids that mate repeatedly (e.g. BICK & BICK, 1963; FINCKE, 1982). Finally, dissection of females revealed that the determinant for remating was sperm volume, rather than the presence or absence of a sperm plug.

Because one female *I. verticalis* fertilized more than 1,000 eggs using the sperm from a single mating, without a drop in fertility (cf. also GRIEVE, 1937), sperm replenishment is probably unnecessary for most females during an average lifespan. Thus, the critical question may not be, "Why do some females mate only once?" but rather, "Why do odonate females mate more often than is necessary to replenish sperm?" I argue that they should only remate if additional matings confer an advantage to them. *I. verticalis* females oviposit above water and thus they do not benefit from exchanging fertilizations for protection by the male as do some female coenagrionids which submerge to oviposit (FINCKE, 1986b). It is probably inefficient for males to try to control oviposition areas, which are abundant and not clumped in any particular area. Consequently female *I. verticalis* would not benefit from exchanging fertilizations for access to oviposition sites (e.g. WAAGE, 1979; FINCKE, 1984b). I propose that male *I. verticalis* are not aggressive because they can offer nothing to make remating beneficial to females. Consequently, female monogamy preempts a male's use of any sperm displacement ability he might have. Comparative experimental studies between populations of *I. verticalis* whose females are monogamous and polygamous (if the latter exist), or between different species of *Ischnura* exhibiting the 2 female mating strategies, hold promise of clarifying the benefits of multiple versus single mating in female dragonflies.

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