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SHORT COMMUNICATION

ISCHNURA AURORA (BRAUER), A DRAGONFLY WITH UNUSUAL MATING BEHAVIOUR (ZYGOPTERA: COENAGRIONIDAE)

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Dragonflies usually undergo a period of several days' maturation before mating. However, ♂♂ of *I. a. aurora* have been observed mating only with freshly emerged ♀♀. After copulation ♀♀ resist further mating attempts, disperse, mature and then lay eggs. Respects in which this behaviour may constitute an adaptation to the colonisation of temporary pools are discussed.

INTRODUCTION

It is widely held that after emergence dragonflies typically undergo a period of maturation and dispersal before becoming sexually active. Maturation times for Zygoptera in temperate climates generally range from one to two weeks (CORBET, 1962; WAAGE, 1972). The shortest maturation time recorded is two days in the case of *Calopteryx splendens* (Harr.) (ZAHNER, 1960). However, according to a personal communication from the late Dr J.S. Armstrong of Taupo (1968), Dr F.C. Fraser believed that in *Ischnura aurora*, recently emerged females mate before dispersal. I observed such behaviour in 1966 and 1970, but my interest sharpened after discussions with Professor P.S. Corbet in 1976. I have since confirmed my earlier observations, photographed the behaviour and established the approximate duration of the maturation period in this dragonfly.

Two colour forms exist in female *I. aurora*: the homochrome form resembles the male in having a red and black abdomen with blue patches on the eighth and ninth segments, and in the heterochrome form the abdomen has green-bronze dorsal surfaces over a light-green background. TILLYARD (1907) and FRASER (1927) indicate that only the heterochrome female is found in eastern Australia

and the Pacific including New Zealand. Changes in colour can be used to determine the approximate age of females in this species.

TILLYARD (1926) and ARMSTRONG (1958, 1975) document the recent colonisation of New Zealand by *I. aurora*. The species occurs widely in the North Island in shallow, well vegetated pools. No colonies are known to occur in the South Island. O'FARRELL (1973) states that *I. aurora* in Australia can "develop from egg to adult in 8-10 weeks".

MATING BEHAVIOUR

I have observed mating behaviour in detail at three sites, and have made casual observations of *I. aurora* behaviour at many other sites in the North Island.

In 1966, 1970, 1972 and 1978, I made observations at a pool on Henderson's farm, Vinegar Hill, Hunterville (39°53'S 175°36'E).

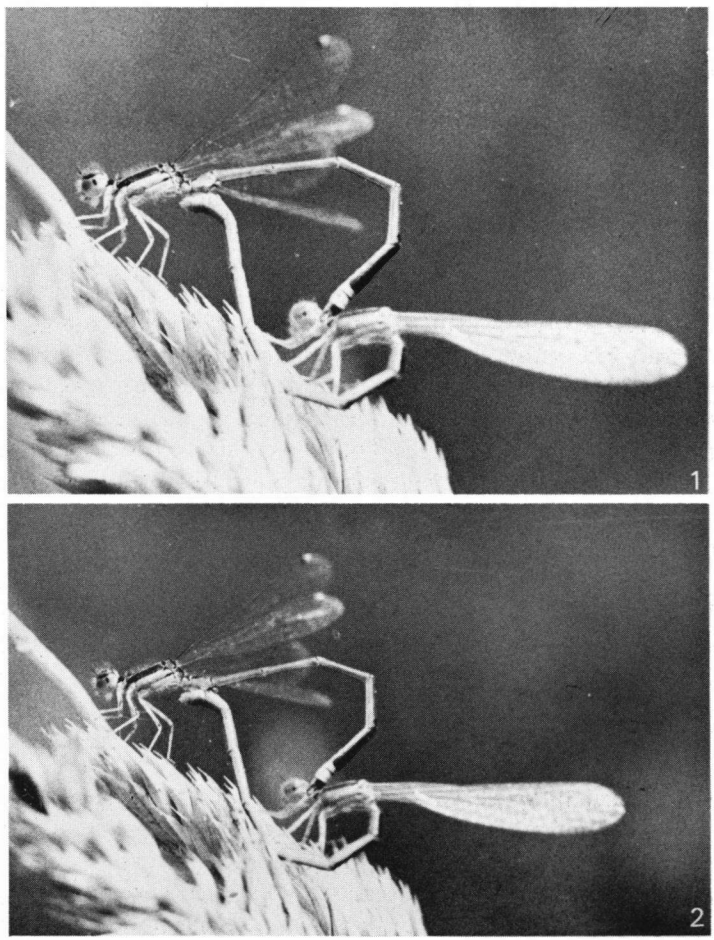
This pool was formed by the damming of a small stream on the upper terrace of the Rangitikei River valley. The pool has a length of 40 m, a maximum width of 10 m, a greatest depth of 0.7 m and an area of about 150 m^2. The site is sheltered from the prevailing wind by its location in the valley and also by a 1.5-m high bank immediately to windward. The pool contains large quantities of aquatic vegetation, this being mostly pondweed (*Potamogeton* sp.) and duckweed (*Lemna*). There is a belt of mature reeds (*Juncus* and *Eleocharis* spp.) 1-5 m deep immediately to the leeward of the pool.

Resident populations of the endemic dragonflies *Xanthocnemis zealandica* (McLachl.) and *Austrolestes colensonis* (White) occur with *I. aurora* in the pool. *Procordulia smithii* (White) adults are active above the pool, and lay eggs in it; and *Hemicordulia australiae* (Ramb.) adults are occasionally found nearby. *Aeshna brevistyla* (Ramb.) exuviae have been found on emergent vegetation and the adults are common in the district. Interspecific adult interactions have been observed between the 25-mm long *I. aurora* and the 32-mm long *X. zealandica*, both species being found on the pool margin and over the pool for much of the day. The colony of *I. aurora* became established on this pool in 1963 or 1964.

I. aurora was observed during the periods 2-5 February 1970, in February 1972 and again during 14-21 February 1978. During these periods adult density was high: on the pool and surrounding vegetation there was about one male per 2 m^2, and there were many females hidden in the reed bed. Activity occurred over the pool, on the pondweed and other emergent vegetation and among the reeds and grasses in nearby pasture.

During the late morning and early afternoon the males rested amongst the reeds close to the pool margin; normally the body was held parallel to the stems on which they sunned themselves. Threat display by wing opening, as illustrated by MOORE (1960, p. 115), occurred whenever a male in flight approached within 30 cm of another male's perch. When a flying male was challenged he either settled or flew away. No males were seen to approach closer after being subjected to such a threat display. Approximately two hours after solar noon, the male behaviour began to change. Flights became both more frequent and

more vigorous. There was a general movement to new perches on weed at the pool margin, drowned grasses and floating duckweed. In these new locations the males perched with the abdomen raised from the substrate by about 20°, and the wings closed above the abdomen. Some males moved to the tips of drowned grasses or made short, direct flights between perches at the pool margin. Other males made long, slow, hovering flights around partly submerged vegetation in the pool. These males spent up to about half their time on the wing, flying backwards 1-5 cm above the water surface.



Figs. 1-2. Mating behaviour of *Ischnura aurora* (Brauer): (1) Wheel position: the female is immature; its genital pore is not in contact with the male accessory genitalia; – (2) Copulation: the female genital pore is now in contact with the male accessory genitalia.

About three hours after solar noon, freshly emerged females appeared, flying clumsily over the pool. Males followed these females until the females landed. No sooner did a female alight on weed pads or poolside vegetation than it was seized by a male. As soon as the male anal appendages had gripped the prothorax of the female, the pair flew in tandem to the reeds or to the long pasture grasses. After the tandem pair had perched for a few seconds, mating ensued. First the male placed his primary and secondary genitalia together (presumably transferring the sperm capsule). Then the female would complete the copulation wheel. Examination of photographs has shown that during this phase (at least in the individuals that were photographed) the female genital pore was not in contact with the male. The wheel position (as distinct from true copulation) lasts approximately twenty minutes. This time is comparable to SCHIEMENZ's (1953) data for *Ischnura elegans* (Vander L.) but contrasts with the three to five hours found by KRIEGER (1958) for *I. elegans*; but Krieger does not indicate the positions of the copulatory apparatus during the long periods in the wheel position. During the late afternoon, as the light intensity decreased, the time spent by *I. aurora* waiting in the wheel position without copulating increased. Actual copulation took approximately two minutes. The male alternately and rapidly curved and straightened his abdomen; then finally, for almost half a minute, he held his abdomen in a position that was noticeably straighter and more rigid. The female then quickly withdrew her abdomen from the male accessory genitalia and the male so placed her that her feet could clasp the stem immediately below the spot he was grasping. He then released her. After being motionless for a few seconds, both insects flew away. The still-teneral females, opaque green in colour with pale wings and with pterostigmata not yet distinct, fluttered upwards until they were caught by wind eddies and blown away. Males which had been attracted to the mating pair, but deterred prior to and during copulation by threat display, often pursued females unsuccessfully for a few metres.

On one occasion (an overcast day following a day of rain) mating occurred in the morning, ceasing four hours before solar noon.

At Lake Pupuke, Auckland (36°50'S 174°47'E) I recorded the behaviour of *I. aurora* on the road separating the flooded quarry (area approximately 1 ha) and the lake (area approximately 8.6 ha). The mating I observed on the afternoons of 6, 12 and 19 March, and 22 December 1977, and on 3 and 18 January 1978 differed in some respects from that seen at Hunterville. The freshly emerged females were intercepted by the males as the females flew over the edge of the quarry bank. Females were occasionally knocked to the ground, whereupon the tandem position was assumed; but more frequently they were picked up from perches at the tips of grass stems by males that had persistently followed them as they flew away from the water. The time spent in tandem prior to the formation of the wheel position varied considerably: on one occasion this

phase lasted more than one hour. As soon as the pair had settled amongst the grass stalks and completed what I assumed to be sperm-capsule transfer, the males appeared to be initiating formation of the copulation wheel by rapidly raising and lowering their abdomens several times. The females, unlike those at the Hunterville site, were often incapable of forming a successful wheel, apparently lacking the strength to curve their abdomen to the male accessory genitalia. When the female seemed unable to complete the wheel, the pair would rest for about ten minutes before the male repeated the raising and lowering of his abdomen, this sequence of attempted initiation and waiting continuing until a wheel was formed. Males in tandem or in the wheel position held their wings partly separated and, if I approached, would move the female around the perch to a less conspicuous place on the perch or else fly with the female to a new perch further from the water. Once the wheel position had been adopted, the pair flew in the wheel position to a new perch if disturbed. The wheel position was maintained for at least ten minutes, and up to twenty minutes, before copulation proper began. The act of copulation was identical to that observed at the Hunterville site. After separating from males, females flew to protected sites in the rank vegetation of the roadside, and were rarely dispersed by wind at that time.

At the seaward end of the Bethel's Beach swamp on the west coast near Auckland I saw mating behaviour in January 1978. Here there was no pond vegetation for the larvae to emerge on and both emergence and mating occurred on the same clumps of *Juncus*. Behaviour was otherwise identical to that observed at Hunterville, including the upward flight into the wind which carried the immature females across the 10-m wide outflow channel and thence inland. Mating started about three hours after solar noon, peaked about four hours after solar noon and had ceased by six hours after solar noon.

MATE RECOGNITION

Mate recognition in *Ischnura aurora* is relatively unselective. On several occasions I have seen male *I. aurora* seizing, and assuming the tandem position with teneral male and female *X. zealandica* as well as with females and immature males of *I. aurora*; indeed, I have even seen them following large craneflies (Diptera: Tipulidae) disturbed near the pool margin. Once a male *I. aurora* obtains a grip with his anal appendages he maintains a firm hold. I separated one which had seized an immature male *X. zealandica* and had held the larger species helpless for more than eight minutes. All of the several hundred females of *I. aurora* which I have seen mating have been freshly emerged. Mature females, and tenerals which have mated, lowered the tip of their abdomen if their perch was approached by a male. The males hovered for a few seconds before moving off and settling. On the rare occasions when a male flying amongst the vegeta-

tion reached a mature female he seemed to be shaken off before he could effect a grip with his anal appendages. A mature female approached by a male while flying, hovered head-on to the male and curved the tip of her abdomen, sometimes through a semicircle. The male also hovered for a few seconds and then moved away. The distance between a male and female during such encounters was 10-20 cm. The smaller the distance the greater the curvature of the female abdomen. Similar behaviours have been reported in *I. elegans* (KRIEGER & KRIEGER-LOIBL, 1958) and *I. verticalis* (Say) (BICK, 1966).

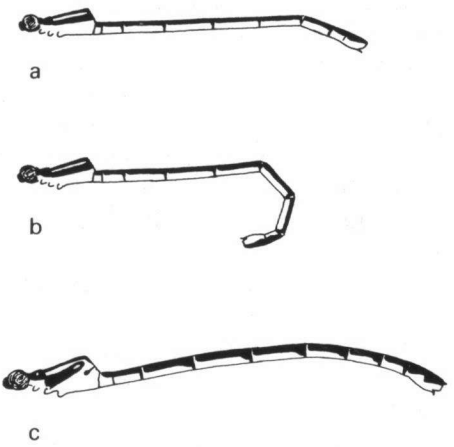


Fig. 3. "Rejection" signals made by (a) mature and inseminated immature females of *Ischnura aurora* (Brauer) when perched or in flight; – (b) flying females of *I. aurora* when closely approached by a male, or during oviposition flights; – (c) *Xanthocnemis zealandica* (McLachl.).

Immature male *I. aurora* leave the vicinity of the water by making short, rapid flights low amongst the vegetation. Each such flight ends in a long motionless wait close to the ground.

In *X. zealandica* males mate with mature females, which are bronzy in colour like *I. aurora* females. The female *X. zealandica* also has a "rejection" signal – a general curving of the abdomen downwards; however, the male *X. zealandica* does not seem to recognise the *I. aurora* "rejection" signal. When approached by an *X. zealandica* male, a female *I. aurora* hovers facing the male and hooks the tip of her abdomen, but on closer approach by the male she flies into any nearby clump of vegetation and there hovers in cover.

MATURATION AND EGG LAYING

Immediately after copulation, female *I. aurora* are still too delicate to be marked for subsequent identification and suffer physical damage if caught. Young females, caught some time after copulation, and then kept in glass vials, took four or five days before they would lay eggs on an artificial substrate. Females judged by their colour shades to be mature laid eggs within one day of capture. Captured immature females have been kept for up to nine days at room temperature (16-20°C) without food. In contrast, mature females taken at the same time and kept under identical conditions rarely survived for more than four days, even when well fed at capture, as evidence by the quantity of faeces found

in their containers.

Female *I. aurora* appear always to lay eggs unaccompanied by a male, which contrasts with the situation in *X. zealandica* where much laying is done in tandem (HUDSON, 1904). In *I. aurora*, flight across pools between ovipositions is usually rapid and low, the abdomen being hooked. Eggs are laid individually in the emergent stems of aquatic vegetation, frequently in the flower stalks of *Potamogeton* spp. both above and below the water level. *I. aurora* females have not been seen to descend below the water surface as *X. zealandica* does (HUDSON, 1904). Thus the laying behaviour of *I. aurora* closely resembles that of *I. elegans* (KRIEGER & KRIEGER-LOIBL, 1958).

DISPERSAL

Dispersal by wind of *Ischnura aurora* is commented on by O'FARRELL (1973) who states that it is found all over South East Asia and the South West Pacific, occurring on oceanic islands and at desert water holes. In New Zealand, solitary females are frequently found 10 km or more from any known breeding site in habitats unsuitable for colonisation. Stokes is reported by PARR (1973) to have found a female *I. elegans* 1.2 km from the nearest breeding site.

DISCUSSION

Ischnura aurora males seize immature Zygoptera of their own and other species near the water's edge, especially in the late afternoon, and attempt to induce copulation. Inseminated females can then disperse, apparently without feeding for several days, and presumably may then colonise suitable habitats that they chance upon. Such a behaviour would appear to have an adaptive value for weakly flying inhabitants of temporary waters. Because insemination occurs before dispersal, every female has the potential to found a colony; thus this pattern provides an operational equivalent, for dispersal purposes, of parthenogenesis. Mating at the emergence site greatly increases the chances of encountering a mate. Similar patterns of mating and dispersal exist in other orders of arthropods. The aberrant New Zealand mosquito *Opifex fuscus* Hutton (Diptera: Culicidae), an inhabitant of isolated brackish pools on rocky shores, mates as the female emerges from her pupal case; males congregate on the water surface and capture pupae when they are ready to emerge, and copulation occurs while the female abdomen is still inside the pupal cuticle (KIRK, 1923). In *Glossina* (Diptera: Glossinidae) mating occurs as soon as the female emerges from her pupation site (NASH, 1969) and MITCHELL (1970) reports mating prior to dispersal in mites.

It is possible that this apparent adaptation to the colonisation of temporary habitats exists only in the Australian and Oceanic populations of *I. aurora*; the

behaviour of the populations with the homochrome female and of the New Guinea subspecies may provide interesting comparisons. Other species of *Ischnura* may show adaptations similar to those of *I. aurora*: PARR (1973) states that *I. elegans* is the only species of dragonfly studied in the British Isles which does not fly away from water to mature. Mated female *I. aurora* at Lake Pupuke, where wind dispersal was uncommon, remained within 3 m of the water's edge while they matured.

There seem to be behavioural similarities between North American, European and Australian species of *Ischnura* (KRIEGER & KRIEGER-LOIBL, 1958; BICK, 1966; PARR, 1973). The descriptions do however differ in detail and a comparative study of behaviour within the genus *Ischnura* may shed light on the evolution of insect behaviours. The differing habitat and ecological requirements of members of this remarkable genus should also prove an interesting study.

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