Odonatologica 12(4): 375-379 *December 1, 1983*

MATING ISOLATION IN TWO SPECIES OF NEHALENNIA (ZYGOPTERA: COENAGRIONIDAE)

D.F.J. HILTON
Department of Biological Sciences, Bishop's University, Lennoxville, Quebec, J1M 1Z7, Canada

Received June 24, 1983 / Accepted August 5, 1983

Two sympatric species of *Nehalennia* breeding in a black spruce-sphagnum bog were effectively isolated from incorrect pairings even though attempts at intermale and interspecific associations were sometimes made. This isolation was probably due to a morphological requirement for the male's anal appendages to mesh with the female's mesostigmal laminae.

INTRODUCTION

Among adult Odonata, vision is considered to be the most highly developed sense and plays an important rôle in feeding and reproductive behaviors such as mating and oviposition (CORBET, 1963). Males of many species are known to rely upon vision for mate discrimination. For instance, *Leucorrhinia dubia* (Vander L.) (Libellulidae) males were able to distinguish conspecific females from those of *L. rubicunda* (L.), apparently solely on the basis of differences in abdominal size, since the body color patterns of both sexes are very similar. In addition, males could distinguish males from females of either species (PAJUNEN, 1964). Sometimes visual discrimination does not prevent occasional instances of interspecies or intermale tandem linkages. BICK & BICK (1981) record all published references to heterospecific pairing and show that greater morphological similarity between individuals results in higher incidences of such pairings. Thus, of the 93 pairs listed, 11 (11.9%) were between members of different families, 21 (22.5%) between different genera and 61 (65.6%) between different species. Similarly, MOORE (1964) determined that interspecific interactions were greatest between species that looked most similar to the human eye. Although interspecific tandem linkages do occasionally occur, copulation wheels are much less frequent, and oviposition by mixed pairs exceedingly rare. BICK & BICK (1981) record only two instances of mixed oviposition, one of which is doubtful. It is thought that mixed pairs do not normally complete the mating sequence because the male's anal appendages cannot properly mesh with the corresponding structures on the head and (or) thorax of the female (CORBET, 1963). For this reason, PAULSON (1974) postulates that mechanical isolation will be more important than visual discrimination in those species with similarly-colored females.

These observations led me to examine the extent to which intermale and interspecific associations occurred between two very similar species of damselflies [*Nehalennia gracilis* Morse and *N. irene* (Hagen)].

Nehalennia is a genus of tiny delicate damselflies which are primarily metallic green above and yellowish below. There are only two species in Canada: *N. gracilis* and *N. irene*. Of the two, *irene* has the widest distribution in eastern Canada and "inhabits almost all still waters that support a stand of emergent vegetation" (WALKER, 1953). In contrast, *gracilis* is restricted to sphagnum-bog ponds and although *irene* can occupy such habitats, it does so in much smaller numbers. Both species are superficially similar in size and color pattern. Diagnostic features used to separate males consist of paired dark spots on the dorsum of otherwise blue abdominal segments 9 and 10 (*irene*) while *gracilis* has these same segments entirely blue. Female *irene* have dark dorsal spots on the blue abdominal segment 10, the hind margin of the pronotum is trilobate and the mesostigmal laminae have strongly reflected hind margins. In contrast, female *gracilis* have segment 10 entirely blue, a bilobate hind margin to the pronotum and mesostigmal laminae without reflected margins. WALKER (1953) provides detailed descriptions and illustrations of each species.

STUDY SITE AND METHODS

This study was carried out in a black spruce-sphagnum (*Picea mariana* *Sphagnum* spp.) bog 13 km SE of Sherbrooke, Québec, Canada 45°20'N, 71°45'W). I have described its odonate fauna (HILTON, 1981; and references therein for vegetation and physiography) and pond topography (HILTON, 1983). The pond is bordered with 1 m high ericaceous shrubs, predominately leatherleaf (*Chamaedaphne calyculata*), which overhang the water's edge. The damselflies fly among, or perch on, the tangled branches and oviposition occurs in water-soaked sphagnum moss at the base of the shrub border.

Observations were made while slowly walking, in a crouched position, once per day around the pond's circumference and through the shrub border. Records were kept of the numbers of solitary individuals of both sexes of each species, tandem pairs, copulatory wheels, or ovipositing pairs. Observations were made on 15/30 days (mean of once every 2 days) beginning 6 July and ending 4 August 1982. The mean starting and finishing times each day were 10.34h (range: 09.30 — 13.45) and 13.01h EST (range: 11.05 — 15.45), respectively. The mean observation period per day was 2 hr 26 min (range: 1 hr, 15 min — 4 hr, 10 min) for a total time of 36 hr, 35 min.

OBSERVATIONS

Solitary individuals totalled 4271, distributed as follows: 3976 (93.1%) *gracilis* [3391 (85.3%) males, 585 (14.7%) females] and 295 (6.9%) *irene* [257 (87.1%) males, 38 (12.9%) females]. This resulted in male:female sex ratios of 5.8:1 and

6.8:1 for *gracilis* and *irene*, respectively. In addition, male and female pairs were engaged in the following reproductive activities: (a) 3491 in tandem [3437 (98.45%) *gracilis*, 52 (1.5%) *irene* and 2 (0.05%) *irene* males with *gracilis* females]; (b) 107 copulating [105 (98.1%) *gracilis* and 2 (1.9%) *irene*]; and (c) 12 ovipositing [9 (75%) *gracilis* and 3 (25%) *irene*]. Combining all reproductive activities, the number of interspecies pairs (2 instances of a male *irene* in tandem with a *gracilis* female) were significantly fewer than expected based upon the numbers of each sex and species ($x^2 = 3607.9$; $p < 0.001$).

A number of other associations were also seen: (a) a *gracilis* male trying to adopt the tandem position with the female of a *gracilis* tandem pair (31); (b) a *gracilis* male trying to adopt the tandem position with the male of a *gracilis* tandem pair (24); (c) a *gracilis* male trying to seize in tandem a solitary *gracilis* male (13); (d) a *gracilis* male perched on the female's thorax of a *gracilis* tandem pair (10); (e) a *gracilis* male perched on the female's thorax of a *gracilis* copulating pair (1); (f) a *gracilis* male perched on the thorax of a solitary *gracilis* male (1); (g) a *gracilis* male trying to seize in tandem a solitary *irene* male (1); (h) an *irene* male perched on the female's thorax of a *gracilis* tandem pair (2); (i) an *irene* male trying to seize in tandem a solitary *gracilis* female (1); (j) an *irene* male trying to seize in tandem the male of a *gracilis* tandem pair (1); (k) an *irene* male trying to seize in tandem a solitary *gracilis* male (1); and (l) an *irene* male trying to seize in tandem the female of an *irene* tandem pair (1). These associations lasted from a few to many sec, the shortest being those where a male was groping with his anal appendages trying to form a tandem linkage with the wrong sex or species. The only exception occurred with a tandem pair of male *gracilis* which stayed together for 2 min.

Frequently a male *gracilis* followed a tandem *gracilis* pair for a short distance and tried to land on the male's or female's thorax when the pair perched. When approached closely like this, the male of the tandem pair performed wing warning (BICK & BICK, 1963) and this usually resulted in the solitary male flying away without attempting tandem formation with either sex. Consequently, the number of triple associations listed above were infrequent occurrences.

DISCUSSION

Although most dragonflies have almost a 1:1 sex ratio at adult emergence (CORBET, 1963), information on damselflies is scanty. JOHNSON (1963) cites studies on *Pyrrhosoma nymphula* (Sulz.) (Coenagrionidae) and *Lestes disjunctus australis* Walker (Lestidae) for which males on emergence comprised 55% and 45%, respectively. In addition, PARR & PALMER (1971) estimated the percent of males in larval populations of *Ischnura elegans* (Vander L.), *Coenagrion puella* (L.) and *Enallagma cyathigerum* (Charp.) (Coenagrionidae) to be 52%, 76% and 50%, respectively. However, emergence sex ratios are soon obscured due to factors differentially affecting the sexes, such as higher female mortality and a tendency for males to congregate at the breeding site (JOHNSON, 1963). This results in a preponderence of males, such as the 65.9%, 81.2% and 90.2% males in populations of *I. elegans, C. puella* and *E. cyathigerum,* respectively (PARR & PALMER, 1971). My data of 85.3% and 87.1% males in the breeding populations of *N. gracilis* and *N. irene,* respectively are similar to these other zygopterans.

Odonates in which one sex far outnumbers the other at the breeding site will be subject to unequal mating expectancies. In the cases cited above, a higher proportion of females than males is likely to mate successfully since so many males are present to compete for available females. Consequently, it may be advantageous for males to approach, and attempt to seize in tandem, any individual that resembles a conspecific female. This would account for the number of intermale, heterospecific and triple associations (or attempts at such) I noted for *Nehalennia* spp. and which have also been recorded for other odonates (e.g. BICK & BICK, 1981; KRIEGER & KRIEGER-LOIBL, 1958; ROWE, 1978). Once tandem linkage is effected it would obviously be advantageous for the sexes to recognize an incorrect association and terminate it as soon as possible so that an eventual correct mating could be achieved. This is especially so for females since they are the active sex in initiating the copulatory wheel position with the male after having been seized in tandem. The most likely mechanism preventing intermale and interspecific associations in morphologically similar species is incompatibility of the male's anal appendages with the female's mesostigmal laminae (or, depending upon the odonate, similar nearby structures used in tandem linkage). This would explain why only 0.05% of *Nehalennia* spp. tandem pairs were heterospecific. Mechanical isolation of this type has been demonstrated for *Enallagma* spp. (ROBERTSON & PATERSON, 1982; TENNESSEN, 1975) and *Ischnura* spp. (KRIEGER & KRIEGER-LOIBL, 1958). There is also the possibility, as suggested by TENNESSEN (1982), that rather than a morphological inability by a male to securely grasp a heterospecific female in tandem, heterospecific pairings are prevented because the female does not respond with the appropriate mating behavior when she perceives incorrect tactile stimuli on her mesostigmal laminae.

REFERENCES

BICK, G.H. & J.C. BICK, 1963. Behavior and population structure of the damselfly Enallagma civile (Hagen) (Odonata: Coenagriidae). *SWest. Nat.* 8: 57-84.

BICK, G.H. & J.C. BICK, 1981. Heterospecific pairing among Odonata. *Odonatologica* 10: 259--270.

CORBET, P.S., 1963. *A biology of dragonflies.* Quadrangle Books, Chicago.

HILTON, D.F.J., 1981. Flight periods of Odonata inhabiting a black spruce-sphagnum bog in south-eastern Quebec, Canada. *Notul. odonatol.* 1: 127-130.

HILTON, D.F.J., 1983. Reproductive behaviour of Cordulia shurtleffi (Anisoptera: Corduliidae). *Odonatologica* 12: 15-23.

JOHNSON, C., 1963. Breeding structure in populations of the Odonata. *Texas J. Sci.* 15: 171-183.

KRIEGER, F. & E. KRIEGER-LOIBL, 1958. Beiträge zum Verhalten von Ischnura elegans und Ischnura pumilio (Odonata). *Z. Tierpsychol.* 15: 82-93.

MOORE, N.W., 1964. Intra- and interspecific competition among dragonflies (Odonata). An account of observations and field experiments on population density control in Dorset, 1954-60. *J. Anim. Ecol.* 33: 49-71.

PAJUNEN, V.I., 1964. Mechanism of sex recognition in Leucorrhinia dubia v.d. Lind., with notes on the reproductive isolation between L. dubia and L. rubicunda L. (Odon., Libellulidae). *Ann. zool. fenn.* 1: 55-71.

PARR, M.J. & M. PALMER, 1971. The sex ratios, mating frequencies and mating expectancies of three coenagriids (Odonata: Zygoptera) in northern England. *Ent. scand.* 2: 191-204.

PAULSON, D.R., 1974. Reproductive isolation in damselflies. *Syst. Zool.* 23: 40-49.

ROBERTSON, H.M. & H.E.H. PATERSON, 1982. Mate recognition and mechanical isolation in Enallagma damselflies (Odonata: Coenagrionidae). *Evolution* 36: 243-250.

ROWE, R.J., 1978. Ischnura aurora (Brauer), a dragonfly with unusual mating behaviour (Zygoptera: Coenagrionidae). *Odonatologica* 7: 375-383.

TENNESSEN, K.J., 1975. Reproductive behaviour and isolation of two sympatric coenagrionid damselflies in Florida. *Diss. Abstr.* (B) 36: 59-61.

TENNESSEN, K.J., 1982. Review of reproductive isolating barriers in Odonata. *Adv. Odonatol.* 1:251-265.

WALKER, E.M., 1953. *The Odonata of Canada and Alaska.* Vol I, Part I: *General.* Part II: *The Zygoptera-Damselflies.* Univ. Toronto Press, Toronto.