

## HETEROSPECIFIC PAIRING AMONG ODONATA\*

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Literature records of naturally occurring heterospecific pairs are summarized on a worldwide basis. The 93 pairs include: 11 between members of different families, 21 between different genera, 61 between different species. In all, 10 families, 34 genera, 124 species are represented. Anisoptera genera with the greatest number of species in the mixed pairs are *Sympetrum* and *Gomphus*; Zygoptera genera are *Lestes* and *Enallagma*. An important factor limiting the number of records of mixed pairs is difficulty in determining the females of many genera. Despite the seemingly numerous records and the taxonomic spread of the mixed pairs (actually only a small proportion of the entire Order), there are only two records of heterospecific pairs ovipositing and two (one very doubtful) of hybrids resulting from observed mixed pairs under natural conditions. The species of Odonata are apparently effectively isolated even though mixed tandems and mixed wheel positions do occur.

### INTRODUCTION

Heterospecific pairings among the Odonata usually are considered to be infrequent. For example, both MOORE (1953) and ASAHIKA (1974) state that pairing between two different species has been recorded only occasionally. Quite differently, our survey of the literature, our own records, and observations of colleagues suggest that mixed pairings are rather widespread. Because of this discrepancy and because the literature records often are hidden among papers dealing primarily with other matters, a summation of all records seems to be appropriate. Also, such a

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summation is needed as background information for current studies of species isolation now underway by others.

## METHODS

In this paper, we record: (1) on a worldwide basis published records of heterospecific pairs, (2) our hitherto unpublished observations, (3) unpublished observations which colleagues have kindly made available to us. We were not able to compare numbers of species recorded in mixed pairs with total number of species on a worldwide basis because of the absence of a worldwide catalogue and because of our lack of knowledge of the odonate fauna of the world. Instead, we compare the number of Nearctic species recorded in heterospecific pairs with the total number of Nearctic species.

Only naturally occurring heterospecific pairs are considered including both ♂-♀ in tandem and ♂-♀ in the wheel position. Mixed pairings in the field resulting from experimental work with models (tethered live individuals, dead ones, or strictly artificial ones), those occurring under laboratory conditions, and ♂-♂ heterospecific tandems are all excluded. Also excluded is the assumption of a mixed pair based on morphological studies of specimens considered to be hybrids (ASAHPNA, 1974).

As recorded in the literature, the exact nature of the pairing often was unclear to us. There are two distinct possibilities: (1) the ♂ grasps the ♀ with his appendages without genitalic contact in a connection now generally referred to as tandem and earlier as per collum, (2) while in tandem, the ♀ abdomen swings upward into the wheel position, the genitalia contacting, in a position variously referred to as copula, coition, coitus, even though it is now clear that sperm need not be transferred from the ♂ to the ♀ throughout the duration of the wheel position (WAAGE, 1979). The literature often does not make clear which of these stages was occurring, and it is particularly unfortunate that terms such as mating, pairing, interbreeding, "struggling to make connection", without further detail, make it difficult to decide if a pair was only in tandem or in the wheel position.

There was no possibility of checking most of the taxonomic determinations. Some of these seem to be based entirely on field identifications, causing us to doubt the accuracy of the identifications of females in certain of the difficult genera. Nevertheless, nomenclature is as originally given except that a few older designations are replaced by current ones when the change is well established. Family considerations are as in FRASER (1957).

## RESULTS

A total of 93 heterospecific pairs is recorded. These are summarized in three tables: Table I shows the 11 (5 Anisoptera, 6 Zygoptera) involving different families, Table II, the 21 (10, 11) mixed genera, and Table III, the 61 pairs (40, 21) involving mixed species. These pairs include (Tab. IV):

Table I

Pairing involving species belonging to different families. The male of each pair is listed at the left. When no notation appears in connection with the reference, it should be understood that the pair was only in tandem

|                                      |  |   |
|--------------------------------------|--|---|
| <b>Aeshnidae</b>                     | <b>Cordulegasteridae</b>               |   |
| <i>Aeshna cyanea</i> (Müll.)         | <i>Cordulegaster boltonii</i> (Don.)   | MÜNCHBERG, 1964                             |
| <i>Anax imperator</i> Leach          | <i>Cordulegaster boltonii</i> (Don.)   | FRASER, 1936, copula                        |
| <b>Aeshnidae</b>                     | <b>Libellulidae</b>                    |   |
| <i>Aeshna cyanea</i> (Müll.)         | <i>Sympetrum striolatum</i> (Charp.)   | MOORE, 1960<br>attempted coition            |
| <i>Brachytron pratense</i> (Müll.)   | <i>Libellula quadrimaculata</i> L.     | MOORE, 1952, 1960;<br>SCHIEMENZ, 1953       |
| <b>Cordulegasteridae</b>             | <b>Corduliidae</b>                     |   |
| <i>Cordulegaster boltonii</i> (Don.) | <i>Somatochlora metallica</i> (v.d.L.) | VOLKER, 1955;<br>MÜNCHBERG, 1964            |
| <b>Protoneuriidae</b>                | <b>Platycnemididae</b>                 |   |
| <i>Elatoneura glauca</i> (Sel.)      | <i>Allocnemis leucosticta</i> Sel.     | PINHEY, 1951;<br>CORBET, 1963               |
| <b>Coenagrionidae</b>                | <b>Lestidae</b>                        |   |
| <i>Argia tibialis</i> (Ramb.)        | <i>Lestes dryas</i> Kirby              | WILLIAMSON, 1919, 1920,<br>attempted copula |
| <b>Lestidae</b>                      | <b>Coenagrionidae</b>                  |   |
| <i>Lestes d. australis</i> Walker    | <i>Enallagma cyathigerum</i> (Charp.)  | SHIFFER, unpubl.                            |
| <i>Lestes viridis</i> v.d.L.         | <i>Erythromma viridulum</i> (Charp.)   | JURZITZA, 1966                              |
| <b>Calopterygidae</b>                | <b>Platycnemididae</b>                 |   |
| <i>Calopteryx splendens</i> (Harr.)  | <i>Platycnemis pennipes</i> (Pall.)    | MOORE, 1953                                 |
| <b>Calopterygidae</b>                | <b>Coenagrionidae</b>                  |   |
| <i>Hetaerina americana</i> (Fabr.)   | <i>Argia plana</i> Calvert             | BICK, unpubl.                               |

10 families (5 Anisoptera, 5 Zygoptera); 34 genera (20, 14); 124 species (74, 50). The number of mixed pairs along with the taxonomic spread, at first impressive and surprising, becomes somewhat less so when it is realized that the species in these mixed pairs form only a small proportion of the entire Order. Also, Table IV shows that rarely is more than half of the species in any Nearctic genus recorded in the mixed pairs.

In the Nearctic region, 27% of the Zygoptera species are included in the

mixed pairs, only 12% of the Anisoptera. This difference is probably related to the greater duration of copula and to the greater frequency of tandem oviposition in the Zygoptera, both of which increase the probability of observation of mixed pairs.

The two Anisoptera genera with the greatest number of species in mixed pairs are *Sympetrum* and *Gomphus* (Tab. IV). The genus *Sympetrum* is interesting for several reasons. One species was involved in a mixed family pair, one in a mixed generic pair, and 12 others in mixed species pairs. In

Table II

Pairing involving species belonging to different genera. The male of each pair is listed at the left except in one case, marked with an s, where the sex is unknown. When no notation appears after a reference, it should be understood that the pair was only in tandem

| <i>Gomphidae</i>                    | <i>Gomphus plagiatus</i> Sel.              |   |
|-------------------------------------|--|---|
| <i>Dromogomphus spinosus</i> (Sel.) |  | WILLIAMSON, 1932;<br>WALKER, 1958   |
| <i>Gomphus crassus</i> Hag.         | <i>Ophiogomphus rupinsulensis</i> (Walsh)  | TENNESSEN, unpubl.  |
| <i>Gomphus plagiatus</i> Sel.       | <i>Dromogomphus armatus</i> Sel.           | WILLIAMSON, 1932, 1934,<br>attempted copula;<br>WALKER, 1958,<br>attempted copula |
| <i>Ophiogomphus carolus</i> Ndhm    | <i>Gomphus lividus</i> Sel.                | TENNESSEN, unpubl.  |
| <i>Aeshnidae</i>                    |  |   |
| <i>Anax imperator</i> Leach         | <i>Aeshna juncea</i> (L.)                  | NEVILLE, 1959, copula;<br>CORBET, 1963, copula                                    |
| <i>Corduliidae</i>                  |  |   |
| <i>Cordulia aenea</i> (L.)          | <i>Somatochlora flavomaculata</i> (v.d.L.) | SCHIEMENZ, 1952, 1953   |
| <i>Libellulidae</i>                 |  |   |
| <i>Diplacodes lefebvrei</i> (Ramb.) | <i>Trithemis arteriosa</i> (Burm.)         | PINHEY, 1970  |
| <i>Leucorrhinia proxima</i> (Caiv.) | <i>Sympetrum pallipes</i> (Hag.)           | BICK & HORNUFF, 1974  |
| <i>Libellula luctuosa</i> Burm.     | <i>Tramea carolina</i> (L.)                | DAVIS, 1898, 1913   |
| <i>Libellula semifasciata</i> Burm. | <i>Celithemis eponina</i> (Dru.)           | SHIFFER, unpubl.  |
| <i>Coenagrionidae</i>               |  |   |
| <i>Argia sedula</i> Hag.            | <i>Enallagma basidens</i> Calv.            | BICK, unpubl.   |
| <i>Coenagrion puella</i> (L.)       | <i>Enallagma cyathigerum</i> (Charp.)      | PARR, 1976, copula  |
| <i>Enallagma basidens</i> Calv.     | <i>Argia apicalis</i> (Say)                | BICK, unpubl.   |
| <i>Enallagma civile</i> (Hag.)      | <i>Argia moesta</i> (Hag.)                 | KELLICOTT, 1895,<br>"heterogeneous union"   |
| <i>Enallagma civile</i> (Hag.)      | <i>Argia vivida</i> Hag.                   | GARRISON, 1979  |
| <i>Enallagma hageni</i> (Walsh)     | <i>Ischnura cervula</i> Sel.               | BICK, unpubl.   |
| <i>Ischnura aurora</i> (Br.)        | <i>Xanthocnemis zealandica</i> (McLach.)   | ROWE, 1978  |
| * <i>Ischnura elegans</i> v.d.L.    | * <i>Coenagrion pulchellum</i> v.d.L.      | BILEK, 1963   |
| <i>Ischnura elegans</i> v.d.L.      | <i>Enallagma cyathigerum</i> (Charp.)      | PARR, 1976, copula  |
| <i>Ischnura perparva</i> Sel.       | <i>Enallagma anna</i> Wmsn                 | BICK, unpubl.   |
| <i>Lestidae</i>                     |  |   |
| <i>Leses sponsa</i> (Hans.)         | <i>Sympetrum paedicea</i> (Br.)            | YAMAMOTO, 1973  |

Europe, *S. sanguineum* males paired with females of three different *Sympetrum* species. In the Nearctic region, 38% of the species of *Sympetrum* are recorded in mixed pairs (Tab. IV). In contrast, in the Nearctic fauna, the number of species of *Gomphus* in the mixed pairs is quite low (12%) compared with the large number of species of *Gomphus* in the fauna.

The two Zygoptera genera with the greatest number of species in the mixed pairs are *Lestes* and *Enallagma*. In the Nearctic region, 44% of the species of *Lestes* and 31% of the species of *Enallagma* are recorded in mixed pairs. One species of *Lestes* was involved in a mixed family pair, one in a mixed generic pair, and nine others in mixed species pairs. In *Enallagma*, one species was involved in a mixed family pair, four in mixed generic ones, and five in mixed species pairs.

Mixed family pairs occurred not only between different families, but also between those considered (FRASER, 1957) to be distantly related. Two of these (Aeshnidae & Libellulidae, Coenagrionidae & Lestidae) involved attempted copula, and in another (Aeshnidae & Cordulegastridae) copula was apparently successful. For the latter, FRASER (1936) emphasized that the ♂ *Anax imperator* "actually copulated with" the ♀ *Cordulegaster boltonii*. In addition, there are three records of copula between different genera (*Anax* & *Aeshna*, *Coenagrion* & *Enallagma*, *Ischnura* & *Enallagma*), and 13 between different species, eight of which belong to the genus *Sympetrum*. Of course, the term copula in the older literature was often used when the pair was only in tandem, and this usage continues at present (YOUNG, 1981). Also, there is no certainty that sperm was transferred from ♂ to ♀ in all of these cases. We now know (WAAGE, 1979) that much time in the wheel position may be taken up by the removal of sperm from a previous mating rather than by transfer of sperm from ♂ to ♀.

Despite the rather large number of heterospecific copulas recorded in the literature, we never saw the actual wheel position or even distinct attempts to reach the wheel in our observations of heterospecific pairs which include one of mixed families, five of mixed genera, and four of mixed species. Moreover, we never noted distinctive behavior among the mixed pairs. This contrasts with TENNESSEN's (1975) observations that all mixed pairs which he observed behaved very erratically and were immediately evident in the field.

It is usually assumed that heterospecific pairing is less probable among species with colorful wing patterns. Tables I-III show that in at least 10 species with colorful wing patterns (*Calopteryx splendens*, *C. aequabilis*, *C. maculata*, *Hetaerina americana*, *Celithemis eponina*, *Libellula lucuosa*, *L. pulchella*, *L. quadrimaculata*, *L. semifasciata*, *Tramea carolina*) species recognition sometimes failed. Moreover, despite elaborate courtship in *Calopteryx*, species recognition is sometimes faulty. Interestingly, mixed

Table III

Pairing involving different species. The male of each pair is listed at the left except in two cases, marked with an s, where the sex is unknown. When no notation appears after a reference, it should be understood that the pair was only in tandem

| <b>Gomphidae</b>  |                                    |  |
|---|------------------------------------|--|
| <i>Gomphus crassus</i> Hag.                                       | <i>G. vastus</i> Walsh             | TENNESSEN, unpubl.   |
| <i>Gomphus exilis</i> Sel.  | <i>G. spicatus</i> (Hag.)          | KORMONDY, 1958   |
| 2 ♂ <i>Gomphus moewanus</i> M.&O.<br>[= <i>Davidius</i> ]         | <i>G. chichibui</i> Fraser ♀       | OKUMURA, 1937, "actually copulating"                                       |
| <i>Gomphus simillimus</i> Sel.                                    | <i>G. vulgatissimus</i> (L.)       | LIEFTINCK, 1965, copula  |
| <i>Ophiogomphus severus</i> Hag.                                  | <i>O. occidentis</i> Hag.          | KENNEDY, 1915, copula;<br>CANNINGS & STUART, 1977, copula                  |
| <i>Trigomphus interruptus</i> Sel.                                | <i>T. ogumai</i> Asahina           | UÉDA, 1977   |
| <b>Aeshnidae</b>  |                                    |  |
| <i>Aeshna canadensis</i> Walker                                   | <i>A. subarctica</i> Walker        | KNOPF, unpubl.   |
| <i>Aeshna cyanea</i> (Müll.)                                      | <i>A. juncea</i> (L.)              | LUCAS, 1895, copula;<br>WESENBERG-LUND, 1913, copula; CORBET, 1963, copula |
| <i>Aeshna juncea</i> (L.)   | <i>A. mixta</i> Latr.              | WESENBERG-LUND, 1913   |
| <i>Aeshna grandis</i> (L.)  | <i>A. viridis</i> (Eversm.)        | WESENBERG-LUND, 1913   |
| <i>Aeshna interrupta</i> Walker                                   | <i>A. canadensis</i> Walker        | WALKER, 1912, copula   |
| <i>Aeshna subarctica</i> Walker                                   | <i>A. canadensis</i> Walker        | WALKER, 1912   |
| <i>Aeshna subarctica</i> Walker                                   | <i>A. juncea</i> (L.)              | SCHIEMENZ, 1953;<br>SCHMIDT, 1964  |
| s <i>Anax junius</i> Dru.   | s <i>A. strenuus</i> Hag.          | PERKINS, 1913;   |
| <i>Anax junius</i> Dru.   | <i>A. walsinghami</i> McLach.      | WILLIAMS, 1936   |
| <i>Boyeria grafiana</i> Wmsn                                      | <i>B. vinoso</i> (Say)             | DUNKLE, 1979, ocular<br>mating marks                                       |
| <i>Corduliidae</i>  |                                    | WALKER, 1958   |
| <i>Epitheca spinigera</i> (Sel.)                                  | <i>E. cynosura</i> (Say)           | KORMONDY, 1959   |
| <i>Somatochlora albicincta</i> (Burm.)                            | <i>S. hudsonica</i> (Hag.)         | WHITEHOUSE, 1941,<br>"struggling to make<br>connection"                    |
| <b>Libellulidae</b>   |                                    |  |
| <i>Leucorrhinia dubia</i> (v.d.L.)                                | <i>L. rubicunda</i> (L.)           | PAJUNEN, 1962  |
| <i>Leucorrhinia glacialis</i> Hag.                                | <i>L. intacta</i> (Hag.)           | DUNKLE, unpubl.  |
| <i>Leucorrhinia hudsonica</i> (Sel.)                              | <i>L. proxima</i> Calv.            | WALKER, 1928, copula;<br>WALKER & CORBET, 1975,<br>copula                  |
| <i>Leucorrhinia rubicunda</i> (L.)                                | <i>L. dubia</i> (v.d.L.)           | SCHIEMENZ, 1953;<br>SCHMIDT, 1964  |
| <i>Libellula auripennis</i> Burm.<br>[as <i>L. jesseana</i> Wmsn] | <i>L. cyanea</i> Fabr.             | WESTFALL, 1942   |
| <i>Libellula auripennis</i> Burm.                                 | <i>L. semifasciata</i> Burm.       | DAVIS, 1913  |
| <i>Libellula flavida</i> Ramb.                                    | <i>L. cyanea</i> Fabr.             | WHITE, unpubl., copula   |
| <i>Libellula pulchella</i> Dru.                                   | <i>L. luctuosa</i> Burm.           | CALVERT, 1893, copula;<br>WILSON, 1920, copula                             |
| <i>Orthetrum albistylum speciosum</i><br>Uhler                    | <i>O. triangulare melania</i> Sel. | ARAI, 1981, attempted<br>copula  |

Table III (continued)

|                                      |                                 |   |
|--------------------------------------|---------------------------------|---|
| <i>Sympetrum danae</i> (Sulz.)       | <i>S. sanguineum</i> (Müll.)    | LONGFIELD, 1952                                   |
| <i>Sympetrum e. eroticum</i> Sel.    | <i>S. darwinianum</i> (Sel.)    | ISHIKAWA, 1981                                    |
| <i>Sympetrum internum</i> Montg.     | <i>S. rubicundulum</i> (Say)    | CARLE, 1978, copula                               |
| <i>Sympetrum kunkeli</i> (Sel.)      | <i>S. darwinianum</i> (Sel.)    | ASAHINA, 1974, copula                             |
| <i>Sympetrum obtrusum</i> (Hag.)     | <i>S. danae</i> (Sulz.)         | WHITEHOUSE, 1941; TAI, 1967                       |
| <i>Sympetrum risi</i> Bart.          | <i>S. infuscatum</i> (Sel.)     | HIROSE, 1977, copula                              |
| <i>Sympetrum rubicundulum</i> (Say)  | <i>S. obtrusum</i> (Hag.)       | TAI, 1967   |
| <i>Sympetrum sanguineum</i> (Müll.)  | <i>S. vulgatum</i> (L.)         | JURZITZA, 1966                                    |
| <i>Sympetrum sanguineum</i> (Müll.)  | <i>S. striolatum</i> (Charp.)   | JURZITZA, 1966, 1978, copula                      |
| <i>Sympetrum sanguineum</i> (Müll.)  | <i>S. flaveolum</i> (L.)        | JURZITZA, 1966                                    |
| <i>Sympetrum striolatum</i> (Charp.) | <i>S. vulgatum</i> (L.)         | JURZITZA, 1966                                    |
| <i>Sympetrum striolatum</i> (Charp.) | <i>S. sanguineum</i> (Müll.)    | JURZITZA, 1966                                    |
| <i>Sympetrum vulgatum</i> (L.)       | <i>S. striolatum</i> (Charp.)   | LUNAU, 1947; SCHIEMENZ, 1953; JURZITZA, 1966      |
| <b>Coenagrionidae</b>                |                                 |   |
| <i>Argia plana</i> Calv.             | <i>A. moesta</i> (Hag.)         | BICK, unpubl., ovipos.                            |
| <i>Argia tibialis</i> (Ramb.)        | <i>A. moesta</i> (Hag.)         | TENNESSEN, unpubl.                                |
| <i>Enallagma aspersum</i> (Hag.)     | <i>E. geminatum</i> Kellicott   | BICK, unpubl.                                     |
| <i>Enallagma civile</i> (Hag.)       | <i>E. carunculatum</i> Morse    | GARMAN, 1917                                      |
| <i>Enallagma pollutum</i> (Hag.)     | <i>E. dubium</i> Root           | TENNESSEN, 1975                                   |
| <i>Enallagma pollutum</i> (Hag.)     | <i>E. signatum</i> (Hag.)       | TENNESSEN, 1975                                   |
| <i>Enallagma signatum</i> (Hag.)     | <i>E. pollutum</i> (Hag.)       | TENNESSEN, 1975                                   |
| <i>Ischnura damula</i> Calv.         | <i>I. demorsa</i> (Hag.)        | JOHNSON, 1975                                     |
| <i>Ischnura demorsa</i> (Hag.)       | <i>I. damula</i> Calv.          | JOHNSON, 1975                                     |
| <i>Pseudagrion rubriceps</i> Sel.    | <i>P. microcephalum</i> (Ramb.) | MITRA & LAHIRI, 1972                              |
| <b>Lestidae</b>                      |                                 |   |
| <i>Lestes barbarus</i> (Fabr.)       | <i>L. viridis</i> v.d.L.        | LOIBL, 1958                                       |
| <i>Lestes disjunctus</i> Sel.        | <i>L. vigilax</i> Hag.          | KELLICOTT, 1895                                   |
| <i>Lestes dryas</i> Kirby            | <i>L. sponsa</i> (Hans.)        | WESENBERG-LUND, 1913, copula; LOIBL, 1958, copula |
| <i>Lestes inaequalis</i> Walsh       | <i>L. d. australis</i> Walker   | SHIFFER, unpubl.                                  |
| <i>Lestes rectangularis</i> Say      | <i>L. congener</i> Hag.         | TENNESSEN, unpubl.                                |
| <i>Lestes rectangularis</i> Say      | <i>L. unguiculatus</i> Hag.     | BICK & HORNUFF, 1965                              |
| <i>Lestes sponsa</i> (Hans.)         | <i>L. temporalis</i> Sel.       | ITO & EDA, 1977                                   |
| <i>Lestes sponsa</i> (Hans.)         | <i>L. viridis</i> v.d.L.        | TIMM, 1906; WESENBERG-LUND, 1913; LOIBL, 1958     |
| <i>Lestes unguiculatus</i> Hag.      | <i>L. dryas</i> Kirby           | BICK, et al., 1977                                |
| * <i>Sympetrum fusca</i> v.d.L.      | s <i>S. paedisca</i> Br.        | BILEK, 1963                                       |
| <b>Calopterygidae</b>                |                                 |   |
| <i>Calopteryx aequabilis</i> (Say)   | <i>C. maculata</i> (Beauv.)     | WAAGE, 1971, 1975, copula & guarding ovipos.      |

pairing has not been recorded for the two U.S. species (*Plathemis lydia* (Drury) and *Perithemis tenera* (Say)) with strongly contrasting wing patterns in the sexes.

There seem to be only two records of heterospecific pairs ovipositing normally in the field. We once observed a ♂ *Argia plana* & ♀ *A. moesta* that seemed to be ovipositing normally, but since this pair had not been constantly observed, there is no way to be certain that these particular individuals had been partners in the immediately preceding copula. WAAGE (1971, 1975) records mixed copula between ♂ *Calopteryx aequabilis* and ♀ *C. maculata* followed by oviposition.

There are two records of progeny resulting from heterospecific pairing in the field. WILSON (1920) captured a ♂ *Libellula pulchella* and ♀ *L. luctuosa* "mating", and the female deposited eggs which yielded a newly hatched nymph considered to be a *pulchella-luctuosa* hybrid. Because of the difficulty of confidently determining the early instars of many libellulids, particularly of the genus *Libellula*, one must wonder about the accuracy of the recognition of a hybrid based only on a second instar *Libellula* larva. ASAHINA (1974) recorded that eggs laid by a ♀ *Sympetrum darwinianum* in tandem with a ♂ *S. kunckeli* yielded adults, all of which were *S. darwinianum*. This seems to be the only record of a next generation adult resulting from a known heterospecific pairing. However, eggs of the female *S. darwinianum* could have been fertilized by conspecific sperm held in the spermatheca from a previous conspecific mating, the heterospecific tandem occurring afterwards.

There are no heterospecific pairs recorded from the diverse Neotropical fauna, very few from the Ethiopian and Australian Regions, but abundant reports from the Nearctic Region. This corresponds to the number of workers and research productivity in these areas. Also, mixed pairs in the Japanese fauna are poorly represented only because of our inadequacy with the language. However, we think that the number of mixed pairs depends more on the taxonomist's ability to accurately determine the female than on the above factors. If all pairs in the world's collections could be studied carefully and if females of all species could be determined confidently, the number of records of heterospecific pairs certainly would increase greatly. Nevertheless, because of the scarcity of hybrids, it is clear that species of Odonata are effectively isolated.

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Table IV

A worldwide list of families, genera and number of species in the heterospecific pairs and a comparison of the number of species in mixed pairs with the total Nearctic fauna

| Taxa                    | No. spp. in<br>heterospecific<br>pairs | Species occurring in Nearctic region |                   |           |
|-------------------------|--|--------------------------------------|-------------------|-----------|
|                         |  | No. spp. in<br>mixed pairs           | Total No.<br>spp. | Percent   |
| <b>ANISOPTERA</b>       |  |                                      |                   |           |
| <b>Gomphidae</b>        | <b>18</b>                              |                                      |                   |           |
| <i>Gomphus</i> (s.l.)   | 10                                     | 6                                    | 52                | 12        |
| <i>Ophiogomphus</i>     | 4                                      | 4                                    | 16                | 25        |
| <i>Dromogomphus</i>     | 2                                      | 2                                    | 3                 | 66        |
| <i>Trigomphus</i>       | 2                                      | 0                                    | 0                 | 0         |
| <b>Aeshnidae</b>        | <b>15</b>                              |                                      |                   |           |
| <i>Aeshna</i>           | 8                                      | 3                                    | 25                | 12        |
| <i>Anax</i>             | 4                                      | 2                                    | 4                 | 50        |
| <i>Boyeria</i>          | 2                                      | 2                                    | 2                 | 100       |
| <i>Brachytron</i>       | 1                                      | 0                                    | 0                 | 0         |
| <b>Cordulegastridae</b> | <b>1</b>                               |                                      |                   |           |
| <i>Cordulegaster</i>    | 1                                      | 0                                    | 7                 | 0         |
| <b>Corduliidae</b>      | <b>7</b>                               |                                      |                   |           |
| <i>Somatochlora</i>     | 4                                      | 2                                    | 24                | 8         |
| <i>Epitheca</i>         | 2                                      | 2                                    | 11                | 18        |
| <i>Cordulia</i>         | 1                                      | 0                                    | 1                 | 0         |
| <b>Libellulidae</b>     | <b>33</b>                              |                                      |                   |           |
| <i>Sympetrum</i>        | 14                                     | 5                                    | 13                | 38        |
| <i>Libellula</i>        | 7                                      | 6                                    | 18                | 33        |
| <i>Leucorrhinia</i>     | 6                                      | 4                                    | 7                 | 57        |
| <i>Celithemis</i>       | 1                                      | 1                                    | 9                 | 11        |
| <i>Diplacodes</i>       | 1                                      | 0                                    | 0                 | 0         |
| <i>Orthetrum</i>        | 2                                      | 0                                    | 0                 | 0         |
| <i>Tramea</i>           | 1                                      | 1                                    | 6                 | 17        |
| <i>Trithemis</i>        | 1                                      | 0                                    | 0                 | 0         |
| Other                   |  |                                      | 134               |           |
| <i>Total Anisoptera</i> | <b>74</b>                              | <b>40</b>                            | <b>332</b>        | <b>12</b> |
| <b>ZYGOPTERA</b>        |  |                                      |                   |           |
| <b>Protoneuridae</b>    | <b>1</b>                               |                                      |                   |           |
| <i>Elatoneura</i>       | 1                                      | 0                                    | 0                 | 0         |
| <b>Platycnemididae</b>  | <b>2</b>                               |                                      |                   |           |
| <i>Allocnemis</i>       | 1                                      | 0                                    | 0                 | 0         |
| <i>Platycnemis</i>      | 1                                      | 0                                    | 0                 | 0         |
| <b>Coenagrionidae</b>   | <b>29</b>                              |                                      |                   |           |
| <i>Enallagma</i>        | 11                                     | 11                                   | 36                | 31        |
| <i>Argia</i>            | 6                                      | 6                                    | 26                | 23        |
| <i>Ischnura</i>         | 6                                      | 4                                    | 13                | 31        |
| <i>Coenagrion</i>       | 2                                      | 0                                    | 3                 | 0         |
| <i>Pseudagrion</i>      | 2                                      | 0                                    | 0                 | 0         |
| <i>Erythromma</i>       | 1                                      | 0                                    | 0                 | 0         |
| <i>Xanthocnemis</i>     | 1                                      | 0                                    | 0                 | 0         |
| <b>Lestidae</b>         | <b>14</b>                              |                                      |                   |           |
| <i>Lestes</i>           | 12                                     | 8                                    | 17                | 59        |
| <i>Sympetrum</i>        | 2                                      | 0                                    | 0                 | 0         |
| <b>Calopterygidae</b>   | <b>4</b>                               |                                      |                   |           |
| <i>Calopteryx</i>       | 3                                      | 2                                    | 5                 | 40        |
| <i>Hetaerina</i>        | 1                                      | 1                                    | 3                 | 33        |
| Other                   |  |                                      | 16                |           |
| <i>Total Zygoptera</i>  | <b>50</b>                              | <b>32</b>                            | <b>119</b>        | <b>27</b> |

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