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BEHAVIOR OF *CHROMAGRION CONDITUM* (HAGEN) ADULTS (ZYGOPTERA: *COENAGRIONIDAE*)*

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The behavior of unpaired males and pairs of *Chromagrion conditum* (Hagen) was studied at Highlands, N.C. between June 18 and July 10, 1975. Population size (maximum 14♂/73m of shoreline) and recoveries (35%♂, 9%♀) of marked individuals were both low. Maximum activity was between 1100 and 1300 hours. Unlike nearly all coenagrionids, unaccompanied males held their wings outspread at an average angle between the front wings of 77 degrees. Male interactions, primarily with *Enallagma hageni* (Walsh), were only 46% successful; the male *conditum* often vacated a perch without defensive activity or turned aside in flight when *hageni* was encountered. Most males cruised for long periods, not always as a result of male interactions and apparently not in search of females. Because of much cruising and little success in interactions, most *conditum* males failed to secure a territory or even a perch favorable for mating. Courtship or display did not occur. Intra male sperm translocation in tandem ($\bar{X}$ = 65 sec) and then copulation ($\bar{X}$ = 36 min) followed seizure of the perched female. After copulation, pairs averaged 67 min in tandem but spent approximately half of this time in exploratory activity. Oviposition was in the typical *Coenagrion* position, the sexes constantly in tandem, the male upright. Neither sex ever completely submerged. Eighty percent of the average 36 min effective oviposition was in *Ludwigia, Gratiola,* and horizontal *Juncus.* Since eggs were deposited at a rate of 5.5/min, a complement of 200 for each sequence would be expected. Eggs hatched after 21 days at ambient temperature of 21°C.

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INTRODUCTION

This study continues our efforts to describe behaviour of representatives of all Nearctic genera of Zygoptera. From June 19 to July 10, 1975, a population of *Chromagrion conditum* (Hagen) was conveniently available at Highlands, North Carolina, and because scarcely any information has been published on the behaviour of this species, we studied activities of unpaired males and pairs even though the population was very small.

Chromagrion, a monotypical genus restricted to eastern North America, is most closely related to the Palaearctic *Erythromma*, and *conditum* was placed therein until 1903 when NEEDHAM erected the genus *Chromagrion* for it. Apart from descriptions and taxonomic placement, information on *conditum* relates almost entirely to habitat (e.g. WILLIAMSON, 1899; WALKER, 1953; KORMONDY, 1958) and to flight season (e.g. MONTGOMERY, 1944; WALKER, 1953; BEATTY et al., 1969; PAULSON & JENNER, 1971; WHITE & MORSE, 1973). Statements on behaviour appear restricted to WALKER (1953) who refers to the *Lestes*-like spread of the wings and to oviposition typical of most coenagrionids, and to NEEDHAM (1903) who states that adults spend little time on the wing.

This investigation was at Lake Ravenel, Highlands Biological Station, Macon County, North Carolina, at approximately 122m elevation. This small (2.4ha), shallow (maximum depth, 2.4m) lake, formed in 1893 by damming the confluence of 3 creeks, is now well stabilized and heavily vegetated. The very irregular shoreline has large areas with typical sphagnum bog conditions at the immediate margin. The bottom is soft and mucky, the acid water usually clear except after rain. This habitat is much like that described by WALKER (1953): "Where a clear rapid brook is dammed to form a small artificial lake in a wooded ravine, *C. conditum* is likely to be found along the margin of the lake, especially where the soil is mucky."

The work was along the neatly mowed 73m length of dam which sloped for 1.2m to water's edge. A 0.6-0.9m zone of weedy terrestrial plants merged with emergent aquatics near the water. The most striking feature of the Lake was *Nymphaea odorata* in full flower, in a 3-4 m zone along the dam and solidly massed at the inlets.

METHODS

All observations were on 18 sunny or partially sunny days in June and July when maximum temperatures never exceeded 25°C. After July 10, the population became too small for further study. This terminal date coincides with PAULSON & JENNER's (1971) limit of the flight season in North Carolina.

Using Testor airplane dope in various color combinations on wings and/or thorax, each of 75 males and 11 females was marked with an individual code readily recognizable in the field without capturing. As in previous studies, we planned to limit observations to these individuals. However, because of the few marked pairs at water, we sometimes watched unmarked ones whenever the three observers were simultaneously free to keep a pair constantly in view. Using stop watch, tape recorder, and cine photography, 20 continuous records of the behaviour of unaccompanied males (Tabs I, II, III) and 14 of reproductive activity (Tabs IV, V) were obtained.

DENSITY AND DIURNAL ACTIVITY

Recoveries of marked individuals were low (35% ♂, 9% ♀), undoubtedly because 3/4 of the Lake, margined with dense shrubs, was almost inaccessible. These low recoveries (Tab. III) contrast with our records (1961, 1963, 1965) for *Lestes disjunctus australis* Walker, *Enallagma civile* (Hagen), and *Argia apicalis* (Say) at smaller and much more sparsely vegetated ponds in Oklahoma. Although a demographic analysis was not attempted because of these low recoveries, the records show that one male, mature when marked, lived for 11 days, was noted at water on seven, but was never seen mating.

Populations of Zygoptera which we previously studied were always larger than those of *conditum* at various localities. At Lake Ravenel, the maximum number of males along the 73 m stretch of shoreline at any one hour was only 14. Populations were also small at several other locations in southwestern North Carolina during June and July, 1975, as well as at northern Michigan in early July, 1974. Likewise, ROBERT (1963) never found *conditum* abundant in Quebec. In contrast, along the same stretch of shoreline at Lake Ravenel, *Enallagma hageni* (Walsh) was always much more abundant, the maximum numbers of males varying between 36 and 72. These large numbers significantly influenced *conditum* behaviour.

Males, females, and pairs were counted hourly between 0900 and 1500 hours E.S.T. on nine days. Only two unaccompanied females were noted and both were seen in tandem shortly afterward. The maximum number of unaccompanied males near noon was 2-14 on different days. Regardless of day to day fluctuations, both males and pairs were consistently most abundant between 1100 and 1300 hours. *E. hageni*, the only other numerous zygopteran at the Lake, was also most abundant at these hours.

BEHAVIOUR OF UNPAIRED MALES

WING POSITION

FRASER (1957) states of *Coenagrionidae*, "All species rest with their wings closely apposed over the dorsum of thorax . . ." *C. conditum* is an exception; males perched with their wings outspread rather than pressed tightly together.

Photographs of *conditum* and *hageni* showed angles between the anterior margins of the fore wings of 74-79 degrees ($\bar{X} = 77, N = 3$) and 19 degrees ($N = 1$) respectively. Photographs of unpaired *conditum* females were not obtained, but one, watched for 6 min prior to seizure, first held her wings outspread as in the male then closed them a little. Regarding the related genus, *Erythromma*, BUCHHOLZ (1950) states that males of *viridulum* (Charp.) frequently keep their wings half open as in lestids. However, among the abundant literature for *najas* (Hansem.), we found no mention of outspread wings, and both ROBERT (1958) and ASAHINA (1973) figure wings tight in the typical coenagrionid position.

FRASER (1957) states of *Lestidae, Lestinae,* "... resting with their wings widely open." Photographs of *Lestes unguiculatus* Hagen in Indiana and *Archilestes grandis* (Rambur) in Oklahoma showed angles between the fore wings of 111-168 degrees ($\bar{X} = 142, N = 3$) and 115-178 degrees ($\bar{X} = 154, N = 7$) respectively. FRASER (1957) also states of *Amphipterygidae*, "In the position of rest, the wings, in some at least, are held wide open (*Diphlebia* and *Philoganga*) as in the Anisoptera." The outspread wing position appears to have developed independently in representatives of three families of Zygoptera.

CRUISING

Early in this study we noted that males often flew low or cruised along the shore for periods longer than required for simply shifting perch or flying to an intruder. To study this behaviour, three observers, on six days between 1026 and 1332, constantly watched marked males for 5-36 min ($\bar{X} = 13$) recording all activity. Among the 18 records of 12 different males (Tab. I), six cruised for more than 36% of the observation periods, one of these for 82%, yet two males did not cruise at all.

Cruising was an important part of the behaviour of most unpaired males, but we cannot account for the variation in cruising time. Percent cruising was not directly related to time of day; at 1140 male F cruised for 82% of the observation period, whereas at 1143 on another day male G cruised for 8%. Percent of cruising could not be correlated with the very variable light conditions. During periods of full and continuous sun, male B-1 cruised 49% of the observation time, male I only 2%. Several males, observed more than once, showed that long or short periods did not characterize any one individual. Twice male A cruised for similar intervals, but male F cruised for 82% on one day, for 2% on another. Percent of cruising was not directly related to the number of all zygopterans at water during any one interval. One day, when 30 zygopterans were present, male D cruised for 52% of one period, 8 min later for 6%. Males cruised for long periods either when few Zygoptera were present (A, H) or when many were present (D-1, F-2).

Table I

Duration of cruising by males relative to time of day, light duration, individual variation, and number of zygopterans at water. (Letters denote individuals, some of which were observed more than once).

Code	Date	Hour	Duration of observation (*min*)	Sunshine (*min*)	Unpaired *conditum* at water	Unpaired *hageni* at water	% time spent in cruising
A-1	VI-21	1026	19	–	0	10	54
A-2	VI-21	1048	22	–	0	10	47
B-1	VI-25	1056	10	10	0	18	49
B-2	VI-24	1110	7	–	1	29	27
B-3	VI-25	1130	10	10	3	38	17
B-4	VI-24	1331	15	1	6	72	7
C	VI-19	1109	36	–	–	–	9
D-1	VI-24	1119	6	–	1	29	52
D-2	VI-24	1127	6	2	1	29	6
E	VI-27	1130	10	10	2	5	36
F-1	VI-24	1139	5	–	1	29	2
F-2	VI-25	1140	10	10	3	38	82
G	VI-26	1143	10	8	3	30	8
H	VI-27	1143	10	8	2	5	40
I	VI-26	1159	10	10	3	30	2
J	VI-26	1243	10	5	4	33	0
L-1	VI-25	1322	10	6	6	44	4
M	VI-25	1332	10	0	6	44	0

INTERACTIONS

While determining duration of cruising, the observers also obtained 20 records of all interactions for 13 different males. The 140 interactions noted in 252 min are summarized in Table II. The frequency of interactions varied among different individuals (0-51/30 min) and in the same individual (2-51/30 min) on different days. Males also differed in success; three won all interactions, five lost all. One male lost all encounters on two days. Regardless of variation, males were generally unsuccessful, winning only 46% of their interactions.

Correlated with the small population were very few intraspecific interactions, only 18 among all 140 encounters (Tab. II). On the other hand, because *hageni* males outnumbered *conditum* by as many as 30 to 1, interactions between them were much more frequent than intraspecific ones.

Four types of interactions were noted (Tab. II). Flight toward and wing warning were as described (BICK & BICK, 1963, 1971) for *civile* and *Argia plana* Calvert with results readily scored as either won or lost. Encounters while cruising were considered as won if the observed male continued along essentially

Table II

Rate per 30 min, number, and success of interactions of unaccompanied males

	Av./male/ 30 min	No. of interactions	Number won	Percent won
Intraspecific				
Flight toward	0.7	6	6	100
Wing warning	0	0	0	0
Cruising interaction	1.2	10	5	50
Avoidance	0.2	2	0	0
	2.1	18	11	
Interspecific				
Flight toward	4.2	35	21	60
Wing warning	3.1	26	23	88
Cruising interaction	1.4	13	9	69
Avoidance	5.7	48	0	0
	14.4	122	53	
Total	*16.5*	*140*	*64*	
Both intra and interspecific				46

Table III

A comparison of percent recovery, number of interactions, and percent of interactions won in six species of Zygoptera

	Percent recovery of		No. of interactions/ male/30 min	Percent interactions won
	Marked ♂♂	*Marked* ♀♀		
*E. civile**	70	27	11.1	84
*A. plana**	72	51	13.7	79
*A. apicalis**	72	40	6.4	87
*L. disjunctus australis**	82	58		
*L. unguiculatus***			33.6	39
C. conditum	35	9	16.5	46

*Adapted from BICK & BICK, 1963, 1968 and 1971, 1965, 1961.
**Adapted from BICK & HORNUFF, 1965.

the same route, as lost if he changed direction. Avoidance, which was a shift or cruise upon the approach of an intruder, was always scored as a loss because it was merely an escape without positive defensive activity. *C. conditum* males won most flights toward, interspecific wing warnings, and half or more of the cruising interactions. Unaccountably, *conditum* did not wing warn conspecific males. This species was notably unsuccessful because of the large number of avoidance or escape flights, all of which were losses. We observed such flights in no species of Zygoptera other than *unguiculatus* in Indiana. Our statement for this species (BICK & BICK, 1965) can be applied as well to *conditum:* "*Enallagma* males, and even the very small *Ischnura verticalis*, not only approached and displaced *unguiculatus*, but also often aggressively pursued them in flight."

The number of interactions per male is not directly related to the percent of encounters won by a species (Tab. III). The number per *conditum* male was similar to the numbers for *civile* and *plana*, greater than the figure for *apicalis*. Yet each of these three species won a higher percentage than *conditum*. On the other hand, the frequency of interactions was twice as great in *unguiculatus* as in *conditum* even though both scored low in percent won.

In summary, the behaviour of the unaccompanied male *conditum* more closely resembled *unguiculatus* than any species for which we have quantitative data. In both, the duration of cruising was long, avoidance flights were frequent, and the percentage of interactions won was small.

TERRITORIALITY

BICK & HORNUFF (1965, 1966) found that *unguiculatus* and *Enallagma aspersum* (Hagen) frequently cruised instead of maintaining territories. When HEYMER (1966) described the distinctive flights of males of *Platycnemis acutipennis* Selys and *P. latipes* Rambur to which females responded, he suggested to us that these species also do not maintain individual territories. Subsequently, BICK (1972) proposed four categories to describe the behaviour of zygopteran males. The fourth group, males which consistently cruise rather than maintain territories, included *Ischnura verticalis* (Say) and *aspersum*, and, we now believe, should have included *unguiculatus*. *Chromagrion* belongs in this category because many males cruised for long periods without securing a territory or even a perch favorable for mating.

HEYMER (1968) showed that males of four species of Anisoptera actively search for females. As evidence of the search, he noted characteristic head movements, distinctive flights, and males seizing females. Among males of species in our fourth category, no such definite evidence of searching was noted, nor did they maintain a perch favourable for mating. Yet, all are successful, *verticalis* remarkably so. Males of these species, unable to long maintain even a perch at sites favorable for mating, of necessity, must move or cruise frequently whenever they are at water. We hypothesize that, if cruising is frequent enough, females could be encountered sufficiently often to maintain populations even without the males actively searching for them, and that neither maintenance of territory nor active searching is an absolute requirement for the success of some species.

REPRODUCTION

An attempt was made to record all reproductive activity by constantly observing pairs from seizure until the sexes separated. However, many pairs were lost because they moved frequently for great distances, often after disturbance by *hageni*. Only after it became evident that the constant attention of three observers was required, did we succeed in obtaining one continuous record complete for all events, two records from sperm translocation until the end, and 11 for at least one event (Tab. IV). The entire reproductive sequence, lasting as long as 150 min, may be divided as follows:

SEIZURE

The female was always perched and apparently motionless near water's edge when each of three seizures was observed. Tandem was achieved very quickly without courtship or display of any kind.

PRE SPERM TRANSLOCATION

In most coenagrionids, intra male sperm translocation quickly follows seizure, but in *conditum* an interval of perching at the same spot often occurred between these events. Twice, when both seizure and sperm translocation were observed, pre sperm translocation (Tab. IV) lasted 6 min, but incomplete pre sperm translocation was longer for three pairs discovered only after seizure.

SPERM TRANSLOCATION

This event was never more than 1.5 m from water, usually 0.3-1 m high in marginal vegetation. Always in tandem, the translocations, exclusive of interruptions, lasted 57-72 sec ($\bar{X} = 65$, N = 6). Four of the events (Tab. IV) were continuous at the same spot; two were interrupted. Once, after 20 sec, a *hageni* male knocked the pair to the ground causing a break of the intra male connection. After 10 min the pair resumed translocation for 45 sec whereupon a *conditum* male knocked the pair to the ground, again causing a break in the intra male connection. A *hageni* male disturbed another pair which had been in sperm translocation for 7 sec, causing a break in the male connection for 1 min; the

Table IV

Hour and duration of reproductive events in 14 pairs. (Sp.tr. = sperm translocation, Cop. = copulation, c = continuous as opposed to interrupted, i = incomplete time record)

Hour	Time of seizure	Pre-sp.tr. (*min*)	Sp.tr. (*sec*)	Pre-cop. (*min*)	Cop. (*min*)	Oviposition/total post copulatory time
1205	1208	6	72(c)	4	37(c)	51/103
1040		16(i)	65	2	35	43/75
1214		8(i)	65(c)	1	24(c)	0/12 (i)
1122				6(i)	36(c)	0/3 (i)
1259						26/31 (i)
1056	1059	6	72(c)	1	29(c)	0/4 (i)
1320						10/37 (i)
1313						23/27 (i)
1215			57(c)	1	40	
1240						22/60 (i)
1123					54	22/49 (i)
1040	1040					
1050		10(i)	57	4	32	28/54
1157					16(i)	24/36
Average			*65*		*36*	*36/67* (complete oviposition only)

connection was resumed for 50 sec and again broken by a *hageni* male. Because copulation and oviposition followed both of these sequences, we consider them successful. These are the first reported instances in Zygoptera of interrupted yet successful sperm translocation.

PRE COPULATION

After sperm translocation were intervals of 1-6 min when most pairs remained at the same spot or shifted small distances so that copulation and sperm translocation were in approximately the same area. During this interval the pair attempted copulatory contact or the female hung motionless.

COPULATION

Contact was almost immediate for five pairs; for three it occurred only after 3-25 forward swings of the female abdomen. In copulation, the female's legs were usually tight against her thorax; the male's wings were more widely spread than when unaccompanied (116-153 degrees, $\bar{X} = 136$, $N = 4$), and the female's wings were always tightly together. A slow, usually weak, pumping of the male abdomen occurred at irregular intervals, yet three males strongly uparched their abdomens just before breaking copula. Near the middle and towards the end of copulation, a male would often "kick" the tip of the female's abdomen with his metathoracic legs.

As in sperm translocation, *hageni* males often disturbed *conditum* pairs in copulation. The average rate was one interaction every 4 min. Occasionally the pair simply shifted perch when a *hageni* male approached, but the most frequent response was wing warning, most often by the male, sometimes by both members. Although usually successful, these warnings sometimes failed, as the following events during one copulatory sequence illustrate. A male *hageni*, first attempting tandem with the female, then contacting the male of the pair, knocked them over into a very abnormal position; later another *hageni* male perched on the female for several minutes even though both members wing warned; subsequently a *hageni* male contacted the vigorously wing warning male of the pair; finally a *hageni* male knocked the pair upside down. These disturbances caused frequent shifting, but surprisingly the pair maintained copulatory contact.

Four copulations were continuous, four interrupted (Tab. IV). The interruptions were always the result of some disturbance including a skipper, the observers, a *hageni* male or a strong gust of wind. Pairs disturbed during copulation did not always break contact but frequently shifted, once as much as 5 m, while maintaining the wheel position. Only pairs which perched close to the ground, well sheltered on the leeward side of terrestrial vegetation, escaped disturbance. Copulatory contact (Tab. IV), exclusive of interruptions, was 24-54 min ($\bar{X} = 36$, N = 8).

POST COPULATION

Exploratory Activity. Records were complete for four pairs from the end of copulation until the sexes separated (Tab. IV). The post copulation interval averaged 67 min, but oviposition was effective for only about half of this interval. For an average of 31 min these pairs frequently shifted, the female seemingly testing for suitable oviposition material by briefly probing almost all material lying horizontally on, or projecting just above, the surface. Such exploratory activity not only followed copulation as in *apicalis* (BICK & BICK, 1965), but also interrupted effective oviposition at irregular intervals.

Effective oviposition. Oviposition was considered effective when a pair probed at the same spot for long rather than brief periods. Twice such oviposition material was examined and eggs were present. Pairs spent 24-51 min ($\bar{X} = 36$, N = 4) in effective oviposition (Tab. IV).

Plants seemingly suitable for oviposition were: *Carex crinita*, *C. scoparia*,

Table V

Minutes spent by 9 pairs in effective oviposition on various substrates
(hor. = horizontal, i = incomplete time record)

Ludwigia	*Juncus* (hor.)	*Gratiola*	*Nymphaea*	*Carex* (hor.)	*Sparganium* (hor.)	Total effective oviposition time
2	17	25			7	51
27	1		7	8		43
	22				4	26 (i)
8	2					10 (i)
	13			10		23 (i)
22						22 (i)
17			5			22 (i)
		21	7			28
24						24
Total 100	*55*	*46*	*19*	*18*	*11*	*249*
% 40	*22*	*18*	*8*	*7*	*4*	

Scirpus expansus, Dulichium arundinaceum, Juncus effusus, Gratiola viscidula, Ludwigia palustris, Sparganium americanum, Nymphaea odorata. Table V shows that of the total effective oviposition time (249 min), 80% was in three plants: *Ludwigia* (40%) and *Gratiola* (18%), extending no more than 5 cm above the surface, and *Juncus* (22%), lying horizontal in the water as a result of our walking. The very abundant, large, mature *Nymphaea* pads were not used; instead, the only effective oviposition in *Nymphaea* (8%) was in soft, new, still rolled up leaves or in well disintegrated old leaves. The female *conditum* selected against the abundant mature *Nymphaea* in favor of *Ludwigia, Gratiola,* and horizontal *Juncus*.

During oviposition, which was always in tandem, pairs assumed the typical *Coenagrion* position. While the female perched, the male usually remained upright, with wings tightly together and motionless, supported only by the female's thorax. Exceptions were two males which briefly leaned forward to perch on plants and two which occasionally beat their wings. Neither male nor female ever completely submerged, although three females very briefly allowed their heads to become wet. A female landed on *Ludwigia* or *Gratiola* usually at or just above the water surface. Here the female began ovipositing with her abdomen well arched, the tip just beneath the surface. Then she slowly extended her abdomen downward until her thorax and wings contacted water. When further submersion seemed necessary, she lifted her abdomen and the pair shifted perch. A comparison of the oviposition behavior of *Chromagrion* and *Erythromma* shows that the *viridulum* female (BUCHHOLZ, 1950), like that of *conditum* never completely submerges. Unlike *conditum*, the *najas* female oviposits both unaccompanied and accompanied, both completely submerged and with head and thorax above the surface (WESENBERG-LUND, 1913; ROBERT, 1958).

The sexes always separated suddenly, without detectable preliminary indication. Quickly afterwards, both sexes flew away from water, usually in several short flights, towards trees and shrubs bordering the dam, and, en route, four of seven females cleaned their abdomens. The departing female left water without pursuit by conspecific males, but each of two *conditum* females warded off a *hageni* male.

On July 3 a pair oviposited constantly for 13 min in a stem of *Gratiola* which was subsequently examined daily in the laboratory to determine incubation period. All 70 eggs were in one side of five internodes, not in the leaves. The eggs were tightly packed just below the water surface in only 32 mm of stem, the maximum distance the female could reach without submerging her thorax. The longitudinal axes of some eggs paralleled the stem; the axes of others formed 45-60 degree angles with the stem. Fifty eggs hatched after 21 days in the laboratory at ambient temperature of about 21°C. Another pair deposited 22 eggs in a horizontal *Sparganium* leaf during a 4 min interval. These eggs, more widely spaced than those in *Gratiola*, were spread along 28 mm of leaf, mostly parallel to the axis. Although kept under the same conditions, these eggs did not hatch after 36 days.

In *Gratiola*, eggs were deposited at a rate of 5.4 per min, in *Sparganium*, 5.5. These rates are greater than those recorded for *unguiculatus* (1.3-2.8/min, BICK & HORNUFF, 1965), for *Coenagrion pulchellum* (Vander Lind) (2-3/min, ROBERT, 1958) and for *grandis* (1.5-4.5/min, BICK & BICK, 1970) but less than the exceptional rate recorded for *Sympecma fusca* (Vander Lind.) (120-180/min, ROBERT, 1958). In *conditum*, the 4 complete episodes of effective oviposition averaged 36.5 min, so that a rate of 5.5 eggs per min would result in an average total complement of 200 oviposited eggs. KENNEDY (1915) records 70-180 eggs for *Archilestes californica* McLachlan, BICK & HORNUFF (1965) 116 for *unguiculatus*, ROBERT (1958) 200-400 for *Lestes viridis* (Vander Lind.) and 413 for *pulchellum*. Apparently species of Zygoptera vary in both rate and total number of eggs deposited in one sequence.

REFERENCES

ASAHINA, S., 1973. Discovery of Erythromma najas in Japan. (Agrionidae). *Tombo* 16: 11-12.

BEATTY, A.F., G.H. BEATTY & H.B. WHITE, 1969. Seasonal distribution of Pennsylvania Odonata. *Proc. Pa. Acad. Sci.* 43: 119-126.

BICK, G.H., 1972. A review of territorial and reproductive behavior in Zygoptera. *Contactbrief Nederlandse Libellenonderzoekers* 1972 (10) (Suppl.): 1-14.

BICK, G.H. & J.C. BICK, 1961. An adult population of Lestes disjunctus australis Walker (Odonata: Lestidae). *SWest. Nat.* 6: 111-137.

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, 1965. Demography and behavior of the damselfly, Argia apicalis (Say) (Odonata: Coenagriidae). *Ecology* 46: 461-472.

BICK, G.H. & J.C. BICK, 1968. Demography of the damselfly, Argia plana Calvert (Odonata: Coenagriidae). *Proc. Ent. Soc. Wash.* 70: 197-203.

BICK, G.H. & J.C. BICK, 1970. Oviposition in Archilestes grandis (Rambur) (Odonata: Lestidae). *Ent. News* 81: 157-163.

BICK, G.H. & J.C. BICK, 1971. Localization, behavior, and spacing of unpaired males of the damselfly, Argia plana Calvert (Odonata: Coenagrionidae). *Proc. Ent. Soc. Wash.* 73: 146-152.

BICK, G.H. & L.E. HORNUFF, 1965. Behavior of the damselfly, Lestes unguiculatus Hagen (Odonata: Lestidae). *Proc. Indiana Acad. Sci.* 75: 110-115.

BICK, G.H. & L.E. HORNUFF, 1966. Reproductive behavior in the damselflies Enallagma aspersum (Hagen) and Enallagma exsulans (Hagen) (Odonata: Coenagriidae). *Proc. Ent. Soc. Wash.* 68: 78-85.

BUCHHOLZ, K.F., 1950. Zur Paarung und Eiablage der Agrioninen (Odonata). *Bonn. Zool. Beitr.* 1: 262-275.

FRASER, F.C., 1957. A reclassification of the order Odonata. *Royal Zool. Soc. N.S.W.*, Sydney. 133 pp.

HEYMER, A., 1966. Etudes comparées du comportement inné de Platycnemis acutipennis Selys 1841 et de Platycnemis latipes Rambur 1842 (Odon. Zygoptera). *Annls Soc. ent. Fr.* (N.S.) 2: 39-73.

HEYMER, A., 1968. Le comportement d'appétence sexuelle chez quelques anisoptères non territoriaux (Odon.). *Annls Soc. ent. Fr.* (N.S.) 4: 891-900.

KENNEDY, C.H., 1915. Notes on the life history and ecology of the dragonflies (Odonata) of Washington and Oregon. *Proc. U.S. Nat. Mus.* 49: 259-345.

KORMONDY, E.J., 1958. Catalogue of the Odonata of Michigan. *Misc. Pubs Mus. Zool. Univ. Mich.* 104: 5-43.

MONTGOMERY, B.E., 1944. The distribution and relative seasonal abundance of the Indiana species of Agrionidae (Odonata: Zygoptera). *Proc. Indiana Acad. Sci.* 53: 179-185.

NEEDHAM, J.G., 1903. Life histories of Odonata. pp. 218-279. *In*: Aquatic Insects in New York State. *N.Y. State Mus. Bull.* 68.

PAULSON, D.R. & C.E. JENNER, 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 52: 96-107.

ROBERT, A., 1963. Les Libellules du Québec. Ministère Tourisme, Chasse, Pêche. Province Québec. *Service Faune Bull.* 1: 223 pp.

ROBERT, P.A., 1958. Les Libellules (Odonates). Delachaux & Niestlé, Neuchâtel. 364 pp.

WALKER, E.M., 1953. The Odonata of Canada and Alaska. Vol. I. Univ. Toronto Press, Toronto. 292 pp.

WILLIAMSON, E.B., 1899. The dragonflies of Indiana. *A. Rep. Indiana Dept. Geol. Nat. Resources* 24: 229-333.

WHITE, H.B. & W.J. MORSE, 1973. Odonata (dragonflies) of New Hampshire: an annotated list. *N.H. Agric. Exp. Stn. Res. Rep.* 30: 46 pp.

WESENBERG-LUND, C., 1913. Odonaten-Studien. *Int. Revue ges. Hydrobiol. Hydrogr.* 6: 155-228, 373-422.