

Behavior of the Damselfly, *Lestes unguiculatus* Hagen (Odonata: Lestidae).

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This work, part of a general study¹ of reproductive behavior in the suborder Zygoptera, adds the genus *Lestes* to our studies on *Enallagma* (2), *Argia* (3), and *Hetaerina* (5), affording a broader ethological basis for phylogenetic considerations. The following notes describe behavior of unpaired males and reproductive behavior in *Lestes unguiculatus* Hagen, a member of the Lestinoidea, a group considered (9) primitive on non-ethological evidence.

Observations were all in the field during June and July in St. Joseph County, Indiana, at a 135 x 144', 1-3' deep bog pond supporting abundant emergent vegetation, primarily *Sagittaria latifolia*, *S. rigida*, and *Sparganium androcladum*. Methods and terminology are essentially as in our studies of *Argia* and *Enallagma*. The primary aim was to describe and time behavior of unpaired males and pairs by constantly observing distinctively marked individuals.

Behavior of Unpaired Males

Hourly counts of marked individuals on five days showed that males were most abundant from 1300 to 1600 hours. Between these hours on various days, we constantly observed and recorded all activity of each of 12 marked males for a 20-minute interval. The 554 events tallied during the 240-minute total provided scarcely any evidence of territorial behavior.

The most frequent event was a shift of perch site for no detectable reason, averaging 21 per individual (Table 1) or approximately one shift each minute. When a male reached a perch, he occupied it only momentarily; when he shifted, it was usually for more than 3 feet, so that during one 20-minute episode a male usually moved around an entire margin of the pond. This frequent shifting gave the impression of consistent and random cruising among or just above the vegetation. In contrast, *Argia apicalis* (3), a species which successfully defended territory, seldom shifted perch, but frequently, and for no detectable reason, darted out from and quickly returned to the same perch in a maneuver considered effective in maintaining territory.

When other Zygoptera approached, *unguiculatus* males seldom (Table 1) reacted, and as a result were displaced an average of once every 2 minutes. *Enallagma* males, and even the very small *Ischnura verticalis*, not only approached and displaced *unguiculatus*, but also often aggressively pursued them in flight. On the other hand, an aggressive species such as *apicalis* (3), always reacted to other Zygoptera and was seldom

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TABLE 1
Total activity of 12 different unpaired males, each observed
constantly for a 20-minute interval.

Activity	Number of events	Average per individual	Per cent won
No reaction, displacement	163	13.6	24
Wing-warning	54	4.5	89
Flight toward	49	4.1	33
Contact	3	0.2	0
			39
Shift, no reason	252	21.0	—
Feeding flights	8	0.7	—
Flight, no reason	13	1.7	—
Grooming	12	1.0	—
	554	46.1	

displaced. Although *unguiculatus* males wing-warned (2) and flew toward intruders, these events were infrequent and unsuccessful with one exception. Males of *unguiculatus* "won" (2) only 39% (Table 1) of all encounters, *apicalis* 87% (3). Because of this striking lack of aggressive behavior, *unguiculatus* males failed to maintain territory, even a single stem.

Loibl (11) states that *Lestes* males flew toward and attempted tandem with any passing Zygoptera. Quite differently, *unguiculatus* usually retreated when any Zygoptera approached. On the few occasions when *unguiculatus* males advanced toward other males, we never noted attempted intra or interspecific tandem.

Reproduction

Between 1330 and 1500, the hours of maximum reproductive activity, we studied 29 pairs. Eleven (Table 2) were observed constantly and timed during at least one reproductive phase, and one of these pairs was followed constantly throughout all phases.

Because the already abundant males immediately seized arriving females, unpaired females were rare at water. So, attempting to observe seizure and then to follow the entire reproductive process, we gave careful attention to the only unpaired female encountered during the season which had not mated earlier in the day. For 17 minutes she perched motionless on *Sparganium* over water. Suddenly, without signals or display of any kind, a male flew to her and instantly achieved tandem. There was clearly no courtship, display, or signals by either member. Experiments with models further demonstrated that activity of the female was not required to bring the sexes together. In 17 different trials, each of 12 males flew directly to and made tandem with a dead female, pinned to a stick and held motionless before him.

Courtship and territorial behavior have been considered (6, 8, 10) characteristic of recent groups. If correct, *unguilatus* appears to be primitive, because territorial activity was very poorly developed and courtship entirely absent in our population. Moreover, the present observations, combined with those on *Lestes disjunctus australis* (1), suggest on ethological evidence a primitive position for the entire genus.

Sperm transfer was always in tandem, as in some other Lestidae (4, 11), and probably in the entire suborder (4). In *unguiculatus*, the event, averaging 29 seconds, was over water or damp mud, between 1307 and 1530, as pairs perched 5-18 inches high on *Sparganium* or *Sagittaria*. Attempts to copulate followed immediately after each sperm transfer at the same perch.

Copulation was never a continuous process; each pair momentarily broke contact at intervals. Once, for example, contact lasted 3, 8, 4, 1, 4, and 7 minutes. Exclusive of the momentary interruptions, copulation averaged 25 minutes (Table 2). Nielsen (in 8) reports only 6 minutes

TABLE 2
Duration of reproductive activity in 11 pairs. For the first, timing was continuous for all events; for the others timing was complete for one or more events, incomplete (inc.) or missing (—) for other events.

Sperm Transfer (seconds)	Copulation (minutes)	Exploration in tandem (minutes)	Oviposition tandem (minutes)	Oviposition alone (minutes)
21	27	25	117	none
—	inc.	21	116	17
—	inc.	42	89	none
—	inc.	26	90	none
34	23	inc.		
—	24	inc.		
—	26	inc.		
21	inc.			
25	inc.			
34	inc.			
38	inc.			
21-38	23-27	21-42	75-117	
28.8	25.0	28.5	99.0	

in copula for *Lestes barbarus*, but we believe this was only one phase of an interrupted sequence. Loibl (11) gives 21-36 minutes of copulatory contact for *L. viridis*, 26-47 for *sponsa*, and 47-75 for *dryas*.

Seven pairs copulated over water or damp mud while perched on *Sparganium*, whereas four were 10-25 feet from water on terrestrial weeds. Regardless of initial site, pairs usually shifted during this period, breaking copulatory contact as they moved. During copulation, the male

abdomen pumped slowly (12/minute) and intermittently, the female's legs clasped her abdomen, and the male's metathoracic legs often contacted (3) the female abdomen in a kicking motion just prior to termination.

Immediately after copulation, pairs shifted frequently from one leaf or stem to another, one pair 106 times in 42 minutes. Since the female probed each stem very briefly, we believe that few eggs were deposited at this time and designate this activity, which averaged 28 minutes (Table 2), as exploratory. After exploration, pairs seldom shifted and settled at some small area for an average of 99 minutes of oviposition in tandem.

Unlike *Ischnura verticalis*, *Enallagma aspersum*, *E. civile*, and *E. ebrium*, which at this pond oviposited at or below the water surface, 10 of 13 *unguiculatus* pairs laid eggs in vegetation over damp mud or dry soil, usually 7-12" above the surface. Even though two pairs laid eggs over water, and one completely submerged for 30 seconds, all oviposition sites became dry as the season advanced and the water level receded.

Sparganium stems near the white flowering heads were utilized for 78% of the total oviposition time; three pairs (Table 2) oviposited here constantly for 90, 116, and 117 minutes; and six of nine pairs observed for a part of oviposition used this material. *Sparganium* flower stems seemed to have been selected because *Sagittaria* and leaves of *Sparganium* were abundant but were never utilized. Pairs often shifted rapidly among such vegetation, yet when they perched near the white flowering heads of *Sparganium* the female quickly began prolonged oviposition.

Our pairs were widely spaced around the pond, never close together at the same stem as Walker (13) reports for *unguiculatus*, or clumped at a few communal sites as we (3) record for *Argia apicalis*. The abundance of *Sparganium* relative to the size of our population obviated the necessity for crowding at the oviposition sites. Crowding is apparently not species specific, but characteristic of the particular ecological situation.

When ovipositing pairs perched near the surface among dense vegetation, other Zygoptera seldom disturbed them, and some pairs spent long periods without defense activity of any kind. However, most maintained a stem when intruders did approach. A 207-minute record of all activity of two pairs showed that both held a stem almost entirely by wing-warning. In spite of the warnings, each of five males momentarily grasped an ovipositing female without achieving tandem or displacing the mate.

During oviposition, both sexes were always vertical in the typical (7) *Lestes* position. The female, constantly in the egg laying position, moved very slowly backwards down the stem pulling the male along as she advanced.

One female laid a complete clutch of 116 eggs in a very slender terrestrial grass stem during 89 minutes of uninterrupted oviposition. Another female laid 173 eggs in a *Sparganium* flowering stem during 68 minutes, but this was not a complete clutch since we were unable to count the eggs subsequently deposited in a brief interval at another stem.

The slower rate of deposition in the grass (1.3/minute) than in *Sparganium* (2.8/minute) seems due to the more abundant vascular and supporting tissue in the grass.

Unlike Robert's (12) figures of other *Lestes* species, egg scars of *unguiculatus* were not elevated above the plant epidermis and were very close together, appearing to the unaided eye as a continuous straight line. A black, scarcely elevated flap of cells covered each egg, lying at an angle of 45 degrees, about 1 mm beneath the surface, and with its more pointed pole outermost.

We noted a male *Lestes rectangularis* in tandem with a marked female *unguiculatus* without seeing sperm transfer or copulation, but the female was in the egg laying position for 3 minutes. The male "bit" (2) the female twice, whereupon the pair flew off and was lost for 25 minutes. We then located and collected the pair, still in tandem and the female still in the egg laying position. Mixed pairs are not unusual among European *Lestes*; Loibl (11) records many, both in the field and in laboratory cages.

Summary

Behavior of distinctively marked unpaired males and pairs were studied under field conditions. Territorial behavior was poorly developed and courtship entirely absent, giving ethological support to the primitive position of the Lestinoidea. Sperm transfer averaged 29 seconds, copulation 25 minutes, exploration 28 minutes, and effective oviposition 99 minutes. Sperm transfer was in tandem, with copulation immediately following at the same site; thereafter pairs shifted widely, eventually settling for prolonged egg laying at one site which was usually a stem of *Sparganium* near a white flowering head. The complete clutch of eggs for one female was 116 in 89 minutes of uninterrupted oviposition.

Literature Cited

1. BICK, G. H., and J. C. BICK. 1961. An adult population of *Lestes disjunctus australis* Walker (Odonata: Lestidae). *Southwestern Naturalist*. 6:111-137.
2. ———, ———. 1963. Behavior and population structure of the damselfly, *Enallagma civile* (Hagen) (Odonata: Coenagriidae). *Southwestern Naturalist*. 8:57-84.
3. ———, ———. 1965. Demography and behavior of the damselfly, *Argia apicalis* (Say) (Odonata: Coenagriidae). *Ecology*. 46:461-472.
4. ———, ———. 1965. Sperm transfer in damselflies (Odonata: Zygoptera). *Ann. Ent. Soc. Amer.* 58:592.
5. ———, and D. SULZBACH. 1965. Reproductive behavior of the damselfly, *Hetaerina americana* (Fabricius) (Odonata: Calopterygidae). *Animal Behaviour* (In Press).
6. BUCHHOLTZ, C. 1955. Eine vergleichende ethologie der orientalischen Calopterygiden (Odonata) als beitrage zu ihrer systematischen deutung. *Z. Tierpsychol.* 12:364-386.
7. BUCHHOLTZ, K. F. 1950. Zur paarung und eiablage der Argioninen (Odonata). *Bonner Zool. Beitr.* 2-4:262-275.
8. CORBET, P. S. 1963. A biology of dragonflies. *Quadrangle Books*, Chicago. 247 p.

9. FRASER, F. C. 1957. A reclassification of the order Odonata. Royal Zool. Soc. N.S.W. Handbook 12, 133 p.
10. JOHNSON, C. 1962. Reproductive isolation in damselflies and dragonflies (Order Odonata). Texas Jour. Sci. 14:297-304.
11. LOIBL, E. 1958. Zur ethologie und biologie der deutschen Lestiden (Odonata). Z. Tierpsychol. 15:54-81.
12. ROBERT, P. A. 1958. Les Libellules (Odonates). Delachaux and Niestle, Neuchatel. 364 p.
13. WALKER, E. M. 1953. The Odonata of Canada and Alaska. Vol. 1, Univ. Toronto Press. 292 p.