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# THE REPRODUCTIVE BEHAVIOUR IN *COENAGRION LINDENI* (SELYS) IN CENTRAL ITALY (ZYGOPTERA: COENAGRIONIDAE)

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The reproductive ethogram of *C. lindeni* is described. Males may show territorial as well as non-territorial behaviour. The tandem position may be assumed either with the female in flight or when perched. One or both members in tandem may display to approaching individuals; a magnification of the warning signal is supposed to result from both members of a pair displaying at the same time. Intra-male sperm translocation occurred while the tandem pairs were perched and preceded copulation. It is suggested that cooperation of the female in the successful forming of the wheel may be caused by a reflex response to the stimulation of her prothorax by the male cerci. Exceptionally a female will copulate twice a day. Surface oviposition is chiefly performed in tandem, seldom by unaccompanied females. If the female tends to complete submersion, the male will drag her out of water and shift to another site. In some circumstances, however, he loses his grip on the female prothorax, leading to the female continuing underwater oviposition alone. Occasionally an emerging female is seized again by her previous mate.

## INTRODUCTION

The present study is chiefly based on 79 hours of observation carried out on 12 days between the 8th and 27th of June, 1972 and on 9 days between May 23rd and August 7th, 1979, by one to four observers, at a permanent pool of 25x16 m in Castel Porziano (Roma). Additional data were also gathered by one or two observers at a small lake of about 100x70 m near Percile (Roma), during 29 hours on 6 days between July 19th and August 8 th, 1979. Besides these two biotopes, data from scattered observations at other localities and on other dates were also collected and herein included.

## METHODS

Direct observation in the field was the chief method employed, but binoculars were also used. The insects were individually marked with enamel paints, according to CONSIGLIO, ARGANO & BOITANI's (1974) method. Timing was effected with a stop-watch only in 1979. Cards arranged in advance were utilized in the field to record events such as seizure in tandem, intra-male sperm translocation, copula, oviposition and threat displays. Some events were also recorded on colour slides. All observed behavioural activities were noted and described in notebooks or with tape-recorders. The recorded times in this paper are given by reference to Central European Time.

Some specimens from the populations studied are preserved in the entomological collection of the Istituto di Zoologia dell'Università di Roma.

## RECOVERY OF MARKED INDIVIDUALS

Of 66 males and 44 females individually marked when mature, 28 males (42.4%) and 10 females (22.7%) were recovered in successive days. These rates are a little lower than those of other coenagrionids, such as *Enallagma civile* (BICK & BICK, 1963) and *Argia plana* (BICK & BICK, 1968), but higher than those of *Chromagrion conditum* (BICK, BICK & HORNUFF, 1976). Furthermore, the mean recovery ratio ( males + females, 34.5%) is higher than that obtained by BORROR (1934) for *Argia moesta.*

The recovery ratio for the two years differs greatly for males (92.8% in 1972; 28.8% in 1979) but not for females (23.1% in 1972; 22.6% in 1979).

As with other Odonata, the lower recovery rate of the females might confirm the greater tendency of females to disperse (MOORE, 1954; BICK & BICK, 1968).

Only one female, marked just after emerging, on June 17th, 1972, gives us an indication on the length of the maturational period, having been recorded ovipositing on June 21st.

## BEHAVIOUR OF SINGLE MALES

### TIME OF PRESENCE AT WATER

Even though reproductive activity was performed mainly during the warmer hours of the day, i.e. 1100 to 1400, a few males were observed at water as early as 0730, with either clear or cloudy skies. The latest time at which individuals were observed near water was 1645.

### POSTURE OF THE BODY

Mature males rest with their body axis near a horizontal line, sometimes slightly angled downwards or upwards, whatever the slant of their perch, and keep their wings folded along the abdomen. Some not very active males keep their body axis lower than the others.

## TERRITORIAL BEHAVIOUR

A number of males perched on reeds or other emerging stems situated from few cm to 2.5 m from the shore towards the centre of the pool. These males made quick straight flights towards individuals of the same or other species (*Coenagrion scitulum, C. puella, Anax imperator*) when these passed 1 to 1.5 m from their perches. If the intruder was a male, it was generally displaced after a short fight, which usually did not lead to physical contact. Males could also perform flights towards intruders while returning after a previous attack.

As these males succeeded in making an area around their perch free from invaders, by means of attack flights, we identify their behaviour with territorial behaviour, according with NOBLE's (1939) definition of the territory as any defended area. In accordance with this, we will refer to these males as territorial males and to the areas they would defend as territories.

The larger dragonflies, as a rule, were not disturbed by the attacks of the territorial males. If the intruder was a conspecific female, seizure generally followed immediately.

Territorial males would also perform quick straight flights even in absence of intruders, over a distance generally not exceeding 1 m from their perch. A similar behaviour has been recorded also for *Enallagma civile, Argia apicalis* and *A. plana* (BICK & BICK, 1963; 1965a; 1971), and these authors hypothesize that these "flights no reason" may be regarded as patrol flights over the territory. We think that an increasing non-satisfied internal drive to attack might explain these flights.

After an attack flight or a "flight no reason" a male would usually return to his previous perch, or another one few cm away. However, ties between a male and any particular area were not rigid. As a rule, a male would change its territorial area one or more times in the same day, sometimes also retreating from the shadow of trees arriving on their previous perch. Male N4, on 16.6. 1972, took the same perch from 0900 to 1200, (timings based on oversights of half-hour interval), then shifted to an adjacent area where it performed territorial activities from 1200 to 1300, and then left the water. On the same date, male N12 was on a perch from 1000 to 1100, then was not recorded at water for an hour, was recorded from 1200 to 1430 at another site not adjacent to the previous one, was at the third site at 1500, and at 1530 was on the vegetation of the surroundings, while not performing any territorial activity. A third male, N15, defended a certain area from 0900 to 1130, and from 1300 to 1530 was defending another one adjacent to the first. This male was not recorded at the pond in the interval. Other males were recorded shifting from perch to perch more frequently.

The boundaries of the territories did not seem to be topographically limited, but they appeared to be based on the maximum range of the flights performed by the resident males. Since these flights were made only over the water, the shore line could be considered a territory border for those males that were perching near the shore.

The distance between two neighbouring males was often the same as the attack distance, i.e. 1 to 1.5 m. Two perched territorial males could tolerate each other at this distance, and interactions between them would generally occur when one of them would take flight. Intruders that had succeeded in perching within a territory either because the resident male was momentarily absent or because he had failed to drive them away, were tolerated even within a distance of few cm. We recorded up to four males perched within a distance of 20 cm from the perch of a territorial male. In such rather rare occasions, the owner of the territory would attack individuals passing nearby, but the perched intruders were ignored, except for some approach flights that the owner would perform towards them while recovering from attacks. Nevertheless, a male with wet wings, put by us on the perch of a territorial male momentarily absent, was disturbed insistently and finally displaced by the owner of the perch when he returned.

Perched males that do not attack an intruder, may perform a threat display as the intruder approaches. This consists of opening, and sometimes slightly and briefly fluttering, the four wings, and often in raising the entire body axis up to a horizontal position or even more, pushing with the legs against their perch. Generally the amount the body is raised, and the time the display posture is held, depend on distance and persistence of the approaching individuals.

A wing display similar to this has been described in many Zygoptera of both sexes ("wing warning" of BICK & BICK, 1963; cf. also PAJUNEN, 1963 and BICK, 1966). In *C. lindeni* males, this display may be accompanied by the bending of the 9th and 10th urites downwards at a right angle, so that the blue dorsal spot on these segments is also displayed. An abdomen-tip display of this kind is also performed by *Ischnura elegans* (KRIEGER & KRIEGER-LOIBL, 1958). The 9th and 10th urites can also be displayed while in flight, as in *Ceriagrion melanurum* (AOYANAGI, 1973) and in *C. tenellum* (UTZERI, unpublished). In this case the tip of the abdomen was bent down during an attack flight, and was also sometimes kept in this position during the recovery flight. As in *C. melanurum* (AOYANAGI, 1973), in *C. lindeni* males the bending of the abdomen in flight has been recorded only in intraspecific encounters, but perched individuals would display their abdomen tip also towards non-conspecific males (Tab. IV).

Thus, based on our observations, *C. lindeni* seems to meet the requirements stated by KORMONDY (1961) for territoriality, via spacing of mature males within the reproductive habitat, fights for territory, superiority of the resident males within their territory and performance of displays, in this respect resembling *Argia plana* (BICK & BICK, 1971).

BICK & BICK (1971) stated that one of the main advantages of territoriality in

*A. plana* is that, in reaching the water, females fly lower, and therefore the territorial males, that perch near the shore, can seize them before those males that are excluded from the peripheral zone of the pond. We think that in *C. lindeni* territoriality performs a similar function.

## NON-TERRITORIAL BEHAVIOUR

In 1972, when the population studied was most consistent, many males could be seen on the open water, and an attempt was made to classify them in the following three groups:

(1) Perchers perched all the time on floating vegetation (*Potamogeton, Nitella*), keeping their abdomen almost parallel to the water and their wings folded. They showed little activity, and some were seen feeding after short flights. It was not discovered if these males were keeping the same perch all the time or if they would shift from time to time. Nevertheless, one of them, momentarily displaced to another perch by an ovipositing tandem, regained his previous position as soon as the tandem left. Only in one case, due to disturbance, was one of these males seen aggressively interacting with a tandem pair.

(2) Hoverers performed a stationary flight for a long time. No other activity was recorded, and they were not disturbed by other males.

(3) Flyers kept continuously in flight without rest, chasing one another similarly to the attack flights of the territorial males. Due to the equal aggressiveness of the opponents, violent clashes could occur, leading on one occasion to both opponents falling into the water. However, these males did not disturb those of the preceding groups.

Two marked males, previously recorded one as a "flyer" and the other as a "hoverer", were later labelled as "perchers" on the same or the following day, and some territorial activity (i.e. flights towards passing individuals) was also performed by them. Also, a territorial male was recorded as spending most of its time in flight on a later occasion, but the few data we could gather concerning these changes in behaviour did not permit us to discover if there was a regular interchange among the males of the four behavioural groups nor what was causing a male to change his behaviour.

In conclusion, it can be assessed that, contrary to indications of BUCHHOLZ (1950), SCHIEMENZ (1953) and HEYMER (1973a), at the pond of Castel Porziano where this study was chiefly performed, *C.lindeni* was active either near the shore (territorial males), or above the free water (perched and flying males).

## BEHAVIOUR OF SINGLE FEMALES

Few single females could be observed at water, due to the fact that they were generally seized in tandem as soon as they appeared at the pond.

Perched females usually keep their body lower than males.

Sexually unreceptive perched females perform a refusal display by opening or fluttering the wings, and their body axis can also be raised, in a way resembling the male threat display. Females can also slightly open their wings and curve the raised abdomen downwards, as is described for *Ischnura elegans* (KRIEGER & KRIEGER-LOIBL, 1958), *Ischnura verticalis* (BICK, 1966), *Argia plana* (BICK & BICK, 1972), *Ceriagrion melanurum* (AOYANAGI, 1973) and *Xanthocnemis zealandica* (CRUMPTON, 1975). A female whose wings we wetted, and who was momentarily unable to fly, succeeded in warding off all the ten conspecific and non-conspecific males that had approached her during a few minutes by this form of display. Another wet-winged female performed a refusal display by opening the wings and curving her abdomen upwards. This behaviour was also recorded in a male that also had his wings wetted by us, but we think that this does not occur in nature. Rather, in our opinion, this pattern might be regarded as a combination of the normal refusal (or threat) display with the "abdominal bobbing" (cf. below), the wetted wings possibly inducing an abnormal sensation to the insects.

The ventral curving of the raised abdomen is also performed while in flight, as in *Ischnura aurora* (ROWE, 1978) and *Xanthocnemis zealandica* (CRUMPTON, 1975). In addition, *C. lindeni* females may perform a zig-zag flight in accordance to the pattern described for *Enallagma civile* (BICK & BICK, 1963) and *E. aspersum* (BICK & HORNUFF, 1966). A female, while escaping from a number of *C. scitulum* males with a flight of this type, allowed a conspecific male to capture her in tandem, thus giving us an opportunity to hypothesize that at least females of *C. lindeni* are capable of recognizing to some degree the males of their own species from the others. On one occasion, a zig-zag flight was recorded as a result of the approach of conspecific males. The female in question, coming from her last ovipisition site, was not curving her abdomen, and quickly flew off from the pond. Possibly, females curve their abdomen during an escaping flight only if driven by reproductive motivation; in this case, this behaviour might originate from the oviposition posture, as CORBET (1962) suggests in relation to *Anax imperator* females. Nevertheless, the evidence of any ritualization process in this behaviour is lacking, females avoiding capture rather by means of escaping flights than by abdomen curving. In other words, it is not clear if the curved abdomen itself may act as a signal warding off the pursuing males.

## ABDOMINAL BOBBING

This behaviour has been recorded by us in single males as well as in females. As a rule, it is performed with the abdomen curved upwards during the raising phase and downwards during the lowering one. Yet, in rare cases the bobbed abdomen was recorded being bent between the 2nd and the 3rd segments, with 3rd to 10th urites kept quite straight (2 records, Fig. 1).

The abdominal bobbing was recorded in unhandled as well as in handled individuals (handled individuals are those that had been marked or had their wings wetted to restrict their movements). The opinion that at least in the Coenagrionidae and Lestidae the abdominal bobbing may have the function of cleaning the wings (LOIBL, 1958; BICK & BICK, 1971; HEYMER, 1972; 1973b) is supported also by our observation that the raised and/or lowered abdomen may contact the wings. Nevertheless, in several cases we recorded no contact between wings and abdomen during the whole bobbing period (cf. also CRUMPTON, 1975, for *Austrolestes colensonis*). We think that a possible function of this behaviour as a territorial display, as was stated by HEYMER (1972; 1973b) for the Calopterygidae, may be excluded for *C. lindeni*, since the abdominal bobbing was also performed by females and by males that were perching far from the places where the territorial activity was performed. We think that this behaviour may not only be related to cleaning of the wings, but sometimes also, to loosening up the abdomen.

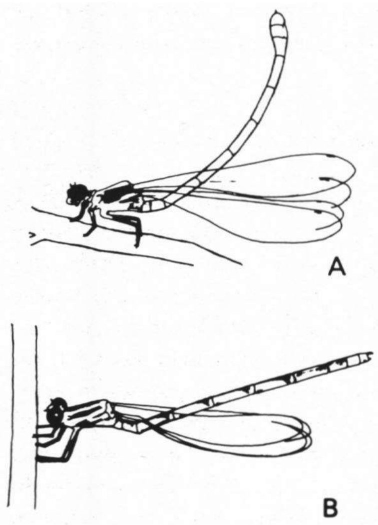

Fig. 1. Abdominal bobbing in *Coenagrion lindeni*. A, normal pattern; B, straight-abdomen pattern. (From slides).

## TANDEM SEIZURE

When mature females arrived at the pond, they were generally receptive to males. They flew straight and uniformly above the water, where they were seized in a short time. Nevertheless we recorded a female that, having avoided capture by some *C. scitulum* males during her flight over the pond, rested on a perch within a territory, where she performed the refusal display to the territorial male that had immediately approached her, and then she left the pond without being seized. Yet, females not taken in tandem while in flight can also be captured by males while perched. Of 14 recorded seizures of non-mated females, 9 were performed in flight and 5 while the female was perching. This indicates that the flight of the female is not necessary for proper sexual stimulation of the male.

The earliest seizure was recorded at 0753.

In no case was the seizure in tandem preceded by courtship behaviour of one or both individuals.

As soon as the tandem position had been attained, the pair flew to the vegetation surrounding the pond, (from its edge up to a distance of 2 m) and the male perched generally at a height of 0.5 to 1.5 m above the ground, the female hanging from the cerci of her mate. In rare cases was a female seen touching the substrate at the beginning of this phase. In the perched position, 1 tandem spent a time of 10 sec, 3 others between 2 to 3 min, before the male began to perform the movements that lead to the sperm translocation.

The male and/or the female of a perching tandem may display their wings towards approaching individuals. If the female is perched, she can also raise her body and bend her abdomen ventrally. Once a female in tandem was seen fluttering her wings during this abdomen bending. Sometimes it seems that also the male makes attempts to raise his abdomen; as a result of this, the male abdomen will take a somewhat downward curved position, its tip being connected to the prothorax of the perched female. This double wing-and-abdomen display may result in a magnification of the signal, that might act as a superstimulus.

The abdominal curving display of a female in tandem while in flight was also recorded.

## INTRA-MALE SPERM TRANSLOCATION

In accordance with what seems to be the rule in the Zygoptera (BICK & BICK, 1965b; BICK & HORNUFF, 1966), we recorded this behaviour in *C. lindeni* while in tandem and just before the copula.

The pattern of intra-male sperm translocation in *C. lindeni* is similar to that of other Zygoptera. The male spreads his wings, sometimes fluttering them from time to time, and at the same time raises and curves his abdomen in order to bring the penis in contact with the genital opening. He remains in this position 7 to 30 sec ($\bar{x} = 14$; $N = 16$, Tab. I) while the female is hanging with her wings folded and her abdomen straight or bending forwards at the proximal third. Sometimes the male makes preliminary attempts in order to attain the proper position for sperm translocation. One male performed 47 such attempts without succeeding in connecting the 9th with the 2nd segment. Then the tandem pair flew shortly above the pond, and after about one minute gained a new perch, where the male unsuccessfully attempted 13 more times to align the genital opening with the penis. After these new attempts the tandem took flight again and was lost.

Sperm translocation was recorded only once while the pair was in flight, contrary to what seemed to be the rule for the populations studied by HEYMER (1973a). Generally our males translocated the sperm while perched on vertical stems, but, also, horizontal or oblique ones were utilized; in these latter cases the tandem pair hung slightly to one side of the perch in such a way that the male could move freely.

After sperm translocation, the pairs would rest generally for not longer than 1 min (8 records), sometimes for a longer time (1 record between 3 to 4 min), or they could at once begin performing the precopulatory movements.

Table I

Sperm translocation in *Coenagrion lindeni:* perch slant is indicated as horizontal (H), vertical (V) and oblique (O); — post-sperm translocation pause refers to the interval between the moment at which the male separates his 2nd and 9th abdominal segments and the beginning of the abdomen bending to form the wheel (or to attempts to do this)

| Time | Duration (sec) | Perch slant | Post-sperm transloc. pause (sec) | Location and year |
|---|---|---|---|---|
| not rec. | 30 | not rec. | not rec. | Castel Porziano, 1972 |
| not rec. | 17 | not rec. | not rec. | |
| 1220 | 7 | H | 0 | Castel Porziano, 1979 |
| 1240 | 19 | V | 8 | |
| not rec. | 15 | V | not rec. | |
| 1120 | 17 | V | not rec. | |
| 1155 | 8 | V | 52 | |
| 1133 | 11 | V | 18 | |
| 1152 | 12 | V | 28 | |
| 1205 | 11 | H | 19 | |
| 1240 | 11 | H | 6 | |
| not rec. | 8 | V | 52 | |
| 1016 | 22 | H | 205 | |
| 1325 | 12 | V | 0 | |
| 1045 | 12 | O | 0 | |
| 1305 | 13 | V | 6 | Percile, 1979 |

## COPULA

In May and the first half of June, at Castel Porziano, most pairs copulated while perched on the vegetation surrounding the pond, at a distance of about 2 m from the water edge and a height of about 1 to 1.5 m above the ground. In the second half of June and in July we recorded most pairs in copula perched on the reeds along the shore, at heights of 0.5 to 0.8 m above the water. This different choice of site for copulation was probably related to the disturbance caused by other species. In fact, *C. scitulum* and *C. puella* were more abundant and more active at the beginning of the season (cf. also UTZERI, FALCHETTI & CONSIGLIO, 1977).

To gain the wheel position, the male raises the proximal segments of its abdomen and curves the distal ones ventrally. At this time, the female bends her abdomen forwards and upwards, till her genital orifice makes contact with the copulatory apparatus of the male.

It is known from the work of LOIBL (1958) that lestid females are capable of discriminating their own males from the other ones by the stimulating action the male cerci have on their prothorax. If the stimulation is a proper one, the female will cooperate to form the wheel, but if it is not, she will rebel against the male. So far, we do not know of any experimental work dealing with this aspect in the Coenagrionidae, but we agree with the hypothesis of KRIEGER & KRIEGER-LOIBL (1958) that receptors with which the female can perceive the stimulation of the male cerci may also be situated on the prothorax of coenagrionid females. It is by means of this stimulation that the male may induce his mate to cooperate in the formation of the wheel. In fact, in *C. lindeni*, as in other Zygoptera, to form the wheel, it is necessary for the female to raise her abdomen actively, while during sperm translocation, when the male is bending his abdomen ventrally, she hangs passively. During the intra-male sperm translocation, the male abdomen is curved upwards at the base, downwards and forwards at the middle and again downwards at the tip, whereas, during the precopulatory phase, it shows only the first two curves, its tip continuing the second one (Fig. 2). In the first case, the female is lifted in the same hanging position she has in tandem; in the second case the male cerci act on the prothorax of the female so that its mesoepisternal area is turned backwards, while she is driven upwards. It is in this turning backwards of the female thorax that the male cerci are most likely to produce a stimulation on the female prothorax, to which she responds bending her abdomen towards the male apparatus. Thus, the cooperation of the female in forming the wheel might be a mere reflex response to the stimulation effected by the male cerci.

Before the wheel is formed, some preliminary attempts may be carried out. Ten pairs made no preliminary attempts (i.e. the genital connection was obtained at the first pre-copulation movement), 1 pair made 1 attempt, 1 pair 2, 3 pairs 3, 1 pair 4 and 1 pair 17 attempts. One tandem pair performed 7 of these attempts, then the male released his grip and flew away. Another pair was seen performing 58 attempts in 11 minutes to make the genital connection, then the female, released by her mate, was seized by another male, and 25 unsuccessful attempts to form the wheel were recorded for this second tandem pair before the male released the female. She was soon caught by a third male, and this tandem attempted 18 times in 25 min to attain the wheel position. At this time we captured the pair in a net, but no morphological anomaly could be discovered in the female. Nevertheless, we believe that this unsuccessful copulation is to be attributed to the female, though in all instances she was recorded bending her abdomen upwards in a manner quite similar to that of the females that had achieved a successful copulation. In fact, it is very unlikely for the same female to have been seized by three males consecutively, all unable to form the wheel.

While raising and bending the abdomen to attain the wheel position, the male keeps his wings spread, and sometimes flutters them from time to time just as when translocating sperm. A male, between two successive attempts to form the wheel, was seen slowly spreading his wings and quickly flapping them some times,

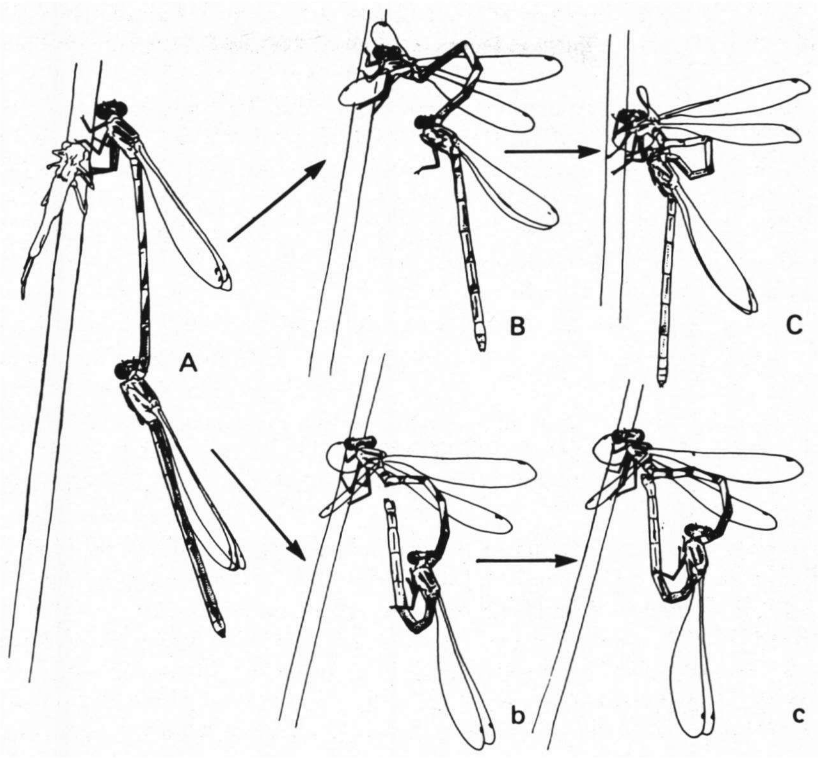

Fig. 2. Subsequent movements of the male abdomen in the pre-sperm translocation (A,B,C) and in the pre-wheel-binding (A, b, c). In the A-B-C sequence the female thorax keeps the same position as in tandem while in the A-b-c one, the female thorax axis is somewhat angled in respect to A. (From slides).

but he did not stroke the female, contrary to what BICK & BICK (1963) recorded for *E. civile* when the female was non-cooperative.

During copulation, the male pumps his abdomen rhythmically all the time and the female seems to follow these movements passively. The abdomen of the male is alternately arched dorsally and depressed ventrally at its base, yet the female thorax axis is not angled by this pumping, while the male one may be angled only slightly. Timing of the pumping cycle in two pairs gave us values of 2.02 and 2.63 sec. HEYMER's (1973a) timing (1.17 sec between the two extreme positions of the male abdomen), taken by means of film recording, may be satisfactorily situated between ours, if we suppose that the time spent to bring the abdomen from the higher to the lower position is equal to that needed for the reverse movement. Thus, it appears that some individual variability does exist in the frequency of the copulatory pumping.

Timing of the pumping of the same male at four different moments of the copula, gave us rather constant values (1.81; 2.17; 2.04; 2.08 sec for one complete cycle).

Perches utilized for copulation were mostly vertical (18 records), in accordance with the statements of BUCHHOLZ (1950) and SCHIEMENZ (1953), but horizontal (4 records) and oblique ones (4 records) would also be utilized. In relation to this, HEYMER (1973a) has already pointed out that in *C. lindeni* the choice of a perch for copulating is less rigid than stated by the previous authors. Furthermore, we recorded pairs in copula shifting from vertical perches to oblique or horizontal ones.

Females in copula generally do not contact the substrate (21 records), but sometimes they may change from a hanging to a substrate-contacting position with one or more pairs of legs (3 records), and vice-versa. Only one female remained in contact with the substrate throughout the copula. Some copulating females were seen to keep their legs by the sides or their abdomen, but only once did we see that the legs (only the first pair) clasped the abdomen, as in lestids (LOIBL, 1958).

During copulation, both partners keep their wings in a rather spread position. A pair can also fly without breaking the wheel, but this event was recorded only as a result of disturbance by the observer. If the disturbance is caused by other damselflies, one or both partners may spread their wings a little more, or flutter them, or the male may spread his wings and increase the dorsal arch of its abdomen, but the pumping rhythm seems not to be affected by this (1 record).

Copula was generally performed without interruption. Nevertheless one pair disengaged the genital organs for 5 min and 10 sec, without any apparent external disturbance, then the wheel was formed again. Another pair interrupted copulation for 39 sec, on account of the rather close approach of a dog. A third pair interrupted copulation two times, the first to flee from the aggression of a frog (*Rana esculenta*) (this lasted 3 min and 56 sec) and the latter as a consequence of being disturbed by other coenagrionids (3 sec). But, as a rule, the disturbance caused by individuals of similar size, whatever the species, did not lead to interruption of copulation, even if physical contact was made.

Timed copulation lasted from 2 to about 30 min ($N = 23$).The mean value of the times recorded at Castel Porziano in 1972 ($\bar{x} =$ between 17 and 18 min; $N = 6$; range 8-30 min) differs from that of 1979 ($\bar{x} = 6.59$; $N = 13$; range 2-13.49 min), but if all these times are considered together we obtain a mean value ($\bar{x} =$ between 10 and 11 min) similar to that computed for the population of Percile lake ($\bar{x} = 9.46$; $N = 4$; range 4.38-15.10 min). The duration of 44 min 10 sec of a copulation timed at Percile was not considered for the calculation of the mean value (Tab. II).

At the end of copulation, the wheel is broken by the male exaggerating the last upward movement of his abdomen.

Table II

Copulation in *Coenagrion lindeni.* The numbers between brackets refer to incomplete timing. Perch slant is indicated as in Tab. I. Female position is indicated as hanging (h) and substrate-contacting (c). Post-copulatory pause refers to the interval between wheel-breaking and the starting of the flight to the first oviposition site. (*) = Double timing due to interruption of copulation

| Time | Duration (min sec) | Perch slant | Female position | No. of preliminary attemps | No. of interruptions (min sec) | No. of shifts | Post-copulatory pause (min sec) | Location and year |
|---|---|---|---|---|---|---|---|---|
| not rec. | ca. 18.00 | not rec. | not rec. | not rec. | not rec. | not rec. | not rec. | Castel Porziano, 1972 |
| " | ca. 8.00 | " | " | " | " | " | " | |
| " | ca. 25.00 | " | " | " | " | " | " | |
| " | ca. 10.00 | " | " | " | " | " | " | |
| " | ca. 30.00 | " | " | " | " | " | " | |
| " | ca. 15.00 | " | " | " | " | " | " | |
| 1200 | not rec. | V | h | 0 | 0 | not rec. | 4.25 | Castel Porziano, 1979 |
| 1220 | 12.22 | H | h | 0 | 0 | 0 | 0.18 | |
| 1240 | 2.33 | V | h | 0 | 0 | 0 | 0.14 | |
| 1200 | 6.53 | V | h | 3 | 0 | 0 | 0.32 | |
| 1135 | 2.38 | V | not rec. | 0 | 0 | not rec. | 0.40 | |
| 1155 | 2.00 | V | h | 2 | 0 | not rec. | 1.10 | |
| 1205 | 2.08 | H | h | 3 | 0 | 2 | 1.21 | |
| 1240 | 2.05 | H | h | 0 | 0 | 1 | 0.00 | |
| not rec. | 6.53 | V | h | 3 | 0 | 0 | 0.32 | |
| 1019 | 12.48 | V | h | 4 | 0 | 0 | 1.20 | |
| 1043 | 6.13 | V | h,c | 0 | 0 | 0 | 1.49 | |
| 1108 | not rec. | V | c | 0 | 0 | not rec. | 1.17 | |
| 1147 | 6.18+3.03* | H | h | 1 | 1; 5.10 | 3 | 0.24 | |
| 1210 | not rec. | O | h,c | 0 | 0 | not rec. | not rec. | |
| 1355 | (9.51) | O | h | not rec. | not rec. | not rec. | 1.05 | |
| 1325 | 13.49 | O | h | 0 | 0 | 0 | 0.45 | |
| 1045 | 11.07 | V,O | h,c | 0 | 0 | 5 | 0.07 | |
| 1120 | (14.34) | V | h | not seen | 0 | 0 | 2.56 | Percile, 1979 |
| 1225 | 4.38 | V | h | 0 | 0 | 1 | 1.02 | |
| 1233 | 44.10 | V | h | 0 | 0 | 0 | 0.25 | |
| 1334 | 7.55 | V,H | h | 0 | 2 | 6 | 0.56 | |
| 1340 | 11.20 | V | h | 4 | 0 | 2 | 0.45 | |
| 1300 | (11.05) | V | h,c | not rec. | 1 | 4 | 0.02 | |
| 1314 | 15.10 | V | h | 17 | 0 | 0 | 1.05 | |

It is rather exceptional (e.g. BICK & BICK, 1963; 1965a; 1968; 1972), at least among the Coenagrionidae, for an individual to couple more than once in the same day. This is true also for *C. lindeni* in our populations. Two females, seized after oviposition, copulated presumably (since we did not observe their previous copulation) for the second time. But, while we may take this for granted in respect to one of these females, that had oviposited in tandem, in the case of the second one, that oviposited alone, it is not known if a female can continue a previously interrupted oviposition on a following day (cf. also BICK & BICK, 1961 and BICK, 1972). The first female, after having copulated for the second time, oviposited again shortly, then the pair perched for a very long while. This possibly indicates that the female had exhausted her drive for egg-laying, while the male's drive to maintain the tandem position persisted (cf. also BICK & BICK, 1965a).

A third female, that had oviposited alone after her mate had released his grip, was seized while flying away from water. We recorded the sperm translocation of her new mate, then this tandem pair was lost.

## OVIPOSITION

At the termination of copulation, the pair would generally rest on their perch for some time. One pair flew immediately towards the water, 12 rested for less than 1 min, 8 between 1 and 2 min, and 2 between 2 and 5 min.

In both biotopes, it was very difficult to continuously observe the ovipositing tandems, since the number of marked individuals that were daily active at the pond was low, and the ovipositing pairs spent most of the time far from the shore; furthermore, tandems would shift from site to site several times, thus eluding the observers even when binoculars were utilized. Therefore, our data were taken from ovipositing pairs, a great number of which were not marked, and our timing data are scarce (Tab. III).

Oviposition may be performed either at the surface or with the female submerged. In both localities where we made our observations, never was a male seen submerging following his mate.

As a rule, surface oviposition is performed in tandem, but females ovipositing unaccompanied were occasionally recorded (4 records). Ovipositing pairs of *C. lindeni, C. scitulum* and *C. puella* would crowd together in particular sites of the pond where suitable vegetation for insertion of eggs is abundant. However, there

Table III

Oviposition in *Coenagrion lindeni.* The numbers between brackets refer to incomplete timings; (*) indicates unaccompanied female. Number of reported shifts refers to movements from site to site where actual egg insertion could be ascertained

| Time | Duration (min sec) | | | | No. of shifts | Location and year |
|---|---|---|---|---|---|---|
| | Total (min sec) | Actual | Surface | Under-water | | |
| not rec. | (120.00) | | | | | Castel Porziano, 1972 |
| not rec. | ca. 120.00 | | | | | |
| not rec. | ca. 45.00 | | | | | |
| not rec. | ca. 60.00 | | | | | |
| 1215 | 96.02 | | few min | 36.02 | | |
| 1255 | 7.12* | 3.34 | 3.34 | — | 12 | Castel Porziano, 1979 |
| 1032 | (69.00) | 32.06 | 32.06 | not-timed | 39 | |
| 1204 | 89.00 | 35.56 | 35.56 | — | | |
| 1255 | not rec. | not rec. | not rec. | 1.43 | | |
| 1330 | not rec. | 20.50 | | 20.50 | | |
| 1050 | not rec. | 7.10 | 7.10 | — | | |
| 1335 | 77.00 | | 77.00 | — | | |
| 1230 | (17.30) | 9.30 | 9.30 | not seen | | Percile, 1979 |
| 1330 | 42.22 | 41.59 | 41.59 | — | | |
| 1415 | (22.42)* | 17.36 | 17.36 | not seen | | |
| 1345 | not. rec. | not rec. | not rec. | 16.05 | | |

did not seem to be any social motivation for this crowding, since a pair in search for an oviposition site would, before perching, explore the substrate in flight near ovipositing tandems for a time almost as long as when there were no pairs laying eggs.

At Castel Porziano, the plant chiefly utilized for egg-insertion was *Potamogeton pusilla*. The female would perch on the emerging portion of the plant, bending her abdomen beneath the water surface. The male would generally stay straight on his cerci, in the "Agrion type" position (WESENBERG-LUND, 1913; BUCHHOLZ, 1950), but sometimes he could slant forwards and even perch on floating vegetation, curving his four distal abdominal segments. It seemed that the male could hold his abdomen at any angle, but his thorax axis was always kept almost horizontal (Fig. 3). This position was likely to allow him to take flight promptly in case of approaching danger.

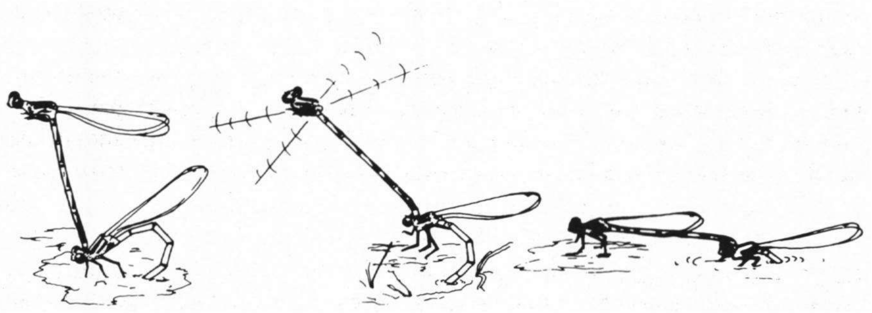

Fig. 3. Observed postures for males of ovipositing tandems. Whatever the abdomen slant, the male thorax axis is kept almost horizontal. (From slides).

Some males of ovipositing tandems were recorded fluttering their wings when individuals of the same or similar species approached (11 records), but we lacked evidence that this was a threatening behaviour, since wings could be fluttered while no damselflies were passing by, and wings could be kept closed when intruders were approaching. Furthermore, wing-fluttering could also be continued after the approaching individual had left. We think that in these occasions wing-fluttering might merely have the function of preserving the balance of the fluttering male, that was possibly perturbed by flying individuals.

In accordance with HEYMER's (1973a) observations, *C. lindeni* ovipositing females may submerge completely, while the males just barely tolerate water wetting their distal abdominal segments. At our ponds, when a submerging female was dragging her mate too far downwards, he would quickly take flight, pulling his female up in a somewhat jerking manner, whether she was inserting the eggs or not. Generally, at Castel Porziano the male would succeed in dragging the female out of the water, possibly due to the fact that the vegetation that the female could grasp (*P. pusilla*) was too thin to allow her a strong grip. We do not think that this jerking behaviour of the male had the function of communicating to the female that the male intended to shift to another site; in fact, if the female was able to maintain her grip on the substrate, the male would lose his grip on the female prothorax, and the female would continue to oviposit unaccompanied. This event was probably more frequent at Percile lake, where the stems that females would grasp to insert their eggs (*Potamogeton perfoliata*) were thicker (3 to 5 mm in diameter).

Submerged oviposition at Castel Porziano, was recorded only three times, in 1979. Only once was a female recaptured by her previous mate, who was perching near the oviposition site at the moment when she emerged, 1 min and 43 sec after being released. In the other two instances the male left, after having hovered shortly above the site where the tandem had broken. One of these two females oviposited, while submerged, for about 36 min (cf. Tab. III), then she bobbed to the surface where she was entrapped by the surface film. We recorded the events followed for 28 min, before stopping the observations. During this time, four *C. lindeni* males passed near this female, that was lying on one side and actively moving her legs and abdomen, but none of them seemed to take an interest in her. Two days later, the yellow marked wings of this female were found at that place.

At Percile lake, submerged oviposition of the unaccompanied female was recorded 4 times (3 times in 1979, 1 in 1974), and as the time spent by us in that biotope was much shorter than at Castel Porziano, we think that this event is probably occurring more frequently at Percile than at Castel Porziano. Nevertheless, even there, recapture of a female by her mate after submerged oviposition was recorded only once, after the female had spent 16 min under water. The tandem flew away at once and was lost. Two other females, that had oviposited under water, were able to reach an emerging stem by their own means, and after a rest of some minutes left the water undisturbed.

Thus, the "communal salvage" of females by their mates after under-water oviposition, reported by HEYMER (1973a), was unlikely to have occurred in the populations we studied.

Only one ovipositing tandem could be observed at close quarters. Most of the time when a female was dipping her abdomen, she seemed to be performing a tactile exploration of the substrate by her ovipositor, and insertion of eggs seemed to be quite rare. One to three eggs were inserted into each appropriate stem. Exploratory activity which preceded actual egg insertion lasted up to 14 sec. As a consequence of this, the times reported in Table III for actual oviposition are unreliable in that we could not tell if a female was actually inserting eggs or just testing the substrate, while the timing was started as soon as she would dip her abdomen.

In those cases where the female did not submerge, it was not evident which partner took the initiative to shift to the next oviposition site. But we recorded one tandem, perched on the vegetation of the shore, in which the female became airborne just before the male when moving to the oviposition site. Furthermore, we twice recorded that during the search for the oviposition site, the female curved her abdomen ventrally, so as to contact the substrate. In these cases, tandems perched at once and the females immediately dipped their abdomens. It seems, therefore, that the female may communicate to the male to stop the searching flight and that the male's cooperation is needed to do this. The control of tandem shifting during oviposition has been ascribed to females in several species of Zygoptera (BUCHHOLZ, 1950; BUCHHOLZ, 1956; ERIKSEN, 1960; BICK & BICK, 1963; 1965a), but based on our own observations, we can affirm that the male, on certain occasions, can drag the female away. This may represent an adaptation for survival, since the male of an ovipositing tandem is in a more favourable position to detect any danger, and having taken flight, may help the female to disengage from the substrate.

The tandem connection during oviposition may last for more than two hours, but generally it takes a shorter time. When the male motivation to keep the tandem position becomes exhausted, he releases his grip without any other particular behaviour pattern, and shortly after, the partners fly away from the pond.

## THREAT DISPLAYS, AND DEFENCE ACTIVITIES OF THE TENERALS

All the types of display described in the text, by which the mature imagoes threaten other individuals, are summarized in Table IV.

UTZERI (1980) suggested that newly emerged tenerals are possibly not able to perform a threat display, as the mature imagoes do.

Newly emerged tenerals may keep their body at an angle of about 45 degrees from the horizontal line, or they hang along their perch. When approached or even struck by an adult individual, or disturbed by the observer, a perched teneral *C. lindeni* specimen will quickly lower the postural angle of its body to the point of bringing it almost parallel to a vertical perch. It will also step around its perch, in such a way as to hide its body from the disturber. This behaviour resembles that of *Ceriagrion melanurum* males, females and tenerals (AOYANAGI, 1973), and SAWCHYN & GILLOTT (1975) report that it is performed also by *Coenagrion angulatum* tandems ovipositing under water, when approached by any object. On one occasion a teneral *C. lindeni*, perching with its body axis parallel to a vertical perch, was approached very close by an *Ischnura elegans* male. The *C. lindeni* quickly raised the angle of its body up to 90 degrees in respect to the perch, without opening its wings, and stepped to the opposite side. The adult male retreated, and after a few seconds the teneral brought its body to the previous position. This rather jerking movement of the teneral did not resemble the

Table IV

Summary of the threat and refusal displays in *Coenagrion lindeni*

| Type of display | Displayer | Target of display | No. of observations |
|---|---|---|---|
| While perching | | | |
| Wing spreading (raising of the body) | ♂ | ♂ *scitulum, puella* | 39 |
| | ♀ | not rec. | 5 |
| | ♂ in tandem | undet. ♂ | 6 |
| | ♀ in tandem | undet. ♂ | 5 |
| | both ♂ and ♀ in tandem | undet. ♂ | 6 |
| | ♂ in copula | not rec. | 7 |
| | ♀ in copula | not rec. | 3 |
| | both ♂ and ♀ in copula | not rec. | 4 |
| Wing spreading with abdomen curving downwards | ♀ | ♂ *lindeni* | 4 |
| | | ♂ *scitulum* | 5 |
| | ♂ in tandem | ♂ *puella* | 5 |
| | ♀ in tandem | undet. ♂ | 8 |
| | both ♂ and ♀ in tandem | not rec. | 3 |
| | ♂ in copula | not rec. | 1 |
| Wing spreading with downward bending of 9th and 10th urites | ♂ | ♂ *scitulum*, undet. ♂ | 2 |
| | | ♂ *lindeni* | 16 |
| Wing fluttering (raising of the body) | ♂ | ♂ *puella*, undet. ♂ | 19 |
| | ♀ | ♂ *lindeni* | 1 |
| | ♂ in tandem | not rec. | 2 |
| | ♀ in tandem | not rec. | 1 |
| | ♂ in tandem, ovipositing | ♂ *scitulum*, undet. ♂ | 11 |
| | both ♂ and ♀ in tandem | not rec. | 1 |
| | both ♂ and ♀ in copula | not rec. | 2 |
| Wing fluttering with abdomen curving downwards | ♀ in tandem | not rec. | 1 |
| In flight | | | |
| Abdomen curving downwards | ♀ | ♂ *scitulum, puella* | 7 |
| | ♀ in tandem | ♂ *lindeni* | 7 |
| Zig-zag flight | ♀ | ♂ *lindeni* | 1 |
| Zig-zag flight with abdomen curving downwards | ♀ | ♂ *scitulum* | 5 |
| Abdominal bending of 9th and 10th urites | ♂ | ♂ *lindeni* | 8 |
| Flights towards intruders, from a perch | ♂ | ♂ *lindeni* | 33 |
| | ♂ | ♂, ♀ *A. imperator* | 4 |
| | ♂ | undet. ♂ | 12 |
| Flight towards intruders, from a recovery flight | ♂ | ♂ *lindeni* | 11 |
| | ♂ | undet. ♂ | 1 |

somewhat regular raising of the body by adults, but it may represent a step towards the adult threatening pattern.

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