Odonatologica 12(2): 141-151 *June 1, 1983*

OBSERVATIONS ON THE BEHAVIOUR OF *AESHNA AFFINIS* (VANDER LINDEN) AT A DRIED-UP POND (ANISOPTERA: AESHNIDAE)

C. UTZERI and R. RAFFI
Istituto di Zoologia, Università di Roma, Viale dell'Università 32, I-00100 Roma, Italy

Received April 6, 1982/Accepted February 12, 1983

Observations on an *A. affinis* population breeding at a temporary pond of Central Italy are reported. Males showed territorial behaviour for less than 3 h over the same area, from which they would chase other males. Females began to oviposit as soon as they came to the pond in the morning, without immediately preceding copulation. Holes dug in the dried-up ground of the pond by wild boars were chiefly utilized as oviposition sites. Tandem formation and intra-male sperm translocation (the latter always closely following the former) took place at the pond and were followed by copulation. Then the pair began to oviposit while still in tandem. After some time the male released the female, who went on ovipositing alone. In the evening, after having been away from the pond, males and females returned and performed the hunting flight, during which they did not show any aggressive or sexual behaviour.

INTRODUCTION

Oviposition of aeshnids in the dried-up ground was briefly reviewed by UTZERI (1978), who outlined that in this family there are species or populations where oviposition may be independent from the presence of water at the oviposition site. UTZERI et al. (1977) reported observations of *Aeshna affinis* females laying eggs in the hardened ground of dried-up ponds. A population of this species was lately found breeding at a temporary pond, and observations on the behaviour were carried out.

METHODS

The pond, located at Castel Porziano (Roma), is a roundish depression in the ground slightly over

40 m in diameter when flooded. At the time when the work was carried out, it was completely dried up, its bottom hardened and richly covered with reed and sedge shrubs. Large oak trees *(Quercus cerris)* surround and partly shade the pond. One to two researchers were in the field from August 5 to 29, 1980. Observations on behaviour were made during 32 hours of 8 days, between August 5 and 27. Marking operations on the insects took place on August 12 and 19, and recording of the marked insects was carried out for over 51 hours of 9 days between August 12 and 29.

The insects were individually marked on the wings with car enamel paint in order to perform direct observations on the behaviour of single individuals. Stop-watches were used to time some events, such as copulation, etc.

In the following, the time will be given as Central European Summer Time.

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

PRESENCE OF THE INSECTS AT THE POND

Presence of the dragonflies at the pond was recorded between 0945 h and 1934 h (August 25, 26), but as these times coincide with the earliest and latest of the researchers' presence at the pond, it is possible that some dragonflies were attending the pond before and after these times. However, at the earliest or latest given times not more than 1 individual was seen, while maximum crowding would take place in the warmer period of the day, i.e. between 11 and 16 h.

Earliest copulation was recorded at 1026 (August 26), and oviposition between 1024 and 1934 (August 26).

MARKING AND RECAPTURE

From the 43 mature males and 12 mature females marked at the pond, 17 males (39.5%) and 6 females (50%) were recaptured from the marking day onwards, while 10 males (23.3%) and no females were recovered from the day following the marking day.

11 males (64.7% of the total recovered) mated once each in the days following marking, and 5 females (83% of the total recovered) mated at least twice on the marking day.

Males attended the pond on successive days as well as at intervals. 33 individuals visited the pond on only one day, 8 on two, 1 on three and 1 on four. The time span during which the pond was visited varied between 1 and 9 days — these figures being inclusive of the marking day. Intervals between two successive visits were from 0 to 8 days.

TERRITORIAL BEHAVIOUR

Males were generally flying over part of the pond, each one patrolling an area of about 8-10 m in width, from which they chased intruders away. As the flights towards intruding males were clearly distinct from those that males would have

performed while approaching females, and as in no case a male attempted to seize in tandem another male as a consequence of an approach flight, we presume that males were distinguishing between males and females, and that their drive when approaching a male was not sexual as when approaching a female. On the contrary, as intruders were generally displaced from an area where a resident male was flying over, we consider the aggressive behaviour of males as territorial behaviour, according to JOHNSON (1964).

Males would attack other males from a distance of up to 6 m, and could chase them for as far as 15 m. Also tandem pairs could be chased from the territory. When chasing intruders off, males kept in a lower position in relation to them. Clashes between males were never seen.

Attacks were recorded also against *Sympetrum* males and tandems, and *A. affinis* males were sometimes attacked by *Sympetrum* males.

Patrol flights as well as hovering flights could be performed by territorial males. The former consisted in the insect flying to and fro within the territory boundaries, sometimes dashing through the entire pond while chasing an invader and soon returning to his territory. The latter were performed over one spot at heights of 1 to 2 m, sometimes alternated with shorter or longer shifts. The flight pattern over the territory could be changed from patrol to hovering and vice-versa several times by the same male. What was leading a male to patrol or to hover over his territory was not clear.

When not involved with aggressive activities, males would often fly low over the ground as though attentively inspecting the ground around the base of reeds and sedge shrubs, and as quite often females would oviposit at places like these, we presume that males were seeking females in these shrubs (cf. HEYMER, 1968).

While males were spending a long time flying over their territories, short rests were frequently recorded, usually perched within the territory borders at heights of 0.5 to 1.5 m. Pauses could last between a few seconds up to some minutes (max. 8 min 04 sec), and were more frequently recorded and longer in the evening. These pauses were sometimes interrupted for no apparent reason. Interruption could be caused to react to individuals passing by. It was not known what was leading a flying insect to perch. In two instances, as soon as a male perched on a *Carex* leaf that bent down to the ground, he took flight again, and remained in flight for quite a long time.

Males were changing their territories within the same day, and there did not seem to be any aggression by other males that was leading them to change their localization. The longest time spans during which two males were on their territories were 2 h 46 min (♂ N5s, Aug. 26) and 2 h 27 min (♂ N3d, Aug. 26). No male was recorded defending the same area in successive days.

A male that insisted in invading the territory of another male, was attacked by the owner several times, but each time he succeeded in momentarily displacing

him, and finally the two males tolerated each other while perched, as well as in flight over the same area. SONEHARA (1964) reported for *A. mixta* that when a male occupies the territory of a perched owner, "both males are usually indifferent to each other".

Thus, in our *A. affinis* males, a "temporial behaviour" such as that described by MAYER (1962) and KAISER (1968, 1974) for *A. cyanea* could not be recognized.

TANDEM FORMATION AND SPERM TRANSLOCATION

Though males were more abundant than females at the pond, and females could be absent from the pond for long periods, some females could be seen from the early morning busy with oviposition. All females we could see prior to mating began ovipositing as soon as they came to the pond.

Everyone of the 8 seizures we recorded, were performed with females that were shifting away from an oviposition site. The male quickly dashed towards the female that generally flew upwards followed by him. At a height of about 2-3 m over the ground, the male gained a higher position in respect to the female, and both male and female began falling headlong, while circling, towards the ground. All females in this phase behaved as if attempting to avoid seizure, but if within a height of about 50 cm over the ground the males contacted them, pairs fell on the ground with a loud wing rustling. As soon as the female perched on the ground, the male bent his abdomen and clasped her head with his cerca (Fig. 1A), then, by shortly stepping forward and depressing the abdomen at its base, contacted the 9th with the 2nd urites for a very short time (Fig. 1B). Both tandem seizure and sperm translocation lasted not more than 1-2 sec. Sperm translocation following tandem seizure was recorded 5 times. Its very short duration, coupled with the lack of male stretching behaviour after the tandem formation (as generally seen in many zygopterans), made it difficult to detect.

It seems that for a successful tandem formation it is necessary for the male to contact the female before the latter perches on the ground. In fact, in two instances in which the female contacted the ground before the male had perched on her thorax, the male renounced taking her, and hovered above her for a time. This behaviour was commonly observed in males in respect to ovipositing females. Though the male that had discovered an ovipositing female seemed to be strongly attracted by her, and would have spent a time hovering over her, males were never seen attempting to take the tandem position with ovipositing females, but as soon as a female took on wings from the oviposition site, the male dashed towards her.

Once a female was seen performing a refusal display similar to that reported by CORBET (1957, 1962) in unreceptive females of *Anax imperator*, i.e. ventral curving of the abdomen while in flight (Fig. 1C); in this instance the pursuing male soon retreated.

COPULATION

As soon as the male translocated the sperm from 9th to 2nd segment, the pair took flight in tandem, and the wheel was usually formed within about 0.5 m. The male stopped his flight for a very short time, while conspicuously raising his abdomen, so the female abdomen swang forwards up to contact the penis (Fig. 1D), where it was restrained. Generally the genital connection occurred at the first attempt. At one occasion the wheel broke three times in the first 30 seconds after seizure. As soon as the wheel was formed, the pair flew to the oak branches leaning over the pond, where they perched (Fig. 1E) at estimated heights of 4 to 9

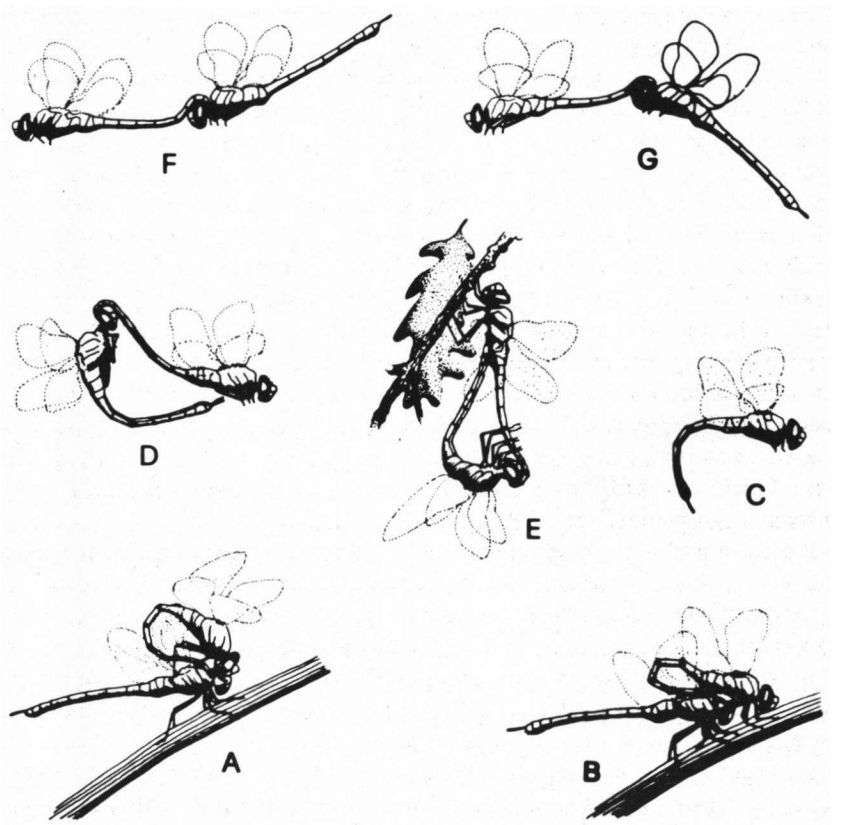

Fig. 1. Reproductive behaviour of *Aeshna affinis:* (A) tandem formation; —(B) intra-male sperm translocation; —(C) female refusal display; —(D) forming the wheel; —(F) tandem flight, with the female swinging her abdomen upwards; —(G) tandem flight, with the female gliding beneath the male while swinging her abdomen downwards. (Freely redrawn by dr. Niccolò Falchi after indications of the Authors).

m; very seldom pairs in the wheel position perched lower, on reeds or other plants of the pond. While in the wheel position, the female grasped the male abdomen with her legs.

During copulation, a slight abdomen pumping was performed by the male, and in concurrence with this, slight starts of the female body were sometimes observed, less frequently also performed by the male, perhaps as a consequence of 1-2 short wing beats that the insects made at intervals.

Table I

Copulation of *Aeshna affinis*. (Figures in brackets refer to incomplete timing. $\bar{x} = 36{:}02$; $n = 5$; $r = 30{:}39 - 47{:}16$)

Height above the ground (m)	Duration (min: sec)	Post copul. pause (min: sec)
2	(23:52)	ca 1 min
3.5	(7:25)	ca 1 min
not recorded	33:24	5:37
not recorded	47:16	not recorded
8-9	not recorded	not recorded
8	not recorded	not recorded
5	35:58	2:13
4	(16)	not recorded
9	32:56	0:44
2	30:39	0:21

The pumping frequency decreased as the time elapsed. In one instance, at the 9th minute, a complete cycle was being performed in 1 sec, at the 17th minute it was performed in 1.86 sec, at the 20th min in 2.8 sec, at the 22nd in 4 sec and at the 23rd in 7.4 sec. These figures representing the average of 5-10 complete cycles. From the 24th minute onwards, the pumping frequency could not be timed with any confidence, because the pumping movements had become very inconspicuous and infrequent. Also the frequency of the slight starts of the female body seemed to follow the decreasing pattern of the pumping.

Pairs in the copulation position could fly without disengaging the wheel, but this was recorded only as a consequence of disturbance by the observer(s), and no pairs were recorded copulating in flight except for a short while between the moment at which the genital connection was obtained and that when the pair gained a perch, contrary to what was reported by ROBERT (1958) for *A. affinis* and *A. juncea*.

Copulation, timed in 5 pairs, lasted between 30 and 50 min, which is comparable with that of *Aeschnophlebia longistigma* (INOUE et al., 1981) but considerably shorter than in *A. cyanea* (KAISER, 1974) and longer than in *Anax imperator* (ROBERT, 1958).

At the end of copulation, male and female genitalia disengaged after the male pushed his mate upwards several times. Then the pair rested a short while on the same perch in the tandem position.

OVIPOSITION

While females firstly coming to the pond in the morning would begin at once ovipositing alone, oviposition following copulation always began with the pair in tandem, the female leaving the perch where copulation took place just before the male.

Only once did a tandem pair land shortly after having taken flight after copulation, and the female immediately began to oviposit. As usual, following the starting from the place where copulation had taken place, tandem pairs were seen flying for a time at a height of 0.1-0.3 m above the ground all over the pond, as if in search of a suitable resting site. While in flight, the distal part of the male abdomen was usually kept on the female frons and clypeus, so the male was in a lower position than the female.

During the exploration flight, the female could swing her abdomen over (Fig. 1F) and under (Fig. 1G) the horizontal plan, resulting in, respectively, increasing and slackening of the tandem-flight speed. In many instances, while tandems were shifting from an oviposition site to another one, we saw the tandem females just gliding wing-motionless behind their mates (Fig. 1G), thus probably slackening the tandem flight speed.

After a time of tandem oviposition (the only exact record was 40 min.; two other incomplete timings: 23, 23 min.) the male released his mate and she continued ovipositing alone. After the tandem release, a male was seen hovering above his ovipositing female for about 1 minute, dashing towards other males and returning after each chase over the place where his female was ovipositing. Then, following a longer chase, he did not return.

It was not possible to continuously watch ovipositing females, as, due to their long shifts, they were frequently lost. Nevertheless, in some instances, it seemed that oviposition was lasting many hours.

Oviposition took place exclusively in holes dug by wild boars in the hardened ground of the dried-up pond. Both tandems and unaccompanied females landed on the edge of the holes, the females immediately beginning to perform oviposition movements and stepping backwards before each successive egg insertion. At other ponds of the same area, where water was present, oviposition was performed in the dry zone of the shore, often at a distance of some metres from the water edge. In all instances, females chose well sheltered and shaded places, and it did not seem that the territories were being utilized for this purpose more intensively than any other part of the pond, contrary to YOUNG's (1965) observations on *Anax junius*. UTZERI et al. (1977) reported *A. affinis* females

also ovipositing in the dry bottom of astatic ponds and in the wet mud. From the above observations, it seems that *A. affinis* is well adapted to temporary water habitats.

Ovipositing females continuously tested the ground by scratching it with their ovipositors, while oscillating their abdomens in the sagittal plane and slightly vibrating their wings, and at times, the ovipositor dived into the ground for a varying length of time. Female N6s, as an example, performed successive egg insertions of 25, 13, 7, 12, 11 and 8 sec.

Females ovipositing alone were easily approached by observers, as also reported by ROBERT (1958) for *A. grandis*, and could be easily caught by hand for marking. Then, as soon as released, they went on with oviposition. The tandem pairs, on the other hand, would generally fly away in case the observers were approaching close by. This strongly suggests that the tandem male has a role in guarding the ovipositing female against common dangers. Wings of *A. affinis* were sometimes found on the ground near the oviposition sites, and we would not be surprised if not only birds (cf. e.g. KENNEDY, 1950) but also lizards (*Lacerta viridis*), perhaps snakes (*Coluber viridiflavus*) and mammals (*Sus scrofa, Mustela nivalis, M. putorius, Martes martes*, various voles) would occasionally prey upon the confident females.

Only once was a female seen stopping oviposition. She quietly took flight from the hole into which she was laying, crossed the pond at a height of 4-5 m, soared over the pond for 1-2 min while continuously raising her flight until she disappeared.

HUNTING FLIGHT

While occasional prey captures were recorded in the period of the day when the insects were busy with reproductive activities, feeding at the pond was particularly intensive in the evening, after both males and females had retreated for some time. For example, on August 26, the last male left the pond at 1703, then 2 males and 1 female appeared at 1737, and in a short time others arrived, in total 4 males and 2 females, of which three of the males, being marked, were known to have attended the pond in the morning and afternoon. The dragonflies fed for about half an hour over the pond and the adjacent part of the cartway, then progressively but in a short while disappeared; their aggregation at the pond being recorded not over 1825. Yet, one marked male made successive visits after that time, and was still feeding at the pond at 1934, when the observations were discontinued.

The *A. affinis* hunting flight was fast and jerky, as though the insects were highly excited. The insects flew at heights of 1 to 10 m above the ground and could crowd or scatter all over the pond, and in no case were interactions among them recorded. KAISER (1974) reports that while feeding, *A. cyanea* individuals

hardly react to conspecifics, while some interactions between individuals are reported for *Anax imperator* (CORBET, 1957).

Preys were taken by horizontal as well as vertical dashes, and captures were sometimes spectacular, as when a dragonfly stooped from a height of about 3-4 metres and reached a small butterfly that was flying near the ground.

Dragonflies did not seem to have any localizations at the pond, though swarming preys could induce some of the hunters to spend some time in the restricted area where a swarm was flying.

Small Diptera and Lepidoptera appeared to be the most available preys in the evening, while various insects, including *Lestes* specimens, could be taken earlier.

CORBET (1957) reported for *A. imperator* a crepuscular flight pattern very similar to that of our *A. affinis.*

OTHER ACTIVITIES

Ventral bending of the abdomen was recorded three times in flying males, once in concurrence with the grooming of the abdomen tip. Grooming of the eyes was recorded in two copulating females. A female of a perched tandem was seen rubbing her legs against each other just after copulation.

Bobbing of the abdomen, recalling that reported for the Zygoptera, was performed in flight by a male just released after marking. KAISER (1974) reported this behaviour for *A. cyanea,* but we did not record in our *A. affinis* male a dorsal raising of the wings comparable with that drawn by that author.

Some males were seen spending some time perched on the walls of the holes dug by boars (15 observations of 7 males), this behaviour being most frequently observed in the afternoon.

DISCUSSION AND CONCLUSIONS

UTZERI (1978) reported *Anax parthenope* tandems ovipositing into the hardened ground of a dry pool, very close to which was a canal provided with water and vegetation commonly utilized by *A. parthenope* to insert eggs in the same area. While in that case it may be assumed that the water in the canal was attracting mature individuals, though females were ovipositing a short distance away from the water, this is surely not the case with our *Aeshna affinis,* whose females were ovipositing when the water was absolutely dried up. Thus, it is not clear to which stimuli mature individuals of *A. affinis* were responding in selecting the oviposition habitat. This question presently exists in all those species that oviposit at temporary ponds in the season when these are completely dried up. These species mostly belong to Lestidae and Aeshnidae (see e.g. UTZERI et al., 1976; UTZERI, 1978), but in the dried-up pond where our *affinis* was

observed, at least two *Sympetrum* species, i.e. *sanguineum* and *meridionale* were scattering eggs on the hardened ground.

While males were attending the pond on a number of days, females were recorded only on the marking day. This may suggest that they were wandering more than males, as is known of other species (MOORE, 1954; BICK & BICK, 1968).

Except when feeding in the evening, never were unpaired females seen at the pond if not busy with oviposition. This induces us to speculate that females would not attend the pond in the morning if not driven to oviposition.

Inter-male aggression was recorded only during the reproductive activity period of the day, while during the hunting flight males did not interact with one another. Hence, territoriality in *A. affinis* appears to be bound to competition for females and not for prey.

Never was a male seen attempting to seize an ovipositing female. It is possible that the male sexual interest for a female is reduced by the oviposition posture of the female. If this is true, we know the first stage of a ritualization process through which the ventrally curved position of the female abdomen developed towards the refusal display.

Females began to oviposit as soon as they came to the pond, perhaps preserving some sperm from an earlier copulation. In no case did their behaviour seem to be affected by the presence or absence of males at the pond. On the other hand, males seemed to be strongly attracted by the ovipositing females, though they would not dash towards them while inserting eggs. In all instances, males mated with females that were shifting from an oviposition site, and a number of marked females were seized at least twice on the same day. This leads us to assume (1) that when coming to the ponds, females may be merely driven to oviposition, while only males play an active role in mating behaviour, and (2) that female behaviour during the wheel formation is probably based on reflex responses, as UTZERI & FALCHETTI (1983) suggest for *Coenagrion lindeni.*

Following copulation, the female firstly takes flight to the first oviposition site and while in flight she seems to be able to communicate to her mate, through the tandem linkage, her disposition to lay eggs at or to go away from a place, acting with her swung abdomen in order to determine the tandem speed acceleration or deceleration. Thus, she is probably the member of the tandem pair chiefly involved with the search for proper sites at which to rest and lay eggs.

Two main functions have been ascribed to the tandem male during oviposition: (1) that of preventing the ovipositing female from being disturbed by other males (CORBET, 1962) and (2) that of preventing his own sperm from being displaced by another male (WAAGE, 1979). Probably these functions are only partially effective with *A. affinis*, as the tandem connection appeared to last considerably shorter than total oviposition. Furthermore, as the ovipositing females were receptive to copulation, we doubt whether multiple mating should be considered

to be a disturbance for females, or rather to represent a strategy permitting a higher fraction of the males to leave some offspring.

REFERENCES

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

CORBET, P.S., 1957. The life history of the emperor dragonfly, Anax imperator Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.

CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

HEYMER, A., 1968. Le comportement d'appétence sexuelle chez quelques Anisoptères non-territoriaux (Odonata). *Annls Soc. ent. Fr.* (NS) 4: 891-900.

INOUE, K., S. OBANA & Y. FUJIWARA, 1981. Life history of Aeschnophlebia longistigma. *Tombo* 23 [1980]: 23-27.

JOHNSON, C., 1964. The evolution of territoriality in the Odonata. *Evolution* 18 (1): 89-92.

KAISER, H., 1968. "Zeitliches Territorial Verhalten" bei der Libelle Aeschna cyanea. *Naturwissenschaften* 55 (12): 657-658.

KAISER, H., 1974. Verhaltensgefüge und Temporialverhalten der Libelle Aeschna cyanea (Odonata). *Z. Tierpsychol.* 34: 398-429.

KENNEDY, C.H., 1950. The relation of American dragonfly-eating birds to their prey. *Ecol. Monogr.* 20: 103-142.

MAYER, G., 1962. Untersuchungen zum territorialen Verhalten von Aeschna cyanea Müll. *Verh. XI int. Kongr. Ent.* [1960] 3: 278-281.

MOORE, N.W., 1954. On the dispersal of Odonata. *Proc. Bristol Nat. Soc.* 28: 407-417.

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

SONEHARA, I., 1964. Discovery of the larva and ecological observations on the adult behaviour of Aeschna mixta Latreille in Komoro-city, Nagano Prefecture. *Tombo* 7: 2-12.

UTZERI, C., 1978. Atypical selection of oviposition site in Anax parthenope (Selys) (Anisoptera: Aeshnidae). *Notul. odonatol.* 1 (2): 26-27.

UTZERI, C., E. FALCHETTI & G. CARCHINI, 1976. Alcuni aspetti etologici della ovideposizione di Lestes barbarus (Fab.) presso pozze temporanee (Zygoptera: Lestidae). *Odonatologica* 5(2): 175-179.

UTZERI, C., E. FALCHETTI & C. CONSIGLIO, 1977. Lista degli odonati della tenuta presidenziale di Castel Porziano (Roma). *Fragm. ent.* 13 (1): 59-70.

UTZERI, C. & E. FALCHETTI, 1983. The reproductive behaviour of Coenagrion lindeni (Selys) in central Italy (Odonata: Coenagrionidae). *Odonatologica* 12. (In press).

WAAGE, J.K., 1979. Dual function of the damselfly penis: sperm removal and transfer. *Science* 203 (4383): 916-918.

YOUNG, A.M., 1965. Some observations on territoriality and oviposition in Anax junius (Odonata: Aeshnidae). *Ann. ent. Soc. Am.* 58 (5): 767-768.