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SUBSTRATE UTILIZATION DURING REPRODUCTION BY *ARGIA PLANA* CALVERT AND *ARGIA MOESTA* (HAGEN) (ODONATA: *COENAGRIONIDAE*)

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Most reproductive features such as: absence of courtship, tandem intra-male sperm translocation, tandem oviposition, interactions during oviposition, and oviposition time, were essentially similar in *Argia plana* Calvert and *Argia moesta* (Hagen), studied simultaneously at a 144 m stretch of Cowan Creek in southern Oklahoma. On the other hand, sperm translocation and copulation were closer to water and briefer in *moesta*. Also, the two species oviposited in different substrates: *plana* in *Nasturtium* and debris, *moesta* only in surface *Salix* roots whose lower portions were used by *Hetaerina americana* (Fabricius) for submerged oviposition. The three species were able to occupy the same small area primarily because each used different substrates for perching and oviposition. The adaptable *moesta* successfully invaded the area by laying eggs in the previously unutilized surface *Salix* roots.

INTRODUCTION

We (1961, 1963, 1965) have described the demography and ethology of various species of Zygoptera by studying a single species at a particular locality. In 1964, assisted by Steve Montgomery, Diane Sulzbach Pexa, and Kieth Rhodebeck, we were able to study simultaneously three species of Zygoptera, *Hetaerina americana* (Fabricius), *Argia plana* Calvert, and *Argia moesta* (Hagen), the only ones common at Cowan Creek in southern Oklahoma. General ecological conditions at this small Creek (BICK & BICK, 1958), reproductive behavior of *americana* (BICK & SULZBACH, 1966), and demography of *plana* (BICK &

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* The research was conducted at the University of Oklahoma Biological Station where the Senior Author was Visiting Professor.

BICK, 1968) have already been described. The present paper presents reproductive behavior in *plana* and *moesta*, based on observations of distinctively marked individuals, and describes how three species of Zygoptera utilized different substrates for perching and reproduction along a 144 m stretch of Creek.

ARGIA PLANA REPRODUCTION

Among six observed seizures, five were at water's edge immediately as the females arrived, and one was 3 m away before the female reached the Creek. Neither sex exhibited courtship or display. Normal females, including two seized after lengthy oviposition, never showed refusal movements, but experimentally tethered ones often spread their wings and bent their abdomen tips ventrally in movements very similar to the refusals (BICK, 1966) recorded frequently in normal *Ischnura verticalis* (Say) females.

Every seizure of a female who had not oviposited earlier that day was quickly followed at the same perch by intra-male sperm translocation in tandem wherein the male applied his ninth to his second abdominal segment and in so doing brought the female's head close to his copulatory apparatus. We (1965) reported six similar episodes in *Argia apicalis* (Say) but doubted that these were sperm translocation. Subsequently we saw the event in many other species and obtained movies of it in several, clearly showing a bridge-like structure between the second and ninth male segments. Because these sperm translocations were exactly as in *apicalis*, we are now convinced that each of the six episodes in *apicalis* was intra-male sperm translocation and that the event occurs in tandem in the entire suborder.

Copulation, observed in 12 pairs and completely timed in six, quickly followed sperm translocation at the same perch, at mean distances of 1.5 m from water and .3 m above the surface. Although most pairs did not change location, a few shifted 2-7 times while maintaining copulatory contact, and one broke contact for three intervals, each less than 1 min. During copulation males frequently pumped their abdomens. Leg positions varied among different females and even in the same female during a single episode; most often her prothoracic legs were pressed tightly against her thorax while her meso- and metathoracic ones were extended, sometimes touching only her abdomen, sometimes extending to the substrate.

Certain aspects of oviposition were observed in 18 pairs, and all aspects from beginning to end of the sequence in five. Egg laying was always above the water surface and in tandem except for one female who oviposited alone at the surface for 65 min. Not having seen her in copulation or the beginning of oviposition, we do not know what preliminary circumstances might have caused this lengthy unaccompanied oviposition. At least one unaccompanied oviposition, usually after a male had left a female toward the end of a lengthy episode, occurred in every species we have studied which oviposits primarily in tandem.

Exploratory activity, wherein the female briefly probed many substrates such as sand, grass, algae-covered rocks, and even a tennis shoe, preceded and interrupted every oviposition sequence. Eggs were probably not actually inserted during most of this period, characterized by momentary probing and frequent shifting. It was sometimes difficult to differentiate such exploration from actual egg deposition and this must be realized when considering time data in Table I.

Table I

Duration of reproductive events in three species of *Argia*

	apicalis*	plana	moesta
Sperm translocation			
No. of pairs	0	9	9
Range (seconds)	-	12-30	5-17
Mean (seconds)	-	21.4	10.6
Copulation			
No. of pairs	15	6	9
Range (minutes)	10-27	19-40	14-31
Mean (minutes)	15.9	26.9	22.2
Exploration			
No. of pairs	7	5	5
Range (minutes)	10-50	16-35	3-49
Mean (minutes)	25.5	21.4	24.0
Oviposition			
No. of pairs	8	5	5
Range (minutes)	53-115	38-56	37-67
Mean (minutes)	72.7	47.2	47.2

* Modified from BICK & BICK, 1965.

Five pairs, observed constantly from the end of copulation until the female left water, spent a total of 236 min in effective oviposition. During this interval, the time spent at every substrate was recorded. Of the total time, 48% was at water cress (*Nasturtium*) and 50% was among debris consisting of decayed leaves and twigs in shallow water.

This population of *plana* utilized *Nasturtium* and debris almost exclusively for actual oviposition even though other materials were present and were contacted in preliminary probing.

Ovipositing pairs were often crowded, particularly at masses of debris. Most often, without wing movement, the male remained rigidly upright on the thorax of the female in the typical "*Agrion* type" position (BUCHHOLZ, 1950). However, all males occasionally leaned forward, contacting the substrate or an adjacent pair. In addition, males of ovipositing *plana* pairs often leaned momentarily against each other, legs touching, in a position similar to ST. QUENTIN's (1965) illustration for *Erythromma najas* (Hansem.) and HEYMER's (1966) for *Platycnemis latipes* (Rambur). The former author interprets this behavior as "mutual assistance", the latter as "attitude de menace". We have seen these brief contacts in *Enallagma civile* (Hagen) and in *apicalis*, as well as in *plana*, and consider them random accidents which are inevitable when pairs oviposit under crowded conditions. In one movie sequence of *civile*, the upright males actively move their legs against each other in what seems more like a boxing match than mutual assistance.

Probably because of crowding, pairs moved frequently, averaging 2.5 shifts each min and 50 cm per shift. Despite crowding and frequent shifting, the five pairs interacted a total of but 38 times, and only with conspecific pairs or males. The observed pair sometimes (9) did not react to the intruder, but usually the male (28) or the female (1) "wing warned" as we (1963) describe for *civile*. As in *apicalis* (BICK & BICK, 1965), *plana* pairs were remarkably tolerant, usually (35) sharing the perch with the intruder. Interspecific interactions did not occur, undoubtedly because neither *americana* nor *moesta* used *Nasturtium* or debris for perching or ovipositing.

Termination of oviposition, observed in 16 pairs, occurred suddenly without preliminary signals. In all, the female withdrew her abdomen from water and extended it, whereupon the pair paused momentarily at the spot. Six pairs then flew, separated in flight, and the female left water. Ten pairs separated at the termination perch with scarcely any discernible movement by either sex. Subsequently as these females flew from water: four were not pursued, three were captured by strange males, two escaped strange males, and one escaped pursuit by her previous mate. The three captured by strange males were in tandem briefly without copulating. One of these pairs performed the zigzag flight, and one male "bit" the female as we (1963) report for *civile*. No female copulated or oviposited twice in the same day.

ARGIA MOESTA REPRODUCTION

A. moesta and *plana* showed similar behavior during seizure and intra-male sperm translocation but differed in one detail of copulation. During copulation, the male *plana* applied the femoral-tibial joints of his metathoracic legs to the female's abdomen ("kicking", BICK & HORNUFF, 1966) primarily near the end of copulation so that he seemed to push away the female abdomen. In contrast, the *moesta* male kicked at irregular intervals throughout copulation suggesting stimulation of the female. Similar kicking in the *apicalis* male (BICK & BICK, 1965) appeared to guide the tip of the female abdomen to the male copulatory apparatus. Thus, it would seem that timing and function of kicking is species specific. However, recognizing the behavioral plasticity of the Zygoptera, we believe that within any species of *Argia* these leg movements may occur at various times during copulation and may serve various functions as BICK & HORNUFF (1966) record for *Enallagma exsulans* (Hagen).

Oviposition in *moesta* is extremely variable. At the Creek, it was always in tandem in red roots of willow (*Salix*) where the female never completely submerged even though splashing water from the rapid current sometimes briefly covered her. In contrast, at nearby Lake Texoma females oviposited while submerged and unaccompanied, and at Lake Erie, Ohio, tandem pairs descended several feet beneath the surface. There are also many earlier records of submerged oviposition, e.g., WILLIAMSON (1899, 1932), KELLICOTT (1899), WALKER (1953), DONNELLY (1961).

The time spent at every substrate was recorded for five *moesta* pairs. Although these females very briefly probed many materials such as algae-covered rocks, debris, grass, and *Nasturtium* in exploratory activity, they remained for long periods only at *Salix* roots, and the total of 241 min of effective oviposition was entirely in these roots at the water surface. This adds still another substrate to the diverse materials already recorded: algae-covered boards (WILLIAMSON, 1899); submerged timbers, algae-covered rock (KELLICOTT, 1899, DONNELLY, 1961); debris in water (WILLIAMSON, 1932, HARWOOD, 1960); sides of a diving raft (WALKER, 1953). Moreover, we have seen *moesta* oviposit in boat mooring ropes at Lake Erie, and in *Polygonum* and old water-soaked sticks at Lake Texoma.

Like *plana*, the *moesta* male usually remained rigidly upright on the thorax of the female. Unlike *plana*, the *moesta* male seldom leaned forward to touch the substrate, and never leaned on other pairs because the small population precluded crowding.

Five ovipositing *moesta* pairs were involved in 40 interactions, all with conspecific pairs or males. On each of nine occasions, a pair, without reacting, shared its perch with an intruder. However, the male (30) or the female (1) usually wing warned an intruder which resulted in sharing the perch 28 times and warding off an intruder three times.

Ovipositing in *moesta* ended as in *plana* without signals. Thereafter four of the five *moesta* females did not mate a second time: one flew away from water without pursuit, one avoided a single pursuit flight by her previous mate, one escaped five such flights, and one remained at water 79 min successfully evading five approaches by her previous mate, 19 by strange males. The female escape always involved flight rather than unreceptive signals which we could detect. The fifth female was seized by her previous mate, and the pair engaged in a completely normal second reproductive sequence during the same day, a most exceptional event for any species of Zygoptera which we have studied.

DURATION OF REPRODUCTIVE EVENTS

Table I summarizes duration of reproductive events in three species of *Argia*. CORBET (1963) states that species which copulate at water do so more briefly than those away from water because of interference by unpaired males. This hypothesis is readily substantiated when copulation times for species of *Calopterygidae* (such as *americana*, BICK & SULZBACH, 1966) are compared with those of many *Coenagrionidae*, and it holds, though to a lesser degree, when members of lower taxa such as *plana* and *moesta* are compared. Copulation times varied greatly among individuals of both *plana* and *moesta* and broadly overlapped in the two species. However, the mean was slightly longer in *plana* (27 min) than in *moesta* (22), and the event was further from water in *plana* (1.5 m) than in *moesta* (.4). Also, the mean number of interactions between copulating pairs and intruders was fewer in *plana* (2.8 per pair) than in *moesta* (7.5) which copulated closer to water.

Even though the distinction between exploration and actual insertion of eggs was not always perfectly clear, mean oviposition time (Table I) in *apicalis* (73 min) was significantly but unaccountably much longer than in *plana* and *moesta* (each 47). Differences in structure of oviposition materials used by these three *Argia* species seem insufficient to account for this time difference.

HABITAT UTILIZATION

Both *plana* and *americana* were present at the study area for many years, but *moesta* was not there prior to 1964 when it invaded from the mouth of the Creek and Lake Texoma. In the summer of 1964, a large population of *plana* and much smaller ones of *americana* and *moesta* were able to successfully occupy the study area because the three species perched in different places and oviposited either in different substrates or in different parts of the same substrate.

H. americana most often perched 1 or 2 m above water on roots and other vegetation of the canyon walls or on large dry rocks in the Creek. The other two species perched much closer to the water surface: *moesta* on smaller rocks distant from those used by *americana*, *plana* on the abundant *Nasturtium*.

A. plana oviposited in *Nasturtium* and in debris, *americana* (BICK & SULZBACH, 1966) only in *Salix* roots. Furthermore, the latter odonate always oviposited in deeper roots beneath the surface leaving those at the surface available for some other species. Even though elsewhere *moesta* uses a variety of material, the invading population deposited eggs entirely in *Salix* roots at the surface apparently because this was the only suitable situation unused by the other two species. *A. moesta* often oviposits while submerged, but it was able to move into our upstream area because its adaptability allowed surface oviposition which resulted in less competition with the previously established *americana.*

Because of these spatial separations among the three species, most of the interactions among unpaired males were conspecific as were all of the interactions during *plana* and *moesta* oviposition.

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