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VISUAL AND TACTILE STIMULI IN CHOICE OF OVIPOSITION SUBSTRATES BY THE DRAGONFLY *PERITHEMIS MOOMA* KIRBY (ANISOPTERA: LIBELLULIDAE)*

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Prior to the establishment of a territory, males select a suitable oviposition substrate which is detected by visual and tactile stimuli. Video films analysed in slow motion revealed that the individuals extend their hind legs while making short dips over the oviposition substrate, touching the ground for 0.01 - 0.02 s with the tarsi. Females use their legs in the same manner during oviposition. By setting up experimental oviposition sites it could be shown that the individuals are first guided by their visual and then by their tactile sensory system. Pancake-like substrates consisting of fine structured, emergent material completely surrounded by water are accepted visually and are subsequently examined physically with the tarsi. Choice experiments with various materials revealed that only those substrates which have a gelatinous surface are accepted. Following site selection the males perch nearby, perform patrolling flights and chase conspecific intruders, while the females oviposit at such localities.

INTRODUCTION

After a short maturation period away from the larval habitat adult dragonflies return to the water where reproduction takes place. As in most temperate-zone species the oviposition sites serve as rendezvous, the highly mobile adults of both sexes must be able to detect habitats favourable for the egg and larval stages (CORBET, 1980). The choice of oviposition sites is of great importance with respect to reproductive success (WAAGE, 1987). It depends on physical and biological features such as size and structure of the site, vegetation, predators and conspecifics (UBUKATA, 1984; WOLF & WALTZ, 1988; BUCHWALD,

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1989; MARTENS, 1989; REHFELDT, 1990; STERNBERG, 1990).

Suitable egg-laying places have to be identified by reliable characteristics (proximate factors) which are easily recognizable. It is generally assumed that oviposition sites are perceived visually (CORBET, 1962). This presumption has been confirmed recently by choice experiments (WILDERMUTH & SPINNER, 1991). The individuals of *Somatochlora arctica* were chiefly attracted by dummies consisting of black plastic foil with shining surface. Both sexes exhibited all the typical elements of the reproductive behavioural pattern. In addition, the males showed repeated dipping movements. When the surface was touched a sound could be heard. This behaviour, which occasionally also occurs at natural egg--laying places, might be interpreted as tactile examination of the oviposition material. However, the significance of „water-touching" (CORBET, 1962) remains unclear, as it does not appear regularly. It is not even known exactly which parts of the body get into contact with the ground during this special flight manoeuvre. In some species it is probably the abdominal tip (MOORE, 1957; WILLIAMS, 1977; PARR, 1983), in others the head (PARR & PARR, 1972).

The aim of the present study was to clarify the roles of the visual and tactile systems for the recognition of the oviposition site by field experiments, and to determine the cues by which the animals identify the suitability of substrates as egg-laying places. For an approach to these problems the neotropical anisopteran *Perithemis mooma* proved a favourable subject because preliminary observations revealed that in this species both the visual and the tactile system are definitely involved (WILDERMUTH, 1991).

MATERIAL AND METHODS

This investigation was carried out from November 1990 to January 1991 at a man-made farm pond near Guaiba, S of Porto Alegre, Rio Grande do Sul, Brazil. The pond was ca 200 m in diameter and surrounded by pasture and small woods. Water plants were lacking except for scattered patches of *Eichhornia azurea*, *Ludwigia* sp., *Nymphoides indica* and *Typha* sp. along the margin (for plan see WILDERMUTH, 1991). These were the localities where the reproductive activities of *P. mooma* were concentrated, thus offering an opportunity to make observations on behaviour at an undisturbed site.

For the experiments a straight stretch of 12 m along the water edge adjacent to a patch of *Eichhornia* plants was chosen. The strip was characterized by shallow water, lack of vegetation and a substrate consisting of muddy sand. After the location had been cleared of dead plant material and other structures, which could have potentially influenced the behaviour of the animals, various experimental oviposition sites were established. Single leaves of *Eichhornia* were offered as perches. For oviposition substrates I used different organic objects (Tab. III). Mouldable materials were shaped into a pancake--like mass of about 10 cm in diameter and subsequently placed in such a way that they emerged in the same way as natural oviposition substrates. Pieces of black plastic foil strewn with glass splinters, which imitated the sparkling light pattern of wet natural oviposition material, were fixed on little floating boards, these being anchored. In some experiments natural substrates were immersed or were placed on land near the water line.

Each of the experiments on the establishment of oviposition sites with natural material, displacement and exchange of oviposition substrates was repeated five times. An experimental oviposition site was considered to be accepted when a male individual had examined the substrate, exhibited patrol flights and finally perched. In choice experiments the reactions of at least 10 male individuals were tested. In two additional cases the reactions of both sexes were analysed quantitatively by referring to six behavioural elements. Simultaneously, at intervals of one minute I noted which of the possible territories was occupied or not.

All observations were made by eye or with the aid of binoculars (Nikon Travelite II, 7 x 20) whose shortest working distance was 2.8 m. In addition certain behavioural elements were filmed with a video camera (Panasonic F 10) equipped with a strobe effect shutter (shutter speed 1/1000 s, 50 video signals per s).

RESULTS

EXAMINATION OF THE SUBSTRATE AT UNDISTURBED SITES

At the pond under observation males in search of oviposition sites flew slowly along the margin at heights of 30 to 50 cm. When they came across floating mats of algae, projecting logs or emergent felts of *Eichhornia* rootlets they stopped and made repeated short dips towards the substrate touching it with the tarsi of the hind legs, obviously in order to inspect the ground more closely. This examination behaviour could be followed by eye, however the details of the movements were only revealed by the film. An analysis of the corresponding sequences at slow motion showed that the hind legs were stretched out quickly and withdrawn after each touchdown (Figs 1, 2). The maximum extension including touching the ground lasted 0.02 s at most. During the flight the mates held their body axis slightly inclined. The flight paths which the individuals performed in the course of this manoeuvre resembled ellipses or figure-of-eight loops when the substrate was small and circular. More extended and linear sites were examined point by point. Actual examples of light patterns and various standardized movements are shown in Figures 3 and 4.

From the first arrival of a male at a suitable site the examination procedure lasted up to several minutes (often interrupted by hovering and patrol flights) before the individual perched, thus demonstrating that he had established his territory. If two or more males were competing for the same site the process could be extended to up to an hour.

The females either detected the oviposition substrate on their own or they were led to the site by a territorial male. When arriving they started immediately making oviposition movements. From a hovering position 5 to 10 cm above the substrate they rapidly dipped down, holding their body axis slightly inclined. While approaching the substrate they extended their hind legs and subsequently, within 0.02 s, bent down the abdomen and beat it down powerfully. For a short moment both tarsi and abdominal tip were in contact with the ground (Figs 1, 2). During the following flight upwards the abdomen was bent back to its original

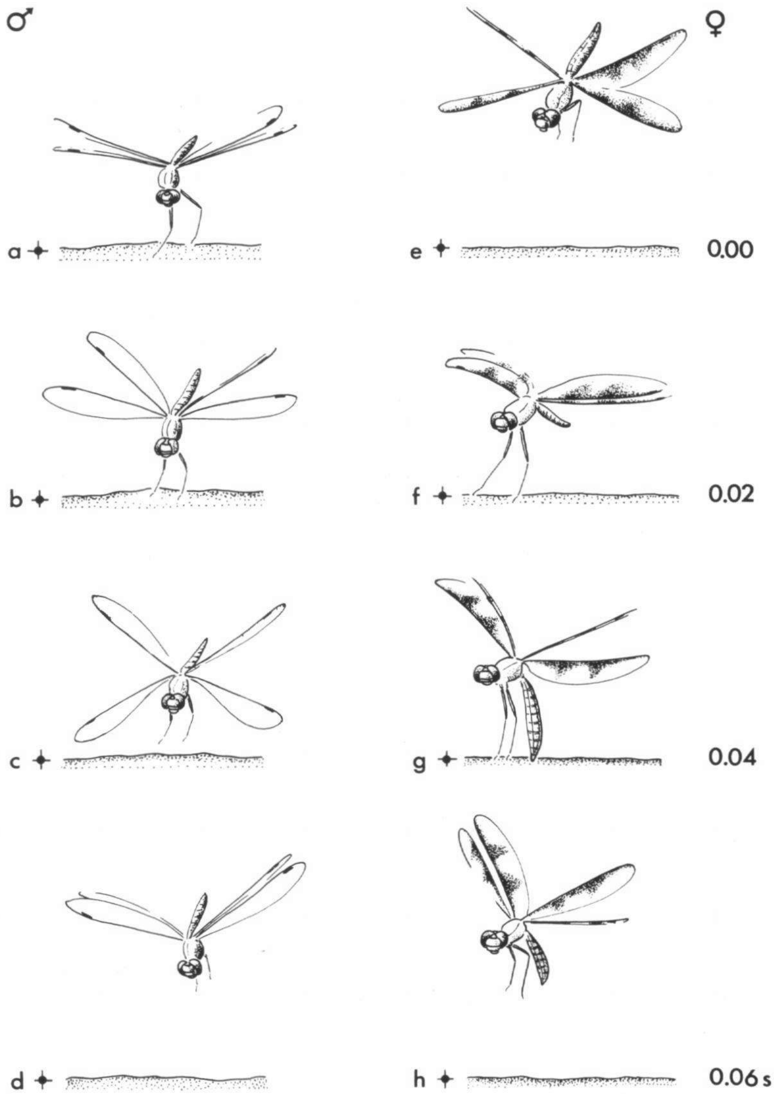

Fig. 1. Male (left) and female (right), physically testing the oviposition substrate. The sequence shows flight manoeuvre and movement of the hind legs in the course of 0.06 s. – [Drawings based on video film; crosses mark reference point on screen].

posture and the individuals returned to the starting position. These circular flight manoeuvres were repeated about twice per s. During oviposition following copulation exactly the same flight movements occurred as described above.

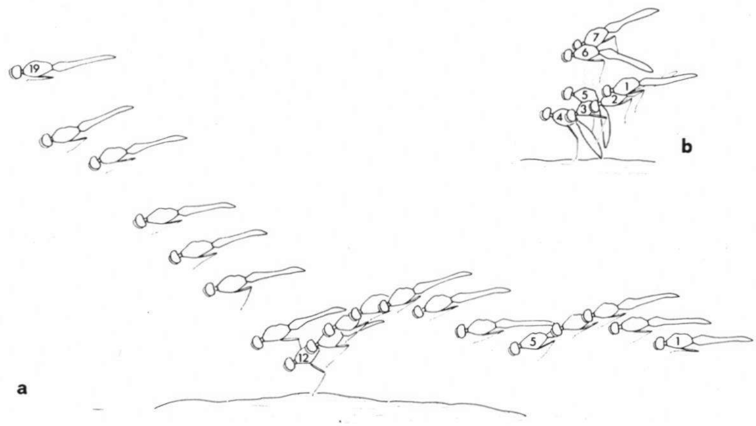

Fig. 2. Movement of hind legs and abdomen during tactile examination of the substrate: (a) The male arriving at the substrate intends to test the latter at the right end (5), however, it moves on to the centre, touches the ground with the tarsi (12) and subsequently folds the legs while flying off. Sequence 1 - 19 lasts 0.36 s. – (b) Female ovipositing. Sequence 1 - 7 lasts 0.12 s. – [Drawings based on video-film].

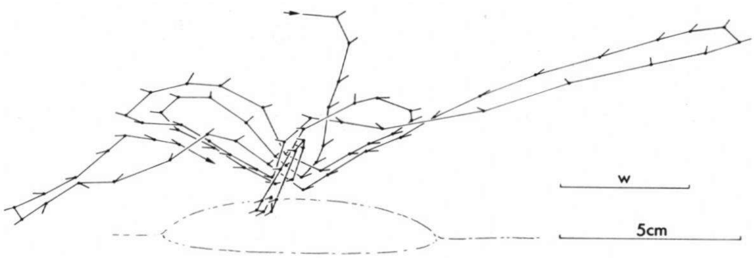

Fig. 3. Lateral view of the flight path of a male testing the oviposition substrate in the course of 1.44 s. The individual is shown at intervals of 0.02 s. – [The symbols show head and body axis, much reduced in size; – w = wing span of male. Drawing based on video film].

ESTABLISHMENT OF EXPERIMENTAL OVIPOSITION SITES

Normally both sexes choose emergent mats of *Eichhornia* rootlets as egg depository substrate. Places partly hidden in the foliage of emergent vegetation were preferred to those on open water. By placing mats of the same oviposition material near the water line, together with a suitable perch similar to a natural situation, males could easily be attracted and stimulated to establish a territory (Fig. 5). As at undisturbed sites they examined the material thoroughly, used the

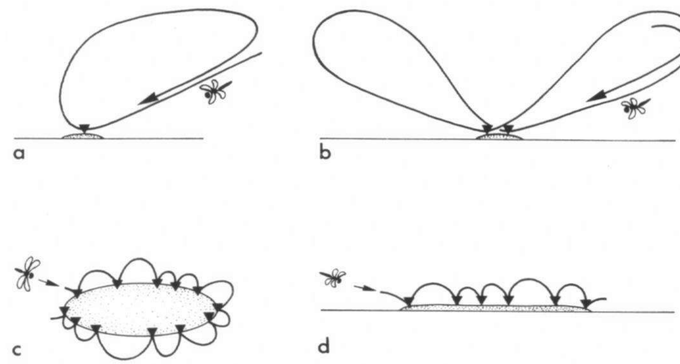

Fig. 4. Flight paths of males physically testing the substrates: (a, b) Circular and figure-of-eight flight path at small substrate; – (c, d) Flight path at more extended substrate; – (c) view from above, – (d) lateral view.

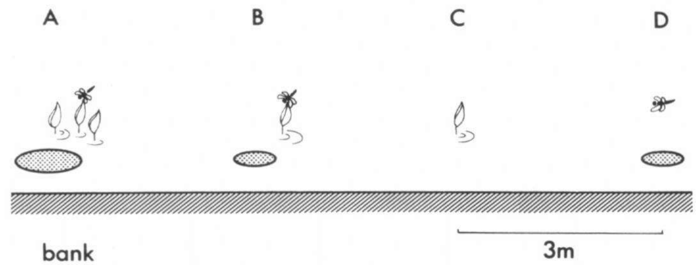

Fig. 5. Natural (A) and experimental oviposition sites (B,C,D) along pond margin. Oviposition substrates are shown by ellipses, perches by leaves. Sites A, C and D are occupied by males. At site D the territory owner hovers over the substrate, due to the lack of a perch.

perch nearby, performed patrolling flights and chased conspecific intruders. The females were also attracted, and sexual behaviour including courtship, copulation and oviposition was exactly the same as at natural places. Substrates lacking perches were also accepted. In these situations the territorial male stayed mainly on the wing and rested only for short intervals on the ground nearby. Perches without oviposition substrates in their vicinity were not used.

DISPLACEMENT AND EXCHANGE OF OVIPOSITION SITE

A patch of oviposition substrate, together with a perch, was placed as described above. After a male had established his territory at the site, I shifted the substrate beside another perch 3 m apart from the original spot. The proprietor of the territory, who had flown off during this procedure, returned for a short while and then changed to the new locality. There he examined the material and subsequently perched. Five min later the substrate was transplanted to the first point. The male soon followed, performed an examination and perched nearby. However, this experiment could not be repeated ad infinitum. The reactions soon became sluggish and unclear. It seemed that the individuals, once having established a territory, would stick to it thus showing a certain site tenacity.

In a further experiment I replaced the oviposition substrate, which was already in the possession of a male, by a dummy consisting of beige coloured plastic tissue, and shifted the original material 3 m apart next to another perch (Fig. 6). In the beginning the male did not react to the alteration and returned several times to his perch, even when chased off by the experimentator. Then the insect examined the dummy briefly, flew to the new site and performed examination behaviour for 3 min, interrupted by short patrol flights, and returned to the first site where it made quick dips towards the dummy. Five min after he had established himself at the new locality I exchanged the oviposition substrates of the two sites, while the owner of the territory was engaged in an aerial fight with an intruder. Both males returned to the territory and soon changed to the locality with the natural substrate. After a period of intensive fighting and examination one of the males perched while the second left. The exchange of the substrates could then be successfully repeated once again. However, not all individuals reacted so promptly as in the example described. After repeated

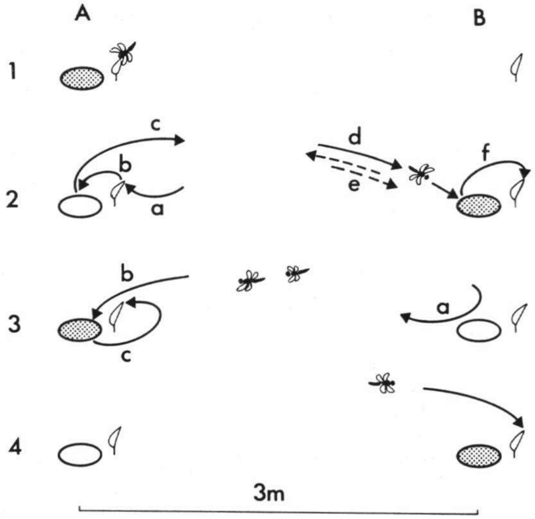

Fig. 6. Exchange of oviposition substrates and subsequent reactions of a territorial male: (1) Male perched at experimental site with natural substrate; — (2) Substrate displaced to B and replaced by dummy. [b - f = sequence of flight movements after the male has returned to his perch (a), — e = repeated flight from B to A and vice versa]; — (3) Exchange of natural and dummy substrates while the territory owner was involved in aerial fight with an intruder [a - c = sequence of flight movements, — c: one male perches while the other male has disappeared]; — (4) Third exchange of oviposition substrates; the male flies from A to B and perches without having examined the substrates. — For details see text.

exchange of the substrates some males obviously became confused, showed unclear reactions or they stuck to the territory which they had set up originally.

CHOICE EXPERIMENTS

In an initial experiment I offered *P. mooma* three possible sites with different substrates arranged in a straight line. The site with natural substrate soon became occupied and there was much sexual activity during the 3.5 h of observation time as shown in Table I. Females also reacted positively to the experimental oviposition site. At the spot with dry and thus hard, unflexible rootlets I noticed 12 flights over the site and 24 bouts of examination behaviour, but no sexual activity. No male established a territory and females did not stop there. Plastic tissue was generally overflown and was examined only once. In a second experiment which I analysed quantitatively I set up three further dummy substrates in competition with natural material (Tab. II). The localities with emergent *Eichhornia* rootlets were clearly accepted again, even if the substrate was placed on a floating plastic disc. A piece of black plastic foil covered with a thin layer of algae was repeatedly examined by males but never accepted. Rafts with black plastic foil strewn with glass splinters of different colours were only overflown.

The results of additional choice experiments with a number of various substrates are summarized in Table III. The reactions showed that material with a relatively coarse looking structure was refused after visual inspection. At substrates with a smooth surface the males stopped and tested them with their tarsi. However, only those which had a soft, gelatinous surface were accepted. The size of the substrate was of minor importance; some individuals even accepted patches of

Table I

Number of different reactions towards natural and dummy substrates in a choice experiment. The substrates were linearly arranged at distances of 3 m. The sequence of the substrates in the table corresponds to the sequence of the experimental arrangement. [t = time during which the sites were occupied by territorial males in the course of the observation period of 3.5 h]

Substrate	Over-flights	Exami-nation	Fights	Court-ship	Copu-lation	Ovipo-sition	*t (%)*
Eichhornia rootlets (experimental site)	2	39	47	7	1	7	*100*
Hard, unflexible rootlets	12	24	-	-	-	-	*0*
Beige coloured plastic tissue	18	1	-	-	-	-	*0*

not more than 3 cm in diameter. Furthermore the substrates had to be above the surface of the water and completely surrounded by it.

DISCUSSION

Dragonflies use their legs in perching (BUCHHOLZ, 1957; HEYMER, 1969), catching prey (ST. QUENTIN, 1953), grooming (ST. QUENTIN, 1936), attacking competitors (RÜPPELL, 1987), repelling males (RÜPPELL, 1989), courting (ROBERTSON, 1982), clinging to the mating partner, walking and climbing (CORBET, 1962). Among dragonflies with exophytic oviposition, the employment of legs in connection with egg-laying has hitherto only be reported for females of *Perithemis tenera* (RUPPELL et al., 1989). These authors state that legs are merely used for keeping an appropriate distance during oviposition. However, if this is a function at all, it is of secondary importance, for in other dragonflies such as *Somatochlora, Sympetrum, Libellula* and other Libellulidae the legs of the females remain folded during oviposition (ROBERT, 1959; pers. obs.). In *P. mooma* at least the hind legs, with respect to the oviposition behaviour,

Table II

Number of different reactions towards natural and dummy substrates in a choice experiment. The substrates were linearly arranged at distances of 3 m. The sequence of the substrates in the table corresponds to the sequence of the experimental arrangement. [t = time during which the sites were occupied by territorial males in the course of the observation period of 3.1 h]

Substrate	Over-flights	Exami-nation	Fights	Court-ship	Copu-lation	Ovipo-sition	*t (%)*
Natural, undisturbed site with *Eichhornia* rootlets	-	18	18	1	1	2	*100*
Black plastic foil (dry), strayed with brown glass splinters	16	-	-	-	-	-	*0*
Black plastic foil (dry), strayed with colourless glass splinters	18	-	-	-	-	-	*0*
Eichhornia rootlets on black plastic dish (wet)	-	19	18	2	1	2	*96*
Black hard plastic foil, partly wet and covered with thin layer of algae	2	15	-	-	-	-	*0*

Table III

Summary of the reactions of *P. mooma* (males) towards experimentally set up oviposition substrates. [+ positive reactions; - no reactions; (+); (-) reactions varied between different individuals. Unless stated, the substrates were pancake-like masses of about 10 cm in diameter]

Substrate	Examined	Accepted
Sand, emergent	-	-
Clump of grasslike waterplants, emergent (green young leaves of *Eichhornia*)	-	-
Clump of olive waterplants with grasslike leaves, emergent	-	-
Brown, tulle, emergent	-	-
Black plastic foil with brown or colourless glass splinters, emergent	-	-
Black hard plastic, partly wet and covered with thin layer of algae, emergent	+	-
Beige coloured plastic tissue, emergent	(+)	(-)
Beige coloured plastic tissue, immersed	-	-
Hard, unflexible rootlets, emergent	+	(-)
Hard, unflexible rootlets, immersed	-	-
Beige coloured plastic foil, covered with thin layer of gelatinous mud, emergent	+	+
Mat of algae, emergent	+	+
Log or stone, covered with thin gelatinous layer, emergent	+	+
Felt of *Eichhornia* rootlets, partly covered with mud and algae, emergent	+	+
Felt of *Eichhornia* rootlets, partly covered with mud and algae, patch of 3 cm in diameter	+	+
Felt of *Eichhornia* rootlets, partly covered with mud and algae, immersed	-	-
Felt of *Eichhornia* rootlets, partly covered with mud and algae, on land, near water line	-	-

are primarily used for tactile examination of the substrate, since this behaviour is not only observed in females but also in males. Furthermore the choice experiments with males revealed that certain substrates were refused after repeated touching while others were accepted. Obviously the individuals are able to discriminate different materials based on their physical properties.

JACOBS (1955) described the reproduction behaviour of *P. tenera* which also performs an examination of oviposition sites. Although the males do not bend down their abdomens during this activity she interpreted the dipping movements as simulation of oviposition, thus indicating to competitors that a specific site is being guarded. However, as shown in this study, the primary function of the short dips is to examine the oviposition substrate. In addition they might have a display function, as in both species so far studied several individuals are often involved in the examination „dances" which sometimes last up to one hour (JACOBS, 1955; WILDERMUTH, 1991).

Male and female individuals flying slowly over the water in search of oviposition sites are primarily guided by their visual sensory system. They react only to experimental substrates if these are emergent, are surrounded by water and have a smooth looking surface (seen by the human eye). Materials with coarse structures such as clumps of grass-like water plants are not further inspected. Obviously, such materials are refused initially at the level of visual information because the image does not fit into the scheme of oviposition substrate.

Table IV

Hierarchy of the types of recognition in finding an oviposition site

Type of recognition	Object	Proximate factor
long-range; visual	water body	horizontal reflecting surface of at least some m^2 in size
medium-range; visual	egg-laying substratum	patch of fine structured material, protruding from and surrounded by water
short-range; tactile	egg-laying substratum	gelatinous (wet?) surface

Finding a suitable egg-laying place in *P. mooma* may be considered as a process which runs stepwise from long-range via medium-range to short-range recognition (Tab. IV). The features of the oviposition place recognized by the visual and tactile sensory system serve as proximate factors which supply the female with information on the ultimate factors determining the survival rate of eggs and larvae. The patterns of proximate factors are specific for each species and usually consist of visually recognizable elements such as size and depth of the water body, water current and vegetation structure (BUCHWALD, 1989; WILDERMUTH, 1986, 1987). As yet such factors have been experimentally tested in only very few species (WILDERMUTH & SPINNER, 1991; WILDERMUTH, 1992; STERNBERG, 1990).

It is a striking fact that in *P. mooma* both females and males choose their oviposition substrate with great care. Both sexes have a highly developed method for precise examination of the egg-laying site. By visually and physically testing the material the female will obtain detailed information about the suitability of the habitat for egg and larva before she decides to oviposit. Male individuals on the other hand will have the best chances of a high copulation rate at locations which are accepted by females for oviposition. If the males select the substrate with the same care and methods as females do, they will increase the probability for encounters with mates.

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