

MALE BEHAVIOUR IN THE MALE DIMORPHIC DAMSELFLY *PARAPHLEBIA QUINTA* CALVERT (ZYGOPTERA: MEGAPODAGRIONIDAE)

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P. quinta is a tropical sp. with 2 ♂ morphs: the black-winged (BW) ♂ and the hyaline-winged (HW) ♂; here their sexual behaviour is described. In general, ♂♂ seem to spend relatively little time in flying activities. This may be explained either by the inability to recognise conspecifics and, hence, engage in social interactions, or by the reduced energetic reserves that prevent them from engaging in expensive activities. BW ♂♂ were more aggressive and site-faithful than HW ♂♂. BW defended spaces containing debris (plant and wood) against conspecifics while HW did not. BW-BW, BW-HW and HW-HW aggressive encounters were common. Despite their non-aggressive nature toward BW ♂♂, HW ♂♂ behaved aggressively when faced by HW ♂♂. The distance flown by each morph from ♂ grasping of the ♀ until she started oviposition was measured: HW flew longer distances than BW. These differences between ♂ morphs are compared to those found in *Mnais p. pruinosa*, another ♂ dimorphic zygopteran. Similar to what happens in that sp., both tactics in *P. quinta* are possibly maintained due to the similar reproductive and energetic costs accrued by and benefits paid to each morph.

INTRODUCTION

Male territoriality represents an ubiquitous phenomenon in many dragonfly taxa (reviewed by CORBET, 1999). In the Zygoptera, territoriality is particularly prevalent among several taxa of the superfamily Calopterygoidea, such as in the genera *Calopteryx* (e.g. WAAGE, 1973), *Cora* (e.g. GONZÁLEZ-SORIANO & VERDUGO-GARZA, 1984; FRASER & HERMAN, 1993), *Heliocypha*

(ORR, 1996), *Hetaerina* (JOHNSON, 1962), *Libellago* (ORR, 1996), *Mnais* (e.g. HIGASHI, 1981), *Platycypha* (ROBERTSON, 1982), and *Rhynocypha* (ORR, 1996). In other zygopteran families, territorial behaviour is a common feature among some genera of Megapodagrionidae, such as *Heteragrion* (GONZÁLEZ-SORIANO & VERDUGO-GARZA, 1982) and *Paraphlebia* (GONZÁLEZ-SORIANO & CORDOBA-AGUILAR, 2003); in Protoneuridae, such as *Chloroneura* (SRIVASTAVA & BABU, 1985) and *Nososticta* (THOMPSON, 1990); in Platystictidae, such as *Palaemnema* (GONZÁLEZ-SORIANO et al., 1982); in Pseudostigmatidae, such as *Megaloprepus* (FINCKE, 1984); in Platycnemididae, such as *Platycnemis* (HEYMER, 1966); and in some Coenagrionidae, such as *Megalagrion* (MOORE, 1983) and *Pseudagrion* (MESKIN, 1986).

Males of the oriental genus *Mnais* are dimorphic. One morph bears pigmented wings and shows territorial behaviour, while the other morph has hyaline wings and behaves as subordinate, non-territorial individuals (WATANABE & TAGUCHI, 1990; SIVA-JOTHY & TSUBAKI, 1989a, 1989b). This phenomenon is not confined to this taxon. Males in some species of the New World genus *Paraphlebia*, such as *P. quinta* and *P. zoe*, are also dimorphic (GONZÁLEZ-SORIANO, 1997; GONZÁLEZ-SORIANO & CORDOBA-AGUILAR, 2003). In *P. quinta*, for example, one morph is the black-winged (BW) male while the other is the hyaline-winged (HW) male. BW males are usually larger individuals, bearing a black transverse band on the wing tips, while HW males are smaller, with entirely clear wings, resembling those of females (GONZÁLEZ-SORIANO & CORDOBA-AGUILAR, 2003). How the two morphs are maintained is uncertain. In *Mnais*, the maintenance of both morphs is possibly due to the balanced reproductive benefits and costs of each phenotype (SIVA-JOTHY & TSUBAKI, 1989a; PLAISTOW & TSUBAKI, 2000).

Here we present a summary of the behavioural components of the male sexual activities of *P. quinta*. Our first aim is to provide a descriptive framework of the behaviour of each morph. Additionally, we present a preliminary analysis of the cost of accompanying a female by each morph, which is discussed in the framework of the possible fertilisation success achieved by both types of males.

MATERIAL AND METHODS

Field work was carried out at a small seepage, divided into 36 quadrants (2 × 2 m), at the Estación de Biología Tropical Los Tuxtlas in the state of Veracruz, Mexico (95°04'–95°09'W and 18°34'–18°36'N). Most observations were performed on 23–26 August 1984 and 19 July–15 August 1986. In both years, males and females were individually marked on their wings, using an indelible ink pen, allocating distinctive numbers. In both years, observations of 30–60 min duration of focal males were carried out. In 1986, daily censuses were made and the position of each marked individual was located on a scale map. By this procedure, daily movements of each individual were measured and tracked with relative accuracy.

On those dates and also on 8–11 July 1988 and 19–23 August 1990, we recorded the trajectories followed by each morph from the male grasping of the female prothorax (at the onset of copulation)

to the beginning of the first oviposition bout.

For the use of parametric tests, we transformed those data that were amenable for such manipulation. Mann Whitney tests are referred to as U tests. Results are presented as means \pm STD unless indicated otherwise.

RESULTS

Daily censuses were carried out during 18 consecutive days (19 July-5 August 1986). The number of individuals of both male morphs found daily fluctuated between 33 and 41 individuals (36.5 ± 2.59). However, males remained in the study sites for variable periods (in days; BW males, 11.5 ± 6.5 , $N = 35$; HW males, 4.8 ± 4.8 , $N = 45$). For BW males, the minimum number of days an individual was found in the same site (during a maximum of a 17-day period) was 1, while the maximum (but not necessarily consecutive days) was 17 ($N = 35$). More than 50% of BW males were found in the same site for 16-17 days, and only 14% were seen on the day of marking. For HW males, the minimum of days present in the same site was 1, while the maximum was 16 ($N = 45$). Only 4.6% of the HW males remained between 15-16 days, 65% were concentrated within a greater interval of 1-15 days, and a large number (almost 30%) were present only on the day of marking. These differences indicate that BW males stayed for longer periods than HW males in the places of marking (U test = 1878.5, $P < 0.0001$). As for females, they were found fewer days (0.5 ± 0.8) compared to BW (U test = 3019, $P < 0.0001$) and HW males (U test = 3653.3, $P < 0.0001$). The minimum number of days they returned to the general area was 1 day, while the maximum was 4.

The four main flying activities, performed by the two male morphs at the reproductive site were: changes of perching site, aggressive flights (mainly directed at same-sex conspecifics), investigatory flights (short-duration flights of a few cm with no clear explanation), and patrolling flights (in which the animal covers the area around its perching site) (Tab. I). Flying activity was fairly low in comparison with total time in activity (0.87% for BW and 0.38% for HW). The only significant difference in flying activities between morphs was in the aggressive flight:

Table I
Account of the different flying activities at the reproductive site
by *P. quinta* black-winged (BW) and hyaline-winged (HW) males

	Perching site change		Aggressive flight		Investigatory flight		Patrolling flight	
	BW	HW	BW	HW	BW	HW	BW	HW
Occurrence	20	17	15	1	55	20	20	1
Mean duration	2.0	2.2	4.3	5	1.6	1.2	0.8	0.4
% occurrence in relation to all flights	18.2	43.5	13.6	2.6	50	51.2	18.2	2.6
% duration in relation to all flights	22.9	25	49.4	56.8	18.3	13.6	9.3	4.5
Mann Whitney U test (P)	57.5	(> 0.05)	69.5	(< 0.05)	66.0	(> 0.05)	66.0	(> 0.05)

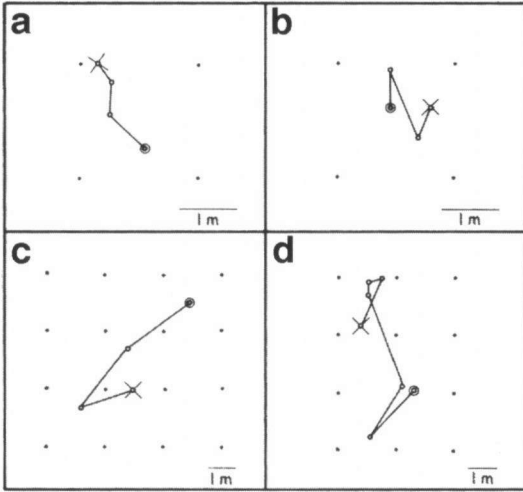


Fig. 1. Examples of distances flown by each *P. quinta* morph while with a female (measured from the onset of copulation to the first oviposition bout): (a–b) two BW males; 1 (c–d) two HW males; —● onset of flight; —× first oviposition bout; — dots represent quadrats (2×2 m).

57.0; wing warning, U test = 56.0; abdominal cleaning, U test = 53.0; all $P > 0.05$).

Agonistic interactions occurred both between (BW–HW) and within (BW–BW and HW–HW) morphs. Most inter-morph interactions consisted basically of a chasing flight of HW males by BW males in which invariably the HW male left the territory (25 out of 25 cases). In the few occasions that escalated flights were observed, they took place mainly between neighbouring BW males. These contests consisted of a frontal, slowly-ascending interaction. In most cases, the owner remained in the territory (3 out of 5 times). As for HW–HW encounters, the intruder was chased and excluded from the territory (5 out of 6 times). In this type of encounters, physical contact was observed.

Interactions were not only intraspecific. *P. quinta* males also chased other damselflies, especially *Palaemnema paulitaba* and *Hetaerina sempronia*. BW males had 9 interactions with *P. paulitaba* and one with *H. sempronia*, while HW males had 12 with *P. paulitaba* and one with *H. sempronia*. *P. paulitaba* has clear wings with black tips, *H. sempronia* clear wings with red bases and small brown spots at the hindwing tips.

TRAJECTORIES OF PAIRS. — There was a difference in relation to male morph in the distance travelled by the pair to the time at which the female first oviposited: HW males flew a longer distance ($N = 4$; 10.65 ± 7.1 m) than BW males did ($N = 5$; 1.28 ± 1.1 m) (t , on log transformed data = -3.36 , $P = 0.015$). Some examples of this difference are shown in Figure 1.

BW males made more of these flights than HW males (U test = 69.5, $P < 0.05$). No further differences were found in changes of perching site (U test = 57.5, $P > 0.05$) or investigatory and patrolling flights (both U test = 66.0, $P > 0.05$). In perched males, three main behaviours were observed: wing clapping (BW: 14.2 ± 12.8 ; HW: 12.60 ± 6.8), wing warning (BW: 0.2 ± 0.5 ; HW: 0.4 ± 0.9) and abdominal cleaning (BW: 6.9 ± 9.2 ; HW: 4.2 ± 3.5). Sample size for all comparisons: $N = 8$ for BW males and 5 for HW males. The morphs differed in none of these behaviours (wing clapping, U test =

DISCUSSION

P. quinta male morphs exhibit clear behavioural differences, which presumably relate to their different mate-seeking tactics. The BW morph is more aggressive (reflected in the number of aggressive flights and their chasing HW males but not being chased by them) and site-attached than the HW morph. An interesting convergence to this dimorphism is the situation in the Japanese *Mnais* (SIVA-JOTHY & TSUBAKI, 1989a, 1989b; WATANABE & TAGUCHI, 1990; PLAISTOW & TSUBAKI, 2000), where the territorial morph is also aggressive, while the non-territorial morph seems to avoid agonistic encounters. Additionally, the territorial morph of *M. pruinosa* requires more mass than non-territorial males, an indication that the territorial tactic is more costly. Our results indicate that the BW males also seem to incur higher costs, as they have to defend a territory. This cost may be balanced by the reproductive benefits. In *P. quinta*, copulations by the non-territorial morph are fewer, they are more frequently genitally interrupted and, during these interruptions, they are likely to result in more sperm-ejection events by females (GONZÁLEZ-SORIANO & CÓRDOBA-AGUILAR, 2003). Given these results, some interesting avenues for research in these species are: (a) to elucidate the genetic basis of male dimorphism (to determine the environmental role in giving rise to each morph); – and (b) to measure the long-term reproductive success of each morph. These aims will shed light on how both morphs are undergoing selection.

BEHAVIOURAL REPERTOIRE OF *P. QUINTA*

Territorial behaviour in *P. quinta* shows two unusual features in comparison with other territorial zygopteran, viz. males are relatively inactive, while the non-territorial morph is fairly aggressive toward non-territorial conspecifics.

Both *P. quinta* morphs showed extremely reduced flight activity: no more than 0.9% of total time. In comparison, males of the coenagrionid *Pseudagrion hageni* invest 6.7% of their territorial occupation in flight (MESKIN, 1986), while HIGASHI (1981) pointed out that “territorial males of *M. pruinosa* seemed to have almost no time perching on their perch sites for pursuing the intruding males”. Also unusual for other territorial zygopterans but concurrent with the above: *P. quinta* engaged in relatively few male-male interactions, with most of them lasting only a few seconds (for a comparison see WAAGE, 1988). At least two explanations can be put forward for this: (a) there is not much light in their habitats, which possibly affects visual recognition of conspecifics; – and/or (b) males may possess a reduced amount of energetic reserves which prevents them from moving too much.

It is also interesting to notice that although HW males always showed a submissive behaviour in the presence of a BW male, they behaved aggressively against

males of their own form. Possibly, the submissive behaviour only emerges in the face of a BW male. Actually, according to the unpublished observations on a related species, *P. zoe*, at the end of the flight season, when no BW males are present, HW males aggressively defend territories (A. Romo-Beltrán, pers. comm.) This indicates that the submissive behaviour of HW males occurs only towards BW males. Perhaps the value of a territory is "appreciated" by HW males, but they do not dispute it with BW males because they are not able to undertake a costly fight (for a similar rationale see PLAISTOW & TSUBAKI, 2000). This cost can be afforded only against HW males.

Pairs formed by HW males flew longer than those formed by BW males during and after copulation. This expenditure is not meaningless. The delay in copulation and/or oviposition could affect fitness of both partners in at least three non-exclusive ways: (1) a greater risk of predation; – (2) an increased number of attacks from conspecific males which may cause tandem disruption; – and (3) a reduced disposition to oviposit by females. We have indirect evidence of the last two. Although not measured, during the increased HW male tandem duration, the couple was more frequently approached by conspecific males which occasionally induced tandem breakage. The increased attack may be "perceived" by the female and affects her disposition to oviposit. This may explain why females spend less time in oviposition after mating with an HW male than with a BW male (GONZÁLEZ-SORIANO & CÓRDOBA-AGUILAR, 2003), though there is also the possibility that HW males may not be good mate guards, as shown in some other species. The reduced oviposition time may be actually translated to the number of eggs laid. In *M. pruinoso* there is a direct relationship between the number of eggs laid and time spent in oviposition (WATANABE & TAGUCHI, 1990). In odonates, the last male inseminates usually most eggs (CÓRDOBA-AGUILAR et al., 2003). If these relationships hold for *P. quinta*, then HW males may see their fertilisation success reduced as a consequence of reduced oviposition bouts.

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