

**TERRITORIAL BEHAVIOUR IN THE GENUS *MEGALAGRION*
(McLACHLAN) (ZYGOPTERA: COENAGRIONIDAE)**

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Preliminary observations were made on the territorial behaviour of 9 taxa of *Megalagrion* in the Hawaiian Islands, July — August 1982. *M. vagabundum* and *M. oresitrophum*, which breed in small streams, showed typical territorial behaviour: highest steady densities of 50 and 38 males per 100 m of water edge were recorded respectively. *M. hawaiiense* (Maui form) and *M. pacificum* are probably also territorial as may be *M. blackburni*. *M. heterogamias* and *M. nigrohamatum*, which spend much time perched on rocks in larger streams, showed aggressive behaviour but were either very weakly territorial or not at all. The form of *M. hawaiiense* in Hawaii, whose larva is probably semi-terrestrial, also appears to be non-territorial. *M. amaurodytum peles* appears not to defend the *Astelia* plants in which eggs are laid and in whose leaf axils the larvae develop. The size of territories in endemic Hawaiian Odonata appear to be proportional to size of insect.

INTRODUCTION

All the native Zygoptera in the Hawaiian Islands belong to the genus *Megalagrion*. However, this one genus has undergone spectacular adaptive radiation, which is comparable in variation and number of species to the avian family of the Hawaiian honeycreepers (Drepanididae). Some *Megalagrion* species breed in still waters, others in fast streams, some in seepages in moss, one in leaf litter below ferns and others in the axils of forest epiphytes (ZIMMERMANN, 1948).

Valuable studies have been made on the bionomics of *Megalagrion* notably by PERKINS (1913) and WILLIAMS (1936), but very little has been published on the territorial behaviour of *Megalagrion*. So the aim of the present investigation was to undertake a preliminary reconnaissance on territorial behaviour within

this ecologically heterogeneous group.

SPECIES, LOCALITIES AND METHODS

Visits were made to rainforest areas in the islands of Kauai, Hawaii and Maui during the period July 30th — August 16th 1982. For sites and dates cf. Table I. Every opportunity was taken to observe the behaviour of imaginal insects, with special emphasis on oviposition and on territorial behaviour. Approximate densities of male insects were measured in terms of "area" and "waterbody edge". "Areas" included sunspots in the forest away from water, when these were occupied by *Megalagrion* during the middle of fine days, as well as sunspots on forest streams. Forest stream "areas" included the whole area which was illuminated by the sun and thus included rocks, banks and plants as well as water. It is very difficult to measure water edge accurately hence the measurements recorded here are only very approximate. All observations were made between 10.00 and 15.30 local time, and hence in the period when it was presumed that species would be showing territorial behaviour. (Sunset was about 18.40). Voucher specimens were collected and their identifications confirmed by Dr. Frank G. Howarth of the Bishop Museum, Honolulu. They will eventually be deposited in the British Museum (Natural History), London.

Table I

Site details

Site No.	Locality	Date(s) visited
1	Cliff forest west of Hanea, Kauai	31-VII
2	Kalahua stream, Alakai Swamp, Kauai	3-VIII
3, 4, 5	Bog c. 4 km from Kalahua look-out, Kauai	3-VIII
6	Pua'alu'u Gulch, 20 km west of Hana, Maui	12/13-VIII
7	Maluhianaiwi Stream 20 km west of Hana, Maui	12/13-VIII
8, 9	Olaa Forest, Volcanoes National Park, Hawaii	5-VIII
10, 11, 12	Forest near Puu Makaala west of Hilo, Hawaii	8-VIII

A few experiments involving subtracting and adding individuals to habitats were made to test density values (cf. MOORE, 1964).

The following taxa were studied: *Megalagrion amaurodytum peles* (Perkins), *M. blackburni* (McLachlan), *M. hawaiiense* (McLachlan) — Maui form, *M. hawaiiense* (McLachlan) — Hawaii form, *M. heterogamias* (Perkins), *M. nigrohamatum* (Blackburn), *M. oresitrophum* (Perkins), *M. pacificum* (McLachlan), and *M. vagabundum* (Perkins).

The Maui and Hawaii forms of *M. hawaiiense* are treated separately because there appear to be morphological differences between them (F.G. Howarth, pers. comm., and N.W. Moore, unpublished). Subsequent studies may show that they represent different species or subspecies.

TERRITORY IN *MEGALAGRION*

The information obtained is summarised in Table II. Conclusions are drawn below and further information added.

M. vagabundum and *M. oresitrophum* are clearly territorial on their breeding sites since aggressive behaviour was observed to limit population

density. Highest steady densities of about 50 and 38 males per 100 m of water edge were observed respectively. These values are very similar to those recorded in several coenagrionids in England, e.g. 40 in *Ischnura elegans* (Van der L.), and 44 in *Pyrrosoma nymphula* (Sulz.) (MOORE, 1964). *M. oresitrophum* was also found at lower densities at Sites 3, 4 and 5 in a bog in the Alakai swamp.

The Maui form of *M. hawaiiense* (cf. Tab. I) was found at a rather similar density (8) by a stream in east Maui (Site 6). Two pairs were seen in copula there but oviposition was not observed. Aggressive behaviour was observed. Four males out of a population of at least 6 males were collected on 12-VIII-82, and by 14.00 hr on 13-VIII-82 the population consisted of 7-9 males.

A single male of *M. pacificum* was found by a small stagnant pool with a circumference of 6 metres (cf. MOORE & GAGNÉ, 1982, for further details). This individual was collected. It had been replaced by another single male by 14.00 on the following day.

From these observations it appears that *M. pacificum* and the Maui form of *M. hawaiiense* are also territorial on what were almost certainly breeding areas, and their highest steady densities are not dissimilar to those of *M. vagabundum* and *M. oresitrophum*.

The population density of male *M. blackburni* at Site 6 was much lower than that of female and immature insects observed away from water near the Akaka Falls, Hawaii. This suggests that the species may be territorial, but since no aggressive behaviour by mature males at water was observed no firm conclusion can be drawn about its territorial behaviour. WILLIAMS (1936) states that it is a rather bold and aggressive insect.

M. heterogamias and *M. nigrohamatum* were observed for several hours on Sites 2 and 7 respectively. Pairs in tandem of both species were watched ovipositing in the quieter parts of quite large streams. Males of both species spent much time perched on rocks in the middle of the stream. Aggressive encounters were observed and these occasionally resulted in one individual moving to another rock, but in no case did it result in an insect leaving the area of the sunspot. Wings and abdomens of *M. heterogamias* were sometimes raised in what appeared to be a threat display. It was also noticed that insects of both species moved freely about the sunspot area perching in different parts of it. On two occasions I caught males of *M. nigrohamatum* and released them near perching males and on another I placed a male beside another male on a stone. In none of these instances was the introduced male pursued. It is concluded that these fast stream species are only weakly territorial, if at all. This lets them live at higher densities than *M. vagabundum* and *M. oresitrophum*. On one occasion no less than 6 *M. heterogamias* were observed perching on two stones in an area of about 0.1 m².

Special interest was attached to the non-aquatic species of *Megalagrion* (cf. WILLIAMS, 1936). Thanks to Mr W.P. Mull, who showed me its locality, I was

Table II

Territorial behaviour: observations on imaginal *Megalagrion*

Site No.	Species	Observed oviposition site or (adult habitat)	Observed aggressive behaviour	Observed expulsion of males	No. of ♂ in area	Density: ♂ per 100 m ² of area	Density: ♂ per 100 m of water edge
1	<i>vagabundum</i>	Moss, dead leaf and slime in small stream	+	+	3	75	50
2	<i>oresitrophum</i>	Water weeds and dead leaf in subsidiary stream pool	+	+	2	63	38
3	<i>oresitrophum</i>	(Bog rivulet)			1	4	4
4	<i>oresitrophum</i>	Detritus in rivulet in bog			2	7	8
5	<i>oresitrophum</i>	(Bog rivulet)			1	2	3
6	<i>hawaiiense</i> (Maui form)	(Rocky stream)	+		6	1	5
6	<i>hawaiiense</i> (Maui form)	(Rocky stream)			9	2	8
6	<i>blackburni</i>	(Rocky stream)			3	1	3
6	<i>pacificum</i>	(Stagnant pool by stream)			1	50	17
2	<i>heterogamias</i>	Rocky stream bed	+	+from stone only	12	75	75
7	<i>nigrohamatum</i>	Dead Koa leaves in rocky stream	+	+from stone only	5	162	69
8	<i>amaurodytum peles</i>	Larvae in <i>Astelia</i> axils (sunspot 2 m from <i>Astelia</i>)			1	25	
9	<i>amaurodytum peles</i>	(Sunspot 4 m from <i>Astelia</i>)			1	11	
10	<i>hawaiiense</i> (Hawaii form)	(Sunny clearing)			5	<1	
11	<i>hawaiiense</i> (Hawaii form)	(Sunny clearing)			2	1	
12	<i>hawaiiense</i> (Hawaii form)	(Sunny clearing)			1	1	

Note: The figures record what was observed during short visits to the sites concerned. For localities and data cf. Table I. Each visit exceeded ¼ hour, none exceeded 3 hours. Thus, all figures represent minimal values. Only in those cases where aggressive behaviour was observed to limit population density can the value be taken to represent a highest steady density for the species concerned. These are shown in **bold type**.

able to investigate *M. amaurodytum peles*. The larvae of this species live in the axils of *Astelia* and of *Freycinetia*. Several larvae were found in *Astelia* plants in Olaa Forest (near Sites 8 and 9). I examined 12 *Astelia* plants to determine whether male *M. amaurodytum peles* held territories on them. No imaginal insects were seen on or close by *Astelia* plants. However, two males were found in Sites 8 and 9. These were small sunspots of about 2 m² and 4 m² on a trail. The males perched about 2/3 m and 2 m above the ground respectively. The perching places were 2 m and 4 m from the nearest *Astelia* plants. When one male was

removed its place had not been filled by another male an hour later.

In a nearby area some more larvae were found. Twenty seven *Astelia* and 7 *Freycinetia* plants were examined but no imaginal insects were observed on them or elsewhere in the neighbourhood.

It is concluded that male *M. amaurodytum peles* do not hold territories over the plants in which their eggs are laid. They may or may not hold territories in sunspots in the general vicinity of the plants.

Mature male and female insects of *M. hawaiiense* — Hawaiian form were found in the middle of a fine day at Sites 10, 11 and 12. These were clearings by a dirt road running through Ohia (*Metrosideros collina*) Forest. There were temporary ponds in ruts on the road elsewhere in the same general area and in some cases these were extensive enough to cover the whole surface of the road. There were no streams in the vicinity. No aggressive behaviour was observed and when two males were caught and released near other males they were not pursued.

On Oahu *M. hawaiiense* lays eggs on vegetation both in and out of water; the later instars of the larva are semi-terrestrial (WILLIAMS, 1936). It appears that the form with a semi-terrestrial larva is not territorial.

The observed population densities of the apparently semi-terrestrial Hawaii form of *M. hawaiiense* appeared to be similar to those of the aquatic Maui form. The apparent behavioural differences between the two forms support the view that they should be separated taxonomically (see Species, Localities and Methods).

From these very preliminary observations and experiments the following generalisations can be made about territorial behaviour in the genus *Megalagrion*:

- (1) Territorial behaviour occurs in at least 2, and probably 4 or 5, of the species with aquatic larvae which were studied.
- (2) In 2 species which habitually perch in the sun on rocks in moderately large streams, territorial behaviour is either weak or non-existent.
- (3) A form with a semi-terrestrial larva also appears to be non-territorial.
- (4) In one species with a terrestrial larva, males do not defend the plants in whose axils the larvae develop.

There are about 28 species and sub-species of *Megalagrion*, hence there is great scope for further work on territory in this very interesting genus.

THE RELATIONSHIP BETWEEN SIZE OF TERRITORY AND SIZE OF INSECTS IN HAWAIIAN ODONATA

The endemic odonate fauna of Hawaii includes two anisopterans. These were observed in association with *Megalagrion* as was the pantropical *Pantala flavescens* (Fab.).

Anax strenuus (Hag.) was seen to patrol long lengths of streams, tracks and roads even when the latter contained no water. The only fight observed was between two males on a waterless track. Two pairs were observed ovipositing in tandem, one immediately above a temporary pool by a road, another in a small stream in an abandoned field. The endemic libellulid *Nesogonia blackburni* (McLachlan) shows aggressive behaviour (WILLIAMS, 1936) and is probably territorial like species of the genus *Sympetrum* to which it is closely related.

In Site 7 on 13-VIII-82 there were 5 *M. nigrohamatum* (length 46 mm) and for a time it was included in the beat of an *A. strenuus* (length 86 mm). In Site 6 on 12-VIII-82 there were 6 *M. hawaiiense* (Maui form) (length 41.5 mm), and 3 *M. blackburni* (length 57.5 mm). Thus, as in European Odonata (MOORE, 1962) the territory size appears to be proportional to size of insect.

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