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REFLEX IMMOBILISATION IN THE HAWAIIAN ENDEMIC GENUS *MEGALAGRION* McLACHLAN (ZYGOPTERA: COENAGRIONIDAE)

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Observations were made on reflex immobilisation in imagines of Hawaiian Zygoptera. The habit appears to be particularly well developed in the endemic genus *Megalagrion*. The origin of this habit in an environment which appears to be unusually free of large predators is discussed.

INTRODUCTION

Reflex immobilisation has been recorded in numerous vertebrate and invertebrate species EDMUNDS (1974). It is frequently called death feigning, but this term begs the question of its function; so the more neutral term is used here.

The habit is well developed in anisopteran larvae (cf. CORBET, 1962 for references), but has been observed less often in zygopterans. It occurs in imagines, but seems to have been rarely recorded. CALVERT & CALVERT (1917) describe how when *Megaloprepus coerulatus* was "caught and held by the wings, the legs were folded against the thorax and remained immobile, even when they were touched or rubbed - the insect seemed to 'play possum'." PARR (1965) describes how individuals of *Ischnura elegans* "frequently exhibited thanatosis (death-feigning) when the top of the pill box in which they were imprisoned was lifted."

In the course of a recent expedition to study the territorial behaviour in Hawaiian Odonata (MOORE, 1983) and the conservation requirements of *Megalagrion pacificum* (McLachl.) (MOORE & GAGNÉ, 1982), I had to collect

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voucher specimens. When transferring a female *M. blackburni* (McLachl.) on Hawaii from one container to another I noticed that it exhibited reflex immobilisation as soon as I picked it up. When placed on a flat surface it lay motionless in its side with its legs tucked in. Repeated handling produced the same response. Subsequently I investigated this habit in specimens of all the imaginal Zygoptera which I collected during the period August 9-16th 1982.

METHODS

In each case I picked up the insect between finger and thumb, thus removing its feet from the substrate, and laid it on its side on a flat surface - often my extended left hand or my field notebook. If the insect lay motionless, either with legs withdrawn or extended, I recorded it as showing reflex immobilisation. If it righted itself I recorded a negative result. Observations were also made on the length of time individuals remained immobilised after repeated experiments and on stimuli which released insects from the immobilised state. When I returned to England I made similar observations on some British Zygoptera.

RESULTS

The results for Hawaian Zygoptera are given in Table I. None among the 23 adults of British Zygoptera tested on 20 or 21 August 1982 showed reflex immobilisation. These adults (all from Cambridgeshire) comprised *Lestes sponsa* (Hans.) 6 males, 3 females, Wood Walton Fen; *Enallagma cyathigerum* (Charp.) 3 males, 1 female, Wood Walton Fen, and 6 males, Fenstanton Gravel Pits; *Ischnura elegans* (Vander L.) 2 males, 2 females, Wicken Fen and *Erythromma najas* (Hans.) 1 female, Wood Walton Fen.

It will be seen that the immobilised reflex response was induced in all save one of the 12 Megalagrions, but in none of the 6 insects belonging to two introduced species in Hawaii, and in none of the 23 insects belonging to 4 British species.

When the experiment was done repeatedly on one insect, reflex immobilisation did not always occur. For example *M. blackburni* specimen 1 was picked up thirteen times between 15.15 and 16.08 hours (c. 2½ hours before sunset) on 10-8-82 and showed the following sequence of response: immobilisation on the first 6 occasions, no immobilisation on the next 4, immobilisation on the next, no immobilisation on the next, immobilisation on the next. The period spent immobilised declined from 7 minutes in the first instance to ½ minute in the last. In other specimens there was no such regular reduction in the time spent immobilised. On one occasion *M. blackburni* specimen 1 remained immobilised for 28 minutes, *M. blackburni* specimen 3 for 18 minutes, *M. hawaiiense* (McLachl.) specimen 7 for 50 minutes and *M. hawaiiense* specimen 8 for 49 minutes. In the last three cases the insects had been kept in specimen tubes for 1, 4 and 4 days respectively and had been experimented on previously and were in a weakened condition and so may not be typical.

Table I
Reflex immobilisation in Hawaiian Zygoptera

Specimen Number	Species	Sex	Locality	Date	Presence or absence of reflex immobilisation
1	*Megalagrion blackburni*	♀	Akaka Falls Hawaii	9-8-82	+
2	*M. blackburni*	♂ *imm.*[1]	Seven pools Maui	12-8-82	+
3	*M. blackburni*	♀	Iao Valley Maui	16-8-82	+
4	*M. hawaiiense*	♂	Seven Pools Maui	12-8-82	+
5	*M. hawaiiense*	♀	Seven Pools Maui	12-8-82	+
6	*M. hawaiiense*	♂	Seven Pools Maui	12-8-82	—
7	*M. hawaiiense*	♂	Seven Pools Maui	12-8-82	+
8	*M. hawaiiense*	♂	Seven Pools Maui	13-8-82	+
9	*M. nigrohamatum*	♂	Seven Pools Maui	13-8-82	+
10	*M. nigrohamatum*	♂	Seven Pools Maui	13-8-82	+
11	*M. pacificum*	♂	Seven Pools Maui	12-8-82	+
12	*M. pacificum*	♀	Seven Pools Maui	13-8-82	+
13	*Enallagma civile**	♂	Kealia Maui	15-8-82	—
14	*E. civile**	♂ imm.	Kealia Maui	15-8-82	—
15	*E. civile**	♂	Kealia Maui	15-8-82	—
16	*E. civile**	♀	Kealia Maui	15-8-82	—
17	*E. civile**	♀	Kealia Maui	15-8-82	—
18	*Ischnura ramburii**	♀	Kealia Maui	15-8-82	—

* introduced species in Hawaii
[1] immature but not teneral.

Repeated experiments on *E. civile* (Hag.) and *I. ramburii* (Sel.) showed that the reflex immobilisation could be induced eventually, especially if the insect was put on its back. Once immobilised in this way these insects, like *Megalagrion*, would

remain inert for quite long periods - 30 minutes in *E. civile* specimen 14, 20 minutes in *E. civile* specimen 15 and 4 minutes in *I. ramburii* specimen 18.

In 65 experiments with British *I. elegans* (specimens 20-23) reflex immobilisation was only achieved once, and then only when the insect was placed on its back.

On one occasion reflex immobilisation was induced in *M. blackburni* specimen 1 by making a threatening movement towards it with my hand without touching it. On two or three other occasions this action failed to elicit a response.

In both *M. blackburni* and *M. hawaiiense* insects could be released from the inert position by blowing gently on them. Slight movements near *M. hawaiiense* also had the same effects. On many occasions there was no obvious stimulus to account for the release from reflex immobilisation.

CONCLUSIONS AND DISCUSSION

It is concluded that members of the endemic Hawaiian genus *Megalagrion* exhibit the behaviour pattern of reflex immobilisation to an unusual degree. It was found to exist in 4 species which differ greatly from each other in appearance, *M. blackburni* being an unusually large, mainly red insect, *M. hawaiiense* a smaller red species, *M. nigrohamatum* (Blackburn) a black and yellow species and *M. pacificum* a small black one. The habit is clearly unrelated to size or colour. The larval requirements of the 4 species differ, but the imagines all live by mountain streams in the forest areas of the Hawaiian Islands. In the past *M. pacificum* also occurred in the lowlands.

Reflex immobilisation is presumed to be a defence mechanism against predators - the predator ignoring the insect because it no longer has the valency of living prey, either because it is not distinguishable from its surroundings or because it appears to be dead.

It is not at all obvious why this form of behaviour is so well developed in Hawaii, for Hawaii appears to contain fewer predators of Zygoptera than most places in the world. There are no wagtails, pipits, buntings, swifts, swallows or insect feeding raptors. None of the existing or extinct honey creepers (Drepanididae) appear to have been adapted to feed on flying prey. There is only one flycatcher - the Elepaio (*Chasiempis sandwichensis*), an endemic species. It occasionally takes flying insects and probably does sometimes catch *Megalagrion*, though I never saw it do so, but there is no evidence whatever to suggest that it exerts an unusual pressure on *Megalagrion*. Further it does not occur on Maui where I made most of my observations.

The spider fauna of the Hawaiian Islands includes some fairly large thomisids and attids, which hunt their prey in the open (SIMON, 1917), but there is nothing to suggest that Zygoptera in the Hawaiian Islands suffer from exceptional pressure from arachnid predators.

PERKINS (1913) records that *Anax junius* (Dru.) sometimes feeds on *Megalagrion* and also that the larger *Megalagrion* species sometimes feed on the smaller ones. Doubtless the 4 libellulid species now present in the islands also feed on *Megalagrion* occasionally. But since *A. junius* and 3 of the libellulids must be recent arrivals and occur mainly in the lowlands, it is most unlikely that they have been the cause of the development of reflex immobilisation. The endemic libellulid *Nesogonia blackburni* (McLachl.) is quite small and also unlikely to be a very significant predator. On the other hand the endemic *Anax strenuus* (Hag.) has been recorded as feeding on *Megalagrion* (WILLIAMS, 1936; ZIMMERMAN, 1948), and since it is a very large insect it could be a very significant predator of *Megalagrion* considering the scarcity of other relatively large prey in Hawaii. This species is abundant in forest areas on all the main islands. Dr Frank Howarth (pers.comm.) reports that the large *Megalagrion heterogamias* (Perkins) of Kauai has been seen to drop into vegetation like a stone when *A. strenuus* flies over it. The reaction of *M. blackburni* to a threatening movement (see p.164) may indicate a similar type of behaviour. Thus it is conceivable that reflex immobilisation has been developed as an escape mechanism from *A. strenuus*, an unusually large odonate predator. Another possibility is that the behaviour originated in the ancestors of *Megalagrion* elsewhere in response to predators not present in Hawaii. Therefore it would be particularly interesting to know if the behaviour occurs in the genus *Pseudagrion* from which it is believed *Megalagrion* is derived. It would also be interesting to learn whether reflex immobilisation is as well developed in the 23 other species and sub-species of *Megalagrion* as in the four species studied here.

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