

**'ACCOMPANYING' BEHAVIOUR AS A MEANS OF PREY  
ACQUISITION BY *BRACHYTHEMIS LEUCOSTICTA* (BURMEISTER)  
AND OTHER ANISOPTERA**

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Adults of the pan-African sympetrine *B. leucosticta* often accompany large vertebrates moving slowly through open grassland or, less often, through shallow water. Such 'accompanying' behaviour, which is shown by solitary individuals and groups, males and females, and immature and mature adults, varies with respect to wind direction and substrate in ways that indicate that the vertebrate is usually perceived as a token stimulus attracting the dragonflies to places where small flying insects are rendered accessible as prey. Certain and probable examples of accompanying behaviour in other Anisoptera are discussed.

**INTRODUCTION**

Adults of the pan-African sympetrine libellulid *Brachythemis leucosticta* appear to associate insect prey with the presence of large animals that thereby serve as 'token stimuli' (CORBET, 1962). Both sexes are attracted towards, and fly close to, large vertebrates such as cattle, hippopotamuses and humans as they move slowly through open grassland where the dragonflies are often abundant. Such 'following' behaviour presumably enables the dragonflies to feed on the small insects that are made to fly up by the vertebrates' movement. Noting 'following' behaviour near Lake Victoria at Entebbe, Uganda (0° 3'N., 32° 29'E), CORBET (1962, p. 154) inferred that initially the dragonflies were responding directly to a large moving object and not to the prey dislodged by it, a view expressed also by WORTH (1962) from observations made in Natal, South Africa. This 'following' behaviour, which we now propose to call 'accompa-

nying' behaviour (AB), is analogous to that shown by many species of birds, such as bee-eaters, cattle egrets, honey guides, robins and seagulls, all of which are attracted to large, slowly moving mammals (or vehicles) which they use as 'beaters' or guides to obtain food. We report here observations on this type of feeding behaviour in *B. leucosticta* and other species of Anisoptera. If not given in the text, authorities for scientific names of species mentioned are to be found in Table I.

### *BRACHYTHEMIS LEUCOSTICTA*

*B. leucosticta* probably acquires much of its food by the usual libellulid method of making sallies from a perch in pursuit of prey and by 'swarm-feeding' (sensu CORBET, 1962, p. 151) during twilight (CARPENTER, 1920 p. 310). AB can be seen as an additional strategy that can be used in situations where large vertebrates move about slowly during the day, usually near a body of water. This species is active throughout the day (ADETUNJI & PARR, 1974) and also during morning and evening twilights (CARPENTER, 1920, p. 310; ADETUNJI & PARR, 1974; our own observations).

Observations made by one of us (P.L.M.) at the eastern end of Lake Kariba, Zimbabwe (16°32'S., 28°51'E.) in April and December 1989 throw further light on AB. Such behaviour, which was examined as a response to the observer, was witnessed on several days intermittently between 10.00 and 18.45 hrs Local Mean Time (sunset being at 18.30 hrs) and continued until the light intensity became too low for the dragonflies to be seen clearly — probably between Civil and Nautical Twilights. AB occurred most often over short grass (less than 20 cm high) but also over bare rocks or sand where no prey was likely to be resting. It could be observed over land within about 100 m of the lake margin but was commonest within 15 m of the margin, where the density of dragonflies was highest.

At Lake Kariba as many as an estimated 50 dragonflies, including both sexes, and immature and mature individuals (as judged by the colour of abdomen and wings; ADETUNJI & PARR, 1974), would fly 10-30 cm above the ground and 1-2 m behind the observer as he walked at 2-3 kmh<sup>-1</sup>. The distance over which individuals accompanied was not measured systematically but many certainly did so for 10 m and some probably for greater distances. When the observer stopped walking some of the accompanying dragonflies overtook him and then turned to face him, hovering and flying in arcs about him for several seconds, after which they either departed or settled on the ground, to fly again when he moved once more.

When there was a wind of a velocity that exceeded the speed of walking, the dragonflies always flew downwind from the observer. Thus in a following wind they preceded him, facing towards him, flying into the wind and progressing backwards with respect to the ground; in a lateral wind they flew alongside the

observer, again facing towards him, into the wind and moving sideways with respect to the ground; and when the observer was walking into the wind the dragonflies followed him, as they did when there was little or no wind. Regardless of the wind direction the dragonflies remained 1-2 m from the observer.

Many individuals of *B. leucosticta* became reproductively active after 16.00 hrs at Lake Kariba in places where reeds stood in the water; male localisation and oviposition were observed in a few individuals in December as early as 11.00 hrs. Thus feeding and reproductive activity occurred at the same time and took place in adjacent areas. However at the lakeside, individuals that showed no sign of reproductive activity always outnumbered those that did so, even towards sunset. No individual was seen to exhibit sexual activity while accompanying.

Observations made (by P.L.M.) from a canoe moving through stands of reeds in the Okavanga Delta, Botswana (ca. 19°S., 23°E.), have shown that *B. leucosticta* will accompany large objects over water also and so would perhaps follow a wading hippopotamus or a floating crocodile.

In Uganda, on Dagusi Island in Lake Victoria (0° 8½'N., 33° 32½'E.), in December 1954, one of us (P.S.C.) noted that adults of this species assembled and hovered behind, but not in front of, a motor vehicle that had just stopped and that had disturbed many small flying insects during its passage. Table I lists other, published accounts known to us of AB in *B. leucosticta*.

#### OTHER SPECIES

In Table I are listed all published records known to us of dragonflies exhibiting certain or suspected AB. We note that all are Anisoptera and that (including *B. leucosticta*) three are sympetrine libellulids.

We ourselves have confirmed that AB occurs in *Brachythemis contaminata* (Fabricius). On 25 January 1988 within an hour of solar noon near Madurai, Tamil Nadu, India (9°57'N., 78°6'E.) a solitary male followed us as we walked slowly along the edge of a large pond. It flew low, 10 cm or less above the ground, which was mostly bare granite rock, and spent much time hovering, usually facing towards the human it was accompanying at the time, and making short, darting flights when the human moved, often taking up a position in front of him. We noted also that some males did not show AB, even when offered the opportunity to do so. However large numbers of *B. contaminata* showed AB near solar noon when one of us (P.L.M.) walked round the margins of a lake close to Nagpur University, Maharashtra, India (79°5'E., 20°56'N.) in September 1990. From our observations we conclude that the propensity for showing AB is sometimes less in *B. contaminata* than in *B. leucosticta*. Although *Diplacodes trivialis* (Rambur) occurred around the pond at Madurai with *B. contaminata*, neither of us was able to induce the former species to show AB — an unexpected result in the light of the report to this effect by MITRA (1974) (see Tab. I).

Table I  
Records of feeding Anisoptera accompanying large, slowly moving objects

Species	Location	Observations
<i>Aeshna grandis</i> (L.)	Denmark	Followed running horses and seized flies from swarms around animals' noses (WESENBERG-LUND, 1913).
<i>Anax junius</i> (Dru.)	Hawaiian Islands	With <i>Pantala flavescens</i> and <i>Tramea lacerata</i> seemed to follow man walking through grass, darting to catch moths disturbed by him (McLACHLAN, 1874).
Anisoptera (unidentified)	India	Groups of 10-50 often flew close to, and parallel with, back wheel of bicycle, adjusting to changing speed of vehicle (ACHARYA, 1961) <sup>1</sup> .
	Natal, S. Africa	Flew close to, and slightly ahead of, walking man and also front wheel of bicycle, adjusting to changing speed of vehicle (WORTH, 1962) <sup>2</sup> .
	Tanzania	Accompanied elephants walking through grassland near shore of Lake Manyara (DOUGLAS-HAMILTON, 1973) <sup>3</sup> .
<i>Brachythemis contaminata</i> (Fab.)	India	With <i>Diplacodes trivialis</i> (Ram.) followed men walking through grass (MITRA, 1974).
<i>B. leucosticta</i> (Burm.)	Nigeria	Both sexes tend to follow moving objects such as man and cattle (ADETUNJI & PARR, 1974).
	Tanzania	Searched backs of humans and other animals for tsetse flies ( <i>Glossina</i> ) (SWYNNERTON, 1936).
	Tchad	Flights of several hundred individuals often follow herds of cattle or sheep through grass (DEJOUX, 1968).
	Uganda	Apparently pursued tsetse flies ( <i>Glossina</i> ) associated with hippopotamuses grazing on land (CARPENTER, 1920).
<i>Crocotthemis servilia</i> (Dru.)	India	Briefly followed motor vehicles on a main road (MITRA, 1974).
<i>Erythemis simplicicollis</i> (Say)	Florida, USA	Followed observer walking through soybean field and caught <i>Heliothis zea</i> adults that he disturbed (NEAL & WHITCOMB, 1972).
<i>Erythrodiplax attenuata</i> Kirby	Brazil	Adults flew low around feet of humans and other large vertebrates among grass by well-trodden paths on muddy banks of Upper Amazon River and in a manner closely resembling <i>Brachythemis leucosticta</i> (J.D. Silsby, 1990, in litt. to P.S.C.).

(Continued Table I).

Species	Location	Observations
<i>Orithetrum brachiale</i> (P. de Beauv.)	Tanzania	Flew a few paces ahead of moving observer, often alighting and waiting until observer had caught up (STORTENBEKER, 1967).
<i>O. chryso stigma</i> (Burm.)	Malawi	Catching tsetse flies ( <i>Glossina</i> ) while hovering around group of humans (CAMPION, 1921).
<i>Pantala flavescens</i> (Fab.)	Hawaiian Islands Siberia, USSR	See <i>A. junius</i> above. Accompanied walking observer, approaching closely and catching mosquitoes that he attracted (BELYSHEV, 1966, p. 471).
<i>Tramea lacerata</i> (Hag.)	Hawaiian Islands	See <i>A. junius</i> above.

<sup>1</sup> From description of behaviour, almost certainly *B. contaminata*.<sup>2</sup> From description of behaviour, almost certainly *B. leucosticta*.<sup>3</sup> From size and style of flight, could be *B. leucosticta*.

The account by ACHARYA (1961) (see Tab. I), which almost certainly refers to *B. contaminata*, reports that the dragonflies followed a moving bicycle for 50-100 yards (ca. 48-91 m), depending on where it stopped.

Concerning the reports in Table I of large vertebrates serving as foci for attracting blood-sucking Diptera we note other, unpublished accounts known to us from subarctic North America of *Aeshna* feeding on mosquitoes, (presumably *Aedes* (*Ochlerotatus*) spp.) assembling over a survey party (personal communication to P.S.C.) and of *Somatochlora hudsonica* (Selys) and *S. sahlbergi* Trybom feeding on horseflies (*Chrysops nigripes* Zetterstedt) (CANNINGS & CANNINGS, 1989), as the latter flew above an observer's head near Old Crow, Yukon Territory, Canada (67°26'N., 14°5'W.).

## DISCUSSION

*B. leucosticta* is extremely common in many parts of Africa (PINHEY, 1961). Adults occur near lakes, large ponds and reservoirs but are usually uncommon or absent at bodies of water less than about 20-30 m in diameter. They prefer exposed parts of lake shores and tend to avoid places with many bushes or trees. They often perch on bare ground such as rock, mud or sand and less often on vegetation, except for emergent plants over water. By contrast *B. lacustris* (Kirby) prefers more bushy areas with taller vegetation and often perches 0.5 m or more above the ground. In India *B. contaminata* occurs at ponds, lakes and sluggish streams (FRASER 1936; MATHAVAN, 1975) and, like *B. leucosticta*, appears to prefer open ground where it often perches low on vegetation.

Over exposed grassland small insects seldom fly spontaneously during daytime

at lower latitudes. Moreover open lakeside areas are sometimes exposed during the day to strong winds which likewise would inhibit flight of potential prey. So, without an adaptation to offset this, dragonflies in such habitats may encounter little prey. The evolution of AB in *B. leucosticta*, allowing it to prey on insects stirred up by large vertebrates, may have enabled it to exploit such environments: certainly this species is frequently the commonest anisopteran at lakeside areas in Africa. Until recently large wild vertebrates were common in many such habitats, and their presence may have indirectly supported large populations of lakeside *B. leucosticta*. Today, as numbers of humans increase and those of wild animals decrease, *B. leucosticta* presumably depends more and more on humans and their stock animals as 'beaters' to disturb prey.

The related African species, *B. lacustris*, occurs in similar habitats and, like *B. leucosticta*, perches and feeds in groups (PINHEY, 1961) but it has not been reported, or seen by us, to exhibit AB. It has already been noted (CORBET, 1962) that AB, as shown by *B. leucosticta*, is unusual in that most species of dragonfly avoid, rather than congregate around, large animals, a reaction that must be over-ridden during AB. Indeed we have found *B. leucosticta* to be much less readily alarmed by the presence of an observer, and thus much more easily caught, than *B. lacustris* occurring in some of the same places.

The records of dragonflies preying on blood-sucking Diptera that have been attracted to large vertebrates show that AB could result in acquisition of prey by a means other than 'beating'.

The observation that *B. leucosticta* also shows AB over water suggests an additional explanation for the existence in crocodile stomachs of mature adults (see CORBET, 1959, 1962, p. 136); they might have been using the floating crocodile as a target for AB as well as merely flying close to the water at dusk.

We may ask what mechanisms mediate AB. The persistent facing towards the target by the dragonflies suggests the operation of an optomotor mechanism in which the large moving object is fixated. Such behaviour would differ from the pursuit of targets such as prey or mates in that a nearly constant distance from the target is maintained.. In order to remain downwind of the object the dragonflies may merely seek a position with respect to the target that maintains a headwind; or they may use a more complex system in which flight effort is compared with apparent ground speed. By facing towards a large moving object and remaining downwind of it, the dragonflies would be best placed to detect prey that had been disturbed.

Learning is likely to be common in opportunistic predators such as dragonflies, though this has received little attention: an example is the predictable arrival during evening twilight in Costa Rica of *Orthemis ferruginea* (Fabricius) to prey on small insects aggregating over fermenting berries (YOUNG, 1980). Other possible examples may be found among the behaviour of certain large aeshnids, such as *Anax junius* (Drury) and *Coryphaeschna ingens* (Rambur), that localise

near bee-hives (WRIGHT, 1944). However, because AB in *B. leucosticta* seems to take much the same form wherever it occurs, we suggest that it probably results mainly from an inherited responsiveness, although learning may sometimes allow it to adapt to local conditions.

For other species of dragonfly in which AB has been observed or inferred but is apparently not shown consistently (Tab. I), several factors may be involved: individuals of such species may be acting gregariously; they may be responding directly to the abundance of prey disturbed by the large object (thus exhibiting 'swarm-feeding'); and they may have learnt to follow large vertebrates as a result of individual experience. That all three possibilities exist serves to remind us that dragonflies offer fruitful models for the study of insect behaviour.

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