

Ballistic defaecation by anisopteran larvae (Odonata): a way to increase foraging success?

Philip S. Corbet

I.C.A.P.B., University of Edinburgh, Scotland, UK.
present address: Crean Mill, Crean, St. Buryan, Cornwall TR19 6HA, UK.
<pscorbet@creanmill.u-net.com>

Key words: Odonata, dragonfly, larvae, Anisoptera, defaecation, alarm pheromone, chemical cues.

ABSTRACT

The article considers the phenomenon of ballistic defaecation by odonate larvae, exhibited by certain Anisoptera but not by any Zygoptera, and explores two possibilities: (1) that ballistic defaecation in Anisoptera may correlate with increased foraging success (the 'Wudkevich Hypothesis') by distancing the prey's alarm pheromone, persisting in the pellet after defaecation, from the larva's ambush site; and (2) that its absence in Zygoptera may correlate with their much richer repertoire of intraspecific agonistic behaviour, perhaps reflecting the need to change, and compete for, ambush sites more often. Attention is drawn to kinds of information that could throw light on the Wudkevich Hypothesis and to the design of experiments that would sustain or refute it; and mention is made of the possible implications for larvae of Zygoptera of their ability to learn to modify their antipredation behaviour in response to chemical cues emitted by their predators or by injured conspecifics.

INTRODUCTION

In this essay I explore the implications of what has been a puzzling aspect of the behaviour of anisopteran larvae. I then offer an hypothesis to explain its selective value in the hope of eliciting observations that may have a bearing on it. Faeces of odonate larvae are voided in the form of discrete pellets comprising the undigested fragments of food enclosed in a sac composed of peritrophic membrane that is periodically shed from the wall of the midgut (Aubertot 1932). Each resulting faecal pellet is then expelled from the anus. It has long been known that certain anisopteran larvae eject their faecal pellets forcefully so that each pellet can be propelled far from the body of its originator. This action has been termed "ballistic defaecation" (Watson 1982). For example, in confined surroundings and at high density, large larvae of *Anax imperator* Leach (Corbet 1962: 144) and

Polycanthagyna melanictera (Selys) (Nagase 1974), both clasps (see Corbet 1999: 149), sometimes ejected faecal pellets out of the water and for distances exceeding 30 cm. Similar behaviour has been recorded in the terrestrial larva of the gomphomacromiine anisopteran *Pseudocordulia* sp. (Watson 1982). Ballistic defaecation is presumably effected by the muscular abdominal diaphragm (Amans 1881; Mill 1982), constituting yet another function of the versatile rectum of anisopteran larvae which effects, inter alia, rectal respiration, emergency (escape) locomotion by jet propulsion (review by Corbet 1999: 74), and foraging in the hovering mode (see Bay 1974; Rowe 1987). As far as is known, zygopteran larvae, presumably because they lack a muscular diaphragm, cannot practise ballistic defaecation. Among Anisoptera, one would not expect ballistic defaecation to occur beneath the water surface because the density of pellets is high relative to that of water. Or, if ballistic defaecation does occur beneath the water, one would wish to know how far the pellets were propelled, expecting this distance to be far less than in the air. If it transpires that ballistic defaecation can occur only in air, then we may have to regard it as a behaviour that becomes manifest only at a late stage in the drying up of small bodies of water or among larvae that preferentially occupy the upper layers of dense weed (in the manner of certain pond-dwelling aeshnids). It certainly does take place in small bodies of water (Corbet 1962: 144; Nagase 1974), but one may note that larvae defaecating at the surface would thereby make themselves conspicuous to avian predators such as herons (*Ardea* sp.). If, on the other hand, ballistic defaecation occurs beneath the water surface, larvae classified as burrowers would be unlikely to practise it because of the obstruction presented by the investing sediment, unless the larva were to raise the tip of the abdomen above the sediment when defaecating. Perhaps the elongated siphon of *Neurogomphus* (Corbet 1999: 161) and *Stylurus* (Asahina 1960), besides allowing the larva access to sediment-free water for respiration, may also enable it to propel faecal pellets into the open water without obstruction from the substrate.

One may suppose that such well-defined behaviour as ballistic defaecation has adaptive significance. Nagase (1974), who witnessed the behaviour in the laboratory, suggested that it might serve to prevent fouling of the water. Nagase's suggestion (to which I at one time subscribed) would provide a less-than-satisfying hypothesis, if, as is likely, faecal pellets have a low oxygen demand, their contents usually comprising highly triturated, predominantly indigestible, cuticular fragments of prey. However we do not know this, and Nagase's suggestion may well apply in very small residual bodies of water in the hot weather that would prevail as habitats dried up. An alternative (or supplemental) hypothesis that in my opinion deserves consideration is that advanced by Karen Wudkevich, a researcher at the University of Saskatchewan, in a letter to me from 26 January 1996. Her suggestion, which may appropriately be named the 'Wudkevich Hypothesis' arose from her involvement in work with two species of fish: the northern pike, *Esox lucius*, and its habitual prey, the fathead minnow, *Pimephales promelas*.

When a minnow or its fellow shoal member is injured or captured by a pike, the minnow emits an alarm pheromone to which other minnows respond by vacating the site (Mathis & Smith 1993). This alarm pheromone persists, serving as a chemical cue, and retaining its repellent properties, in the faeces of the pike (Brown

et al. 1995). The pike habitually defaecates away from its normal foraging site (Brown et al. 1995), thus avoiding discouraging its prey from congregating at the pike's foraging site. The effectiveness of this action by the pike is diminished by the fact that the pike itself emits a chemical cue that is detectable by the minnows and that induces antipredation behaviour in them (Brown et al. 1995). An experiment, using the amphipod crustacean *Gammarus lacustris* as prey and two kinds of predator – northern pike and final-stadium larvae of the anisopteran *Aeshna eremita* Scudder – revealed that the antipredation response of *Gammarus* appeared to differ according to whether the chemical cue it received had emanated from pike or from anisopteran larvae: in response to the chemical cue from the pike, *Gammarus* spent more time on the bottom (where the pike seldom foraged), whereas, in response to the chemical cue from the benthic anisopteran larva, *Gammarus* spent somewhat less time on the bottom, although the difference was not statistically significant (Wudkevich et al. 1997). Unfortunately one cannot readily infer the extent of this difference from the published account and accordingly cannot be confident that the result was not the outcome of coincidence. Nevertheless, these phenotypic behavioural traits induced by the presence of a predator have their morphological counterpart in the development of defensive spines in certain anisopteran larvae when they are obliged to co-exist with fish (Arnqvist & Johansson 1998).

Like pike, anisopteran larvae are ambush predators, adopting a foraging strategy that offers them an exceptionally favourable energy balance (Lawton 1973). If their faeces were to contain chemical cues derived from their recent prey, I find it plausible to predict that their prospects for prey capture would be improved if they were to position their faeces away from the ambush site, which they were presumably occupying because it was a productive foraging site. Accordingly, ballistic defaecation by an anisopteran larva may benefit the defaecator by removing a prey-repellent stimulus from its foraging site.

The Wudkevich Hypothesis can be readily explored (see proposed Experiments below). Initially it would be informative to discover how prevalent ballistic defaecation is among Anisoptera and to discover the correspondence (if any) between ballistic defaecation and taxonomic affinity and microhabitat occupancy. It would be useful to know, for example, whether ballistic defaecation is practised by all behavioural types of anisopteran larvae, namely claspers, sprawlers, hidiers and burrowers (see Corbet 1999: 149), and also whether it is practised by larvae occupying lotic habitats, where any chemical cues in the faecal pellets would presumably be swept away promptly by the current as a matter of course.

A primary need is to confirm that faecal pellets voided by Anisoptera do indeed contain chemical cues that repel prey organisms, in particular perhaps those taxa whose remains are frequently contained within the pellets (Experiment 1, vide infra). A positive result for Experiment 1 would, in my opinion, be consistent with the Wudkevich Hypothesis. A qualifying factor to be allowed for in Experiment 1 is that anisopteran larvae themselves may be repellent to prey (Experiment 2), either by virtue of their 'presence' (see Trembath & Anholt 2002) or because they have been contaminated externally by the alarm pheromone of their recent prey and on this account may affect the behaviour of prey close to them, regardless of the proximity of a faecal pellet (see Hews 1988).

Ancillary information that would bear importantly on this matter would include the distance over which prey can detect the chemical cues deriving from faeces and the modal distance the pellets are propelled in relation to this detection range. It would also be useful to determine whether ballistic defaecation habitually occurs beneath the water surface and, if so, how far faecal pellets are then propelled. To determine the circumstances that cause faecal pellets to be propelled out of the water (Experiment 3) would also contribute to our understanding of this behaviour. Obtaining information of this kind might be made easier by knowing that (by analogy with *Paragomphus lineatus* Selys) faecal pellets are voided at a predictable interval after a meal (see Mathavan 1976).

IMPLICATIONS

If the Wudkevich Hypothesis is sustained, this has far-reaching implications for odonate behaviour that merit discussion.

In the first place, Zygoptera do not defaecate ballistically and so may in some respects offer a 'control' for Anisoptera. Do zygopteran faeces, which necessarily remain closer to their ambush sites, repel prey from those sites (Experiment 4)? If so, does this imply that, to retain foraging efficiency, zygopteran larvae need to change ambush sites more often, to distance themselves either from their faecal pellets or from a repellent conspecific? Does such a need lie behind their much more elaborate intraspecific agonistic display behaviour?

The presence of chemical cues deriving from a predator's faeces (originating from injured prey) or from the predator itself have both been shown to induce antipredation behaviour in prey organisms. This finding has far-reaching implications for our interpretation of behaviour among odonate larvae, especially Zygoptera that frequently serve as prey, either for fish or for anisopteran larvae. A puzzle of long standing has been the contrast between the rich behavioural repertoires of zygopteran larvae and the paucity of such repertoires in anisopteran larvae. If, as predators, and unlike anisopteran larvae, zygopteran larvae are unable to discharge their faeces far from their foraging sites, they may on that account be obliged to change sites more often and thus to compete more vigorously with conspecifics for favourable sites. It is relevant here to note that perched larvae of *Xanthocnemis zealandica*, facing head downward, curl the abdomen downward when defaecating so that the faecal pellets accumulate around the base of an upright stem (Rowe 1985a: 132). A large part of the behavioural repertoire of zygopteran larvae comprises overt displays that can result in the displacement of a conspecific (Harvey & Corbet 1986). Perhaps this finding helps us to rationalize the richer behavioural repertoires found in zygopteran larvae, although larvae of *Enallagma traviatum* Selys, a species coexisting with insectivorous fish, were less active and exhibited fewer interspecific confrontations than did those of *E. aspersum* (Hagen), a species occupying fish-free habitats (Pierce et al. 1985).

Where such display behaviour has been studied closely it has been found to comprise a rich repertoire of discrete behavioural acts. For example larvae of *Ischnura verticalis* (Say) exhibit more than 30 discrete behaviours (Richardson & Anholt 1995), those of *Xanthocnemis zealandica* (McLachlan) exhibit 25

(Rowe 1985b), and those of *Pyrhosoma nymphula* (Sulzer) exhibit 16 (Harvey & Corbet 1986). In contrast, such behaviour has seldom been reported for anisopteran larvae. An example perhaps is the intraspecific agonistic behaviour of *Anax junius* (Drury), which is evidently confined to unilateral stalking (over distances up to 30 cm), reciprocal staring (the heads of facing adversaries being about 1 cm apart) and the labial strike (Ross 1971; Folsom 1980) which can sometimes have a fatal outcome (Folsom 1980). Final-stadium larvae of *A. junius* are significantly more aggressive towards conspecifics than are smaller larvae (Ross 1971; Folsom 1980); and the level of aggression and the distance travelled during a stalk are greater in food-deprived larvae (Ross 1971). Larvae of both Anisoptera (Ross 1971) and Zygoptera (Crowley et al. 1988) may spend protracted periods (e.g. up to 25 min) motionless, merely staring at one another. It would be useful to know whether any other species of Anisoptera exhibit intraspecific agonistic behaviour. In his study of *Gomphus simillimus* Selys and *Onychogomphus uncatatus* (Charpentier), Suhling (1996) witnessed no interspecific agonistic displays of the kind described above for *A. junius*, but recognized the possibility that such displays might be confined to darkness, when they would have escaped the observer's notice.

If the Wudkevich Hypothesis is sustained, it has far-reaching implications for our interpretation of larval ecology and behaviour. Among Odonata, no longer are prey (mainly Zygoptera) to be regarded as passive victims of predation, but rather as potential prey possessing an arsenal of chemical-cue-induced antipredation strategies, each of which may be tailored to the predation behaviour of a particular predator. As mentioned above, the amphipod crustacean *Gammarus lacustris* may respond differently to chemical cues emitted by two of its predators: pike and anisopteran larvae respectively, although this remains to be confirmed. Likewise, larvae of *Enallagma*, probably comprising *E. boreale* (Selys) and *E. cyathigerum* (Charpentier), exhibited antipredation responses appropriate to predators to which they had been previously exposed (Chivers et al. 1996). If zygopteran larvae exhibit a similar ability to vary their antipredation behaviour to enhance avoidance of predators that are active in different microhabitats, we can expect this to have a significant effect on the microdistribution of zygopteran larvae and therefore upon conclusions drawn about that distribution. The demonstration that species-specific chemical signals emitted by a variety of predators can influence the movements and behaviour of zygopteran larvae (Wudkevich et al. 1997) constitutes an important qualifying factor for our interpretation of their ecology. That such behaviour has a learnt component is shown by the antipredation responses of larval *Enallagma* (including *E. boreale* and *E. cyathigerum*) which are appropriate to predators to which they were previously exposed (Chivers et al. 1996). An early need is to characterise the types of microhabitat in which such stimuli are effective. It appears that some of these antipredation responses are innate and that some are learnt. Thus *E. boreale* larvae from sites lacking pike responded first (with antipredation behaviour) only to chemical cues from injured conspecifics (Wisenden et al. 1997). Later they responded similarly to chemical cues from pike. Such a flexible learning programme enabled the *E. boreale* larvae rapidly to acquire the ability to recognise (and to distinguish) kinds of local predation risk based, respectively, on chemical stimuli from predators, conspecifics, and heterospecific

members of their prey guild; i.e. organisms exposed to the same predators as themselves (Wisenden et al. 1997). If zygopteran larvae, which are known to be habitual prey of fish, can detect and respond to chemical cues that warn of the proximity of a predator, this may constitute an additional reason why they may be encouraged to vacate some ambush sites and to compete with conspecifics for the occupancy of others.

EXPERIMENTS

The following experiments would throw light on the possibilities identified above:

- (1) Determine whether faecal pellets of anisopteran larvae emit chemical cues that repel prey organisms (i.e. that modify the latter's antipredation behaviour).
- (2) Determine whether anisopteran larvae themselves (in the absence of their faecal pellets) emit chemical cues that repel prey organisms.
- (3) Determine the factors that induce anisopteran larvae to project their faecal pellets out of the water.
- (4) Determine whether the faecal pellets of zygopteran larvae emit chemical cues that repel prey organisms.

Apart from these experiments designed to test the Wudkevich Hypothesis, it would improve our understanding of larval behaviour if the following questions could be addressed:

- (1) Are there other observations of ballistic defaecation by larval odonates, besides the ones cited in this article? If so, which taxa are involved?
- (2) Are there other observations, besides those cited here, of intraspecific agonistic behaviour by larvae of Anisoptera?

ACKNOWLEDGEMENTS

I am greatly indebted to Karen Wudkevich for alerting me to the notion that ballistic defaecation by anisopteran larvae might be analogous to the strategic defaecation behaviour of pike. I also thank Hal White for providing literature, Sally Corbet and Hal White for commenting on an early draft of the manuscript and Richard Rowe, Göran Sahlén and Frank Suhling for commenting on a late one.

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