

Death feigning in sexual conflict between dragonflies (Odonata): does it exist?

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Abstract. Death feigning, sometimes designated as thanatosis, reflex immobilization, tonic immobility or faking death is generally assumed a last-resort antipredator defence, attempting to avoid being killed and consumed. Recently, faking death has also been claimed to exist with respect to sexual conflict in Odonata. Here we review a number of published cases in Anisoptera that describe how non-receptive females during oviposition escape male harassing by fleeing, plunging into vegetation, freezing immediately and remaining motionless in random body position, no longer being noted by the male hovering nearby. We argue that this reaction of the female does not match the definition of death feigning and propose a new term for it: ‘drop and stop’ behaviour. In this context it is reasoned how and under what circumstances males, if at all, are able to recognize immobile females and react to them. The adaptive value of ‘drop and stop’ is discussed and it is suggested that this behaviour in sexual conflict could have evolved from a predator avoiding tactic.

Further key words. Thanatosis, reflex immobilization, tonic immobility, catalepsy, playing possum, female recognition, review

Introduction

Death feigning or thanatosis is considered an antipredator tactic in which the potential prey freezes, giving an animal the appearance of being dead. It is assumed to be an adaptive behaviour to the extent that it reduces predator attention and increases survival in the presence of a potential predator (Ed-

MUNDS 1974; HONMA et al. 2006; HUMPHREYS & RUXTON 2018). This defense behaviour is found in a wide range of animals and is especially impressive in the case of 'playing possum' in the Virginia opossum *Didelphis virginiana* (e.g., FRANCO 1969) or in snakes as, e.g., the grass snake *Natrix natrix* (GREGORY et al. 2007) and the water snake *Erythrolamprus miliaris* (MUSCAT et al. 2016). It also is known in arthropods such as the blue death feigning beetle *Asbolus verrucosus* (EVANS & HOGUE 2006) and the harvestman *Eumesosoma roeweri* (CHELINI et al. 2009). Thanatosis has likewise been described in terms of sexual cannibalism in the preying mantid *Mantis religiosa* (LAWRENCE 1992) and the nursery web spider *Pisaura mirabilis* (BILDE et al. 2006). In adult dragonflies it is less clear if they actually exhibit thanatosis, especially in the context of reproductive behaviour. Recently, KHELIFA (2017) reported on »faking death« in adult females of *Aeshna juncea*, stating his account was the first record of sexual death feigning in odonates. He made the case that the adaptive function of the behaviour by females was to »avoid male coercion« as a way to »extreme sexual conflict resolution«. His report prompted us to review a number of past cases of 'death feigning' in the Odonata and assess its function with respect to sexual conflict resolution.

What are the criteria of thanatosis in arthropods?

Death feigning as phenomenon was first mentioned as early as 350 BC by the Greek philosopher Aristotle who summarized the knowledge on animals of his culture period, laying the foundation of zoological taxonomy. In his work 'Parts of Animals' (Book IV, §6; BARNES 1984: 87) he described death feigning in the example of soldier beetles (Cantharidae): »This can be felt quite plainly by putting the finger on one of the insects, for instance, known as canthari. The touch frightens the insect, and it remains motionless, while its body becomes hard.« Meanwhile death feigning has been found in all classes of vertebrates as well as in many invertebrate taxa. A variety of terms is used for it such as thanatosis (from Greek *ho thánatos* – death), apparent death, reflex immobilization, tonic immobility, freezing behaviour, akinesis, animal hypnosis, catalepsy, catatonia or playing possum. Although its phenotypical expression may vary between different animals, death feigning is characterized by a number of features that are generally accepted to be common to all protagonists. In regard to Odonata, discussed here, we would restrict our

review to a few traits that we consider typical for arthropods. Thus, considering views and studies of several authors (*e.g.*, NISHINO & SAKAI 1996; WILDERMUTH 2000; NISHINO 2004; ROGERS & SIMPSON 2014; HUMPHREYS & RUXTON 2018), death feigning in arthropods may be defined as

- immediate reaction to strong physical stimuli (grasping, gripping, biting) by a real or simulated, *i.e.*, experimental, predator
- adoption of a distinctive rigid body posture, sometimes rolling over and laying on the back, the legs either retracted over the body or extended in a characteristic fashion
- immobility with a prone but stiff posture to be maintained by pronounced tonic muscular activity
- the flexed-leg posture maintained by the flexor tibiae muscle, giving the limbs a 'waxy flexibility'
- unresponsiveness to external stimuli while remaining fully aware of the environment
- duration of few seconds to minutes or even hours
- usually spontaneous rapid resumption of activity, with the righting reflex reasserting itself

Although thanatosis is far from being understood in many cases, it is generally assumed a last-resort antipredator defence, attempting to avoid being killed and consumed (*e.g.*, EDMUNDS 1974). Death feigning exceptionally occurs also in the context of sexual selection: males of mantids may make use of it in terms of sexual cannibalism (LAWRENCE 1992; KYNASTON *et al.* 1994). The same has been found in the nuptial gift-giving spider *Pisaura mirabilis* (BILDE *et al.* 2006, 2007; HANSEN *et al.* 2008). However, in these cases too, thanatosis may assist a male to evade predation by his mate. As revealed in the red flour beetle *Tribolium castaneum*, death feigning has an underlying genetic basis, suggesting that thanatosis is adaptive (PROHAMMER & WADE 1981; MIYATAKE *et al.* 2004).

The term 'death feigning' needs to be scrutinised. Do death feigning animals actually look as if they are dead? When entering thanatosis, a spider or harvestman collapses and remains completely motionless, often laying on the back with legs retracted over the body and indeed appearing to be dead (*e.g.*, BILDE *et al.* 2006; POMINI *et al.* 2010). The same would apply to

anisopteran larvae, which press their legs closely against their sides, remaining immobile with anal valves closed (ABBOTT 1926; ARAI 1987; WILDERMUTH 2000; WILDERMUTH & MARTENS 2019: 432, 538). Other arthropods, although motionless as response to predator attack, judged by their posture, do not always look as if they were dead. The pigmy grasshopper *Criotettix japonicus* may be an extreme example. It adopts a special rigid posture when attacked by a frog (*Rana nigromaculata*), a gape-limited predator. By stretching the spiky pronotum, the hind legs and the lateral spines in three different directions it enlarges its operational body size, thereby making it difficult for the predator to swallow the prey (HONMA et al. 2006). In this posture the insect does not mimic death *per se* and looks decidedly different to a dead individual. Thus, 'death feigning' would not be an appropriate term for the behaviour in this case.



Figure 1. Unreceptive female *Aeshna grandis* plunged into meadow vegetation as reaction to male follower. Sihlsee, Switzerland, 08-x-2007, 14:50 h CEST. Photo: HW

Do odonate imagines display death feigning in the narrower sense?

Besides larval dragonflies imagines may also exhibit thanatosis. As described by CALVERT & CALVERT (1917) in *Megaloprepus coerulatus* (Drury, 1782), the damselflies when »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'.« 'Reflex immobilization' is especially distinct in most of the Hawaiian *Megalagrion* species (MOORE 1983). Furthermore, it is a common experience of any observer in the field that freshly emerged odonates immediately drop from their support and disappear in tangled vegetation when disturbed. The same may happen in adult zygopterans or anisopterans at low temperatures or in rainy weather when flight is virtually impossible. HÜBNER (1983) and SCHMIDT (1995) observed how individuals of *Sympetrum vulgatum* and *Somatochlora metallica*, respectively, dropped to the ground »like dead« or plunged into dense vegetation when they were closely pursued in flight by a barn swallow *Hirundo rustica*. In this situation *S. vulgatum* remained motionless even when taken into the observer's hand for some seconds before it departed. In all aforementioned cases the odonates tried to escape a predator, however,

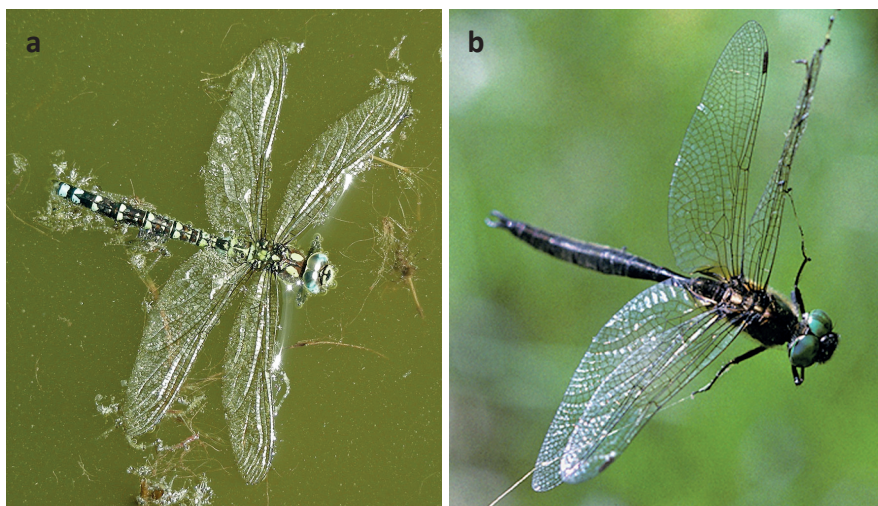


Figure 2. Aspects of naturally dead dragonflies. a – *Aeshna cyanea* floating on pond surface. Rüti ZH, Switzerland, 31-viii-2011; b – *Somatochlora arctica* in spider web. Nauders, Austria, 07-viii-2011. Photos: HW

not all examples meet exactly the above definition of death feigning. In the last two cases, *e.g.*, triggers of the behaviour were visual – and not tactile – stimuli, and motionlessness was preceded by escape reaction, thus obviously being more complex than a simple reflex.

Another point is that ‘death feigning’ dragonflies lying on herbaceous ground or in shrubby vegetation do not necessarily look dead. They may cling completely motionless to the substrate, often nose-down, or are entangled in random position among plant structures (Fig. 1; photo in GRAND & BOUDOT 2006: 58). Instead, dead odonates look different when encountered, mostly being caught in spider webs or floating on the water with their wings sticking to the water surface (Fig. 2).

Does ‘death feigning’ exist in context of reproductive behaviour?

‘Death feigning’ has also been described in the context of reproduction. KHELIFA (2017) reports on »sexual death feigning« in *Aeshna juncea*. He »witnessed a dragonfly dive to the ground while being pursued by another dragonfly. « [...] Then he realized »that the individual that crashed was a female, and that she was lying motionless and upside down on the ground. [...] The male hovered above the female for a couple seconds and then left.« Exactly this behaviour of *A. juncea* was described by at least four independent observers: most probably for the first time by ROBERT (1959: 177) and then explicitly by SCHMIDT (1964), STERNBERG (2000a) and WILDERMUTH & MARTENS (2014: 314). Meanwhile the same has been recorded in at least 15 aeshnid, corduliid and libellulid species (Table 1) but only exceptionally designated ‘death feigning’ (CORBET & BROOKS 2008: 202; WILDERMUTH 2008: 203).

In all published cases the females reacted to a fast approaching, visually detected male and dashed to the ground or, in tall herbaceous or shrubby vegetation, the way they behaved as described above when chased by hunting swallows. Immediately after touching the substrate they remained motionless for seconds to minutes and were no longer noted by the males hovering above them. In the typical case of *Somatochlora arctica*, *e.g.*, females escaping from pursuing males were repeatedly observed to plunge speedy into vegetation, to freeze immediately and remain motionless in a random body position among stems and blades (WILDERMUTH 2003).

Table 1. Published records of ‘drop and stop’ behaviour in female Anisoptera. MA – male attack, PA – predator attack.

Species	References	Trigger
<i>Aeshna cyanea</i> (O.F. Müller, 1764)	KAISER (1974): 416	MA
<i>Aeshna juncea</i> (Linnaeus, 1758)	ROBERT (1959): 177	MA
	SCHMIDT (1964): 340	MA
	STERNBERG (2000a): 80	MA
	WILDERMUTH & MARTENS (2014): 314	MA
	KHELIFA (2017): video	MA
	WILDERMUTH & MARTENS (2019): 359	MA
<i>Aeshna subarctica</i> Walker, 1908	STERNBERG (2000b): 104 f.	MA
	SCHMIDT (1964): 340	MA
<i>Cordulia aenea</i> (Linnaeus, 1758)	ROBERT (1959): 258	MA
<i>Cordulia aenea amurensis</i> Selys, 1887	UBUKATA (1975): 823	MA
	UBUKATA (1983): 78	MA
	UBUKATA (1984): 77	MA
<i>Procordulia grayi</i> (Selys, 1871)	ROWE (1988): 56	MA
<i>Procordulia smithii</i> (White, 1846)	ROWE (1988): 56	MA
<i>Somatochlora alpestris</i> (Selys, 1840)	KNAUS (1999): 28 f.	MA
	GRAND & BOUDOT (2006): 58, 377 + photos	MA
	BOUDOT et al. (2006): 56 + photo	MA
<i>Somatochlora arctica</i> (Zetterstedt, 1840)	WILDERMUTH (2003): 69	MA
<i>Somatochlora flavomaculata</i> (Vander Linden, 1825)	WILDERMUTH (1998): 232	MA
<i>Somatochlora metallica</i> (Vander Linden, 1825)	SCHMIDT (1995) in WILDERMUTH (2008): 155	PA
	WILDERMUTH & KNAPP (1998): 68	MA
	GRAND & BOUDOT (2006): 58 + photo, 372	MA
	BOUDOT et al. (2017): 56 + photo, 339	MA
<i>Somatochlora meridionalis</i> Nielsen, 1935	WILDERMUTH & MARTENS (2014): 516	MA
	WILDERMUTH & MARTENS (2019): 592	MA
<i>Leucorrhinia dubia</i> (Vander Linden, 1825)	PAJUNEN (1963): 112 f.	MA
	PAJUNEN (1964): 66	MA
<i>Leucorrhinia rubicunda</i> (Linnaeus, 1758)	SCHMIDT (1964): 340	MA
	RÜPPELL (1990): 6	MA

Species	References	Trigger
<i>Libellula quadrimaculata</i> Linnaeus, 1758	SCHMIDT (1964): 340	MA
<i>Orthetrum brunneum</i> (Fonscolombe, 1837)	CHOVANEK (2017): 140	MA
<i>Sympetrum danae</i> (Sulzer, 1776)	SCHMIDT (1964): 340	MA
<i>Sympetrum vulgatum</i> (Linnaeus, 1758)	HÜBNER (1983): 90	PA

‘Drop and stop’ behaviour of unreceptive females

Dropping to the ground and suspending movement is also observed in some libellulids and corduliids that typically exhibit non-contact guarded oviposition. At high male density and intensive mating activities females of several libellulid species may drop and perch on algae carpets or emergent plant substrates at the oviposition site and in most cases are no longer molested by conspecific males. That way they avoid male harassment, why we interpret motionless sitting on floating vegetation as a variant of ‘drop and stop’ behaviour (see below). In this situation, female *Orthetrum brunneum* and *O. taeniolatum* (Schneider, 1845) seem to interrupt oviposition (CHOVANEK 2017; WILDERMUTH & MARTENS 2019: 721) or the females may continue laying eggs as reported in *Orthetrum cancellatum* (JÖDICKE & BORKENSTEIN 2019) and *Leucorrhinia rubicunda* (PAJUNEN 1963; RÜPPELL 1990; AB unpubl.). In *Zygonyx natalensis* (Martin, 1900) and *Z. torridus* (Kirby, 1889) sedentary oviposition is one of four alternative oviposition modes (MARTENS 1991, 2015). Similar behaviour is reported in *Procordulia grayi* (Rowe 1988), and in *Orthetrum nitidinerve* (Selys, 1841) sedentary oviposition is the only known style of laying eggs (KHELIFA et al. 2012; PRUNIER 2015; WILDERMUTH & MARTENS 2019: 638). In *Trithemis kirbyi* Selys, 1891, unusual oviposition behaviour was observed at high male density. After copulation, females settled on the ground at the pond’s edge, released a drop of eggs, flew quickly to the water, dipped the abdomen with the eggs in the water and settled again until the next drop of eggs had formed (KOCH 2006). In all these cases this behaviour may be interpreted as avoidance of male harassment during oviposition.

As argued for odonates, crash landing and staying motionless as response to attacking bird predators, non-receptive females reacting in the same way on harassing males do not actually fake death because this behaviour does not meet the crucial criteria for thanatosis as defined above: (i) It is not triggered by strong physical contact but rather by sight of a fast attacking male, *i.e.*, by a visual cue, (ii) Immobility is preceded by downward escape and follows only after physical contact to solid substrate, (iii) There is no characteristic 'death feigning' posture; the females just plunge into vegetation and stop in accidental posture. Body, legs and wings are positioned passively, determined by the vegetation structure, and not actively by the animal itself. Usually they alight headfirst nose down (Fig. 1) or in perching position (GRAND & BOUDOT 2006: 58), landing on the back is rather exceptional.

Taking into account all these factors, we consider 'death feigning' as described by KHLELIFA (2017) simply as »hiding, remaining motionless« (FINCKE 1997: Table 1) or as »hiding by dropping to substrate and suspending movement«, defined by CORBET (1999: 471) as a variant of the female's refusal behaviour. Its function is considered avoidance of coercion by non-receptive females. Just like many modes of behaviour, it can be used effectively in different contexts. Given the fact that dropping and suspending movement is a general feature in Odonata, which is not restricted to a reaction on a potential predator, we avoid the term 'death feigning' and propose a new term: 'drop and stop' behaviour.

Males' response to 'drop and stop'

We can generally assume that visual signals such as size, shape and colour pattern combined with motion are the principal cues for mate recognition (*e.g.*, FINCKE 2015). SCHULTZ & FINCKE (2009) found in *Megaloprepus coerulatus* that the sexually dimorphic wing pattern cues sex to males. Especially in species with camouflage pattern as in *Aeshna* spp. or inconspicuous dull coloration as in *Somatochlora* spp., motion would be the most important cue (UBUKATA 1983). Even wing whirring during sedentary oviposition would disclose a female to a male. As observed in *A. juncea*, ovipositing females would freeze and stop wing whirring as soon as they are aware of an approaching male (STERNBERG 2000a: 80). Accordingly, male *Anotogaster*

sieboldii (Selys, 1854) only react to rotating models but not to motionless objects (ISHIZAWA & ARAI 2003). Visual acuity in odonates is highly evolved compared to other insects, *e.g.*, their spatial and temporal resolution are high. The most important criterion for spatial resolution is the interommatidial angle. The smallest angle that has been measured amounts to 0.24° in *Anax junius* (Drury, 1773) (SHERK 1978), *i.e.*, its maximal visual acuity is at least 25 times lower than in humans. On the other hand, the temporal resolution of odonates is higher than ours: *Pachydiplax longipennis* (Burmeister, 1839) may perceive up to 200 light stimuli per second under optimal conditions (RUCK 1958), *i.e.*, its temporal resolution is at least three to four times better than in humans. Based on these visual traits one might suppose that male Anisoptera would even recognize somatolytically coloured motionless females blending with tangled vegetation. This is in contrast to traditional interpretations which are basing on the assumption that frozen females become invisible to males (*e.g.*, SCHMIDT 1964). But why do they desist from grasping them and cease from hovering close to them after some time? We are convinced that 'drop and stop' is a clear behavioural message to chasing males with the meaning of: 'stop at once, I am unreceptive, do not invest any further energy in me'. Such a message is an effective refusal display and as such only comparable with the downwards curved abdomen of some aeshnid females (reviewed in BORKENSTEIN *et al.* 2016) but may work in an even more effective manner. In both variants of refusal display females are obviously no longer attractive in this posture.

Indeed, there is evidence that some *Aeshna* species are able to recognize immobile females unrestrictedly. This seems to be the case when basking females are perched on sunlit tree trunks. STERNBERG (2000a: 80) reports on males of *A. cyanea*, *A. grandis* (Linnaeus, 1758), *A. juncea* and *A. subarctica* systematically scanning such tree trunks from bottom to top and he interpreted this behaviour in the first place as foraging behaviour. Due to the fact, however, that these scanning flights seem to be exhibited exclusively by males and furthermore took place only in the vicinity of breeding habitats, the author also considers the possibility that in fact this behaviour might rather be sexually motivated and males are trying to detect sunbathing females. He explicitly mentions an observation of a male *A. juncea* tracking and catching flushed flies, but also flushing females resulting in subsequent

mating attempts. SCHMIDT (1964) interprets the tree-scanning behaviour as an exclusive strategy to search for mates. He observed males of *A. juncea* and *A. subarctica* grasping sun-bathing females for copulation but never saw feeding on flushed prey objects. This has been confirmed on the basis of tree-scanning male *A. crenata* Hagen, 1856 (AS unpubl.), thus supporting the assumption of a purely sexual comportment.

Additionally, there is further evidence that odonate males are able to recognize motionless females. AB and RJ (unpubl.) studied the reaction of male *A. grandis* during matutinal searching flight to dead females which were pinned on reed leaves in a position like that of roosting females (cf. BORKENSTEIN et al. 2017). In fact, a searching male spotted and approached such a decoy. He grasped the thorax of the female but was unable to attach his appendices due to the decoy being headless (Fig. 3), so the formation of a copulatory 'twisted wheel' (see below) failed.

How do *Aeshna* males recognise somatolytically coloured and completely motionless perching females? A plausible explanation might be the pattern of reflected light including UV, from the females' wings which, depending of the angle of approach of the hovering males, disclose the motionlessly basking or roosting females, even in twilight (see, e.g., HILTON 1986).

A special case: 'twisted wheels' are immobile

'Twisted wheels' are only reported from *Aeshna grandis* and *A. viridis* Eversmann, 1836 (BORKENSTEIN et al. 2016, 2017). Both species share the same unique mating tactic: males perform a matutinal searching flight, i.e., at sunrise they enter dense thickets of vegetation at the terrestrial rendezvous site and search for perching receptive females. The pairing wheel is not, as is usual, formed in flight, but the females remain in their perching position when being grasped by a male. He then drops downwards and achieves a typical hanging position with his head facing down and his abdominal tip having slipped onto one of the female's eyes in an oblique position.

The striking point of 'twisted wheels' with regard to the subject of this paper is their lack of any escape attempt which makes them *de facto* immobile, although the males show copulatory movements and both mates are able to optimize the grip to their perching substrate. Obviously, the predation risk of a couple is lowest in this combination of motionlessness and hidden

perch position. Most probably the loss of any reaction to visual or even tactile irritation is an adaptive result of an evolutionary process, but it remains unclear if this interpretation may cover all aspects of the freezing behaviour of 'twisted wheels'.

Recognition of an immobile female, even in twilight, has been demonstrated by the experiment with dead specimens as mentioned above. Yet, it is an unanswered question if males can differentiate between receptive and unreceptive females. It is reported that some unmated females of *A. grandis* were seen after the searching flight (BORKENSTEIN et al. 2017), sitting in a position which was fully accessible to the males. Such females might have been unreceptive and have possibly refused the formation of a mating wheel.

Are there parallels in other arthropods?

We are aware of only very few examples of 'death feigning' in the context of sexual selection. In their study on reproductive behaviour of robber flies, DENNIS & LAVIGNE (1976) noticed that some females of *Efferia varipes* and *Scleropogon neglectus* exhibited 'thanatosis' as soon as they were grasped by males: »Once the females ceased to move, the males would release them and fly off«. This behaviour comes closer to our definition of thanatosis as



Figure 3. Male *Aeshna grandis* approaching (a) and grasping (b) a dead pinned female at the natural rendezvous site during matutinal mate search flight in Rheiderland, Germany, at 06:18 h CEST. Note that any genital linkage failed due to the lost head of the decoy. Photos (flashed) by AB (03-viii-2018)

it is elicited by grasping, *i.e.*, by tactile stimulus. However, it is not known whether this behaviour also meets the other criteria of 'death feigning'.

A second example of thanatosis in the context of sexual selection in arthropods is the reproductive behaviour of the nuptial gift-giving spider *Pisaura mirabilis*. BILDE et al. (2006) showed that males display death feigning as part of the courtship prior to mating with cannibalistic females: »When entering thanatosis, the male would collapse and remain completely motionless«. This behaviour can indeed be judged as death feigning as it is released by physical contact and by collapsing, *i.e.*, the legs typically retracted over the body. However, this is not comparable with 'drop and stop' behaviour in female odonates trying to avoid harassment by males. First, it is the male spider that displays thanatosis, and not the female, and second, death feigning in *P. mirabilis* males constitutes an anti-predator tactic, *i.e.*, it may be considered a pre-copulatory cannibalism avoidance behaviour, and not avoidance of sexual harassment by males wanting to mate. The same would apply to male mantids that sometimes freeze when they are moving away from the female after copulation (LAWRENCE 1992), a behaviour being assessed a post-copulatory cannibalism avoidance.

Evolutionary aspects

It is conceivable that the 'drop and stop' behaviour in sexual conflict of anisopteran females could have originated from predator avoiding behaviour, *i.e.*, a flight reaction of low flying dragonflies to bird attacks as mentioned above. The reactions in both situations would be similar, only the triggers – predation on one hand, male harassment on the other – being different. Yet, the reaction would also depend on the individual's motivation as only non-receptive females would try to escape an attacking male. So far, 'drop and stop' behaviour has only been recorded in a few representatives of corduliids, aeshnids and libellulids (Table 2). Oviposition in all these species either occurs alone (unguarded) or with the male guarding closely (non-contact guarded) (CORBET 1999: 21 ff., 527 ff.), and the oviposition mode, as shown in some libellulids, may vary in detail depending on the current situations, such as changing weather conditions, arrival of predators, changing male density and male harassment (KOCH 2006). Thus, male harassment may be considered the main factor which promoted the evolution of 'drop and stop' behaviour.

Occurrence of ‘drop and stop’ could also be connected with the duration of copulation of a species. Noticeably, in representatives of Aeshnidae and Corduliidae, typically exhibiting ‘drop and stop’, copulation lasts relatively long; e.g., 1–1.5 h in *Aeshna cyanea* (KAISER 1974), up to more than 4 h in *A. grandis* and *A. viridis* (BORKENSTEIN et al. 2017), and 0.5–2.5 h in *Somatochlora arctica* (WILDERMUTH 2013), while in several species of libellulids, duration does not exceed 1 min (CORBET 1999: 663), 3–7 s in *Diastatops intensa* Montgomery, 1940 (WILDERMUTH 1994) and 3–30 s in *Libellula quadrimaculata* (STERNBERG 2000c; HW unpubl.). Thus, for a non-receptive female of a species with long copulation, the costs of undesirable mating would be higher than for a species with short copulation. Lower costs could therefore explain that multiple mating of non-receptive females during oviposition, as often observed in *D. intensa* and *L. quadrimaculata*, is preferred over escaping and hiding in vegetation. On the other hand, for a species with long lasting copulation the risk of time loss and injury by additional copulation would be higher than of rapid flight and ‘drop and stop’.

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