

## Faking death to avoid male coercion: extreme sexual conflict resolution in a dragonfly

I spent the summers of 2014 and 2015 in the Swiss Alps, collecting the eggs of odonates (dragonflies and damselflies) for laboratory experiments on larval responses to temperature. This involved many hours spent waiting beside ponds to capture females as they came to the water to lay eggs. On 5 July 2015, while I was waiting at a pond near Arosa, at about 2000 m elevation, I witnessed a dragonfly dive to the ground while being pursued by another dragonfly. I grabbed my camera and started filming (Video S1). As I approached the two insects, I realized that they were *Aeshna juncea* (moorland hawker or sedge darter), that the individual that crashed was a female, and that she was lying motionless and upside down on the ground. Upside down is an atypical posture for a dragonfly. The male hovered above the female for a couple seconds and then left. I expected that the female could be unconscious or even dead after her crash landing, but she surprised me by flying away quickly as I approached. The question arose: did she just trick that male? Did she fake death to avoid male harassment? If so, this would be the first record of sexual death feigning in odonates and probably the fifth in the animal kingdom after a nuptial gift-giving spider (Bilde et al. 2006, Hansen et al. 2008), two species of robber fly (Dennis and Lavigne 1976), and a European mantis (Lawrence 1992). Kaiser (1985) described motionless hiding by females in another dragonfly (*A. cyanea*; blue hawker), but did not indicate that they were faking death. I also wondered how common

this behavior might be. The observation near Arosa prompted me to remember several other instances during the previous season in which I had seen dragonflies diving into the ground or vegetation. *Aeshna juncea* is common at each of the ponds where those observations occurred; could sexual death feigning occur regularly in this species?

To answer these questions, I studied the reproductive behavior of *A. juncea* for 72 h in July and August 2015 at two sites (the Arosa pond, 46.80°N, 9.67°E and another pond near Lenzerheide, 46.73°N, 9.55°E) from 10:00 to 16:00. In both ponds, the bank vegetation, where most egg laying takes place, was relatively dense with most patches not exceeding 60 cm height. As for many other dragonflies, the female reproductive episode of the moorland hawker may be divided into four important sequential events: female arrival at reproductive site, copulation, oviposition, and departure from reproductive site. To summarize, mature males remained close to the water waiting for females. When the female came to the pond, the male intercepted her in the air and both formed the copulatory wheel. Copulation took place near the pond, often perched on a plant support (Fig. 1a). After copulation, the male detached himself from the female and flew away. The female laid eggs (oviposition) solitarily without male protection (Fig. 1b), unlike many other dragonflies (Corbet 1999). Female became vulnerable to male coercion at that time because conspecific males were constantly patrolling each corner of the pond looking for a mate. To overcome this pressure, females showed both preventive and protective behavioral strategies to avoid coercion during oviposition and departure from reproductive sites.

To reveal potential preventive behavioral strategies of females, I estimated the vegetation density (percentage of 1 m<sup>2</sup> water area covered by vegetation) around oviposition sites of 56 and 46 ovipositing females during five days in Arosa and Lenzerheide, respectively (Appendix S1). I hypothesized that females choose sheltered areas

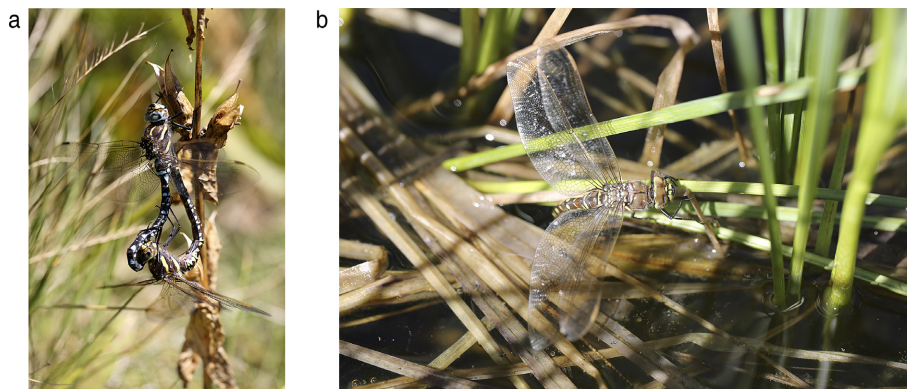


FIG. 1. Moorland hawker (*Aeshna juncea*). (a) Reproductive pair; (b) oviposition of a single female.

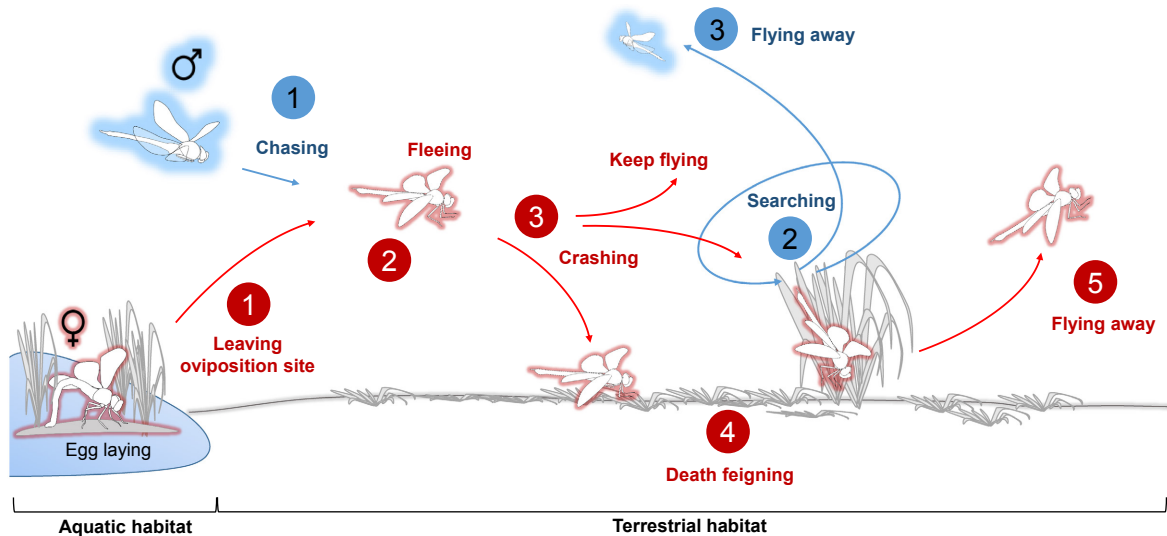


FIG. 2. Death feigning of female (in red) against male (in blue) coercion of the moorland hawkfly (*Aeshna juncea*). Numbers refer to the succession of the events. Numbers in black and white are males and females, respectively. When the female leaves oviposition site (red 1), a male usually chases her (blue 1), which induces the female to flee (red 2). The female either keep flying or crash on the ground or vegetation (red 3). She performs death feigning right after crashing (red 4) while the male is searching for her (blue 2). The male does not detect the female and leaves the crashing area (blue 3). The female, knowing that she is no longer coerced, flies away (red 5).

of the pond to reduce its visibility to coercive males. On average, females laid eggs in sites with high vegetation density of 70.9% in Arosa ( $n = 56$ ) and 69.2% in Lenzerheide ( $n = 46$ ). I conducted an experiment in which I reduced male density by  $\geq 50\%$  in the two sites during one day (Appendix S1), which reduced of the average density of oviposition sites in vegetation (Appendix S1: Fig. S1a) and decreased the number of male coercion events (Appendix S1: Fig. S1b). These results suggest that males shape habitat selection of females, and thus the occupancy of densely vegetated parts of the pond during oviposition could be a behavior to reduce male coercion.

To assess the protective behavioral strategies of females during coercion, I assessed female behavior during departure from the reproductive site, which is probably the phase where the female is most vulnerable to coercion. Fig. 2 illustrates behavioral responses of females to male coercion after oviposition and Appendix S1: Table S1 presents the respective statistics for both sites. When the female tried to leave the oviposition site, males always chased her on the air. Females ( $n = 35$ ) usually crashed on the ground (88.6%,  $n = 31$ ), and rarely kept flying (11.4%,  $n = 4$ ; chi-square test,  $P < 0.0001$ ; Appendix S1: Table S1). Females who did not crash to the ground or vegetation were all intercepted by a male. Females crashed-landed ( $n = 31$ ) more often within vegetation such as bushes and dense grasses (71%,  $n = 22$ ), than on open areas on the ground (29%,  $n = 9$ ; chi-square test,  $P = 0.02$ ). Following the crash, death feigning was observed in 27 out of 31 cases (87%). Of the 27 motionless females, 21 (77.7%) were successful in deceiving the coercive male.

The high frequency of sexual death feigning in both sites suggests that this behavior is common for the species. In addition, that males could not detect the motionless females highlights the importance of movement for males to detect females, which is the case for many odonates (e.g., Bick and Bick 1961, Ubukata 1984).

To test whether females are sensitive to touching during death feigning, I performed an experiment in early August 2015 at Arosa pond in which I attempted to catch by hand females performing death feigning after male harassment. Usually, it is impossible to catch an active dragonfly by hand because they rapidly escape. Of 31 catching attempts, 27 females successfully escaped (87%). Therefore, when females display death feigning they are perfectly conscious and readily avoid disturbance and probably predators.

So how did sexual death feigning evolve? On one hand, this behavior could have resulted from exaptation. Since death feigning already exists in the behavioral repertoire of dragonflies (Corbet 1999), females of the moorland hawkfly expanded the use of this antipredatory function to avoid male coercion. On the other hand, the origin of this exaptation is probably sexual conflict where each sex adopts reproductive strategies that best serve its own survival and reproductive success (Parker 1979). The mating system of the moorland hawkfly is predisposed to sexual conflict because the vulnerability of solitary oviposition, the fitness costs of male harassment (Rice 1996, Crudgington and Siva-Jothy 2000), and the highly male-biased sex ratio in oviposition sites (Wildermuth 1993) put the females under extreme reproductive conditions that require effective

behavioral responses to overcome survival and reproductive costs. Thus, females that perform death feigning probably undergo less coercion, survive longer and produce more offspring, hypotheses that warrant testing.

Sexual death feigning is one of the rarest behaviors in nature, and due to its scarcity, it has received little attention in behavioral ecology. Currently, it is restricted only to arthropods. It would be interesting to know whether this scarcity is true or just an artefact related to the lack of behavioral investigations or difficulty in detecting this behavior. Further studies should investigate how widespread sexual death feigning is among arthropods and whether it occurs in other phyla. Moreover, it is time to develop an informative classification for death feigning behavior that takes into account both behavioral and physiological information because death feigning could be strictly behavioral in which the animal is conscious and sensitive to touching and handling (moorland hawk-like), but could also include physiological changes where the animal is “unconscious,” physiologically shut down and unresponsive to physical contact (opossum-like). Finally, the new case of sexual death feigning reported here demonstrates discoveries even in common species and well-studied areas of the world remain. Although the diversity of sizes, shapes, structures and colorations of organisms on earth is astonishingly high, the diversity of behaviors might be surprisingly comparable.

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#### RASSIM KHELIFA

*Department of Evolutionary Biology and Environmental Studies, University of Zurich  
Winterthurerstrasse 190, CH-8057, Zurich, Switzerland  
E-mail: rassimkhelifa@gmail.com*

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