# How do the molluscivorous beetles *Carabus granulatus* and *Phosphuga atrata* (Insecta, Coleoptera) deal with sinistral and dextral prey?

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## ABSTRACT

Predators of asymmetric prey (such as snails) are often asymmetric themselves or display a predation behaviour that is adapted to the asymmetry of their prey. We studied predation of sinistral and dextral forms of the freshwater snail *Lymnaea stagnalis* (Linnaeus, 1758) by two snail-feeding beetle species, *Phosphuga atrata* (Linnaeus, 1758) and *Carabus granulatus* Linnaeus, 1758. We investigated a possible preference for or more efficient predation of prey items with a certain coiling direction. We found that *C. granulatus* displayed a preference for dextral snails, as opposed to *P. atrata*, which did not show any preference. We also looked at the asymmetry of the mandibles. In *C. granulatus* the left mandible overlay the right one in a higher proportion of specimens (93.7%) than in the non-molluscivorous carabid, *Calosoma inquisitor* (Linnaeus, 1758) (86.7%), whereas these differences were reversed in *P. atrata* and the non-molluscivorous silphid *Oiceoptoma thoracicum* (Linnaeus, 1758) (77.0% and 87.4%, respectively). We discuss our results in the context of differences in feeding behaviour: *C. granulatus* uses its mandibles to tear the body of the snail as it has withdrawn itself in its shell, whereas *P. atrata* feeds by pre-digesting the snail.

## INTRODUCTION

Throughout the animal kingdom, we find less or more strongly developed external asymmetry in the body shape of many species. In Coleoptera, for example, the left mandible is no exact mirror image of the right one, which is connected with the fact that the jaws lock and fit into or onto each other (McManus 2002). Gastropods, too, are asymmetric. They may be coiled sinistrally (anti-clockwise) or dextrally (clockwise). Most snail species consist entirely of individuals of the same coiling direction; usually dextral (Arthur 2000; Vermeij 2002).

In animal species that are obligate molluscivores, the morphology and/or the behaviour is often adapted to the most common chiral morph of the prey (e.g., in snail-eating snakes and crabs; Hoso et al., 2007; Dietl et al., 2006). As previous research has shown that some snail-feeding beetles also display a clear preference for prey of a certain coiling direction (Inoda et al., 2003), we investigated whether similar adaptations exist in two snail-feeding (Barker 2004) beetle species occurring in the Netherlands, namely *Phosphuga atrata* (Linnaeus, 1758) and *Carabus granulatus* Linnaeus, 1758. In Europe, 84.0% of gastropod species are dextral (Gittenberger et al., 2012), so we expect that *P. atrata* and *C. granulatus* would display a preference and a jaw adaptation towards dextral prey.

## MATERIAL AND METHODS

### Beetles and snails

We obtained 22 live individuals of *P. atrata* from Mr. Ed Colijn (EIS Nederland), from the vicinity of Weert. Of these animals, 14 individuals had the left jaw on top of the right jaw, four had the right jaw on the left, and in the remaining four, jaw asymmetry could not be determined unambiguously. Two live individuals of *C. granulatus* were collected by ourselves in Koudenhoorn near Warmond. Both had their left jaw on top of the right. To study predation of snails of both coiling types by *P. atrata* and *C. granulatus* we used the pond snail, *Lymnaea stagnalis* (Linnaeus, 1758) (6-7 weeks old, height of the aperture 9-14 mm). Although this freshwater species presumably is no regular prey for *P. atrata* and *C. granulatus* (which normally feed on terrestrial snails), we chose this species because it was easy to obtain individuals of both coiling types, thanks to the *Lymnaea*-cultures of Dr. Joris Koene (VU University, Amsterdam). For the morphological studies we used material from the world collections of Carabidae and Silphidae of Naturalis Biodiversity Center.

### Experiments and observations

The beetles were kept in trays of approximately 100 cm$^2$, provided with moist soil and litter. Each tank contained one or two beetles of the same species. Each day, a sinistral and a dextral individual of *L. stagnalis*, live and of the same size, were offered to the beetles. After 10-12 hours we checked the result. An empty shell or traces of predation (such as remains of the soft body of the snail, in or near the shell) were recorded as signifying successful predation. During the experimental research, the feeding behaviour of *P. atrata* and *C. granulatus* was also observed. We did not consistently keep track of the prey consumption and feeding behaviour of the beetles on an individual basis, but rather aggregated the data for all experimental animals.

### Mandible shape

We selected 207 specimens of *C. granulatus* and 200 specimens of *P. atrata*, and determined jaw asymmetry in these. We selected specimens that had been mounted in such a way that the mandibles were well visible under a dissection microscope. For comparison with non-molluscivorous species from the same subfamilies, we also investigated the mandibles in 218 specimens of the caterpillar-feeding *Calosoma inquisitor* (Linnaeus, 1758) and 159 specimens of the carrion-feeding *Oiceoptoma thoracicum* (Linnaeus, 1758).

## RESULTS

*Phosphuga atrata* feeds by regurgitating discharges from its mouth that appear to pre-digest the snail, and then to feed with the liquefied snail tissue. This manner of feeding took a long time, in some cases more than 12 hours per snail. During this process, the beetle enters further and further into the snail shell, in the end disappearing almost entirely. Besides this, almost no other movements of *P. atrata* are visible during feeding. When the beetle stops feeding, the remaining shell is almost never completely empty.

| | eaten (offered), sinistral | eaten (offered), dextral | $\chi^2$-test |
|---|---|---|---|
| *P. atrata* | 25 (104) | 18 (108) | $P = 0.182$ |
| *C. granulatus* | 2 (35) | 12 (37) | $P = 0.004$ |

**Table 1**. Results of the predation experiments with dextral and sinistral *Lymnaea stagnalis* prey items.

*Carabus granulatus* does not insert its entire head and thorax into the prey shell. It feeds by inserting the front of its head into the aperture (Fig. 1), and pulling soft parts of the snail's body out of the shell and then tearing them off. The beetle is very mobile and agitated during this process. Afterwards, the remaining shell is almost completely empty.

Only a relatively small proportion of the total number of offered prey items were eaten by the beetles (20.3% in *P. atrata* and 19.4% in *C. granulatus*). The results of the experiments are shown in Table 1. This demonstrates that *P. atrata* does not appear to display a preference for either dextral or sinistral prey, whereas *C. granulatus* does display a preference for the coiling direction that is most common in nature (namely, dextral).

In our assessments of mandible asymmetry (Table 2), the majority of individuals, in all four species, was found to have their left mandible positioned over their right mandible. Nevertheless, the differences were significant: the proportion of left over right was lower in *P. atrata* than in *O. thoracicum*, and in *Carabus granulatus* it was higher than in *Calosoma inquisitor*.

**Fig. 1**. *Carabus granulatus* feeding on a dextral *Lymnaea stagnalis* in a laboratory setting.

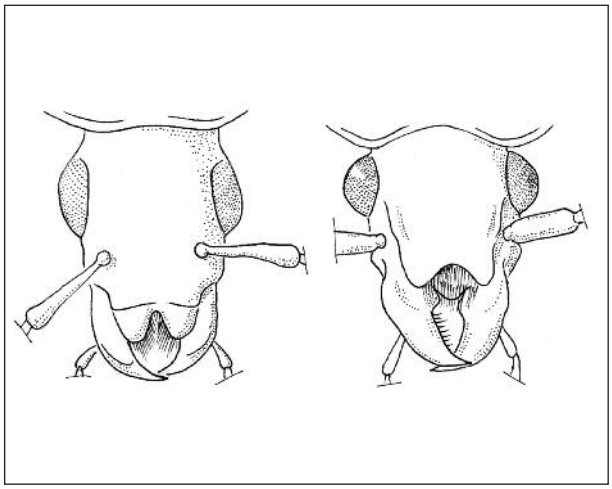

**Fig. 2**. Head of *Phosphuga atrata* (left) and *Carabus granulatus* (right), both with right mandible on top of the left mandible.

| | Total | N right jaw up | N left jaw up | % right jaw up | % left jaw up | $\chi^2$-test |
|---|---|---|---|---|---|---|
| *Phosphuga atrata* | 200 | 46 | 145 | 23.0 % | 77.0 % | *P* = 0.015 |
| *Oiceoptoma thoracicum* | 159 | 20 | 139 | 12.6 % | 87.4 % | |
| *Carabus granulatus* | 207 | 13 | 194 | 6.3 % | 93.7 % | *P* = 0.011 |
| *Calosoma inquisitor* | 218 | 29 | 189 | 13.3 % | 86.7 % | |

**Table 2**. Results of the assessment of mandible asymmetry of the molluscivorous *Phosphuga atrata* and *Carabus granulatus*, and two non-molluscivorous related species. All material derived from the world collections Silphidae and Carabidae of Naturalis Biodiversity Center. The $\chi^2$-test indicates the difference between the molluscivorous and non-molluscivorous species.

## DISCUSSION

Surprisingly, in *P. atrata* we found no preference for dextral or sinistral *L. stagnalis*. In addition, it also appears to show a less strong directional asymmetry in the mandibles than the other three beetle species we studied. These results may be related to the manner of prey subduing and handling in *P. atrata*, where the beetle first bites the snail and exudes a discharge on it, which presumable causes pre-digestion. The beetle then enters the shell almost completely in order to eat the softened snail body. This hunting method may possibly allow this beetle species to kill and eat prey of both coiling directions. In contrast, we did find a significant preference for dextral *L. stagnalis* in *C. granulatus*. However, our experiments on this species were conducted with only two individuals, which means our results should be interpreted with caution. In addition, we found that this species shows a more strongly directional mandible asymmetry than *Calosoma inquisitor*. From observations of feeding beetles we deduced that *C. granulatus* uses its jaws to slice up the body of the snail and to feed itself with the resultant morsels. Moreover, the beetle only inserts the front part of its head into the shell aperture. Given the limited moveability and the mandible asymmetry (which in both experimental animals was left over right) we may perhaps surmise that the beetle is unable to handle sinistral prey. This may explain the beetle's prey preference, but our work will need to be confirmed with a larger number of experimental animals (of both mandible asymmetry types).

Also, in future studies a larger number of molluscivorous Coleoptera will need to be included, to check whether the differences in percentages of animals with left-over-right and right-over-left type jaw asymmetry are consistently correlated with molluscivorous habits.

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