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Flexible trophic position of polyphagous wireworms (Coleoptera, Elateridae): A stable isotope study in the steppe belt of Russia

Ekaterina S. Samoylova*, Alexei V. Tiunov

A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071, Moscow, Russia

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ABSTRACT

Larvae of Elateridae beetles, known as wireworms, are widespread pest species damaging various crop plants. In spite of a general morphological similarity, wireworms demonstrate a wide spectrum of trophic modes ranging from phytophagy to predation. In many wireworm species, facultative carnivory ensures the acquisition of proteins necessary for metamorphosis, whereas feeding on living plant tissues (especially juicy roots and tubers) can be stimulated by water deficiency. We therefore hypothesized that polyphagous wireworm species inhabiting three types of steppe (grassland) ecosystems should be more phytophagous in dry conditions. To assess the trophic position of wireworms, we compared their isotopic signatures with those of plants and the soil, as well as of reference species including carnivorous centipedes and Diptera larvae, herbivorous weevils and saprophagous earthworms. Larvae of *Agriotes obscurus*, *Agriotes lineatus*, *Selatosomus aeneus* and *Selatosomus latus* inhabiting well-drained soils were 3–4‰ enriched in ^{15}N compared to larvae inhabiting wet floodplains, suggesting a difference in at least one trophic level. A comparison with soil animals with known trophic positions indicates that omnivorous wireworms tend to be phytophagous and saprophagous in floodplain, but carnivorous in well-drained habitats. The capability of changing the diet is confirmed by the age-related shift in the trophic position of some species. Elder *A. obscurus* larvae are significantly depleted in ^{13}C and enriched in ^{15}N, likely indicating a switch from saprophagy to carnivory. Overall, our data suggest a considerable flexibility in the feeding behavior of elaterid larvae in steppe habitats.

1. Introduction

Polyphagy is defined as a capacity of organisms to use different preys or food types, including trophic-level polyphagy, i.e. feeding on more than one trophic level. Polyphagy by carnivorous insects is well-known, being important for the management of insect pests (Albajes and Alomar, 2004; Finlay-Doney and Walter, 2012; Zalewski et al., 2016). Larvae of Elateridae beetles, known as wireworms, are widespread pest species damaging various crop plants (Parker and Howard, 2001; Traugott et al., 2015). In spite of a general morphological similarity, wireworms demonstrate a wide range of different trophic modes: phytophagy, saprophagy, predation, necrophagy and coprophagy.

More than fifty years ago, Dolin (1963) elaborated an ecological classification of elaterid larvae according to their feeding requirements. A few groups including Agripninae, Cardiophorini, Melanotini, Ampedini and some Athouini species are obligate predators with different feeding preferences. Their feeding ecology is beyond the scope of this study. *Agriotes* larvae form a group of omnivorous wireworms that can pupate on a plant diet without animal food. Other omnivorous wireworms from Ctenicerini, Agriotini and other tribes, e.g. *Selatosomus* larvae, feed largely on fresh plant tissues, but cannot pupate without animal food (Bobinskaya et al., 1965). Furthermore, when having a choice between animal and plant food, all omnivorous wireworms including *Agriotes* choose the protein-rich animal diet or at least use both types of food (Zacharuk, 1963). Cannibalistic interactions and necrophagy were reported for many omnivorous elaterid species (Furlan, 1998; Kabanov, 1975; Langenbuch, 1932). Stable isotope analysis further suggests that carnivory is very common among wireworms. In particular, species from the tribes Athoini and Ctenicerini that were earlier considered as predominantly herbivorous seem to be predatory (Traugott et al., 2008). Even in the typically herbivorous *Agriotes obscurus* about 8% of individuals collected in a maize field demonstrated δ^{15}N values characteristic of carnivores (Traugott et al., 2008).

Since many wireworm species are agricultural pests, the most well-known peculiarities of their feeding behavior are related to crop damage. In wet/humid conditions wireworms have long been known to cause less damage to plants (Herk and Vernon, 2012; Langenbuch, 1932; Schaerffenberg, 1942). It was therefore concluded that in the dry

* Corresponding author.
E-mail address: askofa@gmail.com (E.S. Samoylova).

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Table 1
Sites sampled for plants, soil, litter, wireworms and other soil invertebrates. Hash mark (#) indicates plants with measured isotopic composition. There were no plants with C4 photosynthetic pathway among investigated species (Supplementary Table S1).

Type of the steppe	Site	Coordinates	Plant community	Most abundant plant species	Soil type
Meadow steppe	Dry habitat: well-drained plain	51.917 N, 44.678 E	Festuca-Bromopsis-forbs	*Potentilla anserine#* *Medicago falcata#* *Galium ruthenicum#* *Achillea millefolia#* *Festuca valesiaca#* *Elytrigia repens#* *Thymus marshalianus#* *Plantago major#* *Bromopsis inermis#* *Trifolium repens#* *Artemisia austriaca#* *Europhorbia cyparissias#*	Udic Boroll (Typic Chernozem)
Meadow steppe	Wet habitat: floodplain of Atkara River	51.913 N, 44.679 E	Elytrigia-Bromopsis-forbs	*Fragaria vesca#* *Galium ruthenicum#* *Festuca valesiaca#* *Elytrigia repens#* *Bromopsis inermis#* *Poa pratensis*	Mollic fluvisol (Alluvial-meadow soil)
Typical steppe	Dry habitat: well-drained plain	51.313 N, 45.414 E	Stipa-Festuca-forbs	*Thymus marshalianus#* *Elytrigia repens#* *Stipa capillata#* *Poa pratensis* *Festuca valesiaca* *Artemisia austriaca*	Typic Boroll (South Chernozem)
Typical steppe	Wet habitat: floodplain of Karamysh River	51.305 N, 45.407 E	Elytrigia-Bromopsis-forbs	*Elytrigia repens#* *Bromopsis inermis* *Urtica dioica#* *Rubus idaeus#* *Humulus lupulus* *Falcaria vulgaris*	Mollic fluvisol (Alluvial-meadow soil)
Dry steppe	Dry habitat: well-drained plain	50.698 N, 47.051 E	Stipa-Agropyron	*Stipa lessingiana* *Elytrigia repens#* *Artemisia austriaca#* *Festuca valesiaca* *Agropyron cristatum* *Lactuca tatarica*	Aridic Boroll (Kashtanozem)
Dry steppe	Wet habitat: floodplain of Solyanka River	50.708 N, 47.081 E	Elytrigia-forbs	*Elytrigia repens#* *Carex* spp. *Geranium pratense* *Festuca valesiaca* *Salvia tesquicola* *Artemisia austriaca*	Mollic fluvisol (Alluvial-meadow soil)

soil wireworms consume plant roots or tubers as a source of water, whereas in the wet soil they can feed on soil organic matter (SOM) (Campbell, 1937; Lees, 1943; Schaerffenberg, 1942), thus switching from phytophagy to saprophagy. There is evidence of some *Athous* and *Agriotes* species feeding on SOM (Hemerik and de Fluiter, 1999; Strey, 1972; Wolters, 1989), but other experiments showed that SOM is an inappropriate food source for wireworms, as *Agriotes* larvae feeding on the moist soil only exhausted their adipose tissues and died after two months at the latest (Bobinskaya et al., 1965; Cherepanov, 1965; Evans and Gough, 1942; Furlan, 1998). Using stable isotope analysis, it has also been shown that the input of SOM in wireworms' diet is inessential (Traugott et al., 2007, 2008). The discrepancy is likely to be accounted for by different experimental settings and variations in the quality of SOM available for larvae. Indeed, humified SOM intermixed with mineral fractions is only palatable for a limited number of specialized animal groups of soil animals, e.g. endogeic earthworms. On the other hand, decomposing plant residues densely populated by microorganisms may provide a suitable food for wireworms. For instance, larvae of certain *Agriotes* species (*Agriotes lineatus*, *Agriotes sputator* (L.)) preferred rotten potatoes over fresh potatoes, and rotten wheat seeds over fresh ones (Dolin, 1963).

Polyphagy therefore seems to be quite common in elaterid larvae. Transient circumstantial switches from saprophagy to phytophagy and back are reported commonly for a wide range of soil saprophages, e.g. millipedes (Mikhaljova, 2004), epigeic earthworms (Baylis et al., 1986; Bouché and Kretzschmar, 1974), scarabaeid larvae (Ritcher, 1958). Interchanges between predation and phyto-/saprophagy seem to be much less common, although they have been recorded in some soil invertebrates as well. The carabid beetle subfamilies Harpalinae and Psydrinae are generalist predators that switch between carnivory and granivory (Goldschmidt and Toft, 1997; Hurst and Doberski, 2003), herbivorous Orthoptera occasionally behave as predators or scavengers (Martín-Vega et al., 2013), while carnivorous centipedes, *Lithobius variegatus* and *Lithobius forficatus*, have been found to feed on litter (Lewis, 1965). Many species of largely mycophagous springtails and oribatid mites consume nematodes (Heidemann et al., 2011). Some collembolan species like *Desoria tigrina* and *Protaphorura cancellata* can even prey on enchytraeid worms (Chernova et al., 2007).

As noted above, facultative carnivory ensures the acquisition of proteins necessary for metamorphosis, whereas feeding on living plant tissues (especially juicy roots and tubers) can be stimulated by water deficiency. It cannot be ruled out that water deficiency could also