Observations on the growth of *Dytiscus dimidiatus* (Coleoptera: Dytiscidae) larvae reared on single or multiple prey species

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Only anecdotal information is available on the choice of prey by the king diving beetle *Dytiscus dimidiatus*. The habitat of *D. dimidiatus* larvae often contains a limited number of abundant prey species. To test whether *D. dimidiatus* larvae were able to grow on only one species of prey, larvae were reared on *Asellus*. Their growth was compared with larvae that were reared on various prey species. Our results indicate that larvae of *D. dimidiatus* are generalists that can both grow on one or on a variety of prey species. We suggest that the quantity of available prey is more important than its diversity.

Introduction

Larvae of larger dytiscid beetles are known to be voracious predators, often feeding on a large variety of prey species (Culler *et al.* 2014, Johansson & Nilsson 1992). Prey is usually caught by surprise with the sickle shaped mandibles of the larvae, is externally digested by injected enzymes and sucked up (Naumann 1955, Sutton 2008). The larvae go through three larval instars (L1, L2 and L3) often within less than a month and pupate in the bank of the water body in which they grew up (Korschelt 1924, Naumann 1955). The feeding behaviour of larvae of several dytiscid beetle species has been studied already for more than a century (Formanowicz 1987, Inoda 2012, Korschelt 1924, Ohba 2009, Scholten *et al.* 2018). For some species, the larvae are known to be generalists in choice of prey, like *Dytiscus marginalis* Linnaeus (Korschelt 1924). Specialists are also found among these species (Ohba, 2009), such as the larvae of *Dytiscus latissimus* Linnaeus that mainly feed on caddisfly larvae (Johansson & Nilsson 1992, Scholten *et al.* 2018). For several other dytiscid beetles, only anecdotal information about prey preference is available, amongst them the king diving beetle *Dytiscus dimidiatus* Bergsträsser.

Dytiscus dimidiatus is frequently found in shaded habitats of wet forests (Lenders 2018, Serjeant 2013) and is considered rather uncommon in the Netherlands (Drost *et al.* 1992). Temporary, shallow pools with thick layers of leaf litter provide a habitat for larvae of *D. dimidiatus*. Such habitat often contains a limited number of invertebrate prey species in high abundances. Larvae of *D. dimidiatus* (figure 1) are also found in more sun-exposed ditches and pools near wet forests (Lenders 2018, Serjeant 2013, personal observations). Such habitats contain a larger diversity of more abundant prey species. Given their presence in both habitats, we assume that larvae of *D. dimidiatus* most probably can develop on a variety of prey species but may as well be able to develop on a limited number or even only one prey species. Whether feeding on one or a multiple number of prey species affects the larval growth is yet unknown.

In this study, we explored whether feeding on multiple prey species improves the growth and development of larvae of *D. dimidiatus* compared to feeding on a single prey species.

1. *Dytiscus dimidiatus* mature L3 larva. Photo: Paul Hendriks
1. Volgroeide L3-larve van *Dytiscus dimidiatus*.

2. The glass tanks used in the single prey test. Photo: Paul Hendriks
2. De glazen bakjes, gebruikt in de 'één prooissoorttest'.

3. The aquarium used in the multiple prey test. Photo: Paul Hendriks
3. Het aquarium, gebruikt in de 'meerdere prooisoortentest'.

We expected that the growth and development would improve when larvae are fed on a variety of prey species. To explore this expectation, we compared the larval growth at the presence of a single or a variety of prey species. We fed *D. dimidiatus* larvae with only water louses (*Asellus*), a prey species that is very abundant in forest pools (single prey test). We also fed larvae with a variety of prey species (multiple prey test) in a vegetated aquarium wherein natural conditions were mimicked. We individually reared the larvae fed on a single prey species because of their expected reduced growth and established their growth and amount of feeding during the larval development.

Material and methods

Culture

Adult female *D. dimidiatus* caught in the wild, oviposited in an indoor vegetated aquarium. With the larvae gained from this oviposition, six rearing trials were performed. The single prey test (S) consisted of rearing trial S1, S2 and S3 with a total of eight larvae. The multiple prey test (M) was performed in rearing trial M1, M2 and M3 with a total of three larvae. Mature larvae from both the single and multiple prey test, were placed in a pupation terrarium (25 × 15 × 32 cm), according to Hendriks (2020). All larvae pupated in captivity, some of the adults were released, others were kept to oviposit in a subsequent rearing trial.

Experimental set-up

Larvae in the rearing trials S1 to S3, were individually housed in indoor glass tanks (10 × 9,5 × 15,5 cm), containing 1 l of water (figure 2). The bottom consisted of a 1 cm thick layer of washed river sand. A twig was placed in every tank on which a larva could rest. The water in the tanks was refreshed at intervals of a few days to once a day when it became smelly and/or turbid. Thereby 80% tap water and 20% water of the indoor aquarium was used.

Rearing trials M1 to M3 were performed in a vegetated indoor aquarium (55 × 20 × 28,5 cm), containing 27 l of water (later referred to as aquarium, figure 3). The bottom consisted of a 3 cm sludge layer, covered with 2 cm of washed river sand. The aquarium contained emerse and submerged water plants: *Glyceria maxima*, *Iris pseudacorus*, *Berula erecta*, *Mentha aquatica*, *Sparganum erectum*, *Elodea nuttallii*, *Hottonia palustris* and *Lemna trisulca*. During all rearing trials, the water was refreshed with tap water when it became smelly and/or turbid.

Growth experiments

In rearing trial S1 to S3 a total of eight larvae was tested. For each rearing trial, young first instar (L1) larvae were taken from the aquarium that was used for the multiple prey test, before they started feeding. Each larva was placed in an individual glass tank. To establish the growth, larvae were measured and weighed at the beginning and end of each larval stage. In the L3 stage, when larvae were more robust, this was done daily. The cumulative weight increase of the larvae in both the single and multiple prey tests was defined as growth.

Groups of living *Asellus* specimens in different life stages were added to the tanks. After consumption by the larvae, their remains were collected each morning and evening with tweezers or by suction with a plastic tube. The number of *Asellus* specimens added varied with the larval instars from two to six in the L1 stage, two to seventeen in the L2 stage and seven to 94 in the L3 stage. The variation in the number of *Asellus* offered, depended on the size of the specimens that we were able to collect. When only smaller individuals were available, larger numbers of *Asellus* were offered. The weight of *Asellus* specimens consumed was calculated by subtracting the weight of the unconsumed remains from the total offered weight.

In rearing trial M1 to M3 three larvae eventually developed to mature larvae. In these trials, the larvae were reared on a variety of prey species known to be predated by dytiscid larvae (table 4), and comparable to the food of *D. marginalis* (Korschelt 1924, Naumann 1955, Sutton 2008).

Rearing trail S1 and M1 started on February 18, 2018 with the oviposition of a wild caught female beetle from Kolham, province of Groningen, The Netherlands (53.195°N 6.733°E). From this oviposition, twelve L1 larvae hatched in the aquarium of which two were placed in the glass tanks (trial S1). With the remaining larvae in the aquarium, trial M1 was performed. Trial S2 and M2 started on April 10, 2018, whereby a wild caught female beetle from Lettelbert, province of Groningen, The Netherlands, 53.193°N 6.428°E oviposited in the aquarium. Three L1 larvae hatched from this oviposition. Two were placed in the glass tanks (trial S2) and one larva remained in the aquarium (trial M2). Trial S3 and M3 started on February 2, 2019 with the oviposition by a female beetle from rearing trial S2 of which nineteen L1 larvae hatched in the aquarium. Four larvae were placed in the glass tanks (trial S3) and with the remaining larvae, trial M3 was performed. In trial M1, M2 and M3 one L3 larva remained due to placement of L1 larvae in the glass tanks for the single prey test or cannibalism.

The number of prey specimens that were offered to the larvae depended on their size. Smaller prey specimens were expected to be less easily detected by the larvae and therefore added to the aquarium in larger numbers to approach about the same biomass offered. In rearing trial M1 and M2, we registered at random, the time needed for a larva to catch a prey specimen and whether this attack was successful. We collected the remains of successfully caught prey specimens. In rearing trial M3, we made no further observations on the feeding behaviour.

In three additional tests, we presented two or more times (if available) several dead prey species to the larvae by offering them using tweezers. These dead specimens consisted of species that were not caught in the multiple prey test, predaceous species that were considered to be harmful to the larvae and of dead terrestrial invertebrate species that do not occur in the natural habitat of *D. dimidiatus* larvae. By the use of tweezers, we mimicked the movements that attracted the larvae.

Measurements

The length and weight of larvae in the L1, L2 and L3 larval stage in the single prey test and of the L3 larval stage in the multiple prey test were measured. The total length of the adults was also measured. Before measuring the length and weight of larvae, adhering water was removed by letting the larvae walk on a towel. The length was measured from the end of the terminal abdominal segment to the labrum in stretched position. All length measurements on larvae and adults were taken with callipers to 0.01 mm accuracy. All *Asellus* specimens fed were counted and weighed after removing the adhering water by letting them walk on a towel. The remains of *Asellus* specimens were gently pressed dry on a towel, counted and weighed. All weights were taken, by using a Mettler PM100 weighing scale (d = 0.001 g).

Statistical analyses

All data were first checked for the criteria of normality (Shapiro-Wilk test) and equal variance (Levene's test). For the growth of larvae, missing data on growth were imputated by using linear regression per larva, as each growth line was best explained by a linear regression line (linear grow trajectories were found by Aiken & Wilkinson 1985). We calculated the correlation between growth lines of each pair of larvae and tested the correlation using a Pearson correlation test. Finally, we used an ANOVA on the residuals around the predicted linear regression line per larva, to test whether lines significantly deviated from each other. Furthermore, we tested whether the amount of food (*Asellus*) consumed by each of the eight larvae differed using an ANOVA. The mean difference in weight between fully-grown larvae in the single and multiple prey tests were tested using an independent T-test. All statistical analyses were performed using JASP version 0.12.2.

Results

The growth of larvae

The larvae in both the single and multiple prey test developed to maturity within three weeks. All larvae pupated and emerged as adults in three to four weeks. The difference in mean, minimum and maximum weight between the larvae before pupation in both tests differed by 1%, 7% and 3%, respectively (table 1). The mean weights of the mature larvae from both series of trials did not differ significantly (Student T-test; $p=0.882$). In adults, the differences in length were 2%, 3% and <1%, respectively. The growth of the larvae in the single prey test increased per larval instar. In the L1 stage, the mean weight of larvae before moulting was 5%, and in L2 25% of the weight of the mature L3 larvae.

The growth trajectories of the larvae in the single prey test did not significantly differ (figure 4, table 2). The L1 stage lasted until day 5 to 6, the L2 stage until day 10 to 12, and the L3 stage until day 23 to 24. During the moulting periods a sudden increase in weight for several larvae is visible, due to the intake of water. From day 22 to 24 a decline in weight for nearly all larvae was observed. At the end of the L3 stage, shortly before leaving the water to pupate, the larvae stopped feeding. Larva 3 was placed in the pupation terrarium prematurely. Because it remained restless, the larva was placed back in the glass tank to further feed until it was mature. This took two days in which it gained weight (figure 4, larva 3, day 23 and 24).

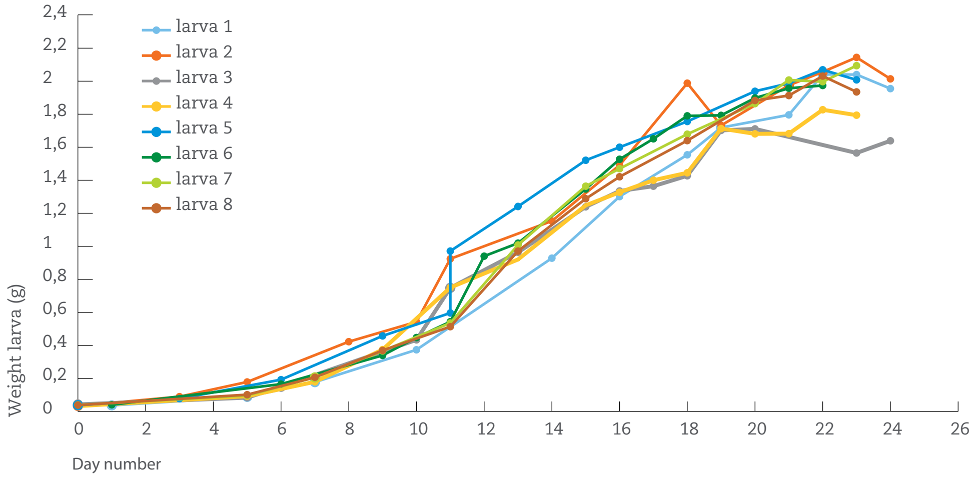
Table 1. The weight and length of the larvae and adult beetles of *Dytiscus dimidiatus* grown in the single and multiple prey test.
Tabel 1. De gewichten en lengtes van de larven en volwassen kevers van *Dytiscus dimidiatus*, gekweekt in de 'één prooisoort- en meerdere prooisoortentest'.

Instar	Mean	SD	Min.	Max.	n
Single prey test					
Weight (g)					
L1	0.089	0.007	0.077	0.101	7*
L2	0.489	0.079	0.373	0.596	8
L3	1.927	0.135	1.639	2.094	8
Before pupation	1.927	0.144	1.639	2.094	8
Length (mm)					
Before pupation larvae	57.5	2.7	53.0	62.0	8
Adult	35.8	0.9	34.4	37.4	8
Multiple prey test					
Weight (g)					
Before pupation	1.911	0.133	1.772	2.037	3
Length (mm)					
Before pupation larvae	58.3	1.2	57.0	59.0	3
Adult	36.6	1.1	35.4	37.3	3

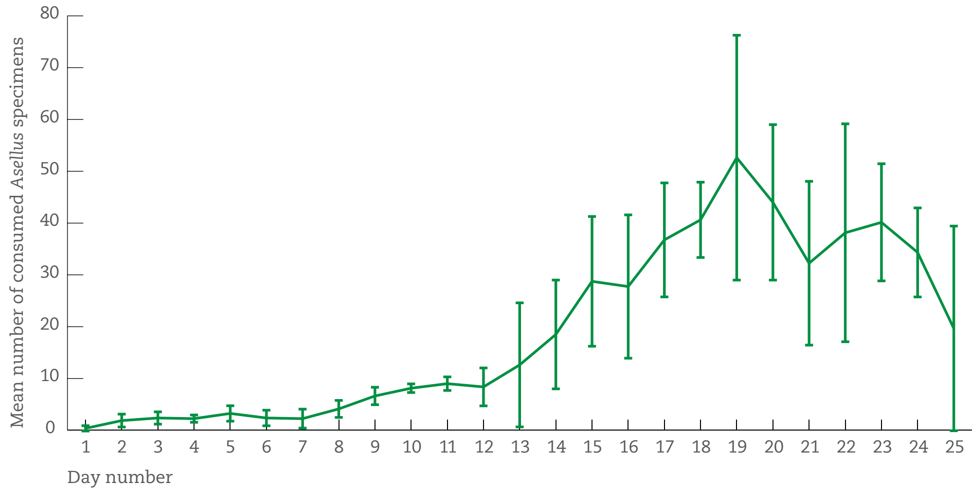
*) One L1 larva could not be measured.

Table 2. ANOVA of the residuals of the growth curves of eight larvae of *Dytiscus dimidiatus* from the single prey test.
Tabel 2. ANOVA met de residuen van de groeicurven van acht larven van *Dytiscus dimidiatus* uit de 'één prooisoorttest'.

ANOVA - residuals Homogeneity Correction	Cases	Sum of Squares	df	Mean Square	F	p
None	Larvae	1.866e-5	7.000	2.666e-6	1.719e-4	1.000
	Residuals	2.978	192.000	0.016		



4. Weight increase (g/day) of the eight larvae of *Dytiscus dimidiatus* within the single prey test.
4. Gewichtstoename (gr/dag) voor de acht larven van *Dytiscus dimidiatus* in de 'één prooisoorttest'.



5. Number of *Asellus* specimens daily consumed by the larvae of *Dytiscus dimidiatus* in the single prey test.
5. Aantallen dagelijks geconsumeerde *Asellus*-individuen door de larven van *Dytiscus dimidiatus* in de 'één prooisoorttest'.

All growth data met the criteria of normality and variance. The growth curves all were significantly correlated ($R^2 > 0.98$, Pearson's $p<0.01$). The ANOVA did not show any significant deviance in residuals.

Feeding in the single prey trials

All larvae were able to feed exclusively on *Asellus* during their entire larval development. A mean number of 451 *Asellus* specimens per larva was captured of which 7.8 g was consumed, being 42.6% of the initial weight of the *Asellus* specimens offered (18.4 g, table 3). The number of *Asellus* consumed in relation to the total consumption during the larval development, increased per larval instar (figure 5), being 3% in the L1 stage, 8% in the L2 stage and 89% in the last (L3) stage.

The minimum and maximum average weight of individual *Asellus* specimens varied from 0.014 g to 0.062 g. The number of *Asellus* consumed dropped sharply at the end of the L3 stage when the larvae stopped feeding. This coincided with the loss of weight in the larvae on day 23 and 24 (figure 4). No significant difference between the amount of consumed *Asellus* specimens per larva was observed (ANOVA).

Feeding in the mutiple prey test

In rearing trial M1 and M2, 347 prey specimens consisting of eighteen living prey species were presented to the larvae in the aquarium (table 4). Fourteen prey species were being attacked and fed on. Four prey species were not seen being successfully attacked and no remains were found. These were: water boatmen (*Corixa,* table 4), water snails (*Lymnaea* and *Planorbis*) and leeches (*Erpobdella*), Observations confirmed that in the last three prey species, the larvae showed relatively less interest.

Additional feeding test

In the additional feeding test, dead specimens of two of the three prey species in which the larvae showed little interest (the water snail *Lymnaea* and leech *Erpobdella*) were offered manually. Also two predator species: saucer bug *Ilyocoris cimicoides* and backswimmers (*Notonecta*) and two terrestrial invertebrate species, centipedes (*Lithobius*) and earthworms (Lumbricina) were offered (table 4). All of the above were attacked and consumed by the larvae.

Observations on feeding behavior

In both the single and multiple prey test, according to our observations, the feeding behaviour of larvae was similar. Larvae mainly sat still with opened mandibles, either at the water surface or on the bottom of the aquarium or glass tank. In this position, the attention and focus of a larva towards prey was drawn when a prey was moving and caused vibrations in the water. Attacks normally took place from a distance of less than 2 cm. Larger prey specimens that were moving intensely, could

Table 3. Number and biomass of *Asellus* prey offered and consumed in the single prey test.
Tabel 3. Aantallen en massa van *Asellus*-prooi gevoerd en geconsumeerd in de 'één prooisoorttest'.

	L1 Mean	SD	L2 Mean	SD	L3 Mean	SD	total Mean	SD
Total number consumed	11.9	3.1	36.4	11.0	403.0	70.7	451.3	60.5
Total biomass fed (g)	0.446	0.163	1.610	0.430	16.329	1.204	18.385	1.313
Total biomass consumed (g)	0.153	0.070	0.603	0.082	7.072	1.267	7.829	1.236
% consumed	34.0%	8.5%	38.9%	6.5%	43.2%	6.6%	42.6%	6.4%

Table 4. Prey species presented to *Dytiscus dimidiatus* larvae in rearing trial M1 and M2. - = prey species was not presented to *D. dimidiatus* larvae in that trial.
Tabel 4. Prooisoorten gegeven aan de *Dytiscus dimidiatus*-larven in kweek M1 en M2. - = prooisoort is niet gegeven aan de *D. dimidiatus* larven in de betreffende kweek.

Species	observed successful/ unsuccessful attacks trial M1	observed successful/ unsuccessful attacks trial M2	collected remains trial M1/ trial M2	dead specimens fed from tweezers trial M1/ trial M2
water louse *Asellus*	12/12	2/0	13/6	
fresh water shrimp *Gammarus*	3/5	-/-	12/-	
lesser water boatman *Corixa*	0/2	-/-	0/-	
water boatman *Sigara*	3/6	0/0	3/0	
backswimmer *Notonecta*				3/4
saucerbug *Ilyocoris cimicoides*				3/7
water scorpion *Nepa cinerea*	-/-	1/0	-/1	
larvae/pupae mosquito Culicidae	1/0	1/0	1/0	
larvae alderfly *Sialis*	1/0	0/0	0/0	
larvae caddisfly Trichoptera	1/13	-/-	10/-	
larvae damselfly *Coenagrion* and larva mayfly Ephemeroptera	1/0	1/0	2/0	
larvae dragonfly *Aeshna*	-/-	0/0	-/2	
ninespine stickleback *Pungitius pungitius*	2/0	0/1	0/2	
tadpoles Anura	-/-	2/6	-/0	
leech *Erpobdella*	0/1	0/1	0/0	-/2
pond snail *Lymnaea*	0/0	0/0	0/0	-/2
ramshorn snail *Planorbis*	0/1	0/0	0/0	
larvae king diving beetle *Dytiscus dimidiatus*	4/2	-/-	5/-	
larvae lesser diving beetle *Acilius*	-/-	1/0	-/1	
larvae marsh beetle *Scirtes*	-/-	2/1	-/3	
terrestrial species				
centipede *Lithobius*				-/3
earthworm Lumbricina				-/2
total	28/42	10/9	46/15	6/20

be detected from a greater distance. Active searching for prey only occurred when larvae had not fed for some time. Moving larvae were less successful in catching prey as they were noticed more easily by the prey. Unsuccessful attacks occurred regularly (table 4), especially when prey moved fast. Larvae never pursued prey after an unsuccessful attack. Small preys with lengths starting from 0.5 cm, were noticed by the larvae and attacked and consumed at all larval instars (figure 6).

Larvae of *D. dimidiatus* were also observed to be cannibalistic. Attacks often occurred when larvae floated towards each other while respiring at the water surface. When larvae were too near to each other and moving, successful attacks took place (table 4).

Discussion

Development of larvae

Larvae of *D. dimidiatus* were reared to the adult stage in both single and multiple prey tests. Under both food conditions adults were equally sized (table 1). The adults were of average to a large size in comparison to the size variation given in literature: 31(32)-38 mm (Lenders 2018, Drost *et al*. 1992,). The weight of mature larvae did not differ significantly in both conditions. Both tests provided equal results which strongly indicates that larvae of *D. dimidiatus* can develop equally well on single (in this case *Asellus*) and multiple prey availability. A female beetle from rearing trial S2 that was kept together with the other beetles from trial S1 and S2, successfully reproduced in trial S3. It shows in this case that feeding on one prey species did not compromise reproduction.

Generalists

We did not notice any preference in *D. dimidiatus* larvae for certain prey species and consider them to be indifferent in their choice of prey. As frequently mentioned before, movement of prey proved to be crucial for larvae to attack (Formanowicz 1987, Inoda *et al*. 2009, Korschelt 1924). Even the smallest prey was caught when moving near to a larva. We did not notice a preference for larger moving prey, despite being suggested in earlier studies (Inoda *et al*. 2009). Whether prey moves and the way it moves, determines the chance of being attacked. Formanowicz

6. *Dytiscus dimidiatus* L3 larva consuming a small *Asellus*. Photo: Paul Hendriks
6. Een L3-larf van *Dytiscus dimidiatus* consumeert een kleine *Asellus*.

7. *Dytiscus dimidiatus* young L2 larva near a water snail. Photo: Paul Hendriks
7. Jonge L2-larf van *Dytiscus dimidiatus* bij een waterslak.

(1987) mentioned that chemical cues appeared to be necessary to fulfil an attack. We observed that larvae also attacked tweezers that were without a scent of prey species and with a force that is shown when prey is caught, suggesting that chemical cues are less important. This is in line with observations of Inoda *et al*. (2009), who reported that movement of prey is enough to be attacked by larvae.

We noticed that prey which causes vibrations while moving, is noticed more easily by the larvae than prey that glides through the water, such as water snails. This was also reported by Korschelt (1924). It coincides with our findings whereby the water snails *Lymnaea* and *Planorbis* rarely drew the interest of the larvae (figure 7). For the leech *Erpobdella*, we witnessed no successful attacks, though Korschelt (1924) described an attack on a leech by a *D. marginalis* larva. The leech immediately responded to the attack with the production of slime, which ended the attack. We cannot verify this response because of the witnessed unsuccessful attacks on *Erpobdella*, but this might have been the case. Dead specimens of *Lymnaea*, *Planorbis* and *Erpobdella* were attacked and consumed by the larvae. The lack of slime production in the dead prey specimens could possibly have made them more accessible for consumption. Female beetles that were placed in the aquarium for oviposition occasionally consumed small *Lymnaea* specimens with lengths up to approximately 1 cm. Serjeant (2013) reported a possible preference for water snails by *D. dimidiatus*. Furthermore, non-selective feeding behaviour by *D. dimidiatus* larvae was shown when dead terrestrial prey species were offered and readily taken and consumed. Feeding on dead prey was already observed before by (amongst others) Korschelt (1924) and Culler *et al*. (2014).

We suggest that the more limited possibility for *D. dimidiatus* larvae to catch fast moving prey species, such as *Corixa* specimens, is caused by the fact that larvae have little to no time to orientate and position themselves to strike fast moving prey.

Availability of prey in natural habitats

The possibility of *D. dimidiatus* larvae to both feed and equally develop on a single prey species as well as on a variety of species, supports the idea that these larvae are flexible and opportunistic. We expect that the biomass of prey specimens is of greater importance for the development and survival of *D. dimidiatus* larvae. It is known for several other dytiscids that their presence influences the biomass of prey (Cobbaert *et al*. 2010, Culler *et al*. 2014) The results of our experiment indicated that larvae only actively search for prey when they were not able to feed for some time. Lack of food probably initiates the larvae to move to places with higher prey densities. Also, cannibalism occurs more often when preys are limited and will reduce the number of larvae (Inoda 2012). This enables a few larvae to fully develop. Larvae of *D. dimidiatus* are frequently found in shaded and temporary pools and ditches. Large numbers of just a few prey species are often found in such habitat of which we observed that this is sufficient for *D. dimidiatus* larvae to develop successfully.

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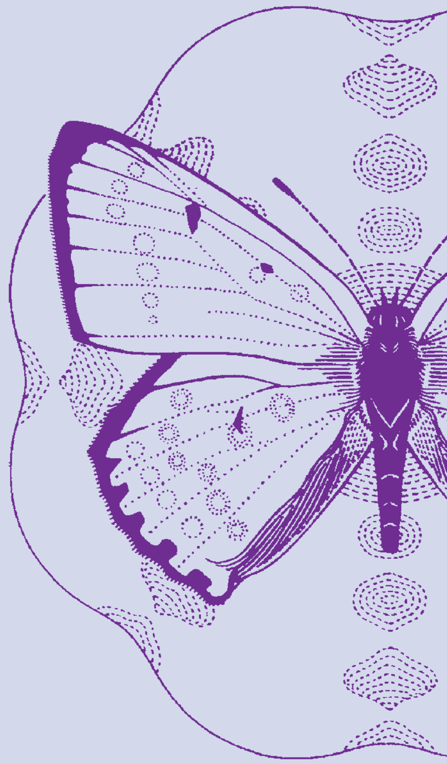
Samenvatting

Observaties aan de groei van *Dytiscus dimidiatus*-larven (Coleoptera: Dytiscidae) die op één en op meerdere prooisoorten gekweekt zijn

Er is nog weinig bekend over de prooikeuze van larven van de veengeelgerande waterkever *Dytiscus dimidiatus*. Deze wat zeldzamere waterkever wordt geregeld aangetroffen in en rond broekbossen. Daar zijn de larven te vinden in bospoelen en (beschaduwde) sloten. Dergelijke milieus bevatten vaak een beperkt aantal soorten evertebraten, maar wel in hoge abundantie. Larven van *D. dimidatus* die zich in dergelijke milieus ontwikkelen en voeden met deze evertebraten, hebben vaak maar één of enkele van deze soorten als prooi ter beschikking. Om het effect van één enkele prooisoort op de groei van larven van *D. dimidiatus* te onderzoeken, zijn larven met waterpissebedden *Asellus* opgekweekt. De groei van deze larven is vergeleken met de ontwikkeling van larven die zijn gevoerd met verschillende prooisoorten. Wij veronderstelden daarbij dat de groei van de larven gekweekt op één prooisoort geringer zou zijn. Onze resultaten laten echter zien dat zich geen significante verschillen in de eindgewichten van gekweekte, volgroeide larven voordeden. Ook de vergelijking van de onderlinge groei van de larven die zijn gevoerd met één prooisoort, laten geen verschillen zien. Alle opgekweekte larven zijn succesvol verpopt en de adulten waren allen relatief groot. Ook een met *Asellus* opgekweekt vrouwtje legde eieren waaruit larven voortkwamen die ook weer succesvol zijn opgekweekt tot kevers. Deze resultaten zijn een sterke aanwijzing dat de larven van *D. dimidiatus* flexibele generalisten zijn die hun ontwikkeling kunnen doorlopen op zowel één als meerdere prooisoorten. De beschikbaarheid van voldoende prooi lijkt daarbij belangrijker dan de prooisoort.



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