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Predatory *Poiretia* (Stylommatophora, Oleacinidae) snails: histology and observations

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ABSTRACT

The predatory behaviour of *Poiretia* snails is studied. One aspect of this behaviour is the ability to make holes in the shells of prey snails. The radula and the histology of the mucous glands support the assumption that *Poiretia* secretes acidic mucus to produce these holes. Observation of a *Poiretia compressa* (Mousson, 1859) specimen yielded the insight that its activities relied on the availability of moisture and not on light conditions. It preyed on a wide range of snail species, but only produced holes in shells when the aperture was blocked. It usually stabbed its prey with a quick motion of the radula. The time it spent feeding on a prey specimen is most likely correlated to prey size.

INTRODUCTION

Poiretia is a genus of predatory snails, mainly preying on other snails. According to Subai (1980), it contains six recent species: the type species *P. algira* (Bruguière, 1792), and furthermore *P. dilatata* (Philippi, 1836), *P. cornea* (Brumati, 1838), *P. delesserti* (Bourguignat, 1852), *P. compressa* (Mousson, 1859), and *P. mingrelica* (Boettger, 1881). *Poiretia dilatata* (Philippi, 1836) is further subdivided into three subspecies: *P. d. dilatata* (Philippi, 1836), *P. d. marginata* (Westerlund, 1886) and *P. d. peloponnesica* Subai, 1980. These snails are found in the Mediterranean area, except for *P. mingrelica* (Boettger, 1881), which occurs in the Caucasus. Along with *Sardopoiretia emanueli* (Bodon, Nardi, Braccia & Cianfanelli, 2010), *Poiretia* snails are the only extant European Oleacinidae. The other extant members of this family occur in Central America and the Caribbean.

Poiretia belongs to the subfamily Euglandininae of the Oleacinidae. The family falls within the superfamily Testacelloidea, which also contains Testacellidae and Spiraxidae (Bouchet & Rocroi, 2005). Thompson (2010) moved the subfamily Euglandininae from Oleacinidae to Spiraxidae, following Baker (1962), but Thompson and Baker did not provide sufficient argumentation for this change, so the widely accepted taxonomy by Bouchet & Rocroi (2005) is used here.

The Mediterranean species occur in rather dry, often rocky habitats, which are openly to sparsely vegetated. However, they also occur in anthropogenically affected areas such as gardens and parks (Kittel, 1997). The snails are mainly active at night and are hidden away under rocks and leaf litter during the day, although they can also be found crawling around during daytime if the weather is rainy or cloudy and moist (Wagner, 1952; Maassen, 1977; Kittel, 1997). During the hot summer months, *Poiretia* snails aestivate by burying themselves in soil or under rocks and sealing their apertures with an epiphragm (Kittel, 1997).

Poiretia snails prey on a wide variety of pulmonate snails. The full extent of this variety is not well known, but it appears that any snail is fair game. They attack their prey's soft tissues with their radula. Even snails that are larger than *Poiretia* themselves, such as adult *Cornu aspersum* (Müller, 1774) and *Eobania vermiculata* (Müller, 1774), are eaten (Wächtler, 1927). *Poiretia cornea* is observed to rotate snails that have retracted into their shell, in order to expose their aperture (Kittel, 1997).

It is unclear whether *Poiretia* snails also prey on slugs in the wild. A captive *P. cornea* was provided with a *Deroceras* slug by Kittel (1997), who observed that the snail attacked its potential victim, but could not maintain a grip on the fleeing slug. It seems that its slimy and tough skin repels the predatory snail and it also appears to be able to flee more quickly than most shelled snails. Kittel's (1997) observations suggest that *Poiretia* snails might not be able to routinely capture (larger) slugs in the wild, but it might still have a chance against small or weakened slugs.

Furthermore, captive *Poiretia* snails will attack and feed on lumbricid earthworms of over 15 cm in length (Wächtler, 1927; Maassen, 1977; Kittel, 1997). When the snail bites the worm, the worm will contract and then try to escape by writhing wildly, but it fails in all the observed cases (Wächtler, 1927; Maassen, 1977; Kittel, 1997). Its movements will grow weaker after only a few seconds and will cease altogether, while the snail continues feeding, using its radula to ingest the worm's inner tissues. After a few minutes, the snail will abandon its partially eaten victim, which will always be dead. The worm's death is remarkable, because a worm attacked by any other predatory snail, such as *Daudebardia*, will still be alive when it is half eaten. This, along with the rapidly weakening movements of the worm, led Wächtler (1927) to suggest that excretions from *Poiretia* snails' salivary glands might be venomous.

According to Wächtler (1927), captive *Poiretia* snails will also feed on cucumber. It is unknown whether they feed on plants in the wild, but, as their physiology is well-adapted to carnivory (Barker & Effort, 2004), it seems unlikely that plant matter would make up a significant portion of their diet.

Snails with a blocked shell aperture, such as the operculate caenogastropods *Pomatias* and *Cochlostoma*, as well as the pulmonate Clausiliidae, or with a narrowed aperture, such as *Chondrula* and *Lindholmiola*, will have a hole made into their shells by *Poiretia*, so that it can reach their tissues (Erjavec, 1885; Maassen, 1977; Schilthuizen et al., 1994; Kittel, 1997; Fanelli, 2012; Helwerda & Schilthuizen, 2014). These holes are elongated and their edges are eroded. In *Albinaria* populations, the number of empty shells with a hole made by a *Poiretia* may reach up to 21% (Helwerda & Schilthuizen, 2014).

It is thought that *Poiretia* snails do not use their radula to produce these holes, as e.g. Naticidae do, but that they use acid secretions to dissolve part of the shell of their prey. Fanelli (2012) observed that a *Poiretia cornea* settled on the shell of a *Pomatias elegans* (Müller, 1774) and stayed on it for over a day to create a hole. This is similar to Fabio Liberto's observation (on online forum naturamediterraneo.com) of a *P. dilatata* keeping its foot on a *Pomatias elegans* for two days. The observed *Poiretia* specimens sat perfectly still, whereas if they would have used their radulae, they would have moved their heads. This potential use of acid by *Poiretia* could be comparable to the little-known saxicavous habits of helicid snails. Helicidae, most notably *Cepaea nemoralis* (Linnaeus, 1758), are capable of producing tubular holes in limestone, presumably by dissolving the rock with an acid secretion (Quettier, 2011 and references therein).

It is unclear how *Poiretia* snails, and saxicavous helicids, produce this acid, but it is most likely localised in the pedal mucus, because the sole of the foot is kept in contact with the shell or rock that is dissolved. The pedal mucus is a mixture of mucus from the suprapedal gland, also known as pedal mucous gland or pedal gland, and from single-celled sole glands or mucous cells (Luchtel & Deyrup-Olsen, 2001), but the relative contributions of these glands to the mucus is unknown. The mucus of some gastropods has been shown to contain acidic mucoproteins and mucopolysaccharides (Campion, 1961; Cook & Shirbhate, 1983; Cook, 1987; Shirbhate & Cook, 1987), but this has not been widely studied.

In this study, the pedal gland and foot tissue from *Poiretia* specimens are investigated histologically, because these tissues are the most likely origin of the acid supposedly used by *Poiretia* to make holes. Radulae were also investigated, because the shape of the radular teeth might also contain clues to the function of the radula and whether it may be used to make holes. A live specimen of *Poiretia* was obtained for behavioural observations. The range of prey species is explored and predatory behaviour is observed in detail. To establish whether *Poiretia* snails are mainly nocturnal or diurnal, day-time and night-time activities were logged by continuously observing a captive snail using an infrared camera.

MATERIAL AND METHODS

Specimens of *Poiretia* from the collection of Naturalis Biodiversity Center were dissected in view of the observations of *Poiretia* making holes in shells by excreting acid, instead of radulating. Radulae were dissected, placed on SEM stubs, coated and imaged in a Jeol SEM. Contents of the digestive system of the *Poiretia* specimens were examined microscopically. In several specimens, transverse sections of about 1 cm thickness were cut out of the foot, incorporating the pedal gland, to be used for histology. For the preparation of histological sections of foot and pedal gland tissue, protocols from the online immunohistochemistry protocol database http://ihcworld.com/protocol_database.htm were adapted and used. The final protocol is given in the Supplementary data (Appendix 1). Measurements were also taken on the dissected specimens. The shell height was measured with a caliper. The average radular tooth length was calculated by measuring four entirely visible teeth from the SEM images. The height and width of the pedal gland was measured from the histology slides. The average number of gland cells in the pedal gland was calculated by counting gland cell nuclei in all the sections on the slide, in alternating halves of the pedal gland, using 100x magnification. The average number of foot sole gland cells was calculated by counting gland cell nuclei in a 500 µm stretch parallel to the epidermis in all the sections on the slide, using 100x magnification.

A live specimen of *Poiretia compressa* was found on the west side of the island of Corfu, near Paleokastrites, GoogleMaps coordinates 39.670600, 19.701214, on the 23th of September 2014, in the afternoon, crawling around in a shaded area among damp leaf litter. This specimen was placed in a plastic container with paper towels on the bottom, which were watered weekly, as well as a limestone rock. Four live *Pomatias elegans* (Müller, 1774) were collected on the same site. Additional live prey snails of *Alinda biplicata* (Montagu, 1803), *Cornu aspersum* (Müller, 1774), *Cepaea nemoralis* (Linnaeus, 1758), *Aegopinella nitidula* (Draparnaud, 1805) and *Discus rotundatus* (Müller, 1774) were collected in the Hortus Botanicus in Leiden, as well as in the garden of Naturalis Biodiversity Center, Leiden, the Netherlands.

Observations of the live *Poiretia* specimen were made using a surveillance infrared camera (obtained from lightinthebox.com, product number 65943), which saved one frame every minute. This camera automatically switched to infrared mode in the dark, enabling night-time observations. However, only about one third of the bottom of the plastic container fitted into the frame of the camera. Each frame was examined for the presence of the *Poiretia* specimen. If the snail was present, it was determined whether it was active or not, by checking whether its head and tentacles were visible and by comparing the frame with the previous and the next frame. If the snail was active, it was noted whether it was light or dark and whether the *Poiretia* was attacking a prey snail or just moving about. Whether it was light or dark was defined by whether the camera switched to infrared mode or not (the camera produced colour images by daylight and greyscale images in infrared mode). If the *Poiretia* was attacking a prey snail, the species was identified, as well as the prey being juvenile or adult. If the *Poiretia* snail was inactive, it was determined whether it has crawled under the limestone rock or the paper tissues, covering at least the front of its shell, or it has withdrawn into its shell without anything covering the front of its shell.

Furthermore, periods of activity were scored for light or dark; these periods started with the *Poiretia* snail becoming active or entering the frame after being out of frame for more than six hours and they ended with the snail becoming inactive or exiting the frame for more than six hours. If the light level changed from light to dark or vice versa during a period of activity, it was scored for both light and dark. The numbers of periods of activity in light and darkness were tested for deviation from an even distribution using the binomial test in Excel.

Additionally, an act of predation was filmed in high resolution using a Nikon camera on a camera stand.

RESULTS

The radulae of *P. dilatata peloponnesica* (Fig. 1a) and *P. compressa* (Fig. 1b) are quite similar, consisting of rather long, slightly curved, aculeate unicuspid teeth. The teeth are 1.6 times larger in *P. dilatata peloponnesica* than in *P. compressa*, whereas the shell is two times taller (Table 1).

No shell raspings are observed in the contents of the digestive system of the *Poiretia* specimens. Dissections and histology reveal the position of the suprapedal gland in *P. dilatata peloponnesica* and *P. compressa* to be on top of the foot tissue, but still connected to it by fibres of tissue in the anterior part of the body and sunken into the foot tissue in the median part of the body. The length of the gland is difficult to assess because it is integrated into the foot tissue, but appears to be about two-thirds of the body length.

The histological sections through the pedal gland (Fig. 2) show the excretory canal, surrounded by glandular cells. The excretory canal is usually located in the dorsal section of the gland. The canal is lined with a single layer of cells. The cells in the floor of the canal are ciliated and elongated and excrete mucus granules from the glandular cells into the canal. In the anterior part of the body, the floor is folded to create a groove flanked by two humps. This folding disappears in the median part of the body, where the canal is rounded. Here, the roof of the canal bears a proliferation of cells projecting into lumen of the canal. The glandular cells are mostly granulated, filled with mucus granules, which are stained blue by hematoxylin, but sometimes vacuolated. The amount of interspaces between glandular cells seems to vary throughout the gland. The interspaces sometimes contain muscle fibres, especially when the gland is surrounded by foot tissue. The amount of glandular tissue, as well as the amount of granules within the glandular cells, is higher in *P. dilatata peloponnesica* than in *P. compressa* (Table 1).

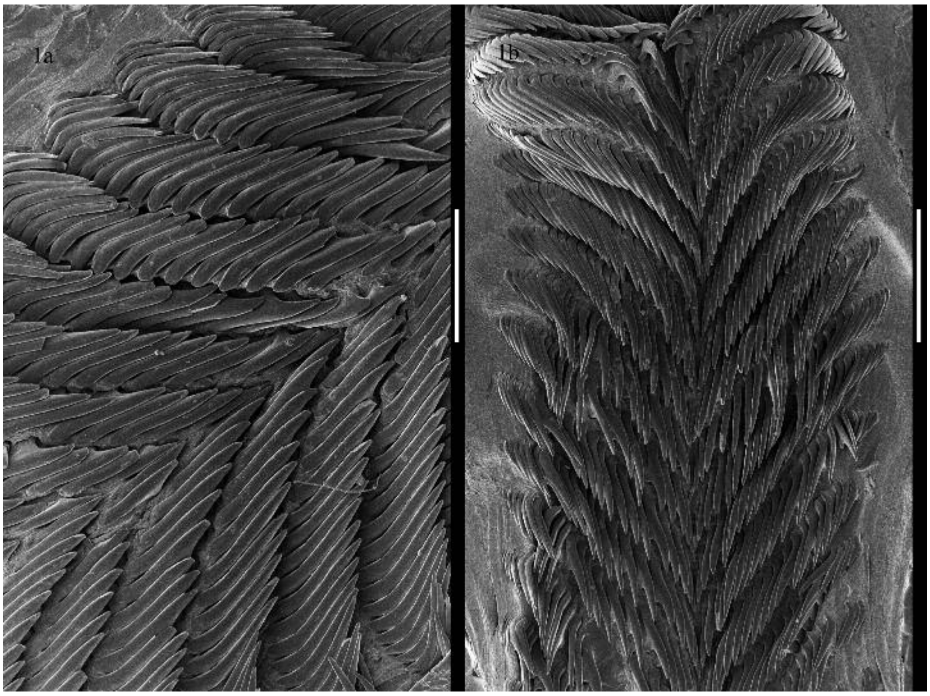

Fig. 1. Radulae of *Poiretia* snails. Scale bars indicate 500 µm. **1a.** *P. dilatata peloponnesica* Subai, 1980, RMNH.MOL.266443. **1b.** *P. compressa* (Mousson, 1859), RMNH.MOL.324813.

Species	RMNH. MOL registration number	Shell height (mm)	Average radular tooth length (µm)	Ant PG H*W (mm)	N GC in Ant PG	Med PG H*W (mm)	N GC in Med PG	N GC in Ant FS	N GC in Med FS
Poiretia dilatata peloponnesica	266442	39.7		0.82 1.38	110			57	
Poiretia dilatata peloponnesica	266443	55.6	489	0.76 1.81	116	1.42 1.31	120	64	52
Poiretia compressa	324811	28.8				0.99 0.91	44		9
Poiretia compressa	324813	27.9	304						
Poiretia compressa	324814	23.2		0.34 1.12	40	0.99 0.75	84	35	38

Table 1. Measurements taken on specimens used for dissections and histology. Ant PG H*W is height and width of the anterior part of the pedal gland. N GC in Ant PG is the number of gland cells in the anterior part of the pedal gland. Med PG H*W is height and width of the median part of the pedal gland. N GC in Med PG is the number of gland cells in the median part of the pedal gland. N GC in Ant FS is the number of gland cells in the anterior part of the foot sole. N GC in Med FS is the number of gland cells in the median part of the foot sole.

Histological sections of the foot soles of *Poiretia* (Fig. 3) show the presence of unicellular mucus-excreting sole glands. These cells are called type C mucous glands, following Campion (1961). They are commonly found in the foot soles of pulmonate snails. They are either packed with blue-stained mucus granules, or vacuolated, containing only a few threads of mucus. The mucus is excreted through ducts, which are partly visible near the surface of the foot sole. The outer surface of the foot sole is covered with cilia. The sole glands in *P. compressa* appear to be smaller, containing fewer mucus granules, and slightly less numerous than in *P. dilatata peloponnesica*.

The live *P. compressa* specimen was provided with two of the four live *Pomatias elegans* specimens at first. It preyed on both of them in October 2014 by producing a hole in their shells. It was photographed sitting on a *Pomatias* shell on 15 October (Fig. 4). An attempt was made to measure the pH-value of its pedal mucus using pH-paper, but this method proved to be too coarse due to the small amount of mucus. The next day, the *Poiretia* snail had abandoned the *Pomatias*, leaving a scar on its shell, but not a complete hole. It had, however, consumed two juvenile *Cepaea nemoralis* instead (without producing a hole). It completed the hole in the shell of the *Pomatias* a few days later, after which the shell was found empty (Fig. 5a). Unfortunately, it was not under continuous observation in October.

The continuous observation of the live *P. compressa* specimen took place from 15 December 2014 until 26 June 2015, except for a few short periods in which the camera system malfunctioned. The camera produced a total of 192,185 frames. With one frame per minute, this stands for about 123 days of observation. The *Poiretia* snail is visible in 34,916 of the frames, which is about 18%. Of these frames, it is moving (i.e. crawling, feeding or moving its head or tentacles) in 2,084, or 6%, of the frames. Of the frames in which it is active, 1,312 (63%) are light and 772 (37%) are dark. Of the frames in which it is inactive, it has crawled under the limestone rock or the paper tissues, covering at least the front of its shell, in 30,803 (95%) of the frames, versus 1,509 (5%) of the frames in which it has withdrawn into its shell without anything covering the front of its shell. An overview of its activities can be found in Fig. 6.

In total, 74 periods of activity were recorded, 40 of which were in the light and 34 in darkness. This distribution does not deviate significantly from an even distribution ($P = 0.0727$). The periods of activity are clustered in one to four days that follow watering of the *Poiretia* snail's enclosure (Fig. 7). The watering is not always followed by activity (thirteen out of eighteen times), but activity is always preceded by watering.

Fifteen instances of predation were counted (Table 2 and Supplementary film 1 https://youtu.be/9zsyvtjig2Y); in eight of these instances, the prey species was *Discus rotundatus*; in three, *Aegopinella nitidula*; in another three, *Alinda biplicata*, two of which were juveniles and one adult; in one instance, the prey was a juvenile *Cornu aspersum*. The time the *Poiretia* snail spent feeding varied from one minute to seventeen minutes. Eleven of the predatory acts occurred in light, three in darkness and one started in light and ended in darkness. However, the predatory acts cannot be viewed indepen-

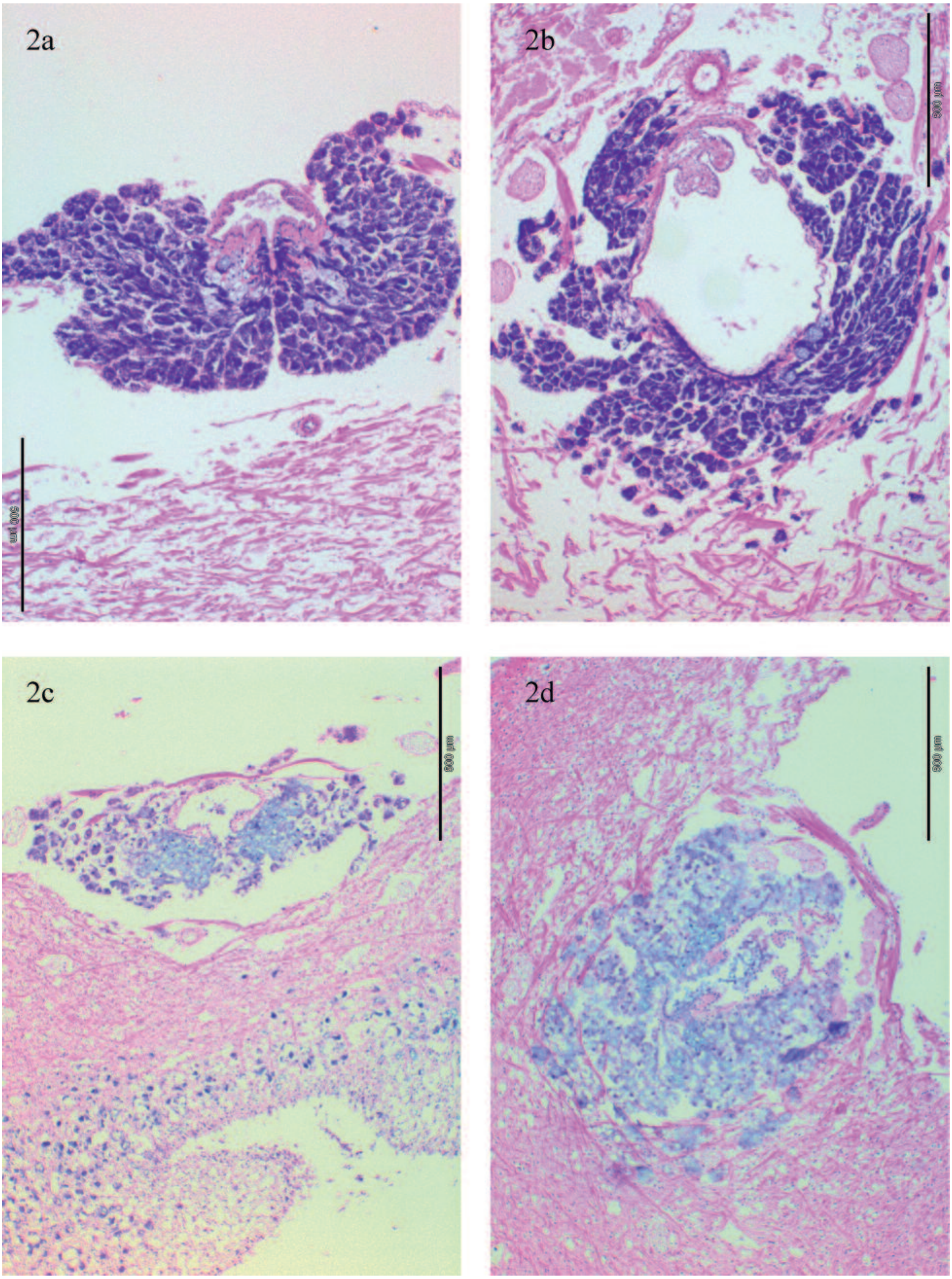

Fig. 2. Histological sections through pedal glands of *Poiretia*. Scale bar indicates 500 µm. **2a.** Anterior part, *P. dilatata peloponnesica* Subai, 1980, RMNH.MOL.266443. **2b.** Median part, same specimen as a. **2c.** Anterior part, *P. compressa* (Mousson, 1859), RMNH.MOL.324814. **2d.** Median part, same specimen as c.

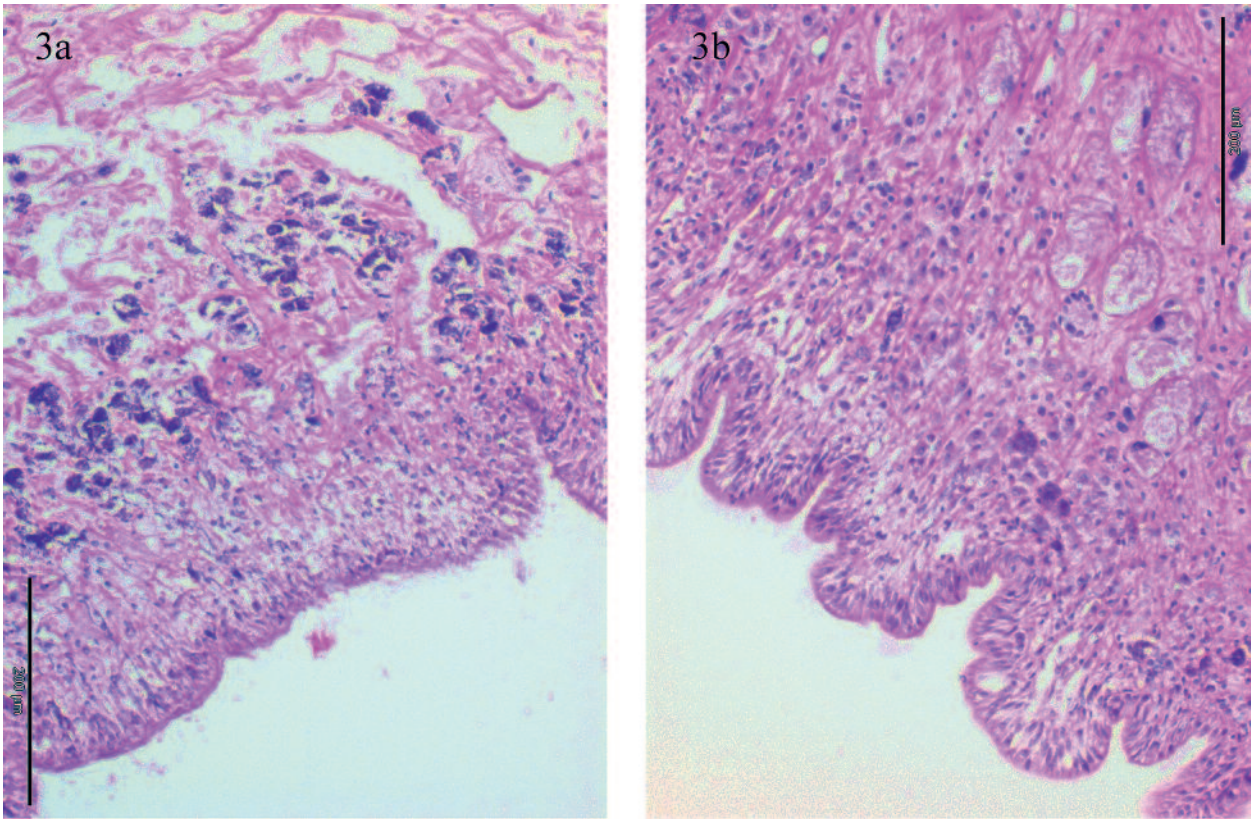

Fig. 3. Histological sections through anterior part of foot sole of *Poiretia*. Scale bar indicates 200 µm. **3a.** *P. dilatata peloponnesica* Subai, 1980, RMNH.MOL.266443. **3b.** *P. compressa* (Mousson, 1859), RMNH.MOL.324811.

dently of each other: the six predatory acts on *D. rotundatus* that occurred in the light, all happened within half an hour, consecutive to each other. The two predatory acts on *D. rotundatus* in the dark took place within an hour and a half. The thirteen minute predation of the *A. biplicata* juvenile and the four minute predation of the adult took place within one hour. The predatory acts on *Aegopinella nitidula* in the light also took place within one hour. Therefore, there are seven periods of predation: four in the light, two in the dark and one that started in the light and ended in the dark.

One act of predation, the thirteen minute predation of the *Alinda biplicata* juvenile, was filmed in detail on 13 January (Plate 1; Supplementary film 2 https://youtu.be/x9-NXfbJI4c). The *Poiretia* snail was put in front of 28 *Alinda biplicata* specimens and activated by watering the tissue paper. It took about 50 minutes before the snail started crawling towards the *Alinda* specimens. Its tentacles were extended and its head moved slowly from side to side. It appeared to lock its eyes onto an active adult *Alinda* specimen and moved towards it. When its head was very close to the *Alinda*, about 2 mm away, the latter quickly retracted into its shell. The *Poiretia* snail contracted its head and shot out its radula with a fast motion, but it hit the edge of the aperture of the *Alinda* shell. It relaxed again and looked about, then moved towards an active *Alinda* juvenile. It moved its mouth to the *Alinda*, which retracted into its shell, then shot its radula into the aperture of the *Alinda* and ingested it, which was visible as a dark blob moving into its slightly transparent head. It continued feeding on the *Alinda* juvenile for about thirteen more minutes, with its radula through the aperture. It kept the *Alinda* shell in the air, spire up, while feeding.

The *Poiretia* snail was given the other two *Pomatias* specimens on 19 May. One of the *Pomatias* specimens became active, while the other remained inactive. The active *Pomatias* specimen was "inspected" by the *Poiretia* snail on 25 May, but it was not eaten (Supplementary film 3 https://youtu.be/ICNZmSBSer8). The *Pomatias* had only partially emerged from its shell as the *Poiretia* moved its head close to its aperture. It is not clear if the *Poiretia* attacks the *Pomatias* with its radula or not, because this footage only has one frame per minute, but it appears that the gap between the *Pomatias*' aperture and operculum is too small or that the *Pomatias* retracts into its shell too quickly. This repeats itself four more times, but the *Poiretia* fails to prey on the *Pomatias* or perhaps it is merely browsing. The *Poiretia* also crawls towards and over the other *Pomatias* specimen. It later inspects the previously active *Pomatias* while the latter is completely retracted into its shell, two times, but it does not employ its hole-making technique. Instead, it retracts into its shell and becomes inactive. It enters into aestivation the next day, securing its shell to the tissue paper and sealing its aperture with an epiphragm, without anything covering its shell.

Fig. 4. A captive *Poiretia compressa* (Mousson, 1859) sitting on the shell of a *Pomatias elegans* (Müller, 1774) to produce a hole.

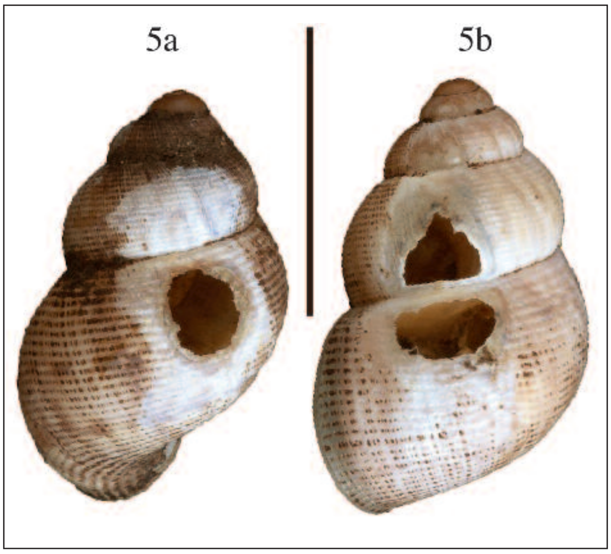

Fig. 5. *Pomatias elegans* shells after attack by *Poiretia* **5a**. The *P. elegans* specimen from Fig. 4, after being consumed by the *P. compressa* specimen. **5b**. Another *Pomatias elegans* specimen preyed upon by the *P. compressa* specimen. Scale bar indicates 1 cm.

DISCUSSION

Radulae with elongated, unicuspid teeth are consistent with a carnivorous diet (Taylor, 1894-1900; Simroth, 1901; Solem, 1974), as pulmonates with such a radular dentition are predominantly carnivores. This fits the assumption and observations of *Poiretia* snails being carnivores. However, interpreting function from radular dentition should be treated with caution, because species with similar radulae can have very different feeding behaviours (Barker & Efford, 2004). For instance, there are also pulmonates with aculeate teeth and a strictly herbivorous diet (Barker & Efford, 2004). It is therefore impossible to prove that *Poiretia* snails do not ingest plant matter as well by only studying the radula. It also seems unlikely that *Poiretia* uses these aculeate teeth to scrape holes in shells, but again this is impossible to tell for sure. The teeth are smaller in *P. compressa* than in *P. dilatata peloponnesica*, which fits the smaller overall body size of *P. compressa*.

Dissections and histological sections of *Poiretia* support the idea that they do not use their radula to make holes in the shells of their prey, because there were no shell scrapings in their gut contents. Instead, their pedal glands and foot sole glands seem capable of producing acidic mucus to dissolve prey shells. These glands are well developed in *Poiretia* and their contents are stained blue by haematoxylin, which means they are acidic and/or negatively charged. The pH-value cannot be assessed through this method, but is likely below 7. The pedal gland is larger and the foot sole glands more numerous in *P. dilatata peloponnesica* than in *P. compressa* and this also appears to be proportionate to their body size.

The observation of a live *Poiretia compressa* specimen confirmed results obtained in previous studies (Wächtler, 1927; Maassen, 1977; Kittel, 1997; Fanelli, 2012) and yielded new insights into their behaviour. The *Poiretia* preyed on specimens of all the different species of prey snail provided to it. These were *Pomatias elegans*, *Alinda biplicata*, *Cornu aspersum*, *Cepaea nemoralis*, *Aegopinella nitidula*, and *Discus rotundatus*. It only produced holes in the shells of *Pomatias elegans*. This indicates that *Poiretia* snails prey on a wide range of snail species of different shapes and sizes, but that they only produce holes in shells when they cannot attack their prey through the aperture. It is notable that the *Poiretia* specimen did not produce holes in *A. biplicata*, which, being a species of Clausiliidae, blocks its aperture with a clausilium. However, the *A. biplicata* specimens often emerged from their shells when water was provided and the *Poiretia* was capable of preying on them at such times, without having to make a hole. There were also plenty of prey specimens available at this stage of the experiment, whereas there were only two *Pomatias elegans* specimens and a few juvenile *C. nemoralis* specimens at the time when the *Poiretia* produced holes, so prey availability might also influence *Poiretia*’s hole producing behaviour. Another factor that might influence this, is the *Poiretia* specimen's feeding status, because it was only recently collected, and it probably emerged from its aestivation not long before that, at the time it produced holes in *Pomatias elegans*, whereas it had fed on many prey snails by the time it was provided with *A. biplicata*.

The statement that *Poiretia* snails are mainly nocturnal (Wagner, 1952; Maassen, 1977; Kittel, 1997), is not confirmed by the activities of the observed specimen, as the number of periods of activity in the light is actually greater than the number of periods in the dark, although the periods did not deviate significantly from an even distribution. The distribution is even more skewed when the number of minutes of activity is compared, but this distribution cannot be statistically tested, due to

PLATE 1

Figs 1a-j. Stills from Supplementary Film 2, of a *Poiretia compressa* (Mousson, 1859) snail preying on *Alinda biplicata* (Montagu, 1803). **1a**. *Poiretia* snail starts crawling. **1b**. Moving towards adult *Alinda*. **1c**. Attacks adult *Alinda* with radula. **1d**. Contracts after failed attack. **1e**. Moves towards juvenile *Alinda*. **1f**. Puts its mouth very close to juvenile *Alinda*. **1g.** Shoots radula into aperture of juvenile *Alinda*. **1h**. Ingests prey. **1i**. Feeds while lifting prey up. **1j**. Still feeding 5 minutes later. For complete footage see https://youtu.be/x9-NXfbJI4c

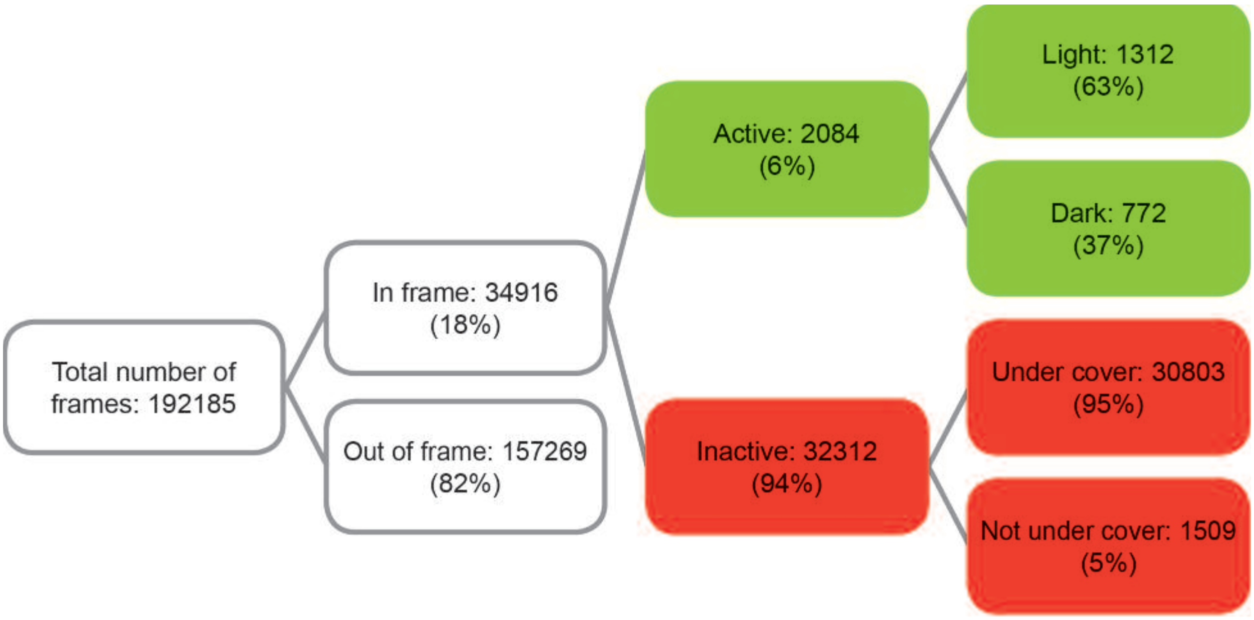

Fig. 6. The activities of a live *Poiretia compressa* (Mousson, 1859), observed with an infrared camera producing one frame per minute.

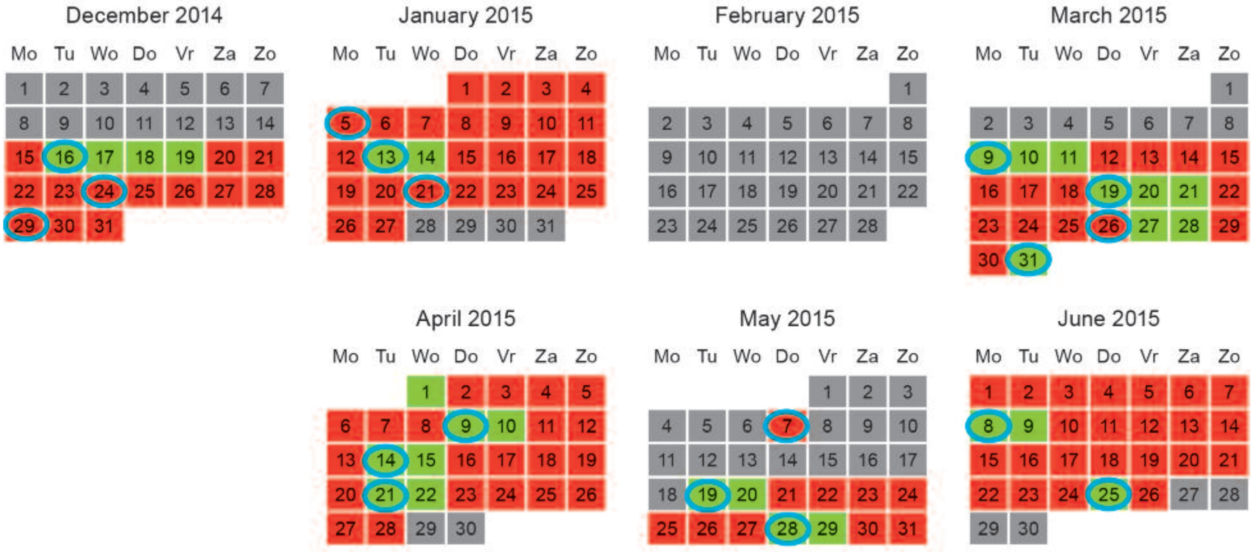

Fig. 7. A calendar timeline of the *Poiretia compressa* (Mousson, 1859) observation experiment. Days in which the *Poiretia* specimen showed activity are coloured green, days in which it did not show activity are red and days in which the camera did not function are black. The days when the enclosure was watered are encircled with blue.

the interdependence of consecutive minutes. There is a much clearer link between the availability of water and the activity of the *Poiretia* specimen, as its activities always took place within one to four days after the enclosure has been watered. Its nocturnality in the wild is therefore better explained by moisture conditions than light conditions, as nights are cooler and more moist, and snails will have to remain inactive during the heat of day to avoid heavy water loss. This is also congruent with observations of active *Poiretia* snails on rainy or clouded and moist days (Wagner, 1952; Maassen, 1977; Kittel, 1997). It might be advantageous for *Poiretia* snails to hunt during daytime, because then they can use their eyesight. The observed *Poiretia* specimen seemed to actively observe its prey before striking them with its radula. It also hunted in the dark, but then it presumably had to rely on smell and touch.

When the observed *Poireita* was inactive, it was resting under cover 95% of the time. However, it entered its aestivation out in the open. This is difficult to explain and contrary to observations of *Poiretia* snails in the wild, which aestivate by burying themselves into the topsoil or under rocks (Kittel, 1997). Perhaps it could not find an adequate place to bury itself in the unnatural enclosure.

Prey species	Feeding time (minutes)	light	dark
Discus rotundatus	1	x	
Alinda biplicata juvenile	2	x	
Discus rotundatus	2	x	
Discus rotundatus	2	x	
Discus rotundatus	3	x	
Discus rotundatus	3	x	
Alinda biplicata adult	4	x	x
Aegopinella nitidula	6	x	
Aegopinella nitidula	8	x	
Aegopinella nitidula	8		x
Discus rotundatus	9	x	
Discus rotundatus	9		x
Discus rotundatus	9		x
Alinda biplicata juvenile	13	x	
Cornu aspersum juvenile	17	x	

Table 2. Observed acts of predation by a *Poiretia compressa* (Mousson, 1859) specimen.

The time that the observed *Poiretia* specimen spent feeding on different species of prey, varied from one minute to seventeen minutes. The longest feeding time was spent on a *C. aspersum* juvenile, a relatively large prey, which follows the expectation that feeding time is correlated with prey size. Prey shape may also influence feeding time, but its influence is difficult to assess from the small sample of fifteen acts of predation. However, feeding time varied from one to nine minutes with *D. rotundatus* prey, which were all similar in size and shape. Therefore, other factors, such as light and moisture conditions, may also have a significant influence on feeding time. Many more observations will be necessary to clear this up.

The predatory behaviour that the *Poiretia* specimen shows on the detailed film, is similar to the behaviour of the well-studied Central American oleacinid *Euglandina rosea* (Férussac, 1821) (Barker & Efford, 2004 and references therein) in the use of the radula to ingest the soft tissue of the prey. However, *E. rosea* moves its head from side to side, while also moving its enlarged labial palps, more conspicuously than *P. compressa* does, before attacking prey. *Euglandina rosea* also swallows small prey snails whole, including their shells, and is known to follow mucus trails to locate prey. These behaviours have not been observed in *Poiretia*. Furthermore, *E. rosea* is observed to turn its prey's shells over on their spire to expose their aperture, similar to *P. cornea* (Kittel, 1997), but this is not observed in the captive *P. compressa* specimen. Perhaps *P. compressa* does not show this behaviour, or shows it less frequently, because of its smaller size. This might also explain the observation that predatory holes made by *P. compressa* in *Albinaria* occurred most frequently on the abapertural side, whereas holes made by *P. dilatata* occurred most frequently on the apertural side (Helwerda & Schilthuizen, 2014).

Fanelli (2012) suggested that *Poiretia cornea* possibly feeds exclusively on *Pomatias elegans*, because he could only find holes made by *P. cornea* in shells of *Pomatias elegans*. However, in light of the observations done here and by Kittel (1997), it is most likely that these *P. cornea* predate other snails as well, by attacking them while they are crawling or reaching through the aperture. It is more time-consuming and probably more costly in terms of resources for *Poiretia* to produce a hole in a shell, so they will only resort to this mode of predation if the only prey available are snails with a blocked aperture, such as *Pomatias elegans*.

The infrared camera was instrumental in acquiring most of the data in this study and proved to be a useful tool for observational studies in snails. The set up could be perfected further, especially by ensuring that the entire enclosure fits in the frame. With such a set up, many more snails' secrets could be revealed. A subject that requires further research, is the acidity and the composition of the pedal mucus of *Poiretia*, because this is the missing piece in the puzzle of *Poiretia*'s hole making behaviour. Advanced laboratory techniques, e.g. a pH-microelectrode, will be needed to clear this up once and for all.

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APPENDIX 1. HISTOLOGY PROTOCOL

1. Fix tissues with 10% formalin for 24-48 hours at room temperature. Fixative volume should be 5-10 times of tissue volume.
2. Paraffin embedding schedule is applied as follows:
   - 70% Ethanol, two changes, 1 hour each
   - 80% Ethanol, one change, 1 hour
   - 96% Ethanol, one change, 1 hour
   - 100% Ethanol, three changes, 1.5 hour each
   - Xylene, three changes, 1.5 hour each
   - Paraplast paraffin wax (58-60 ºC), two changes, 2 hours each
   - Embed tissues into paraffin blocks by allowing araffin to dry at room temperature
3. Trim paraffin blocks as necessary and cut at 8 µm.
4. Select 4 paraffin ribbons of about 6 sections for each paraffin block to mount onto slides.
5. Apply Riopel adhesive and 6 drops of distilled water to slide, then place paraffin ribbon on slide.
6. Allow slides to air dry for 30 minutes and then bake in 30 ºC oven overnight.
7. Deparaffinizing, staining and dehydrating schedule is applied as follows:
   - Xylene, 2 changes, 10 minutes each.
   - 100% Ethanol, 2 changes, 5 minutes each.
   - 96% Ethanol, 2 minutes
   - 70% Ethanol, 2 minutes.
   - Wash briefly in distilled water.
   - Mayer hematoxylin solution, 8 minutes.
   - Wash in warm running tap water (35 °C), 10 minutes.
   - Rinse in distilled water.
   - Rinse in 96% alcohol, 10 dips.
   - Eosin-Phloxine B solution, 30 seconds to 1 minute.
   - 96% Ethanol, 5 minutes.
   - 100% Ethanol, 2 changes, 5 minutes each.
   - Xylene, 2 changes, 5 minutes each.
8. Mount with Depex, cover with cover glass and dry overnight in a well-ventilated room.

Solutions used:

Formalin Solution (10%, buffered neutral):

Formaldehyde (37-40%)	100 ml
Distilled water	900 ml
$NaH_2PO_4.H_2O$	4.6 g
$Na_2HPO_4.2H_2O$	8.15 g

Mix to dissolve.

Eosin-Phloxine B Solution:

Eosin Stock Solution:

Eosin Y	1 g
Distilled water	100 ml

Mix to dissolve.

Phloxine Stock Solution:

Phloxine B	1 g
Distilled water	100 ml

Mix to dissolve.

Eosin-Phloxine B Working Solution:

Eosin stock solution	100 ml
Phloxine stock solution	10 ml
Ethanol (96%)	780 ml
Glacial acetic acid	4 ml

Mix well.

Hematoxylin Solution (Mayer):

AluminiumPotassium Sulphate (alum)	50 g
Hematoxylin	1 g
Sodium iodate	0.2 g
Citric acid	1 g
Distilled water	1000 ml

Stir to dissolve the chemicals in the order listed above. For example, dissolve alum in 1000 ml distilled water first. When alum is completely dissolved, add hematoxylin. When hematoxylin is completely dissolved, add sodium iodate, etc.

APPENDIX 2. OBSERVATIONS ON A CAPTIVE *POIRETIA COMPRESSA* SPECIMEN

Start:
15-12-2014: 16.21 not in frame
16-12-2014: 13.54 watered enclosure, provided *Alinda biplicata*, put in frame withdrawn into shell
    14.11 emerges from shell
    14.20-14.22 predates juvenile *Alinda*
    14.24 exits frame
17-12-2014: 12.55 enters frame
    12.58 settles under rock
    15.59 shifts position under rock
18-12-2014: (dark)16.40-17.17 crawls out from under rock, cralws around until out of frame
19-12-2014: (light) 8.37-8.42 enters frame, crawls around, exits frame
24-12-2014: (light) 15.49 watered enclosure
29-12-2014: 13.10 watered enclosure
05-01-2015: 12.28 watered enclosure
06-01-2015: 12.16 camera moved
    14.29 camera moved
13-01-2015: 15.30 made movie with other camera
    17.27-17.37 (light) put in frame with prey snails, crawls around "inspecting" prey, exits frame
    17.55 enters frame again, crawls around "inspecting" prey
    18.00 predation of one active *Alinda biplicata*
    18.01 becomes dark
    18.04 finished eating the *Alinda biplicata*
    18.10 exits frame
14-01-2015: (dark) 9.09-9.16 enters frame, "inspects" *Alinda biplicata* shells, none are active, exits frame
    9.19-9.23 (light) enters frame, crawls around, exits frame
    9.43-9.47 enters frame, crawls around, exits frame
    11.45-11.49 enters frame, crawls around, exits frame
    12.00-12.03 enters frame, crawls around, exits frame
    12.27-12.33 enters frame, crawls around, exits frame
21-01-2015: 12.20 watered enclosure
28-01-2015: 17.39 until 09-03-2015: 14.08 camera malfunctions, (light) put in frame
    14.38-15.50 becomes active, looks around but doesn't move much, looks under rock
    16.31-16.34 crawls around, exits frame
    16.37-16.38 enters frame, crawls around, exits frame
    16.47-16.54 enters frame, crawls around, exits frame
    17.28-17.31 enters frame, crawls around, exits frame
    17.36-17.41 enters frame, crawls around, exits frame
    18.02 becomes dark
    18.43-18.52 enters frame, crawls around, exits frame
10-03-2015: 5.14-5.29 enters frame, crawls around, exits frame
    5.32-6.03 enters frame, crawls around, exits frame

6.25-6.40 enters frame, crawls around, exits frame
7.10 enters frame, crawls around,
7.18-7.38 hides under rock,
8.03 crawls around, exits frame
8.25-8.32 enters frame, crawls around, exits frame
9.11-9.33 enters frame, crawls around, exits frame
9.48-9.58 enters frame, crawls around, exits frame
10.34-10.39 enters frame, crawls around, exits frame
10.42-10.45 enters frame, crawls around, exits frame
11.13 becomes light
11.26-11.46 enters frame, crawls around, hides under rock
16.28-17.05 crawls out from under rock, exits frame
17.12-17.25 enters frame, crawls around, exits frame
17.36-17.42 enters frame, crawls around, exits frame
17.55-18.00 enters frame, crawls around, hides under rock
18.10 becomes dark
11-03-2015: 4.02-4.10 crawls out from under rock, hides under rock
8.23-8.47 crawls out from under rock, hides under rock
9.24 becomes light
9.25-9.35 crawls out from under rock, hides under rock
10.49-11.00 crawls out from under rock, hides under rock
19-03-2015: (light) 14.32 watered enclosure, added *Aegopinella*
16.10 crawls out from under rock
16.13 predates small *Aegopinella*
16.19 abandons *Aegopinella*, crawls around
16.25 exits frame
16.39 enters frame
16.40 predates small *Aegopinella*
16.48 abandons *Aegopinella*, crawls around
17.10 exits frame
17.36-17.39 enters frame, crawls around, exits frame
20-03-2015: (dark)8.03-8.12 enters frame, crawls around, inspects *Aegopinella* specimen, exits frame
8.19-8.21 enters frame, crawls around, exits frame
(light)15.37-15.42 enters frame, crawls around, exits frame
(dark)16.22 enters frame
16.29 withdraws into shell
16.41 becomes light
16.51 resumes crawling
17.05 exits frame
(dark)18.10 enters frame
18.14 withdraws into shell
18.25 resumes crawling
18.32 exits frame
18.34 enters frame
18.40 exits frame
21-03-2015: (dark)6.45-6.54 enters frame, crawls around, exits frame
26-03-2015 16.30 watered enclosure
27-03-2015: 6.04 enters frame
6.09 predates *Aegopinella*
6.17 resumes crawling
6.30 exits frame
6.42 enters frame
6.48 exits frame
6.55 enters frame
6.59 exits frame
8.17-8.25 enters frame, crawls around, exits frame
9.11-9.25 enters frame, crawls around, exits frame
9.28-9.40 enters frame, crawls around, exits frame
(light)13.48-13.55 enters frame, crawls around, exits frame
14.26-14.39 enters frame, crawls around, exits frame
16.27-16.43 enters frame, crawls around, exits frame
16.46-16.50 enters frame, crawls around, exits frame
16.57-17.00 enters frame, crawls around, exits frame
17.20-17.40 enters frame, crawls around, hides under rock
17.52-17.58 crawls out from under rock, exits frame
18.01-18.08 enters frame, crawls around, exits frame
18.12-18.29 enters frame, crawls around, exits frame
(dark)19.08-19.17 enters frame, crawls around, exits frame
28-03-2015: (dark)7.15-7.18 enters frame, crawls around, exits frame
7.42-7.49 enters frame, crawls around, exits frame
8.02-8.06 enters frame, crawls around, exits frame
8.25-8.43 enters frame, crawls around, exits frame
(dark)9.10-9.26 enters frame, crawls around, exits frame
31-03-2015: 14.30 watered enclosure
(light)17.12-17.16 enters frame, crawls around, exits frame
(light)17.30-17.36 enters frame, crawls around, exits frame
01-04-2015: 0.49-0.53 enters frame, crawls around, exits frame
1.57-2.11 enters frame, crawls around, exits frame
5.09-5.14 enters frame, crawls around, exits frame
5.18-5.28 enters frame, crawls around, exits frame
6.12-6.18 enters frame, withdraws into shell
6.30-6.35 resumes crawling, exits frame
6.55-7.00 enters frame, crawls around, exits frame
7.24-7.34 enters frame, crawls around, exits frame
7.45-7.59 enters frame, crawls around, exits frame
8.08-8.12 enters frame, crawls around, exits frame
8.59-9.04 enters frame, crawls around, exits frame
(light)9.08-9.30 enters frame, crawls around, exits frame
(dark)10.18-10.28 enters frame, crawls around, exits frame
(light)18.58-19.00 enters frame, withdraws into shell
(dark) 19.25-19.41 resumes crawling, exits frame
09-04-2015: 15.12 watered enclosure
18.16-18.23 enters frame, crawls around, exits frame
18.35-18.46 enters frame, crawls around, exits frame
10-04-2015: (dark) 7.45-7.56 enters frame, crawls around, exits frame
8.00-8.05 enters frame, crawls around, exits frame
8.38 enters frame
8.40-9.03 withdraws into shell
9.25 light
9.30 exits frame
18.04-18.11 enters frame, crawls around, exits frame
14-04-2015: 15.52 watered enclosure
18.11 enters frame
18.14-18.31 predates juvenile *Cornu aspersum*
18.35 exits frame
18.38-19.07 enters frame, crawls around, exits frame
19.10-19.16 enters frame, crawls around, exits frame
19.22-19.27 enters frame, crawls around, exits frame
15-04-2015: (dark) 7.40-7.52 enters frame, crawls around, exits frame
8.08-8.14 enters frame, crawls around, exits frame
8.48 enters frame
8.52-9.06 withdraws into shell
9.10 exits frame
9.19-9.23 enters frame, crawls around, exits frame
10.10-10.13 enters frame, crawls around, exits frame
21-04-2015: 15.22 watered enclosure, added prey *Aegopinella* and *Discus rotundatus*
16.11 enters frame
16.14-16.23 predates *Discus*
16.26-16.29 predates *Discus*
16.30-16.32 predates *Discus*
16.33-16.34 predates *Discus*
16.35-16.38 predates *Discus*
16.40-16.42 predates *Discus*
16.49 exits frame
16.52-16.55 enters frame, crawls around, exits frame
18.23-18.27 enters frame, crawls around, exits frame
18.56-19.16 enters frame, crawls around, exits frame
19.18-19.23 enters frame, crawls around, exits frame
22-04-2015: 6.12 (dark) enters frame
6.13-6.22 predates *Discus*
6.32 exits frame
7.23 enters frame
7.25-7.34 predates *Discus*
7.44 exits frame
7.53-8.08 enters frame, crawls around, exits frame
8.21-8.26 enters frame, crawls around, exits frame
9.20-9.24 (light) enters frame, crawls around, exits frame
9.37-9.49 enters frame, crawls around, exits frame
9.54-9.56 enters frame, crawls around, exits frame
11.21-11.24 enters frame, crawls around, exits frame

11.47-11.49 enters frame, crawls around, exits frame
12.14-12.19 enters frame, crawls around, exits frame
12.24-12.33 enters frame, crawls around, exits frame
12.47-12.54 enters frame, crawls around, exits frame
13.13 enters frame
13.28 withdraws into shell
13.37 emerges from shell
13.50 exits frame
17.49-17.56 enters frame, crawls around, exits frame
29-04-2015 8.51 camera moved accidentally
18.58 camera malfunctioning
06-05-2015 12.12 camera functioning again
07-05-2015 13.42 watered enclosure
14.04 camera malfunctioning
19-05-2015 14.19 camera functioning again, in frame resting under rock
14.32 watered enclosure, prey added
18.55 crawls out from under rock
19.39 exits frame
20-05-2015 2.44-2.45 enters frame, crawls around, exits frame
21-05-2015 13.13 camera moved, put *Poiretia* in frame, resting
28-05-2015 15.06 watered enclosure
15.43 becomes active
15.47 inspects active *Pomatias*, but does not attack (gap between aperture and operculum too small?)
16.10 inspects active *Pomatias*, but does not attack
16.27 inspects active *Pomatias*, but does not attack
16.35 withdraws into shell
17.20 emerges from shell
17.35 withdraws into shell
17.50 emerges from shell
18.03 exits frame
18.17 enters frame
18.20 inspects active *Pomatias*, but does not attack
18.37 withdraws into shell
18.48 emerges from shell
18.54 exits frame
19.21 enters frame
20.09 withdraws into shell
(dark) 22.25 emerges from shell
22.54 crawls under rock
29-05-2015 6.14 crawls out from under rock
6.27 withdraws into shell
7.00 emerges from shell
7.10 exits frame
7.23 enters frame
7.33 exits frame
(light) 9.30 enters frame
9.51 crawls under rock
(light) 12.53 crawls out from under rock
13.13 exits frame
14.22 enters frame
15.28 withdraws into shell under tissue paper
(dark) 16.53 emerges from shell
17.01 exits frame
17.05 enters frame
17.18 withdraws into shell
01-06-2015 (light) 8.57 exits frame
06-06-2015 2.20-8.45 camera malfunctions
07-06-2015 3.26-11.18 camera malfunctions
08-06-2015 16.22 watered enclosure
17.16 enters frame
17.19 inactive
18.31 active
18.54 exits frame
19.40 enters frame
19.45 withdraws into shell
20.17 emerges from shell
21.22 becomes dark
21.30 becomes inactive
09-06-2015 2.05 becomes active
2.10 becomes inactive
3.40 becomes active
3.43 exits frame
4.51-8.55 camera malfunctions
12.50 enters frame
13.31 exits frame
14.17 enters frame
14.41 withdraws into shell
15.43-15.48 emerges from shell, shifts position, hides under rock
10-06-2015 8.40 camera moved accidentally, out of frame
25-06-2015: 15.25 watered enclosure, put in frame, still in same position under rock
16.44 crawls out from under rock
17.04 exits frame
17.14 enters frame
17.18 inspects inactive *Pomatias*
17.32 withdraws into shell
18.08 becomes active
18.46 inspects inactive *Pomatias*
18.50 exits frame
(dark) 20.54 enters frame
21.06 withdraws into shell
22.14 becomes active
22.25 withdraws into shell
26-06-2015: 11.59 camera malfunctions