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# Host distribution, larviposition behaviour and generation time of *Sarcophaga penicillata* (Diptera: Sarcophagidae), a parasitoid of conical snails

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**Abstract**

Host characteristics, hyperparasitism, larviposition behaviour and generation time of *Sarcophaga penicillata* Villeneuve a parasitoid of the conical snail, *Cochlicella acuta* Müller (Mollusca:Helicidae) in southern France are described. Only snails which aestivated on vegetation were found to be parasitized by *S. penicillata*. *Sarcophaga penicillata* preferred *C. acuta* which were both significantly higher off the ground and larger in size than the population averages. Of the 2768 snails collected at the study site, 4% (112) were parasitized by *S. penicillata*, of which 36.6% (41) failed to emerge while 34% (38) were hyperparasitized. The predominant hyperparasite was *Novitzkyanus cryptogaster* Bouček (Hymenoptera: Pteromalidae) which was responsible for 79% (30) of the hyperparasitism. Larvipositing *S. penicillata* were observed to fabricate a hole in the epiphragm of resting snails in which they deposited one larva. After larviposition, female *S. penicillata* remained with the freshly parasitized snail a mean time $\pm$SE of $25.2 \pm 10.3$ min. It is suggested that this may be an adaptive response to avoid superparasitism. The mean generation time of *S. penicillata* when reared in the laboratory was 18 days, indicating that more than six generations are possible during summer in the south of France. During winter, *S. penicillata* enters diapause in the pupal stage within a host snail for up to 6 months. The possible utility of *S. penicillata* as a biological control agent of introduced conical snails is discussed.

## Introduction

The polymorphic, conical snail, *Cochlicella acuta* Müller, is found throughout the littoral zones of the Mediterranean and along the Atlantic coasts of France and Britain to the Outer Hebrides (Lewis, 1975). This species has been introduced into Australia where it is now a serious pest in both pastures and grain fields (Baker, 1986; Baker *et al.*, 1991). Since 1991, surveys of natural enemies of *C. acuta*, and other pest helicid snails such as *Cochlicella barbara* Linnaeus, *Theba pisana* Müller and *Cernuella virgata* da Costa have been carried out in the Mediterranean region. In preliminary collections of aestivating *C. acuta*, the sarcophagid fly *Sarcophaga penicillata* Villeneuve was found to parasitize this snail.

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The association between snails and sarcophagids has been known for a long time (Perris, 1850; Keilen, 1919, 1921). However, the nature of the relationship between snails and many sarcophagids is based largely on speculation, with few detailed studies having been carried out. Many sarcophagids are described as being reared from dead snails (Keilen, 1991; Beaver, 1986a, 1986b) with several described as being reared from live snails (Keilen, 1919, 1921; Askew, 1971). Keilen (1919) described the life history of the calliphorid *Melinda cognata* Meigen and determined that it was a true parasitoid of *Cernuella virgata* (as *Helicella virgata* da Costa). In the family Sarcophagidae, Keilen states that only *Sarcophaga filia* Pandellé can be assumed to be a parasitoid of snails (Keilen, 1921) based on the study of Rostand (1920) who discovered larvae attacking supposedly healthy snails in the genus *Helix*. *Sarcophaga nigriventris* Meigen has been quoted as a parasitoid of snails (Askew, 1971) based largely on a note by Bowell (1917) who reared it from dead and moribund *H. itala* (Linnaeus). Keilen (1921) in contrast, only reared this species from snails which had previously been killed by *M. cognata*. Recently, *Sarcophaga creuntata* Meigen (as *haemorrhoidalis* Fallén) along with several other sarcophagid species were reared from collections of *Theba pisana* and *C. virgata* in the south of France (Berner, 1973; Hopkins & Baker, in press) while *Sarcophaga pumila* Meigen was reared from the same species in Israel (Harpaz & Oseri, 1961). However, no direct evidence was given to indicate that any of these flies attack living snails. Other flies which also attack *C. acuta* may yet be found; a dipterous 'parasite' was observed by Aubertin *et al.* (1930) when they studied *C. acuta* populations on the south coast of England. They observed that this 'parasite' may have been responsible for the high mortality of *C. acuta* populations at two localities, although they never identified the fly.

This paper describes the larviposition behaviour and life history of *S. penicillata* in the laboratory and its host distribution in the field along with its associated hyperparasite fauna.

## Materials and methods

### *Field collections*

Collections were made of *C. acuta* from a fallow field on the Mediterranean coast near Palavas-les-Flots (Hérault, France) about 100 m from the sea during July and August, 1992. This site supports a large population of *C. acuta* ($210 \pm 89$ individuals/m$^2$) along with smaller numbers of *T. pisana*. During the summer, when collections were made, the snails aestivate either in clusters attached to vegetation or attached to the underside of stones. Vegetation and rocks with attached snails were collected and transported back to the laboratory, care being taken not to disturb the clusters of *C. acuta*. In the laboratory the height above ground level of the clusters on plants (taken as distance from base of stalk) was measured. Snails from each cluster on plants or beneath rocks were then removed, and the snails' size (as height from base of the mouth to the apex) measured to the nearest 0.2 mm. Snails were screened for evidence of attack by being placed on a photographic light table. Attacked snails were easily observed due to the lack of flesh at the apex, a pupa near the shell aperture (fig. 1) and occasionally a faecal plug produced by the fly, sealing the aperture of the snail shell.

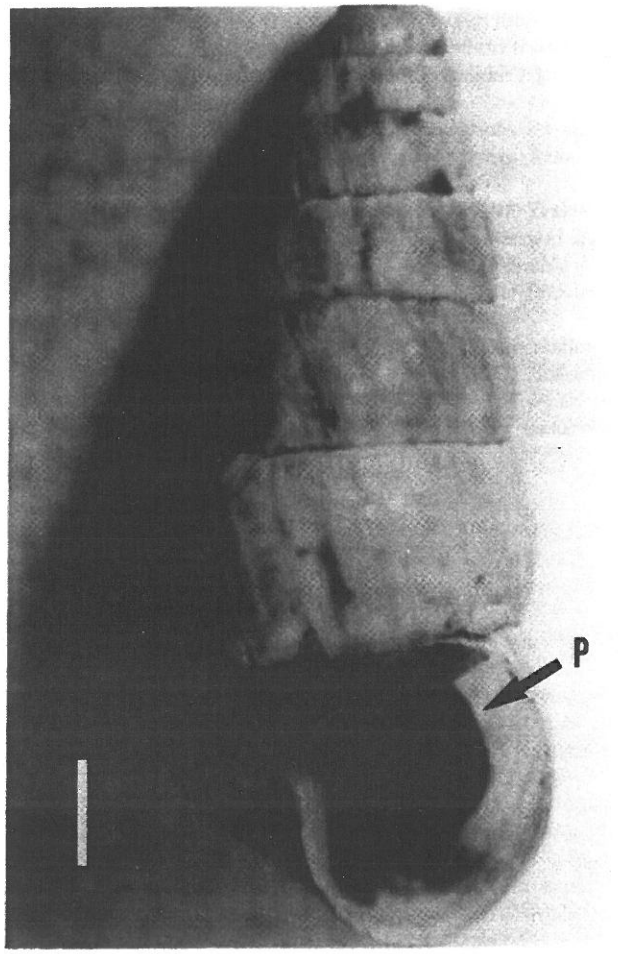


Fig. 1. Infected *Cochlicella acuta* showing position of the pupa (P) in relation to the aperture of the shell. Scale bar=1 mm.

Snails with a pupa or larva present were placed in two 6×3 cm vials sealed with fine mesh (0.1 mm). Snails were maintained under ambient light and temperature conditions. Hyperparasitoids and emerging flies were then collected. Flies which emerged were anaesthetized using $CO_2$ and their wing length measured using a binocular microscope. Over 2500 snails were examined.

### *Laboratory studies*

Cultures were started using *S. penicillata* which emerged from field-collected snails. Flies were maintained in male-female pairs in circular clear plastic rearing boxes (10 cm diameter, 13 cm high) with 20 live *C. acuta* and provided with a mixture of honey, yeast and skim milk powder along with several crushed snails. In these boxes it was easy to view both fly behaviour and snail attack since *C. acuta* tended to rest on the clear sides. Male-female pairs were observed for approximately 2 h daily (usually in the morning) for a period of at least 3 weeks after emergence. Times to mating and first larviposition were recorded when observed. *Sarcophaga penicillata* were always maintained with an excess of host snails. Total lifetime fecundity could not be determined due to the possibility that not all larvipositions are successful, though the number of snails

which were successfully attacked was determined for each female during its lifetime.

Preliminary observations identified three discrete behaviours occurring during a larviposition event after the initial contact with a potential host snail; initial probing of the snail with the proboscis and hole formation (if needed) in the host snail's epiphragm, larviposition, and post larviposition grooming, occasional probing and resting on the host snail. Each behaviour time was recorded for each of the 31 complete larviposition bouts (arrival of the fly on the snail to departure) that were observed. Interactions with other flies were also noted.

Immediately after larviposition, snails were numbered on the shell using a fine point marker pen (Scotch Brand). Time to pupation and adult eclosion were determined by observing attacked snails daily for evidence of pupa formation. Once pupae were observed snails were removed from the rearing boxes and placed in vials until adult emergence. On emergence, flies were anaesthetized, sexed and their wing length measured along with host snail height.

## Results

### *Distribution of parasitized snails*

Clustering snails aestivating beneath rocks were never found to be parasitized by *S. penicillata* and of the snails that were collected from vegetation only 4% were parasitized (table 1). The mean size of parasitized snails was significantly larger than the population average and parasitized snails tended to be higher off the ground than the population average.

### *Hyperparasitism of parasitized snails*

Of the 112 snails containing pupae that were collected, 36.6% (41) failed to emerge and 34% (38) were hyperparasitized. The main hyperparasite was the pteromalid *Novitzkyanus cryptogaster* Bouček which was responsible for 79% (30) of the hyperparasitism, with the eulophid *Barsyscapus* sp. (*daira* group) and the pteromalid *Norbanus* sp. parasitizing 15.7% (6) and 5.2% (2), respectively.

### *Larviposition behaviour*

Thirty-one larvipositions were observed and the results of subsequent dissection confirmed that only one larva was deposited per snail. During the larviposition sequence the longest mean time was spent by *S. penicillata* in the post larviposition phase at 25.2 min (SD=10.3 min, range, 5–65 min) followed by the initial landing, probing and hole making phase (5.3 min, SD=3.4, range, 0.5–24 min). Larviposition was relatively quick (2.6 min, SD=1.8, range, 0.2–8 min) and entailed the fly placing its abdomen either in the aperture of the snail or pointing it in the direction of the hole which it previously formed in the epiphragm of the snail. Larvae were deposited head first and if placed on the outside of the shell aperture moved directly forward, usually entering the snail's epiphragm within several seconds. Larvae which did not enter immediately would normally find the entrance to the snails interior after several minutes. Those which were unsuccessful however, died after several hours. Larvae which entered could be seen moving on the foot of the snail which usually contracted violently, dragging the larvae deep into the snail.

Of the 31 larvipositions observed, aggressive encounters occurred between adult female flies in 20 instances, all of which occurred in the post larviposition phase. Females which had larviposited and which were resting on the host snail were observed to wave their fore legs rapidly, occasionally tapping females which approached.

### *Generation time*

The mean overall generation time was relatively short at only 18 days (table 2) indicating that there may be up to six generations during the summer period. Fly larvae which pupated in snails during late October did not eclose until the following April, suggesting that the flies may diapause in the pupal stage during winter. During this period flies were maintained at 21°C under ambient light conditions. This suggests that light may be the determining factor in induction and completion of diapause in this fly.

The size of the emerging flies was found to be significantly correlated with the size of the snail host (fig. 2). There was no significant difference in the mean wing size ($\pm$SE) between females ($3.47 \pm 0.10$ mm) and males ($3.7 \pm 0.11$ mm, $F_{(39,1)}=2.63$, $P > 0.05$) which emerged in the laboratory.

## Discussion

While much anecdotal material has been written on the parasitism of snails by sarcophagids, remarkably only one previous study (Rostand, 1920) has observed this phenomenon. The present study indicates for only the second time that a sarcophagid can be a true parasitoid of terrestrial snails (as opposed to slugs, of which *Sarcophaga melanura* Meigen is a parasitoid according to Keilen (1921)). The larviposition habit of *S. penicillata* is very similar to that of *S. filia* described by Rostand (1920) who also found that only one larva per snail was deposited. Pupation of *S. filia* occurred within the host snail and the pupae were often hyperparasitized by hymenopterous parasitoids. The penetration of *S. penicillata* into the body of the host snail was not observed though it may be similar to *S. filia* in entering the pneumostome of the snail. Larval feeding is similar in that they both penetrate to the apex of the snail (at the hepatopancreas) and work towards the shell aperture. This characteristic enables the determination of snails which are parasitized by the lack of flesh at the apex. The relatively long post larviposition phase where females were seen to drive off other females may be an adaptive behaviour which reduces superparasitism. As each snail can only support one

Table 1. Comparison of mean ($\pm$SE) size and aestivation height above ground in parasitized and non parasitized *Cochlicella acuta*

| | Non parasitized | Parasitized | F[1,2768] | *P* |
|---|---|---|---|---|
| Size (mm) | $8.47 \pm 0.04$ | $10.81 \pm 0.31$ | 114.7 | $<0.001$ |
| Height above ground (cm) | $50.84 \pm 0.85$ | $64.39 \pm 3.5$ | 10.51 | $<0.01$ |

Table 2. Life history parameters (±SE) for *Sarcophaga penicillata* reared at 23°C and 30% relative humidity under natural light conditions.

| | | |
|---|---|---|
| Days from eclosion to mating | N=30 | 1.5±0.4 |
| Days from eclosion to first observed larviposition | N=21 | 4.2±1.5 |
| Days from larviposition to pupation | N=24 | 4.2±0.7 |
| Days from pupation to eclosion | N=36 | 8±2.1 |
| No. of snails successfully parasitized per female/day | N=30 | 0.7±0.4 |
| Longevity (days) | | |
| Males | N=30 | 36.6±4.3 |
| Females | N=30 | 37.5±4.5 |
| Mean generation time (days) | N=21 | 18±4 |

larva, it may be adaptive that the female waits and guards the host until the freshly deposited larva has entered the snail. Furthermore this may allow sufficient time for the larva to indicate its presence, perhaps by excreting a chemical marker which conspecifics could recognize. The occasional probing by females prior to larviposition may be to test for the presence of such markers.

The potential of sarcophagids for use as biological control agents of pest terrestrial snails has so far not been studied. Detailed host specificity testing is now being carried out for *S. penicillata*. If it proves to be host specific it may be a very safe and effective control agent, particularly if released from its hyperparasitoids. Its potential for several generations per summer also increases its attractiveness as it may have the ability to quickly increase in numbers in a relatively short period. In Australia, where *C. acuta* is a major agricultural problem, its habit of attacking snails aestivating on plants, makes it a particularly desirable agent. One of the main problems with *C. acuta* is its habit of aestivating on the ears and stalks of cereals where they clog machinery and contaminate grain during harvest. Flies which attacked these particular snails and which caused the snail shell to fall during the flies' emergence would help alleviate this contamination. Secondly, the life-cycle of *C. acuta* in the agricultural fields of South Australia is primarily biennial (Baker *et al.*, 1991). Large mature snails produce many offspring during the autumn to spring breeding season. This new generation predominates in pastures though many are killed if pastures are burnt prior to the following crop being sown. In winter crops the largest snails, while having mature gonads, produce few if any young. Instead they continue to grow until spring and reproduce the following season in the pasture phase. Since *S. penicillata* was found to prefer larger snails in the field it follows that the large non reproducing snails would be a preferred host, thus reducing the number of potentially breeding snails in the pasture phase. Finally, the recorded distribution of *S. penicillata* has to date only been in countries bordering the Mediterranean region (its type-locality is actually Palavas, Hérault, Soós & Papp, 1986) a region with a similar climate to that in South Australia where the parasitoid would be introduced.

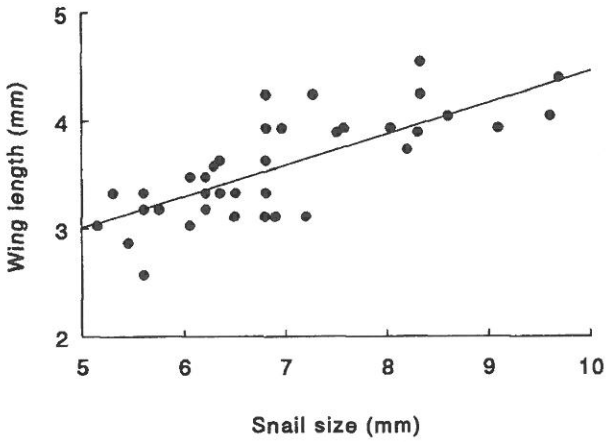


Fig. 2. Relationship between the wing length of *Sarcophaga penicillata* and the host snail from which it emerged. The relationship is best described by the equation: wing length (mm)=1.57+0.28 (snail height mm), $r^2=57.29$, $P < 0.001$.

Among the family Sarcophagidae other promising biological control agents of snails may also be found, especially in the genus *Heteronychia* most of which seem to have an association with snails. Within this genus, fly species in the subgenus *Ctenodasypygia* are particularly promising as potentially specific parasitoids. In this group more than half have been reared from snails. Apart from *S. penicillata*, *Sarcophaga fertoni* Villeneuve was reared from *Trochoidea simulata* (Ehrenberg) in Israel (J. Heller, pers. comm.) while both *Sarcophaga graeca* Rohdendorf and *Sarcophaga uncicurva* Pandellé were reared from *C. virgata* and *T. pisana* Müller, respectively (unpublished data). More studies are needed to confirm whether these sarcophagids are true parasitoids.

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