

water was sprinkled on the control box from a watering rose before applying 200 ml of the inoculum to the experimental box with the same rose. The viability of the nematode culture was checked using a McMaster counting cell, and applied at the dilution recommended by the manufacturers.

Activity was recorded from the time the slugs were introduced by a time-lapse videorecording on a National Panasonic AG6010 time lapse recorder with a 3 h tape running for 180 h and replayed at normal speed. Lighting was matched to daylength for the time of year, and recording was made with a National Panasonic WV-1850/B videocamera in infrared light from a safelight fitted with Wratten 87C infra-red filters. The arenas were watered daily, and recording continued until most of the experimental animals exhibited little activity. Tapes were replayed at normal speed and movements tracked on an acetate sheet placed on the monitor screen. The times of start and end of crawling, feeding and courtship were also recorded. Tracklengths were measured with a Graf-Bar 7 sonic digitizer (Bailey, 1994). The tendency for slugs to move within a small area, rather than move over the whole arena was measured by an index of recursion. This was the number of 1 cm squares entered more than once during the execution of a track, divided by the number of 1 cm squares which the final track occupies (Figure 1). Tracks which encountered a corner of the box were not included in the estimation.

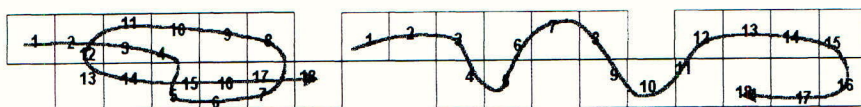


Figure 1. The index of recursion. Both trails pass through 18 squares, but that on the left passes through six of them twice: the index of recursion of the left hand trail is therefore $6/12$ or 50%, that of the right hand trail is $0/18$ or 0%.

RESULTS

In all trials, activity levels declined in both the experimental and control groups (Figure 2a). Measures of activity in experimental animals are therefore compared with those of the control group. In a late autumn trial with large individuals, locomotory movements had declined in the experimental group below those of the controls by the fourth night (figure 2a). In this trial, unusually the slugs continued activity for 11 days, although the swollen mantle symptomatic of parasitisation by *P. hermaphrodita* was observed by day 8. The distances moved each night after the first three nights were significantly less in the experimental group (Figure 3a). In one summer trial, the movements were again clearly reduced by the fourth night when larger individuals (mean weight $331 \pm \text{SD } 110$ mg) were used, but by the third night when using smaller individuals ($220 \pm \text{SD } 68$ mg) in another trial. In one trial all experimental animals, but none of the control group, were dead after the third night.

The speed of a slug can vary tremendously even on a single track. Before moving away, slugs usually extend the front of the body from side to side, then move slowly forward, but they can then change to a very rapid gait, until they meet an obstacle. A measure of the average speed throughout 24 h, ignoring local movements which result in a translocation of less than one body length, showed that parasitized slugs move more slowly (mean speed 0.91 cm/min) than uninfected slugs (1.27 cm/min) (Figure 3b).

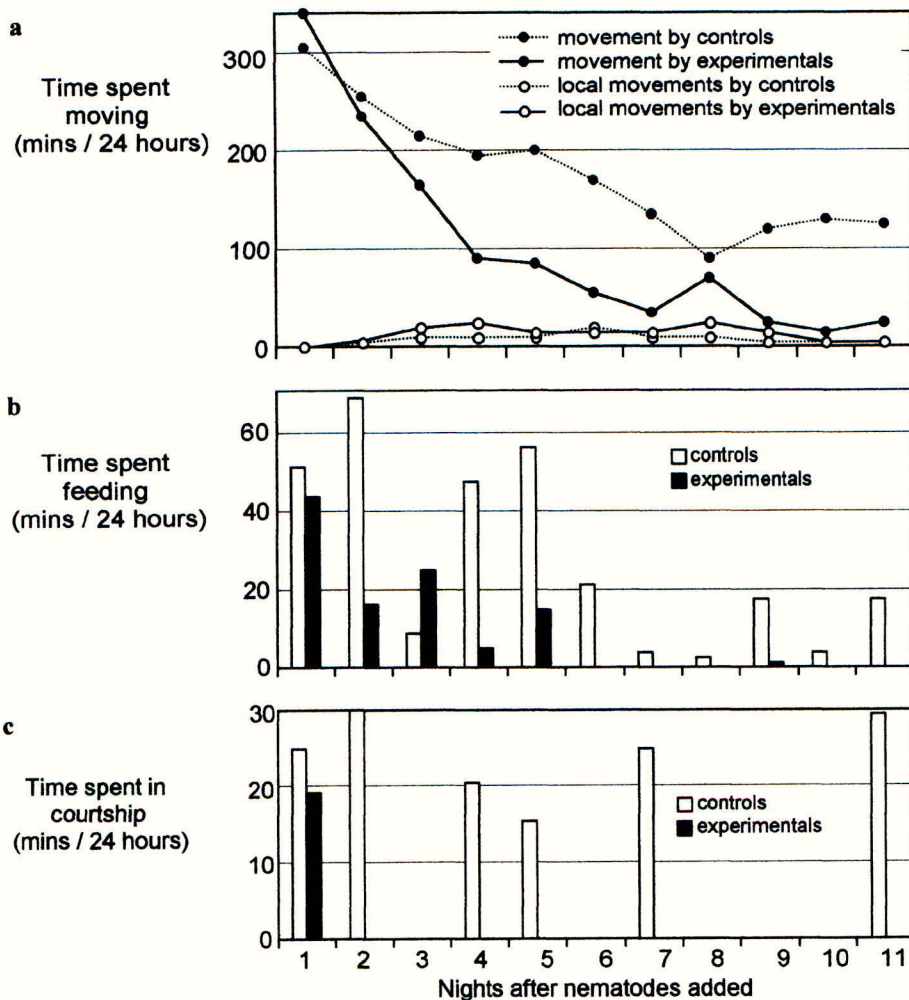


Figure 2. Mean time spent in each 24 hours in (a) locomotory and local movements, (b) feeding, and (c) courtship.

In addition to locomotory movements, small local movements were observed, in which the animal moved less than a body length, reversed its position, or contractions passed over the experimental animals (Figure 2a). These movements were mostly within the confines of the shelters, where most slugs remained throughout the daytime – and parasitized slugs throughout the night as well. More recursive excursions were also seen by parasitized slugs after four nights, although the data suitable for analysis (i.e. movements clear of the edges of the boxes) were too limited to yield a significant difference (Figure 3c).

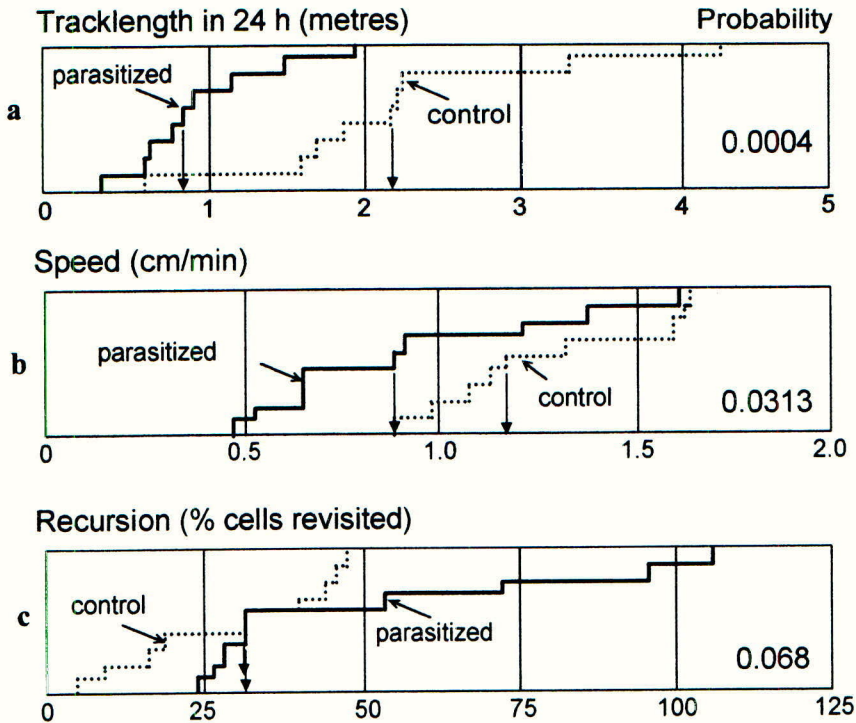


Figure 3. Track lengths (a), speeds (b) and indices of recursion (c) for parasitized and control slugs, on the fourth to eleventh night after adding nematodes. Median values are indicated by arrows. The probability that the two groups are not significantly different is given by the Wilcoxon-Mann-Whitney test.

In two trials, the activity of the experimental group was higher than that of the control group in the first 24 h after the nematodes were added, in a third trial activity of the experimental group was greater than that of the controls only for the first six hours. However, activity levels are so variable that it is uncertain if this represents a real effect or not.

Feeding and courtship decline earlier than locomotor activity (Figures 2b and c); although feeding was sometimes seen up to five nights after inoculation, this was uncommon, and no courtship was seen after the first night in any of the experimental groups.

A further distinction between parasitized and non-parasitized slugs is the timing of their activity patterns. The proportion of activity falling in each hour reveals a clear nocturnal behaviour in non-parasitized slugs with a peak at dusk and another around dawn (Figure 4). In contrast, parasitized slugs, at least those in a long or equinoctial night, show almost as much activity in the daytime as at night. However, in the case of parasitized slugs during the short nights of summer, there is a peak of activity at dawn.

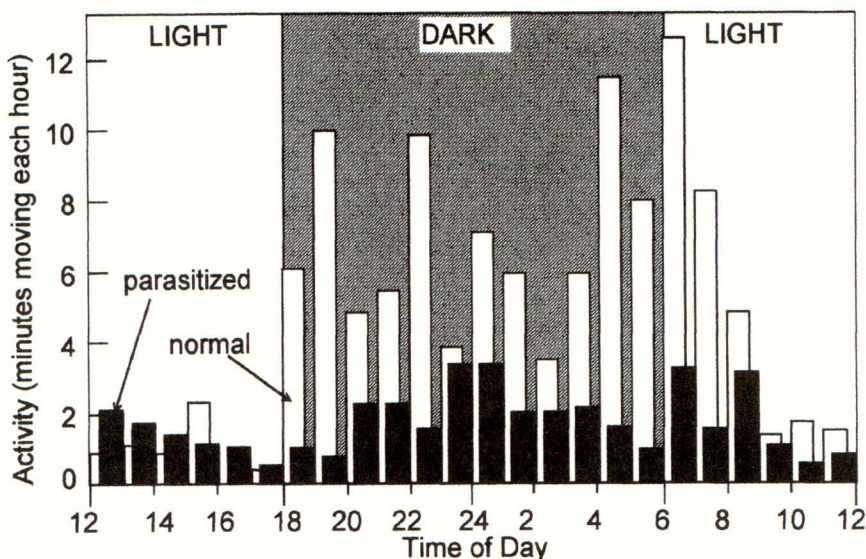


Figure 4. Timing of activity over 24 h averaged over days 4 to 11 after adding nematodes. Only 55% of activity of parasitized slugs falls in the nocturnal phase, compared to 75% in normal slugs.

DISCUSSION

The rapid decline in feeding supports Wilson, *et al.*'s (1994) suggestion that this is the primary means of crop protection offered by this method. The earlier onset of locomotor immobilization in smaller specimens is consistent with findings that the nematode is more effective against smaller species of slugs and snails.

The effects of parasitization on locomotion are a decrease in time spent moving and a reduction in speed of movement, which combine to reduce the distance travelled. This is accompanied by a relative increase in the number of local movements, with the slugs tending to confine themselves to shelters. The possible initial increase in activity has been suggested as due to irritation of the slug by the nematodes penetrating the mantle.

Even ignoring the possible increase in recursive tracks, the decreasing length of tracks will reduce the movement of parasitized slugs before they become immobilized and die, releasing the next generation of infective larvae. The mean distance of dispersion of a population of animals moving at random can be expressed by a simple random walk model (e.g. Bailey, 1989), using the track-length distances each night. The mean distance from the point of inoculation would be about 1.5 m after 5 days, changing little thereafter, whereas unparasitized slugs would be 2 metres away at that time, and 3.5 metres away after 11 days. Many slugs travel further than the mean distance of course, and it is also possible that unparasitized slugs encountering parasitized slugs and sharing their shelter, would spread the infection further,

producing a saltatory spread of infection. However, the present formulation acts inundatively, requiring repeated applications, which suggests that secondary infections are less effective than the initial application. The power of slugs to act as the dispersive agent for the parasite therefore appears weak.

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Hybridisation in Arionids: the rise of a super slug?

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ABSTRACT

The respiration of some large slug species was investigated using a closed respirometry set-up. The slugs were tested at temperatures of 4, 10, 15 and 20 °C. Preliminary data show that the respiration is fairly uniform amongst the slug species, except for *Arion ater*, which is native to Sweden, *Arion rufus*, which was introduced over a century ago, and a hybrid between *A. ater* and *A. lusitanicus*, the latter being a newcomer in the Swedish fauna. These species show a considerably higher respiration rate at high temperatures.

Neither *A. lusitanicus* nor *Limax maximus*, both introduced to the Swedish fauna, show any such adaptation. The difference in respiration rate at high temperatures may be an adaptation to the cold climate of Sweden. That the hybrid shows this adaptation may indicate the appearance of a "super slug".

INTRODUCTION

Respiration in the large arionid and limacid slugs has been studied on several occasions (e.g. Prior, *et al.*, 1983, Rising & Armitage, 1969). The main objective of the present study was to compare the autochthonous *Arion ater* (Linnaeus 1758), with the rapidly spreading alien *Arion lusitanicus* (Mabille 1868). As we have detected hybridisation between the two species (von Proschwitz, *et al.* in prep), the hybrid was also included in the study. To broaden the study we also included *Limax maximus* (Linnaeus 1758) and *Arion rufus* (Linnaeus 1758), both introduced into the Swedish fauna. We have used oxygen consumption to estimate the difference in activity at different temperatures. We postulate that the activity of the autochthonous *A. ater* can be considered a good strategy for the cold Swedish climate and that other species who have adapted well should show similar degrees of activity.

MATERIAL & METHODS

For the experiment we used a perspex respirometer chamber containing a fan (to ensure circulation), an oxygen electrode, a grid (to prevent the slugs from crawling into the fan and oxygen electrode or blocking the air inlet or outlet) and a damp piece of cloth (to ensure 100 % humidity in the chamber). Air was supplied by a pump and passed through a wash bottle before entering the chamber. The outlet air hose was submerged in water to indicate flow when the chamber was flushed with air.

Slugs were placed in the respiration chamber one at a time. The oxygen probe was calibrated to 100 % during the flushing period. The measurement was then started by clamping the in-going

hose from the air pump. A computer registered the oxygen consumption until a stable decrease in the chamber was achieved which, in some cases, took several hours.

The slope for oxygen consumption (% s⁻¹) was calculated from the raw data. The data were then transformed to ml/h by the following formula:

$$((V-m)*0.2094)*(((\text{slope}*3600)/100)*3600)$$

where V is the chamber volume in millilitres, m is slug mass in grams (assuming that volume equals mass), and the slope is in % s⁻¹.

All slugs were tested at 4, 10, 15 and 20° C. The slugs were always allowed to adjust to a new temperature for at least 24 hours.

Table 1. Individual slugs used in experiments. For individuals where weights and volumes changed during the experiment, mean values have been calculated and are marked *.

| Species | Collection locality | Weight (g) | Volume (ml) | Temperatures (°C) |
|----------------------------|---------------------|------------|-------------|-------------------|
| <i>Arion ater f. albus</i> | Särö, Sweden | 5.0 | 4 | 4, 10, 15, 20 |
| <i>Arion ater</i> | Floda, Sweden | 24.5* | 24 | 4, 10, 15, 20 |
| <i>Arion "ater"</i> | Galicía, Spain | 21.5 | 20 | 4, 10, 15, 20 |
| <i>Arion "hybrid"</i> | Floda, Sweden | 12.8* | 11.7* | 4, 10, 15 |
| <i>Arion "hybrid"</i> | Floda, Sweden | 19.6 | 15 | 20 |
| <i>Arion lusitanicus</i> | Floda, Sweden | 6.4 | 6 | 4, 10, 15, 20 |
| <i>Arion rufus</i> | Slöinge, Sweden | 15.9 | 15 | 4 |
| <i>Arion rufus</i> | Slöinge, Sweden | 11.4 | 12 | 10 |
| <i>Arion rufus</i> | Slöinge, Sweden | 8.8 | 9 | 15 |
| <i>Arion rufus</i> | Slöinge, Sweden | 14.7 | 20 | 20 |
| <i>Limax maximus</i> | Floda, Sweden | 12.9* | 12.7* | 4, 10, 15, 20 |
| <i>Limax maximus</i> | Floda, Sweden | 9.1 | 10 | 20 |
| <i>Limax maximus</i> | Galicía, Spain | 7.2 | 7 | 4, 10, 15, 20 |

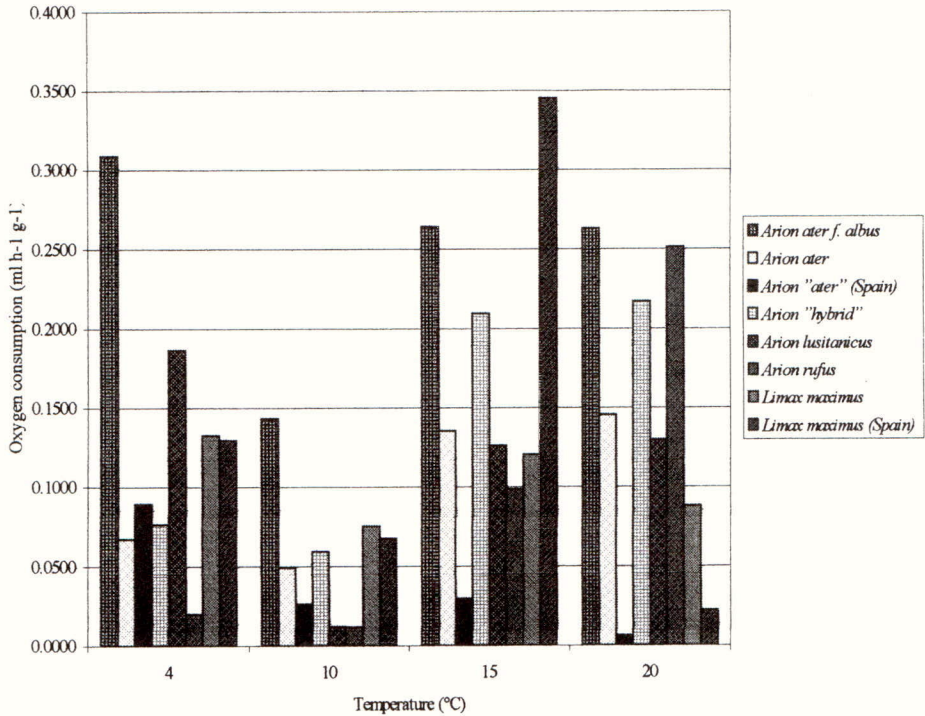


Figure 2. Oxygen consumption in the three arionid and the one limacid slugs of Figure 1, in relation to body mass.

RESULTS

Mean oxygen consumption for the slugs investigated is displayed in Figure 1. Oxygen consumption in relation to body mass is shown in Figure 2. The values in Figure 1 can be divided into two major groups: one with a marked difference in respiration between low and high temperatures (low and high respiration, respectively), the other one without. The former group consists of *A. ater*, *A. rufus* and the hybrid between *A. ater* and *A. lusitanicus*. The latter consist of all the other species investigated except *L. maximus*. When mass is taken into account, the picture changes, but both *A. rufus* and the hybrid still show a broad range in respiration.

DISCUSSION

The hypothesis behind our experiments is that the hybridisation we have observed between *A. ater* and *A. lusitanicus* in Sweden (von Proschwitz, *et al.* in prep.) is leading to the rise of a "Super Slug" which combines the aggressive feeding behaviour of *A. lusitanicus* (e.g. Briner & Frank, 1998; von Proschwitz, 1997) with *A. ater*'s tolerance for a temperate climate. Such a hybrid might compete successfully with *A. ater* and maybe also with *A. lusitanicus*.

Our results show that the autochthonous *A. ater* and the hybrid respond to changes in temperature quite differently compared with both *A. lusitanicus* and the Spanish *A. ater*. If we assume the behaviour of *A. ater* to be optimal for a cold climate, our conclusion is that *A. lusitanicus* still has not mastered the climate of the new temperature region. The hybrids, on the other hand, seem to show a response similar to that of the Swedish *A. ater*.

Also noteworthy is that the Middle European *A. rufus*, which was introduced into Sweden in the mid-19th century, seems to act like *A. ater*, while *L. maximus*, which started to become common in Sweden in the mid-20th century, does not appear to show this behaviour. The fact that these species belong to different genera does not necessarily contradict this suggestion (Rising & Armitage, 1969).

Following this line of argument, we could be watching the rise of a "Super Slug" that is liable to take over in many Swedish habitats. The question is, of course, what the respiration at different temperatures really tells us. Is it valid for measuring activity and, if so, what is good and bad respiration strategy? Dainton (1954), who used slug movement as a measure of activity, showed that lowered temperature induces increased activity. Roy (1962) used oxygen consumption to obtain similar results while both Nopp & Farahat (1967) and Rising & Armitage (1969) used oxygen consumption to show increased activity at higher temperature. Taking mass into account changed the picture somewhat (Figure 2), but there is evidence (Rising & Armitage, 1969) that there is no clear link between mass and oxygen consumption.

We conclude that our results support the theory that the hybrid between *Arion ater* and *Arion lusitanicus* has the potential of becoming a "super slug", i.e. combining the most favourable characters from both species, in one, highly competitive, hybrid form.

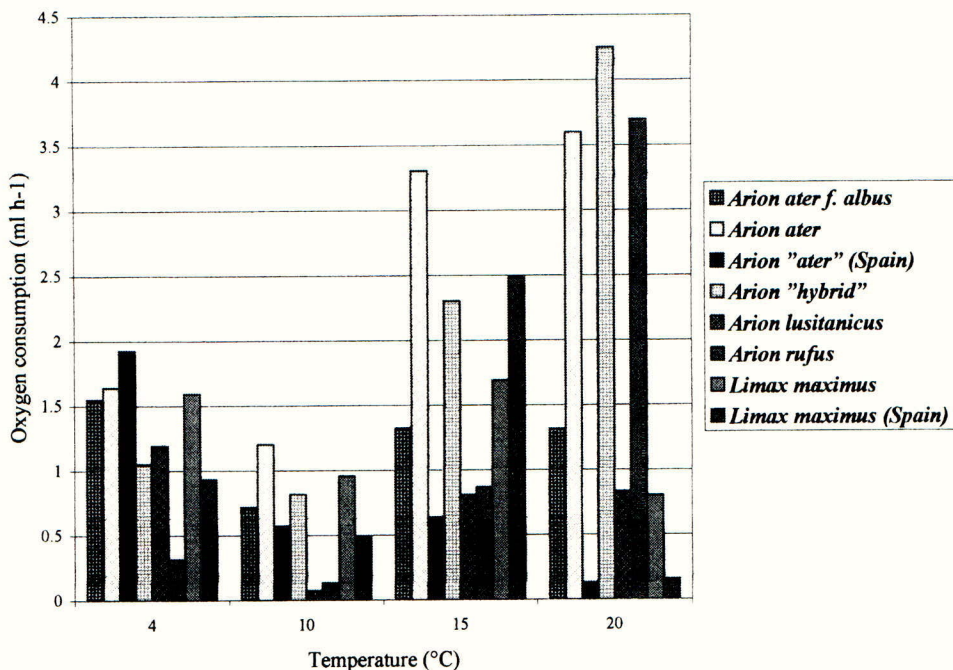


Figure 1. Oxygen consumption in three arionid and one limacid slugs. For *Arion ater*, three forms were used: the ordinary black form from Sweden, the albinistic form (*Arion ater f albus*) from Sweden and one dark specimen collected in Galicia, Spain. The latter may also be a hybrid, hence the quotation marks. *Arion "hybrid"* is what we consider to be a hybrid between *A. ater* and *A. lusitanicus*. The limacid group consists of specimens from Sweden and from Spain.

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SESSION 4

PROSPECTS FOR IMPROVED CONTROL

Chairman: Dr W O C Symondson
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Session Organiser: Professor D M Glen
Styloma Research and Consulting, Cheddar, UK

Development of a decision-aid system for the assessment of slug attack risk in arable crops.

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ABSTRACT

A decision-aid tool called "Activ+ Limaces" has been under test since 1999 and is now fully developed. Slug risk per plot is assessed by means of a climate model and recorded agronomic factors. Studies on a hundred or so agricultural plots have enabled the system to be developed and validated, first on autumn and then on spring crops. At present, the model is being run weekly with data from 170 weather stations during the active slug period in 170 sites spread over all areas of large-scale arable farming in France. The approach adopted and the degree of user satisfaction are presented.

INTRODUCTION

Slugs – and grey and black slugs in particular (*Deroceras reticulatum* (Müller) and *Arion hortensis* species aggregate, respectively) – are very important pests of oilseed rape, sunflowers, maize, wheat and beetroot.

Certain agricultural practices are known to limit slug populations: e.g., ploughing and harrowing, intercrop periods etc, (Ballanger & al., 1990; Glen *et al.*, 1990; Hommay 1995; Taupin & al., 1997). Even so, under present large-scale arable farming systems, it is proving very difficult to keep these pests under control and the problem is becoming very serious. During a year of especially heavy slug attack in France, as many as 5 million of the 12 million hectares given over to arable farming may be under molluscicide treatment.

In view of the scale of the problem, efforts were made to develop a decision-aid system to help farmers assess risk levels per plot and to estimate suitable levels of integrated molluscicide application. To this end, further data were needed in addition to those obtained from studies conducted in 1995-1997 (Chabert & al., 1997), especially as regards the assessment of slug damage. Field trials run all over France enabled the main agronomic factors favouring the development of slug populations to be identified.

The principle was to describe "slug risk" on the basis of climatic parameters, plot-specific agronomic factors, cultivation stage and slug capture levels. These data were weighted so as

to provide farmers with a risk-level per plot so as to enable them to estimate suitable levels of molluscicide application as part of integrated control strategies.

AGRONOMIC FACTOR ANALYSIS

Assessing the field effectiveness of the slug-risk model required tests to be set up in a variety of regions: i.e., the North, Centre and East of France. In 1995-97, some 40 plots had been studied (20 rape, 6 maize, 5 wheat, and 9 sunflower).

In 1999, 30 wheat and 30 rape plots were tested. In 2000 and 2001, the tool was developed for maize and sunflower crops, and in 2002 for beetroot. Other tests, not described here, were quickly abandoned for lack of slugs.

Two non-treated, non-adjacent areas of about 12x20 m each were defined within each test plot. Plants destroyed and plants attacked by slugs were recorded fortnightly for 2 months over 4 m x 2 m for wheat and 3 m x 10 m for rape.

In both non-treated test areas, six INRA-Bayer traps (50 cm x 50 cm damp canvass squares) were laid out in a 2 x 3 grid and lifted at each count. After counting, the traps were moved by at least 1 metre. In the case of wheat plots, traps could be laid ahead of sowing.

Slugs (usually grey or black) were identified and counted under each trap, and classified simply by size: small (<0.7 cm), medium (0.7-1.5 cm), or large (>1.5 cm). Outside of the non-treated test areas, the farmers continued with their normal slug control practices.

On the basis of the main agronomic data for the plot, a table was completed. Each criterion was allocated a certain number of points. The score for each plot gave the corresponding estimated risk level. These data were set *a-posteriori* against the trapping results for the plot and the damage as measured in comparison with a treated plot.

Table 1 gives, as an example, the 1999 findings on the effects of previous crop on slug populations and damage. It clearly emerges that the largest populations were found in wheat plots which had borne a previous crop of oilseed rape. Fallowing also favoured slug population growth. Infestation was lower in rape plots; but, as rape is especially sensitive to slug attack, damage could be considerable despite population levels being less than in plots where rape had been the previous crop.

In this study, the correlation coefficients (*r*) between slug capture and damage levels showed that:

- **for oilseed rape crops**, grey slug population level correlated with damage, whether in terms of plants missing ($r=0.60$) or of plants attacked ($r=0.91$). At the time of observed damage, grey slugs were predominant.
- **for wheat crops**, presence of black slugs correlated with the number of plants missing, as did the presence of grey slugs. There was a clear correlation between grey and black slug capture levels and the number of plants attacked. There was also a correlation between the numbers of grey and of black slugs.