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Candidate session number			
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Examination session (May or November)	MAY	Year	2015

Diploma Programme subject in which this extended essay is registered: BIOLOGY

(For an extended essay in the area of languages, state the language and whether it is group 1 or group 2.)

Title of the extended essay: factors affecting the frequency of
turn alternation in Porcellio scaber (Common
rough woodlouse).

Candidate's declaration

This declaration must be signed by the candidate; otherwise a mark of zero will be issued.

The extended essay I am submitting is my own work (apart from guidance allowed by the International Baccalaureate).

I have acknowledged each use of the words, graphics or ideas of another person, whether written, oral or visual.

I am aware that the word limit for all extended essays is 4000 words and that examiners are not required to read beyond this limit.

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Name of supervisor (CAPITAL letters) _____

Please comment, as appropriate, on the candidate's performance, the context in which the candidate undertook the research for the extended essay, any difficulties encountered and how these were overcome (see page 13 of the extended essay guide). The concluding interview (viva voce) may provide useful information. These comments can help the examiner award a level for criterion K (holistic judgment). Do not comment on any adverse personal circumstances that may have affected the candidate. If the amount of time spent with the candidate was zero, you must explain this, in particular how it was then possible to authenticate the essay as the candidate's own work. You may attach an additional sheet if there is insufficient space here.

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I have read the final version of the extended essay that will be submitted to the examiner.

To the best of my knowledge, the extended essay is the authentic work of the candidate.

As per the section entitled "Responsibilities of the Supervisor" in the EE guide, the recommended number of hours spent with candidates is between 3 and 5 hours. Schools will be contacted when the number of hours is left blank, or where 0 hours are stated and there lacks an explanation. Schools will also be contacted in the event that number of hours spent is significantly excessive compared to the recommendation.

I spent 4 hours with the candidate discussing the progress of the extended essay.

Supervisor's signature: _____ Date: 11-3-05

Assessment form (for examiner use only)

Candidate session number	
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Achievement level

Criteria	Examiner 1	maximum	Examiner 2	maximum	Examiner 3
A research question	2	2		2	
B introduction	2	2		2	
C investigation	4	4		4	
D knowledge and understanding	4	4		4	
E reasoned argument	4	4		4	
F analysis and evaluation	4	4		4	
G use of subject language	3	4		4	
H conclusion	2	2		2	
I formal presentation	4	4		4	
J abstract	2	2		2	
K holistic judgment	4	4		4	
Total out of 36	35				

Name of examiner 1: _____ Examiner number: _____
(CAPITAL letters)

Name of examiner 2: _____ Examiner number: _____
(CAPITAL letters)

Name of examiner 3: _____ Examiner number: _____
(CAPITAL letters)

IB Assessment Centre use only: B: _____

IB Assessment Centre use only: A: _____

As an enthusiastic zoologist and wanting to research animals _____ became motivated to study woodlice. This was based upon a historic research paper that she had discovered. With this topic decided she worked with characteristic interest and efficiency to establish her initial protocol and trials and moved quickly to intensive practical work where she introduced new variables. She was well aware of the delicate nature of the crustaceans with which she was working and was careful to follow appropriate guidelines to avoid harm to these organisms. She investigated the frequency of turn alternation in woodlouse after discovering that this behaviour could be due to either a learned behaviour or a sub-conscious mechanistic behaviour. Turning behaviour is a factor which is found in many different organisms for a range of reasons and in woodlice the direction a woodlouse turns is influenced by the direction of the previous turn and is linked directly to an innate survival mechanism. _____ investigated how size and therefore the age of the woodlice affected this turning behaviour, forming a hypothesis which suggested that if the older woodlice showed more of this behaviour then it was a learned response.

She worked entirely independently and with very little supervision on her project, building and designing her mazes and running her experiments out of school time. During her viva _____ was very clear that her sample size was her limiting factor in this investigation. This was due to particularly dry weather conditions which meant that the number of woodlice available were limited. However she also noted that her data matched very clearly published data and could therefore be seen to be relevant and worthwhile research. Her concise written style indicates her clear thinking and analytical manner of thinking and during her viva _____ showed that her analysis of written work by other scientists was excellent. What was also impressive was the background knowledge which she had acquired during her reading and her ability to apply and understand complex ideas. She was also able to apply her knowledge and link her research to other studies in different animals even linking this with studies of children. A possible criticism of this study could be that _____ has assumed a level of understanding of this topic above that of a lay person, however in her viva she was very clear in verbalising her ideas.

Overall this was a very well researched and very biological project, written in a very mature and scientific manner.



Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

Candidate name:

Candidate Number:

Subject: Biology

Word Count: 3994



Abstract

This investigation researched the effect of different factors upon the frequency with which alternate turning behaviour was displayed by the terrestrial isopods *Porcellio scaber*. The specific research question answered was: 'Does the length of the *Porcellio scaber* individual (measured from head to telson, excluding antennae) affect the frequency with which alternate turning behaviour is displayed within an 'H' shaped maze?'. This was investigated using 35 naïve *P. scaber* of various size categories within an 'H' shaped maze, which forced them to turn in a specific direction before giving them a free choice point at a 'T' junction. An 'alternate turn' was recorded if the woodlouse turned in the opposite direction to the previous forced turn.

Two preliminary investigations were undertaken, the first involving 50 naïve *P. scaber* of assorted sizes using the same apparatus in order to show the presence of alternate turning behaviour within the experimental population. The second preliminary investigation aimed to discover whether *P. scaber* and *Armadillidium vulgare* (another woodlouse species) showed alternate turning behaviour to the same extent, in order to determine whether valid comparisons between research on both species could be compared.

The preliminary investigations concluded that alternate turning behaviour was present in the sample of woodlice used and that *A. vulgare* and *P. scaber* showed alternate turning behaviour to the same extent, meaning that valid comparisons between research on the two species could be made. The investigation of the research question revealed a Pearson's product-moment correlation coefficient of 0 between length of woodlouse individual and frequency with which alternate turning behaviour is displayed showing that there was no correlation between the two factors. This conclusion allows for the evaluation of other pieces of academic research and suggests that alternate turning behaviour is due to a subconscious mechanistic process rather than a form of 'learning' behaviour.

Word Count : 299

Not clear what the line of argument is.

Longer = older = more likely to have learned behaviour?

Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

Acknowledgements

I would like to thank my supervisor, _____ for her guidance and advice during the research and writing of this essay. I would also like to thank _____ for her additional support and advice. I would further like to thank my family for the loans of materials used during the investigation as well as their ongoing tolerance and support, especially with respect to their permission to use the kitchen as a research facility.



Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

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Introduction

Research question:

Does the length of the *Porcellio scaber* individual (measured from head to telson, excluding antennae) affect the frequency with which alternate turning behaviour is displayed within an 'H' shaped maze?

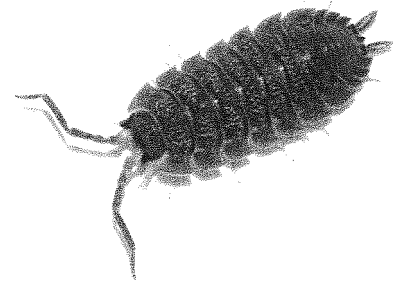
In order to answer this question two further preliminary experiments were carried out to determine whether:

- The specific population of naïve *Porcellio scaber* individuals used in this study displays alternate turning behaviour.
- Members of the *P.scaber* population and the *Armadillidium vulgare* population display the same frequency of alternate turning behaviour.

These investigations enabled comparison with previous studies on alternate turning behaviour across woodlice species.

Figure 1 *Porcellio scaber* (Murray 2005)

Porcellio scaber, (common rough woodlice), are terrestrial crustaceans of order isopoda (Riggio 2013). The species is identifiable from similar species of woodlouse by its inability to roll into a ball, its rough texture and lack of any striped marking, as well as its size and lack of characteristic long tails (<http://www.nhm.ac.uk/nature-online/life/other-invertebrates/walking-with-woodlice/identification.html> no



date). Members of the species can grow to a maximum of 17mm in length (Riggio 2013) although the maximum length of individuals used within this investigation was 14mm. Woodlice increase in size between their birth at which they are approximately 2mm until they reach their maximum size through a series of irregular moults of their exoskeleton throughout their adult life (Capinera 2008).

P. scaber individuals have 14 legs, two attached to each of the seven body segments as well as two pairs of antennae arranged as one long and one short pair, they are bilaterally symmetrical (Riggio 2013). Similarly to other crustaceans, *P. scaber* have gills as part of their respiratory system (Donaldson Becker 1936) alongside mechanisms for breathing air in the form of pseudolungs situated on their abdomen (Riggio 2013). Damp living conditions are necessitated by the presence of these gills.

Like many other species of woodlouse, *P.scaber* prefer to live in aggregated groups (Broly et al. 2012) in dark, damp areas and frequently inhabit grassland, woodland and coastal habitats as well as domestic gardens (Harding and Sutton 1985). They feed on decomposing matter such as decaying wood, leaves and fungi as well as the bacteria living upon these items (Broly et al 2012). They protect themselves from desiccation and predation by living under wood and rocks.

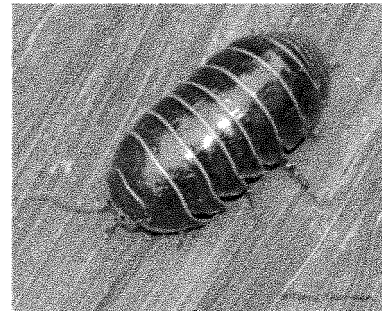
Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

P. scaber is a species of woodlouse originally native solely to mainland Europe but which now populates all continents barring Antarctica (Riggio 2013) causing it to be described as: “probably the most successful woodlouse colonizer” (*Woodlice in Britain and Ireland: Distribution and Habitat* pg.94). It is listed in some areas of the world as an invasive species (Global Invasive Species Database 2009) specifically as a threat to native invertebrates on Gough and Marion Islands.

P. scaber are known to exhibit alternate turning (or correcting) behaviour (Hughes 1966). This behaviour is present in many other invertebrate species including Boxelder bugs (*Leptocoris trivittatus*) (Dingle 1961), and involves individuals making a turn in an opposite direction to one which they had been forced to make immediately prior. For example, an individual forced to make a left turn to avoid an obstacle will then make a right turn at the next available ‘free turn’ opportunity such as a ‘T’ junction. Studies have shown the frequency of this behaviour to be increased by placing the woodlice in unfavourable conditions such as desiccation (Hughes 1967) and the presence of predatory animals, in particular the spider *Dysdera crocata* (Carbines, Dennis and Jackson 1992). This has led to the suggestion that the behaviour is an adaptation intended to enable an individual woodlouse to escape an unfavourable situation quickly (Hughes 1967) as it enables the animal to remain travelling in as close to a straight line as possible whilst avoiding obstacles .

Figure 2 *Armadillidium vulgare* (Thormin 2010)

There is however some discussion over how the woodlice develop this behaviour. *Armadillidium vulgare*, another woodlouse species has been shown during investigations to increase “variant patterns” (Moriyama 1999 pg 154) including escaping from the apparatus as an investigation progressed, when tested through consecutive ‘T’ mazes in order to escape from desiccation. The variation between different individuals adaption to the scenario is argued to be due to “the bugs’ own decision making” (Moriyama 1999 pg. 153) arguing that they are capable of conscious decision and learning over time (Moriyama 1999).



However it has also been proposed that woodlice follow this pattern of behaviour due to the theory of bilaterally asymmetrical leg movements (BALM) (Hughes 1985) which states that woodlice place more stress on one side of the body when turning in a particular direction and so redresses this by turning in the opposite direction at the nearest possible opportunity.

This investigation aims to provide evidence for either one of these theories by answering the research question stated above. This will show whether variation between woodlouse size (and therefore age) suggests woodlice adopt alternate turning behaviour over time or whether individuals of all ages display it to the same extent. If longer individuals show a higher frequency of alternate turning behaviour, it would suggest that some level of learning had taken place throughout the woodlouse’s lifespan. However, if all individuals display the behaviour to the same level it would suggest a more ubiquitous, biologically mechanistic origin to the behaviour. It is hypothesised that longer (and therefore older) woodlice may display alternate turning behaviour with a greater frequency, either because the behaviour is learnt over time or because woodlice individuals that do

Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

not display the behaviour are less adept at escaping disadvantageous situations and hence are more likely to die before growing to a longer length. This investigation aimed to indicate whether learning behaviours could be present in invertebrates such as *P. scaber* or whether such behaviours are likely to be due to instinctive, subconscious controls.

The supplementary investigations aimed to show whether it is possible:

- To replicate the results of Hughes' (1966) experiment and show a prevalence of alternate turning behaviour within the specific population of *P. scaber* used in this investigation.

It is hypothesised that the specific sample of woodlice used in the investigation will show alternate turning behaviour, therefore confirming the presence of the behaviour within the experimental population as well as adding validity to Hughes' (1966) experiment.

- To make valid comparisons between alternate turning behaviour patterns in *A. vulgare* and *P. scaber*.

This will show whether observations and theories made regarding alternate turning behaviour in *A. vulgare* can be transferred to *P. scaber* and therefore whether the observations of Moriyama (1999) can be applied to *P. scaber* and used as an explanation for the behaviour. It is hypothesised that both species will show alternate turning behaviour to the same extent.

Investigations

Care of Organism

During these experiments, whilst not actively involved in investigation, woodlice were kept in small groups in plastic trays containing leaf litter and soil regularly moistened with water, which gave the subjects access to darkened areas. They were fed carrot and potato. Conditions were further kept damp, cool and dark by placing a damp towel over their containers. This aimed to reduce stress by keeping the woodlice in as close to natural conditions as possible. To further reduce stress, woodlice were handled using soft plastic spoons which prevented damage to their bodies. All woodlice were released back to their site of capture after two days.

Initial investigation 1

This investigation seeks to recreate the results of Hughes (1966) and show that alternate turning behaviour is present within this population of woodlice.

clear ideas / good
line of argument.

Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

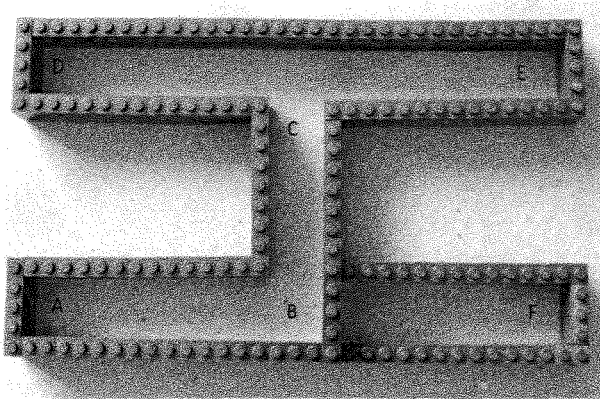


Figure 3

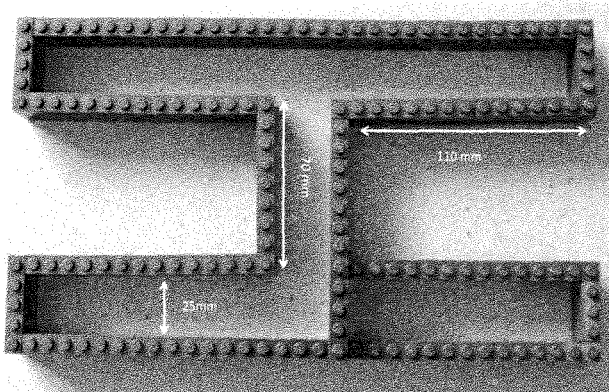


Figure 4

Equipment

- 1x 'H' shaped maze (Figures 3 and 4).
- 50 x naive *Porcellio scaber* (assorted lengths).
- 2 x plastic spoons (for handling *P. scaber*).

Method

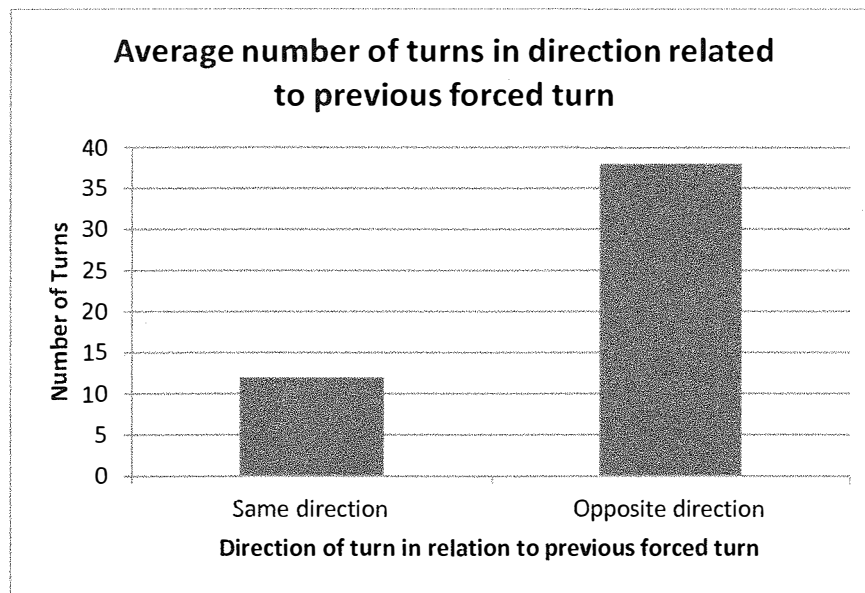
1. Place woodlouse in the maze at point A (Figure 3)
2. As the woodlouse progresses through the maze, it will be forced to turn left at point B as access towards point F is blocked.
3. Woodlouse will arrive at point C
4. If woodlouse turns left again, towards point D a turn in 'same direction' will be recorded
5. If woodlouse turns towards point E a turn in 'opposite direction' will be recorded.
6. Remove the woodlouse from the maze.
7. Place the next woodlouse in the maze, alternate starting point from point A and point F each time (ensuring to move the block to the other side of position B). This ensures the woodlice turning do so because of the direction, rather than a preference for points D or E. Ensure recording of 'opposite' or 'same' direction turn is taken from the opposite position, e.g. if starting at point F, a turn to point D will be recorded as 'opposite' direction.
8. Run all 50 woodlice through the maze 3 times.
9. Calculate an average of results.

Results

Table 1 – Results of Preliminary Investigation1

	Trial 1		Trial 2		Trial 3		Average	
	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction
No. of turns	13	37	15	35	7	43	12	38

Graph 1 - Results of initial investigation1



Analysis

These results show that alternate turning behaviour is present within this population of *P. scaber* and show that the results are similar to those recorded by previous studies. On average this sample of woodlice made approximately 3.2 (2sf) (table 1) more turns in the opposite direction to the force turn than the same direction as the forced turn. This compares to the data of Hughes 1966 who found that woodlice in a maze with a distance of 60 mm between the forced turn and choice turn made 1.7 (2sf) times more turns in the opposite direction to the forced turn than the same direction.

The disparity in these result could be a result of a difference in sample size (Hughes 1966 trialled 200 woodlice, 4 times more than used in this investigation), or environmental conditions on the day, which could have led to desiccation which has been shown to affect the frequency of alternate turning behaviour (Hughes 1967). Also the maze used in this investigation had a distance between

Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

turns of 70mm and as distance between forced turn and choice point has been shown to influence the frequency of alternate turns (Hughes 1967), this could have affected the result.

Initial Investigation 2

This investigation was intended to show whether alternate turning behaviours are displayed with the same frequency between *A. vulgare* and *P. scaber* in an attempt to investigate whether it is valid to compare experimental results and theories involving alternate turning behaviour between the two species.

Equipment

- 1 x 'H' shaped maze (see Figure 3)
- 6 x naïve *Porcellio scaber*
- 6 x naïve *Armadillidium vulgare*
- 2 x plastic spoons (for handling woodlice)

Method

1. Place an individual *P. scaber* in the maze at point A (Figure 3).
2. As the woodlouse progresses through the maze, it will be forced to turn left at point B as access towards point F is blocked.
3. Woodlouse will arrive at point C.
4. If woodlouse turns left again, towards point D a turn in 'same direction' will be recorded
5. If woodlouse turns towards point E a turn in 'opposite direction' will be recorded.
6. Remove woodlouse from the maze.
7. Repeat with other *P. scaber* individuals so that each woodlouse is run through the maze 3 times, alternate starting point from point A and point F each time (ensuring to move the block to the other side of position B. This ensures the woodlice turning do so because of the direction rather than a preference for points D or E. Ensure recording of 'opposite' or 'same' direction turn is taken from the opposite position, e.g. if starting at point F, a turn to point D will be recorded as 'opposite' direction.
8. Repeat with all 6 woodlice 3 times and record the results.
9. Repeat steps 1-7 using *A. vulgare*.
10. Calculate an average for both sets of results.

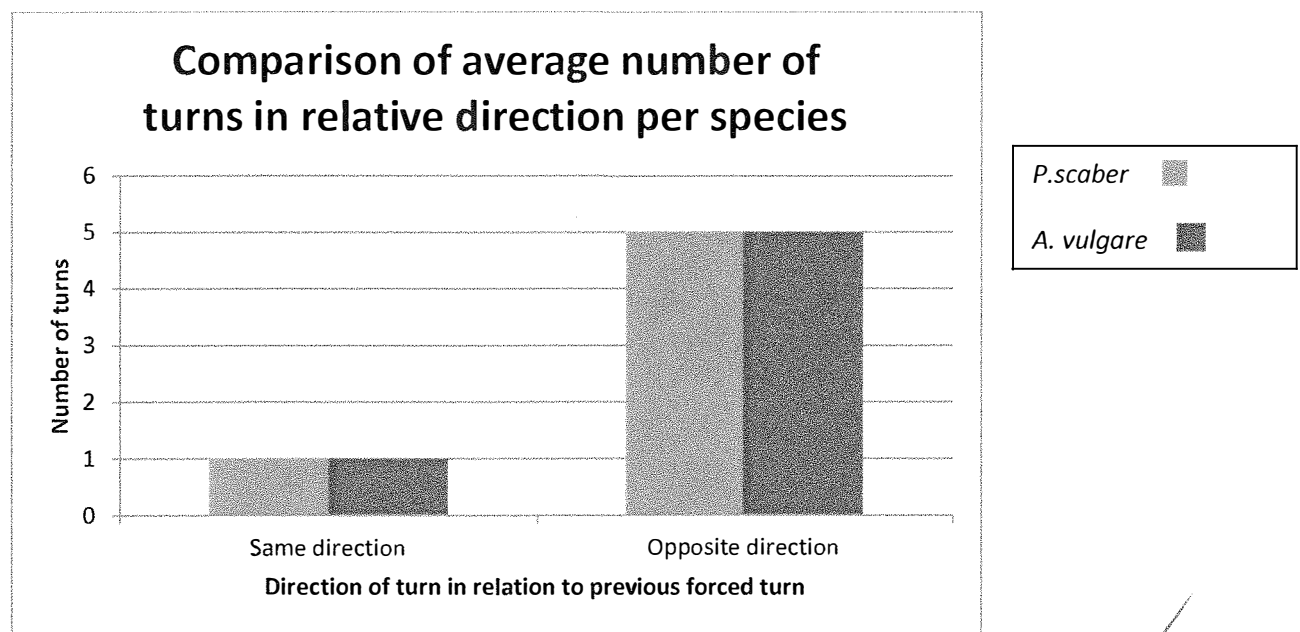
Results

Table 2 – Results of Initial Investigation 2

Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

Woodlouse species	Trial 1		Trial 2		Trial 3		Average	
	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction
<i>P. scaber</i>	1	5	0	6	2	4	1	5
<i>A. vulgare</i>	1	5	1	5	1	5	1	5

Graph 2 - Results of Initial Investigation2



Analysis

This investigation shows that individuals of *P. scaber* and *A. vulgare* exhibit the same frequency of alternate turning behaviour within maze. This implies that with respect to alternate turning behaviour, valid comparisons can be drawn between the two species and that subsequently they are likely to have the same underlying cause for their behaviour. This suggests that the investigation by Moriyama (1999) could be applied to members of *P. scaber*.

On the other hand, although individuals from *P. scaber* and *A. vulgare* exhibited the same behaviours it does not necessarily follow that they do so for the same reasons and this must be considered when interpreting studies for one species with implications for the other.

Investigation into Research Question

This investigation aimed to show whether alternate turning behaviour alters in frequency between *P. scaber* individuals of different sizes in an attempt to determine whether it is a behaviour which is acquired as they grow or whether it is a behaviour exhibited ubiquitously regardless of age. This will attempt to provide evidence for the debate on whether woodlice display this behaviour as a result of 'learning' as Moriyama (1999) argues or the more mechanistic BALM as Hughes (1985) argues.

Equipment

- 1 x 'H' shaped maze (see Figure 3)
- 35 x *Porcellio scaber*.
- 1 x ruler (15 cm) (+/- 0.5 mm)
- 2 x plastic spoons (for handling *P. scaber*)



Method

1. Measure length of all *P. scaber* individuals from head to telson (excluding antennae) using ruler and hence sort into size categories (4-6cm, 6-8 cm, 8-10cm, 10-12 cm, 12-14cm) so that 7 individual woodlice are in each category.
2. Take a woodlouse from the smallest size category (4-6 mm).
3. Place individual in the maze at point A (Figure 3).
4. As the woodlouse progresses through the maze, it will be forced to turn left at point B as access towards point F is blocked.
5. Woodlouse will arrive at point C.
6. If woodlouse turns left again, towards point D a turn in 'same direction' will be recorded.
7. If woodlouse turns towards point E a turn in 'opposite direction' will be recorded.
8. Repeat with other individuals from that size category so that each woodlouse is run through the maze 3 times.
9. Repeat steps 3- 8 with all other size categories of woodlouse.
10. An average will be calculated of the number of turns in 'opposite direction' and 'same direction' made for each size category.

Results

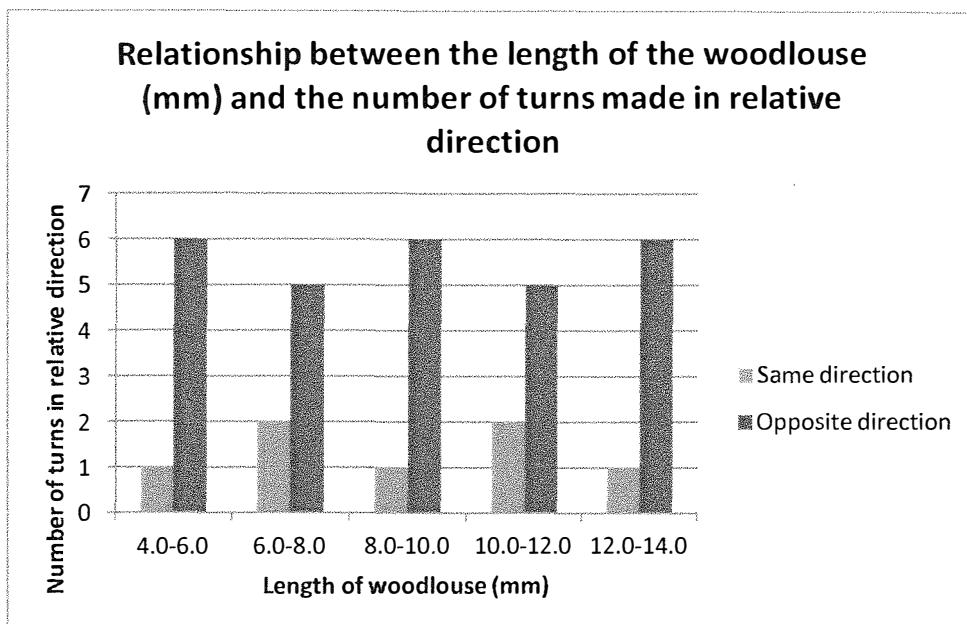


Factors affecting the frequency of turn alternation in *Porcellio scaber* (Common rough woodlouse)

Table 3 – Results of Investigation into Research Question

		Trial 1		Trial 2		Trial 3		Average (1 sf)	
No. of turns	Size of woodlice (mm) (+/- 0.5 mm)	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction	Same direction	Opposite direction
	4-6	1	6	1	6	1	6	1	6
	6-8	2	5	3	4	1	6	2	5
	8-10	0	7	1	6	2	5	1	6
	10-12	1	6	3	4	2	5	2	5
	12-14	1	6	1	6	0	7	1	6

Graph 3 –Results of Investigation into Research Question



Analysis

These results gave a Pearson's product-moment correlation coefficient of 0, showing that there was no correlation between the length of the woodlouse's body and the frequency with which alternate

It would be useful to be able to see the calculation!

turning behaviour was displayed. The results also show that there was no increase in frequency of alternate turning behaviour across the three trials within the different size categories of the woodlice. This suggests that the woodlice have not learnt alternate turning behaviour throughout their lifetime as then it would be expected that larger woodlice would exhibit more alternation within their turns. The results also suggest that the woodlice did not learn alternate turning behaviour as the investigation progressed as in that case the number of turns in 'opposite direction' would have increased between trial 1 and trial 3.

This suggests a lack of learning behaviour as suggested by Moriyama (1999) and as observations during the investigation did not show any increase in "variant patterns" (Moriyama 1999 pg 154) as the investigation progressed it suggests that those observed by Moriyama (1999) on *A. vulgare* may not be a behaviour which is replicated in *P. scaber*. These results therefore seem to support the BALM theory of Hughes (1985) as they suggest a reason for the behaviour which is common to all woodlice regardless of shape and age.

Discussion

The behavioural adaptation of alternate turning behaviour is present within multiple arthropod species (Hughes 1985) and as its frequency increases when faced with disadvantageous environmental conditions (Hughes 1967) or the presence of a predator (Carbines, Dennis and Jackson 1992) it is likely to have developed as behaviour in order to permit efficient escape of the individual from an otherwise dangerous situation in order to reach a more advantageous one (Hughes 1967 and 1978, cited in Hughes 1985). As this investigation shows that there is no increase in the frequency of this behaviour with relation to body length (and therefore age of the woodlouse) it seems unlikely that this behaviour is due to any kind of social or individual learning as this would be expected to progress with age. The result also suggest that it is unlikely that short term learning behaviours used as there is no relationship between the trial number and the reaction of the woodlice. This seems to contrast with the evidence of Moriyama (1999) as there was a little change in woodlouse behaviour over the course of the experiment. However it could be argued contrary to this that there was no incentive during the experiments investigated in this paper for the individual woodlouse to turn in either direction as both turn directions resulted in the same outcome - a dead end and subsequent removal from the maze.

It therefore seems likely that bilaterally asymmetrical leg movements (BALM) (Hughes 1985) are responsible for this action within woodlice. These movements are described as the "mechanistic basis" (Hughes 1985 pg. 259) for alternate turning (or correcting) behaviour and describe the process by which a forced turn stimulates the legs on one side of the woodlouse's body to a greater extent than on the other side as they have further to walk. For example a turn to the left would stimulate to a greater extent the outer set of legs on the right hand side of the body. This then causes the woodlouse to favour a turn in the opposite direction at the next available 'choice point' in order to favour the legs on the other side of the body which have experienced less stimulation (Hughes 1985).

Another behaviour which could be responsible for the prevalence of alternate turning behaviour is the thigmotactic behaviour displayed by woodlice (Pardi and Papi 1961, cited in Hughes

1985). Thigmotaxic behaviour causes woodlice to remain very close to or in contact with the wall of the maze during the course of the investigation. From my observations during these investigations woodlice tended to leave point A (see Figure 3) run in a straight line until they hit the wall at point B and subsequently follow that wall for the rest of the maze until they reach point E. This could therefore be seen as the explanation for the alternate turns made. However, Hughes (1985) argues that this wall following behaviour could just as easily be the result of the implications of BALM as he says that woodlice "travel closer to the wall because of greater locomotor force of the inner legs which were more 'rested' during negotiation of the forced turn(s)" (Hughes 1985 pg 259).

The argument that alternate turning behaviour has its basis in a mechanistic biological behaviour rather than any short term memory or decision making element is supported by the fact that woodlice do not display alternate turning behaviour when they experience a passive rather than forced turn subsequent to a choice point (Beale and Webster 1971). This suggests that without the mechanical movement of the legs of the woodlouse navigating the forced turn of the maze the behaviour is absent and that consequently the physical movement of the legs does play a key role in the displaying of alternate turning behaviour. This view is further supported by further experimentation which shows that when placed in a maze with one set of legs on a moving track (therefore experience greater stimulation) the woodlouse is likely to turn in the direction of the side of the legs that were on the moving track (Beale and Webster 1971). It is suggested that this is to compensate for the increased activity on the one side of the body by forcing the side furthest away from the turn to do more work during the turn. This evidence is described as suggesting "differential activity of the left and right legs is a sufficient condition for producing a strong bias in the direction of the subsequent free turn" (Beale and Webster 1971 pg 356).

However, it has been shown that *P. scaber* are capable of some learning behaviour within mazes over time in response to the reward stimulus of damp after having been previously kept in desiccated conditions (Morrow and Smithson 1969). This suggests that *P. scaber* have the capacity, at least in the short term, to develop learning behaviours, although this would seem to contradict the conclusion of this investigation. This might suggest that learning behaviours in invertebrates such as *P. scaber* are present but are not used over long periods of time to control patterns of behaviour such as alternate turning. However, the experiment used to show learning relates to the actions of an individual *P. scaber* learning from their own experience rather than social learning between different members of the same species. This might not be expected with a behaviour such as alternate turning as, using the example of escaping predation, if an individual does not use alternate turning behaviour and is therefore captured by a predator they are likely to be eaten and therefore will be unable to implement any learned behaviour gained from that experience.

It is also worth evaluating the experimental procedures undertaken during the investigations carried out in this essay. One of the main design errors with these investigations was the small sample size of *P. scaber* individuals tested. For example in the experiment involving the categorisation by length, once the individuals had been subdivided into categories relating to size there were 7 individuals per category which may not have been sufficient to show any trend which may have been present. This could have been improved in a laboratory setting by breeding woodlice specifically for the experiment and so ensuring a ready supply of them or, alternatively, using a wider area from which to collect wild woodlice. This could have prevented any trend in woodlouse behaviour being made clear during the investigations.

A further source of error may have been not using a wide enough range of size categories of woodlouse. When *P. scaber* individuals first emerge from the brood pouch they are considerably smaller than 4mm (Capiner 2008). However it was very difficult to find and handle woodlice smaller than this as well as being very difficult to determine whether they were *P. scaber*. The largest woodlice used within this investigation had a maximum length of 14mm, *P. scaber* are reported to grow up to 17mm (<http://www.nhm.ac.uk/nature-online/life/other-invertebrates/walking-with-woodlice/identification.html> no date) but due to a limited number of specimens being located within this population with a body length of more than 14mm, this size category was not trialled. In order to resolve all issues involving the availability of woodlice in different size categories they could be bred in captivity to ensure a ready supply of all stages of development.

Conclusion

1. As predicted within the hypothesis, this sample of the population of woodlice did display alternate turning behaviour. This confirms that members of the species *P. scaber* do exhibit this behaviour and that this specific sample used in the investigation do display this behaviour.
2. In agreement with the hypothesis, *A. vulgare* and *P. scaber* showed the same frequency of alternate turning behaviour, with neither showing any change in trend of alternate turning behaviour being displayed as the investigation progressed.
3. Contrary to the hypothesis, there is no relationship between the length of the *P. scaber* individual and the frequency with which alternate turning behaviour was displayed. Similarly, there was no relationship between the number of times the individual woodlouse had experienced the maze and the frequency of alternate turning behaviour, as the number of alternate turns did not progress as the number of trials increased.

These investigations appear to contribute to the overall academic debate favouring a mechanistic approach to the origin of alternate turning behaviour, such as BALM (Hughes 1985). This is because they show that the frequency alternate turning behaviour does not increase over a long-term time scale, such as age, or a short-term time scale, such as over the course of the trials. This suggests that the woodlice do not learn alternate turning behaviour as they grow older, and as woodlice of all ages display the behaviour to the same extent, it suggests the behaviour has a cause that is exhibited universally by woodlice of all ages. The theory of BALM (Hughes 1985) would allow for this pattern and would appear to support the results to a greater extent than the proposition of “variant patterns” proposed by Moriyama (1999 pg 154).

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