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Space activity and sheltering behaviour of terrestrial isopods

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UNIVERZITA PALACKÉHO V OLOMOUCI
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Prostorová aktivita suchozemských stejnonožců

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Olomouc 2013

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Declaration

I declare that I have written this thesis only by myself under supervision of RNDr. & Mgr. Ivan H. Tuf, Ph.D. and with using cited sources only.

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Olomouc, 2013 Romana Pálková

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Abstract

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Appropriate behavioural reactions of woodlice contribute to successful adaptation to a terrestrial environment. Therefore, behavioural reactions of terrestrial isopods have been intensively studied. These studies have been conducted mainly under laboratory conditions, whereas field experiments observing behaviour in terms of the real environment have been published less frequently. Therefore a field experiment was conducted within this thesis. There were observed woodlice behavioural reactions such as, sheltering, locomotion and diurnal activity, on 2 model species *Porcellio scaber* and *Armadillidium versicolor.* Individuals of both species were colour-marked and released into the area with artificial shelters and then monitored for several days.

Migration ability was detected at least 5.6 m in 5 hours (*P. scaber*) and 4.4 m in 4 hours (*A. versicolor*). There was not revealed any significant difference in vagility of 2 species (Wilcoxon nonparametric paired test), although vagility rate of *A. versicolor* was assessed to be a slightly higher compared to *P. scaber*. There was found a significant influence of the day period (dusk, night, dawn) on abundance of individuals inhabiting shelters. The shelters were the least inhabited at night period, most individuals sheltered at dusk (tested GLMM). Considering time, spatial arrangement and abundance aspects, the shelters were not inhabited equally. The migration ability, sheltering and also diurnal activity issues are compared to other studies results in a discussion part of the thesis.

Key words: shelter, locomotion, movement, behaviour, marking, terrestrial isopods, diurnal activity, *Armadillidium versicolor*, *Porcellio scaber*

Abstrakt

Pálková R.: Prostorová aktivita suchozemských stejnonožců. Diplomová práce. Katedra ekologie a životního prostředí, Přírodovědecká fakulta, Univerzita Palackého v Olomouci, 31 s., 3 přílohy, anglicky.

Většina současných studií zaměřených na chování suchozemských stejnonožců je prováděna v laboratorních podmínkách, které nereflektují zcela podmínky reálného prostředí. Tato práce se proto zaměřila na terénní výzkum, ve kterém bylo sledováno chování (ukrývání, migrace) 2 modelových druhu *Porcellio scaber* a *Armadillidium versicolor*. Jedinci těchto dvou druhů byli barevně označeni a vypuštěni na vybranou lokalitu s předem připravenými úkryty v podobě cihel. Po dobu několika dní byli jedinci kontrolováni v pravidelných časových intervalech.

Při sledování migračních schopností byla zaznamenána maximální dosažená vzdálenost 5,6 m za 5 hodin (*P. scaber)* a 4,4 m za 4 hodiny (*A. versicolor*). Ačkoliv vagilita *A. versicolor* byla vyhodnocena jako mírně vyšší v porovnání s *P. scaber* (testováno Wilcoxonovým párovým testem), mezi druhy nebyl prokázán signifikantní rozdíl. Počet jedinců zaznamenaných při jednotlivých kontrolách se lišil v závislosti na denní době (testováno GLMM). Úkryty byly nejméně využívány v noci a nejvíce před setměním. Rozmístění jedinců využívající úkryty nebylo rovnoměrné. Některé úkryty zůstávaly dlouhodobě neobsazeny pod jinými byly zaznamenány početné agregace (11-25 jedinců). V diskuzi jsou tyto výsledky reflektující pohybové schopnosti a ukrývání, rozšířeny o téma diurnální aktivity.

Klíčová slova: úkryt, pohybová aktivita,chování, značení, suchozemští stejnonožci, diurnální aktivita, *Armadillidium versicolor, Porcellio scaber*

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1. Introduction

Terrestrial isopods (Crustacea, Isopoda, Oniscidea) (Appendix 1) seem to be moved in a spotlight of recent science for 3 main reasons. First, there exists a clear evidence that terrestrial isopods contribute significantly to the nutrient cycles (Hassal *et al*. 1987), therefore it is not negligible the role of terrestrial isopods as decomposers within the ecosystem processes (Petersen & Luxton 1982). Second, a possibility to keep terrestrial isopods under laboratory conditions, that enables carrying out range of various studies (Hornung *et al*. 1998). Third, their cosmopolitan distribution (Schmalfuss 2008) gives an opportunity to study in detail terrestrial isopods nearly all over the world, also in the Czech Republic. The reasons mentioned above, as well as inspiring world of soil biology, have underpinned my thesis focused on locomotion and sheltering behaviour of 2 terrestrial isopod species (*Armadillidium versicolor* Stein, 1859 and *Porcellio scaber* Latreille, 1804).

Land colonisation introduction

Terrestrial isopods, unlike other aquatic Crustaceans, managed to colonise various land habitats ranged from littoral zones to deserts, from mangrove swamps to woodlands or dry grasslands (Den Boer 1961; Paris 1965; Baker 2005; Araujo & Taita 2007). Edney (1986) described the differences between marine environment, which is supposed to be an original habitat of isopods, and the conquered land environment. The air, as a main medium in terrestrial environment, was compared to water by Edney (1986). He reminded 2 main points: firstly, a density of gaseous air is lower than water, and secondly, a low water potential in the air does not enable to isopods a utilization of osmotic gradient to gain water or salts via gills and integuments contrary to the aquatic environment. Following the evolutionary approach, Hornung (2011) and Schmidt & Wägele (2001) pointed out 4 main challenging problems that were supposed to be resolved during the transition to land.

First, protection against desiccation is considered to be a serious issue by majority of authors, more detailed review is given in following part of the introduction.

Second, nitrogen metabolism and a way how to get rid of nitrogenous waste needed to be resolved. According to Zimmer (2002), the ability of terrestrial isopods to excrete ammonia mainly in volatile form (also called ammonotelism) offered energetic advantage to isopods while colonisation the land. Third, respiratory organs, such as pleopodal lungs (Warburg 1993), have been developed to manage a problem of oxygen uptake from the air. Furthermore, an effect of the air with quite a low water potential (Edney 1986) have already been mentioned above. Fourth, nutrition and terrestrial food sources appeared to be adapted. Zimmer (2002), who offered an evolutionary-ecological approach to the Oniscidea nutrition in his review, considered an ability to utilize microbes as a source of enzymes and essential nutrients as an evolutionary adaptation to terrestrial food.

To sum up, a reduction of dependency on the aquatic environment has been emphasized as a crucial factor for a successful land colonisation by numerous authors (Edney 1968, 1977; Cloudsley-Thompson 1977; Warburg 1989, 1993; Carefoot 1993; Hornung 2011).

Water balance adapting strategies

Since water balance issues have been considered to be a factor of great importance for woodlice, various adapting strategies, such as physiological, morphological and behavioural ones have been studied and discussed in the field of science. A comprehensive review of recent literature dealing with aspects of adaptations, which have contributed to the successful land colonisation and water balance issues, is given by Hornung (2011) and Warbug (1993). Several comparative studies have examined abilities of woodlice species to withstand terrestrial conditions (Edney 1951; Schmidt & Wägele 2001). According to these studies, *Armadillidium vulgare,* which is considered comparable to *Armadillidium versicolor* (Csonka *et al* 2013), was evaluated to be better adapted to dry environment than *Porcellio scaber*.

Morphological adaptations

According to land transition, the morphological changes of organs as well as a whole body construction had appeared to protect woodlice from excessive water loss.

Firstly, water resistant-cuticle development was necessary to protect isopods from desiccation. In the cuticle, unlike Arachnids or Insect, the epicuticular wax layer is missing, that is why the protection is not absolute (Bursell 1955; Edney 1960; Cloudsley-Thompson 1977). Csonka *et al* (2013) studied interspecies variability in cuticle morphology, such as thickness of cuticle layers or cuticle sunlight reflection that rises with shiny cuticle surface. Thick cuticle layers and shiny cuticle surface contributed to a lower evaporation rate.

Secondly, pleopodal lungs with pseudotracheaes have been developed from the gills of marine isopods as an adaptation to uptake oxygen in dry air (Edney 1968; Schmidt & Wägele 2001). The more terrestrial species have evolved more covered lungs, which are connected to the environment through spiracles, these spiracles have been decreasing during adaptation in the closed lungs (Hornung 2011; Csonka *et al*. 2013). Thirdly water conducting system (also called *Porcellio* type) in the body was described by Hoese (1982) and Carefoot (1993). The system is consisting of bilateral ventral ducts and dorsal ducting components articulated between dorsal plates of exoskeleton, water is taken up by uropods as Drobne & Fajgelj (1993) pointed out. There was described also a less developed conducting system (*Ligia* type), where water is taken by 6th and 7th pareiopod (Drobne & Fajgelj 1993), this system was evaluated to be less efficient, while considering water management within a body (Hoese 1982). Water is gained mainly from food (Kuenen 1959) and via mouth and anus (Spencer & Edney 1954). According to Kuenen (1959), who studied woodlice and water uptake from food, *Armadillidium vulgare* was able to uptake water with higher efficiency than *Porcellio scaber*. Finally, brood-bearing adaptations (Kight & Ozga 2001), such as closed brood pouch (marsupium) (Hoese 1984) needed to be developed from an ancestral type (Carefoot 1993; Hornung 2011).

The morphology of whole body construction was examined by Schmalfuss (1984). He described 5 eco-morphological forms, such as runners, clingers, rollers, creepers and spiny forms. These categories were grouped by different skeletal constructions, shape of body, relative length of legs etc. These forms were correlated to ecological strategies and characteristic behaviour that have enabled survivorship in different land habitats. *Porcellio scaber* can be characterized as a clinger, according to flat body and tight fitting to the substrates. Whereas *Armadillidium versicolor,* which is able to form quickly a ball shape, can be classified as a roller, due to conglobation ability and its smooth tergites. The conglobation was assumed to enable withstanding harsh conditions (Schmalfuss 1984; Hornung *et al*. 2011). This suggestion was agreed by Smigel & Gibbs (2007), who found 34% water-loss decrease, when *Armadillidium vulgare* was rolled in a conglobated form in comparison with non conglobated individuals. The morphological adaptations of Oniscidea are closely connected with a physiological reaction, considered in the next paragraph. .

Physiological adaptations

Physiological responses of the organism enable to cope with current changes of environmental factors. Various studies were carried out to explore physiological reactions to air humidity changes (Edney 1977; Carefoot *et al.* 1990), temperature change, light intensity (Warburg 1964). Respiration and oxygen consumption was examined by Carefoot *et al.* (1990), who observed 4 species (*Ligia pallasii, Porcellio scaber, Oniscus asellus, Armadillidium vulgare*) and stated that dehydration caused a drop in oxygen consumption. Wright & Machin (1993) proved woodlice ability of active water vapour absorption and they assumed importance of such ability, when animals can find some water saturated shelter and in such refuge they can maintain a water budget. Lindvist (1986) focused on water redistribution in the body and osmoregulation. It was pointed out in his study, that rising concentration of hemolymph is balanced by relocating water from muscles to the respiratory organs. Wieser *et al.* (1969) highlighted a protein metabolism adaptation based on the fact, that volatile nitrogenous excreting rate is significantly increased during period of inactivity, when animals are hidden in moist shelters and can afford demanding metabolism processes.

Behaviour as an adaptation

Behavioural reactions have been considered to be a contribution to the range of adaptations, equally to morphological and physiological aspects. Appropriate reaction could enable woodlice to survive under demanding environmental conditions, such as dry air or extreme temperatures (Edney 1986; Schmalfuss 1984; Hornung 2011). Terrestrial isopods have developed various strategies to maintain water balance, such as diurnal activity, sheltering, aggregation phenomenon etc. Following text gives more details about such behavioural reactions.

Diurnal activity

First, avoidance adverse environment in time via diurnal activity was studied by Cloudsley-Thompson (1952, 1956), nocturnal activity patterns were described in his papers. It was suggested that there are more suitable conditions at night due to lower temperatures, and thereby higher relative air humidity is favourable. According to Cloudsley-Thompson (1956) the intensity of nocturnal activity correlated negatively with terrestriality of species (*Armadillidium vulgare* was found to be less active at night – 60%, whereas *Philoscia muscorum*, which is supposed to be less adapted, appeared 92% of nocturnal activity). During the daylight period the isopods are expected to be hidden in shelters to protect against desiccation.

Movement reactions

Second, horizontal and vertical movement reactions (Brereton 1957; Den Boer 1961; Davis & Sutton 1977) enable to find suitable microclimate conditions (Cloudsley-Thompson 1977; Warburg 1993). Behavioural responses to the environmental factors, such as phototaxes, thigmokinesis or hygrokinesis, are considered to stimulate moving activity besides other factors.

Photonegative orientation is supposed to be associated with searching for dark habitats (shelters), which provides higher humidity and lower temperatures in comparison to surrounding environment (Cloudsley-Thompson 1977). Phototaxes as a response to light and interactions with humidity reactions were studied in details by Warburg (1964), who observed a reversal responses to light on *Venezillo arizonicus* at high temperatures and high humidity but photopositive reactions of *Armadillidium vulgare* were not affected by such conditions.

Thigmokinetic reactions were linked with sheltering behaviour as well as with aggregation phenomenon by Allee (1926) and Broly *et al.* (2012). Thigmokinesis was characterised by Friedlander (1964) as any inhibition of moving activity in response to contact stimuli. The intensity of thigmokinesis reaction is variable according to various factors: (1) species terrestriality - more terrestrial species such as members of genus *Armadillidium* show less thigmokinesis reactions than less terrestrial forms such as *Porcellio* spp. (Warburg 1968), (2) air humidity – increasing reaction with declining air humidity rate, (3) surface – the rougher surface the appreciable reaction (Friedlander 1964). The fact, that thigmokinetic reactions varied individually, was pointed out by Friedlander (1964) and Warburg (1968). These behavioural responses are supposed to empower or inhibit spatial movement in relationship to environmental conditions.

Sheltering

Third, resting in shelters during day period to avoid unfavourable environment was considered as a behavioural adaptation by Hornung & Warburg (1996), Hassall & Tuck (2007). There was described a trade-off between time spent by foraging and sheltering by Dias *et al.* (2012). The shelters are utilized to avoid predators and negative environmental conditions, such as desiccation. Den Boer (1961) emphasized, according to *Porcellio scaber* observations, that water budget was the major out-of shelter activity driver.

Terrestrial isopods were found to be very flexible while considering time spent in shelters. Oniscidea species spend more time sheltering at a lower relative humidity (Dias *et al.* 2012). Hassall & Tuck (2007) examined sheltering behaviour during the year within 4 species (*Porcellio scaber, Platyarthrus hoffmannseggi, Armadillidium vulgare, Philoscia muscorum*). *P. scaber* sheltered in spring and pre-breeding season (March, June) significantly more than *A. vulgare*. There were also found differences in the main sheltering period during a year. *A. vulgare* preferred spring period (March, April), whereas sheltering peak of *P. scaber* was reached in a pre-breeding season (May, June).

Dangerfield & Hassall (1994) studied spatial variation in habitat-use of 2 species *(P. scaber, A. vulgare*) in connection with the sex ratio. Their findings were as follows, males used artificial shelters less frequently and were more active on the surface, probably due to effort to maximize foraging time and increase mating chance in May and June. And furthermore, female-biased sex ratio in shelters was observed during breeding season (June, July). Shelters offered protection against desiccation and predation to females, and moreover, due to higher average temperatures, staying in the refuges enables shortening of brood development time.

Kuenen & Nooteboom (1963) concerned the question how 3 species (*Oniscus asellus, Porcellio scaber, Armadillidium vulgare*) react when search for shelters after night activity. Authors suggested an influence of olfactory signals besides thigmotaxis and negative phototaxis factors. They found a positive aggregation reaction to smells of other individuals, furthermore to smells of other species. The smell reached higher attractiveness for animals with increasing desiccation, whereas there was a negative reaction to smell of *P.scaber* under wet conditions. The hypothesis of existence of olfactory aggregation signals was supported by researches by Takeda (1980) and Ebisuno *et al*. (1982) on aggregation pheromone contained in faeces pellets of some woodlouse species, including *P. scaber* and *A. vulgare*.

Aggregation

Aggregation phenomenon, that enable animals to evaporate significantly less water while bunching, was studied in details by Allee (1926), who tested effects of various environmental factors on aggregation behaviour. Moisture was found as the most important factor. Bunching reactions were increasing under dry conditions and aggregated animals lost less water than isolated ones. These results were agreed by Warburg (1968), in his study on differences between water loss on aggregated and isolated *Oniscus asellus*. He concluded that bunched animals evaporated 50% less water. Secondary factors, such as light, contact and temperature, were found to influence aggregation less than the main humidity factor (Allee 1926). A study on humidity reactions and aggregation in woodlice was conducted by Friedlander (1965), who believed the aggregation is not only a direct implication of humidity, because he marked significant aggregating behaviour also if the experiment was conducted in the water-saturated air. It was suggested by Friedlander (1964), that aggregation stimuli could be influenced by contact (thigmokinesis) combined with special movements or some chemical substances.

Caubet *et al.* (2008) studied deeply an intraspecific aggregation behaviour and geographical variability within *A. vulgare* populations from different countries. There were revealed significant differences in aggregation behaviour between populations according to moist or dry climate of the original environment.

To conclude, direct connections between water balance issues, temperature, light and other factors have been examined within a scope of reactions, such as: diurnal activity (Cloudsley-Thompson 1956), sheltering behaviour (Den Boer 1961), aggregation (Allee 1926; Friedlander 1964), movement activity (included also phototaxes, thigmokinesis, hygrokonesis etc.; Warburg 1993). On the other hand, Cloudsley-Thompson (1977) recommended a holistic approach, considering the fact that various factors could be hidden beyond, factors could interact frequently, and furthermore, diverse individual reactions to such factors could be received (Cloudsley-Thompson & Constantinou 1987). Since the spatial moving activity have been considered to be a significant behavioural adaptation contributing to the survivorship in the terrestrial environment, the field study exploring locomotion and sheltering activities of terrestrial isopods was carried out within my master thesis to contribute at least a little to a recent knowledge of woodlice behaviour patterns.

Objectives

The aim of the thesis was to describe terrestrial isopods' space activity and sheltering behaviour features based on the field experiment and subsequent data analysis. Expected space activity features were as follows:

- vagility traits, such as maximum migration distances of marked woodlice
- locomotion behaviour (nocturnal activity)
- sheltering behaviour (abundances of recaptured individuals after releasing, tenacity to certain shelter)

2. Materials and Methods

Field study was carried out in summer 2011. Main part of the experiment was monitoring of sheltering and moving behaviour of 1,000 marked individuals in the field, where a grid of artificial shelters was arranged. Pilot study had been conducted in June. The experiment was redesigned according to the feedback and afterwards, the field experiment was run twice, former one in June and the second in September 2011 (Tab 1). As a model species pillbug *Armadillidium versicolor* and rough woodlice *Porcellio scaber* were selected.

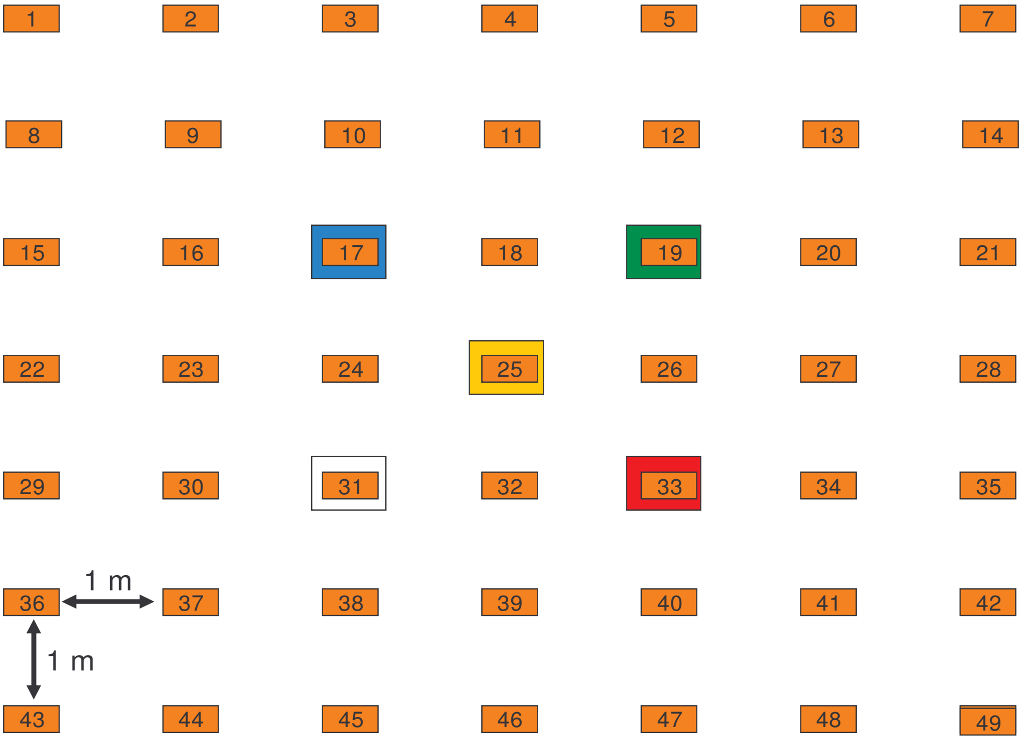
Collecting of individuals and marking

Collecting of individuals took place at 2 localities: (1) fortress Korunní pevnůstka also used as a study site and (2) garage area situated nearby the Olomouc-město railway station. Collecting sites were chosen according to Riedel *et al.* (2009), who explored terrestrial isopods in Olomouc city. Map 1 in Appendix2 illustrates, where both localities were situated.

Acetone-based mother-bee marking polish was used to identify 5 different colour groups (Fig 1). White and green colours were used for *Porcellio scaber*. Red, yellow and blue colours were used for *Armadillidium versicolor*. There were 200 individuals marked for each colour group. Marking was done according to method described by Drahokoupilová & Tuf (2012), she recommended marking by small, but clearly visible dots on dorsal sheet of the first segment of pereion (Fig 2). Emphasized was also a gentle and quick manipulation with individuals to minimize a stressful situation. Specimens had been marked in advance of 48 hours before releasing, to reduce negative marking influence described by Drahokoupilová & Tuf (2012).

Experimental design

Regular grid of 49 shelters (7x7) spaced 1 meter was used to observe sheltering behaviour of 1,000 labelled animals. Bricks (size 29x15x6.5 cm) were used as shelters and there was hollowed a small space (size 15x10x1 cm), beneath each brick, to avoid killing animals during the manipulation with a brick. Shelters had been arranged 10 days in advance of releasing animals. Five shelters were used as release points when experiment started. Each colour group (200 specimens) was released under 1 shelter (Fig 1).



Legend brick position: 18 releasing point for a group of 200 marked individuals: 🟨

Fig1. Experimental design scheme

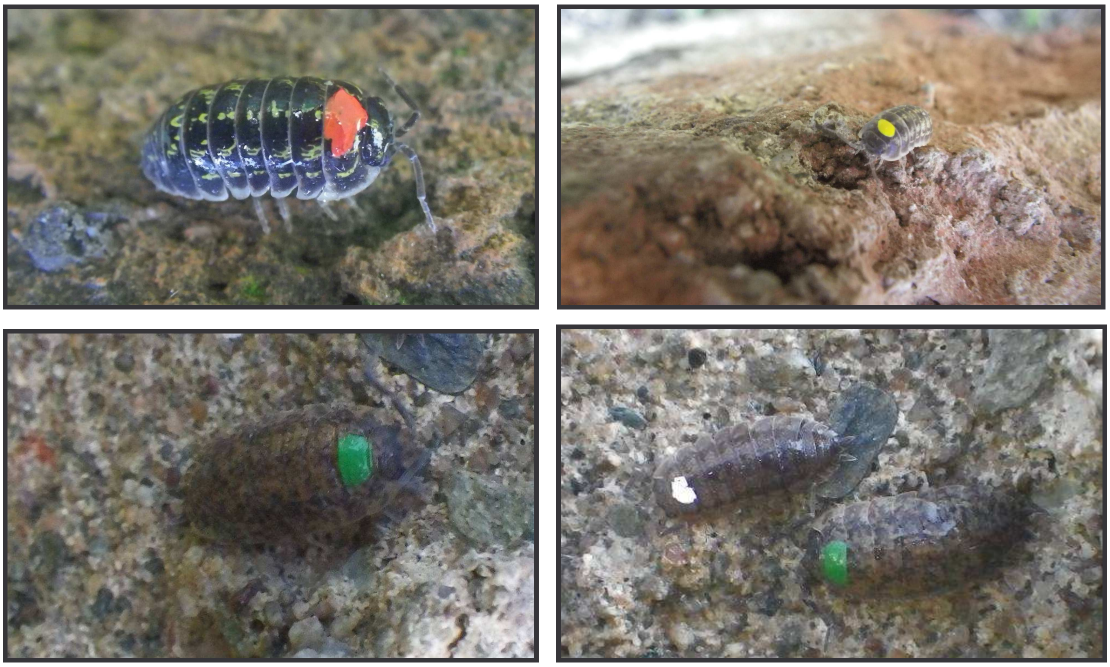


Fig 2. Details of marked individuals *Armadillidium versicolor* (red, yellow – pictures above) and *Porcellio scaber* (green, white – pictures below)

Monitoring of shelters followed. Study site was visited regularly 3 times during each night (at dusk, in the middle of night, at dawn). Monitoring of experiment 1 was provided for 3 nights and experiment 2 for 7 nights. Tab 1 illustrates the monitoring timetable. Each shelter was checked and there were recorded numbers of individuals, who were using the shelter at the moment. Cole's comments (1946) to the counting procedure were taken into account. Furthermore, each monitoring action was recorded on video to ensure that obtained data were correct.

Tab 1. Monitoring timetables

	Date	**Monitoring Timetable**
Pilot study	11-17 June 2011	1:00, 5:00, 21:00
Experiment 1	24-27 June 2011	1:00, 5:00, 21:00
Experiment 2	22-29 September 2011	0:00, 7:00, 19:00

Study site

The field study area took place in front of Olomouc fortress called "Korunní Pevnůstka", which is situated nearby the Olomouc city centre and the park "Bezručovy Sady" (Map 2 in Appendix 2). There was a small grassland area with regularly mowed lawn in front of brick walls of the fortress, 36 m^2 flat square area was used for the experiment. The site was selected as an optimal place considering researches of and Riedel *et al.* (2009), who described the site as a natural habitat for various species of terrestrial isopods, including *Armadillidium versicolor* and *Porcellio scaber*, as well as by presence of bricks.

Data processing and analysing

First, it was necessary to process data sets (each monitoring control) according to colour groups and species. Then individual records were matched with achieved distances from release point, and furthermore achieved distances for colour groups, consequently for species were computed.

Species vagility comparison

Wilcox nonparametric paired test was used to compare vagility of 2 species, therefore 2 equal groups were needed to use the test. It was necessary to include only 2 colour groups (400 individuals) of *Armadillidium* to compare with *Porcellio* (400 individuals). The *Armadillidium* colour group selection was carried out according to the sum of the average distances (meters) of 2 color groups, the middle sum was chosen as a representative. Blue and red colour groups were selected by this method.

Firstly, it was necessary to count subtractions of mean achieved distances for each night ("dusk distance mean" minus "dawn distance mean"). The limit of 10 individuals was set to decrease random effects. These figures were counted for each species. Secondly, obtained figures were used for Wilcox nonparametric paired test. Experiment 1 and 2 were tested separately. Prism 6 software was used to compute the test (GraphPad Software Inc. 2013).

Diurnal activity

The effect of diurnal activity of woodlice was tested by evaluating the abundances of 3 periods of the night (dusk, night, dawn). Because time was expected to affect the abundances significantly, generalized linear mixed model (GLMM) was used to justify effect of 2 fixed variables, such as time (categorical: 1–3 in experiment 1, 1–7 in experiment 2) and day period (categorical: dusk, night, dawn). It was set Poisson error distribution and logarithmic link function to model the effect of both predictors. While creating the model, it was necessary to consider predictor time for replication, because of repeated measurements. Program SAS 9.2 (SAS Institute Inc. 2007) was used for the statistical analysis.

To enable comparison of 2 species (Fig 3, Fig 5), it was necessary to select only 2 color groups for *A. versicolor* to create graphs. In the graphs in Fig 3 and Fig 5, there were visualised comparisons of 2 groups of 400 individuals released in the beginning of the experiment. Similar process, as described above for vagility comparison, was used to select data for the graphs but the abundance category was used for the selecting process. According to the process, 2 colour groups (blue and red) were chosen to represent *A. versicolor* species in the figures.

3. Results

Movement

Dispersal within the grid of artificial shelters was fast, shelters in various distances (1-5 m) were inhabited in 20 h after releasing, such results were performed by species in both experiments. According to the experimental design, the maximum noticeable distance to observe migration was 5.66 m. The distance of 5.66 m was firstly achieved by *P. scaber* in 5 h and by *A. versicolor* in 12 h in experiment 2. Detailed information about other maximum distances observed during experiments is given in Tab 2, which illustrates moving capability in the day following releasing. Particular data from monitoring period are available to check in Appendix 3.

Tab 2. Maximum observed distance (m) measured from releasing point

Experiment 1	*Porcellio scaber*	*Armadillidium versicolor*	Experiment 2	*Porcellio scaber*	*Armadillidium versicolor*
Time	Max .dist.(m)		Time	Max .dist.(m)	
4 h	4.12	4.47	5 h	5.56	3.16
20 h	4.47	4.47	12 h	5.56	5.56
24 h	5.56	4.47	24 h	5.56	5.56
28 h	5.56	5.56			

Vagility

There was not affirmed any significant difference in vagility of the species, results of Wilcox paired test are represented in Fig 3. While zooming in experiment 1, that appeared to be equal in vagility of species (*P. scaber* mean = 0.54 m, *A. versicolor* mean = 0.57 m; $p_{\text{experiment 1}} > 0.9999$), whereas there was revealed a higher vagility of *Armadillidium* in experiment 2 although statistics did not proved to be significant (*P. scaber* mean = 0.007 m, *A. versicolor* mean = 0.5140 m; $p_{\text{experiment 2}} = 0.0938$).

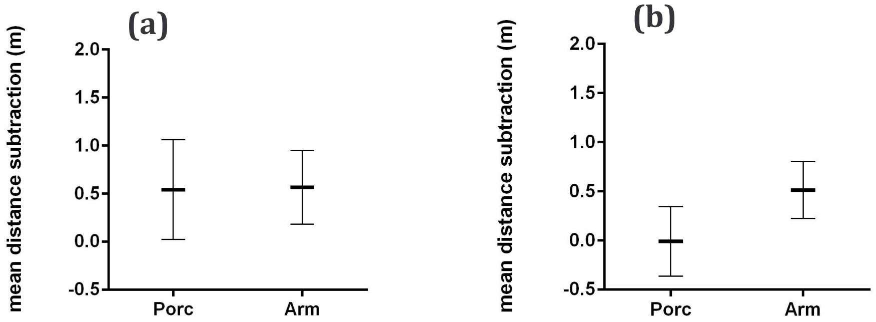


Fig 3. Species vagility comparison (a) experiment 1, (b) experiment 2 represented by mean distance subtractions (± SE)

Diurnal activity

Abundance of sheltering individuals was different while comparing experiments as well as species, as could be seen in Fig 4 and Fig 5. Higher abundances of individuals in experiment 1 were noticed, such as 289 individuals and 179 individuals recorded in the 1st and 2nd evening after releasing, compared to 111 and 102 individuals from experiment 2. Individuals of *A. versicolor* species were detected at a higher abundance compared to *P. scaber*, as is shown in Fig 6.

Time (each night was considered to be a category of time) was confirmed to affect negatively abundance of individuals observed under shelters (Fig 4). This negative effect was affirmed significant for *P. scaber* and also for *A. versicolor* in both experiments. 1,000 individuals had been released and 198 individuals were observed 24 h later in experiment 1 and 111 in experiment 2. Despite the amount of 1,000 released individuals, only 25 (experiment. 1) and 28 (experiment. 2) specimens were found at the end. The low abundance has always been the main factor that influenced the duration of the experiment. To check p values and F-test values see Tab 3.

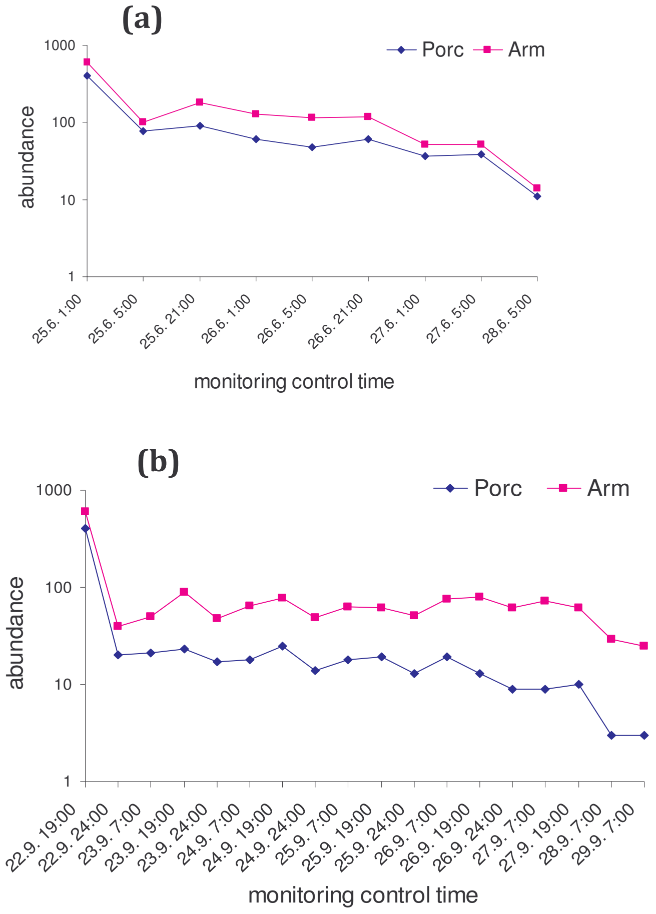


Fig 4. Species abundance of detected individuals according to monitoring control time, (a) experiment 1, (b) experiment 2

Significant differences in abundances between day periods (dusk, night, dawn) were identified. While comparing abundances according to day period, the results between experiments were different. The results also varied between species in experiment 1, contrary to the similar patterns for species in experiment 2. *Dusk* period was found to be the most sheltered period (*A. versicolor* in experiment 1, both species in experiment 2). *Night* was evaluated to be the least sheltered period for both species in experiment 2. In contrast to behaviour of *P. scaber* in experiment 1, where the night was revealed to be the most sheltered period. *Dawn* was identified as the least sheltered period in experiment 1 for both species, but these results did not fit with results of experiment 2 precisely, where dawn was although close, yet evaluated as a second least sheltered (night was first). Tab 3 contains values, such as p value and F-test value separately for species and experiments. Fig 5 and Fig 6 visualise the results of experiments, where kind of day period cycles in sheltering pattern could be noticed in graph (b).

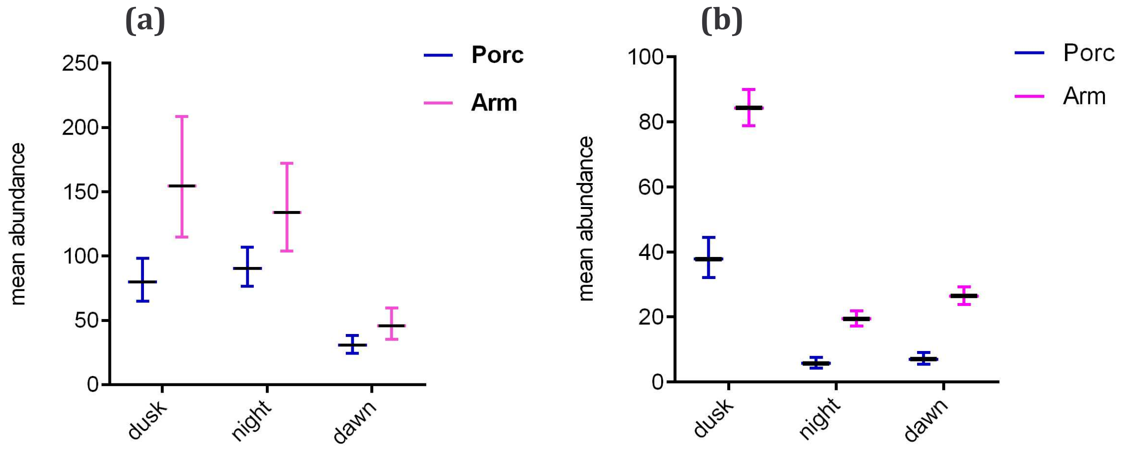


Fig 5. Influence of day period (dawn, dusk, night) on abundance (mean ± SE), (a) experiment 1, (b) experiment 2

Tab 3. Influence of variables "Time" and „Day period" on species abundance, (F) F-test value (power of test), (p) p-value (probability of achieving such a result randomly)

Experiment 1	*Porcellio scaber*		*Armadillidium versicolor*		Experiment. 2	*Porcellio scaber*		*Armadillidium versicolor*	
Variable	F	p	F	p		F	p	F	p
Time	333.93	<.0001	500.64	<.0001		477.14	<.0001	411.49	<.0001
Day period	77.27	0.0002	128.54	<.0001		195.35	<.0001	240.80	<.0001

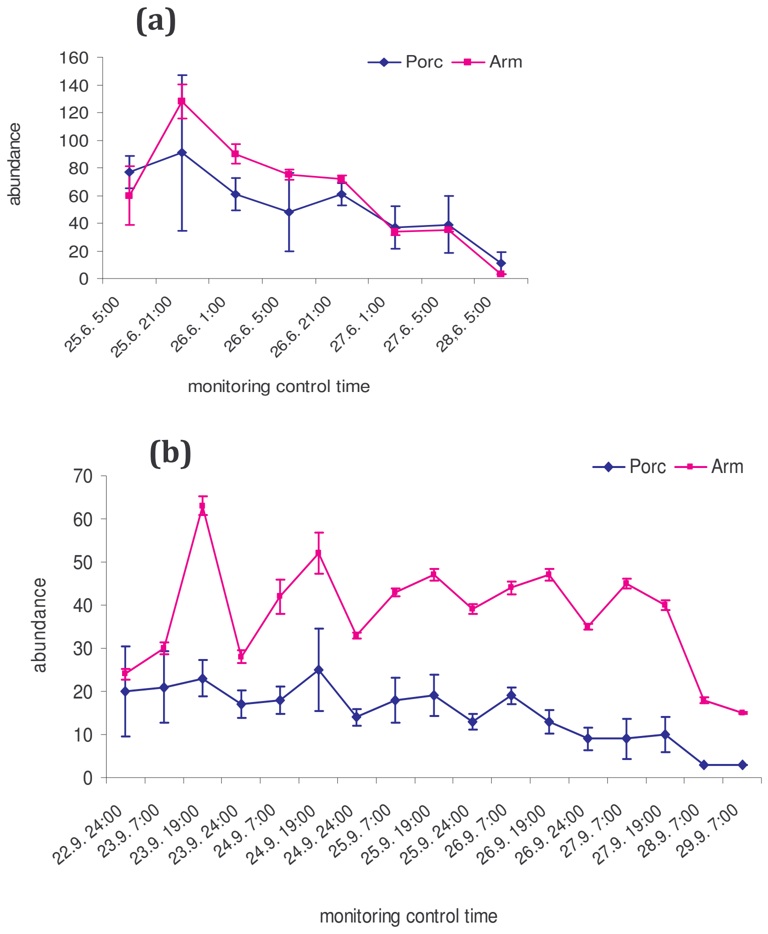


Fig 6. Species abundance (total abundance ± mean squared error (MSE), MSE was computed according to number of individuals inhabiting each shelter, MSE was used to reflect differences in aggregation size between shelters within a control**,** (a) experiment 1, (b) experiment 2. To enable comparison of 2 equal groups only blue and red color groups of *A. versicolor* were included.

Shelters were not inhabited equally, the sheltering varied in time and in aggregation size. The effects of time and day period have been described above. Some shelters had never been inhabited, such as bricks No. 11, 21, 36 (experiment 1) and No. 6, 45, 47 (experiment 2). On the other hand, under some shelters, there were observed individuals of all 5 colour groups at the same moment, such as shelters No. 6, 16, 20, 27, 36 (experiment 1) and No. 15, 24 (experiment 2).

The sum of individuals under each shelter (aggregation size) varied among shelters and according to time as well. The sums of individuals, who use a shelter (aggregations size), were structured in categories according to the sum of individuals under each shelter (categories – 0, 1, 2–5, 6–10, 11–25, 26 and more). These categories were visualised in Fig 7 and data could be seen in Appendix 3 in Tab 11 and Tab 12 And furthermore, a higher range of mean squared errors, which is displayed by error bars in Fig 6, indicates also a presence of higher abundant aggregations, which were observed in the monitoring control.

There were only 13 shelters found not to be inhabited during the 1st control after releasing in experiment 1 and 16 in experiment 2, these results reflected the minimal phase of empty shelters. The frequency of empty shelters increased in the last quarter of monitoring period. Zooming to other categories, category with 2-5 inhabitants was more frequent than the category with 1 individual, similar situation was observed every control besides the last one in experiment 1 and there were 11 such findings in experiment 2. The aggregations sized 6-10 woodlice were observed in each control except the last but one control in experiment 2. The very abundant aggregations (category 11-25) were found under some shelters, such as No. 12, 19, 20, 25, 31 in experiment 1 and under No. 10, 19, 24 in experiment 2. Draft outline of sheltering tenacity and aggregation behaviour could be derived according to the data in Tab 5 and Tab 8 in Appendix 3 but has not been analysed within the thesis.

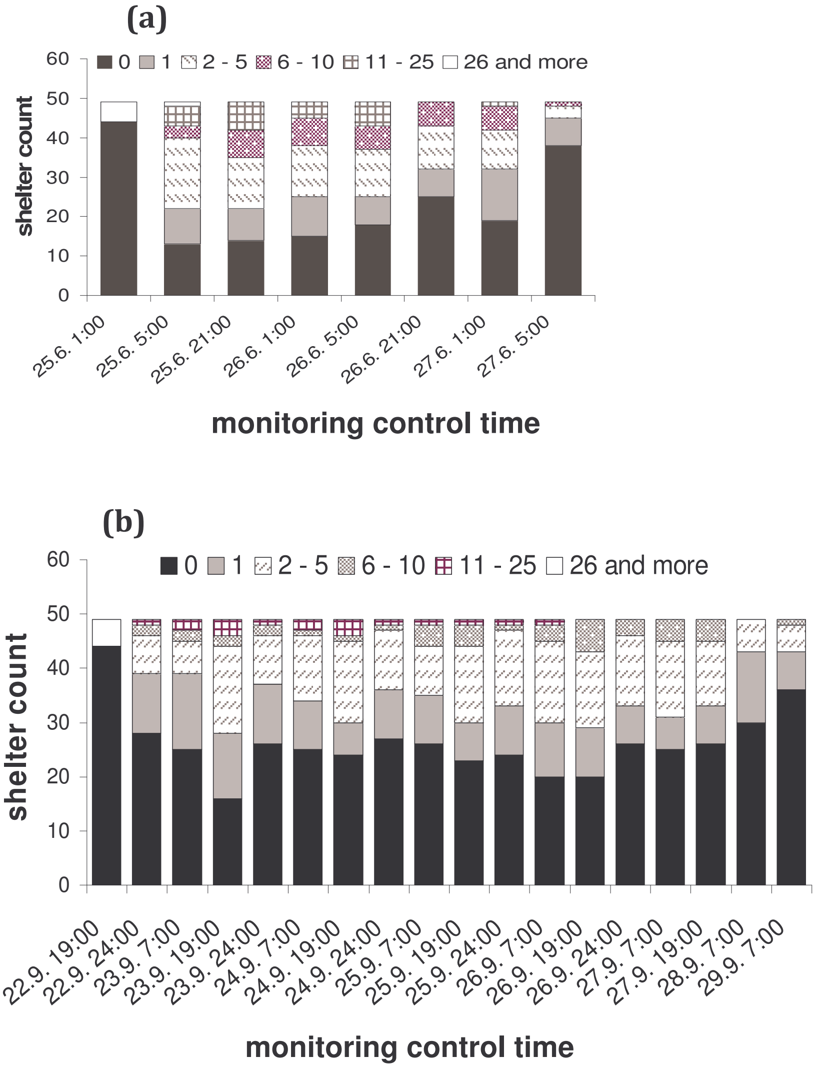


Fig 7. Frequency of aggregation categories according to sum of individuals (both species *P. scaber* and *A. versicolor*) observed under each shelter during (a) experiment 1, (b) experiment 2

4. Discussion

Locomotion

Woodlice movement belongs to the behavioural features (Friedlander 1964; Edney 1968; Warburg 1968), therefore it has been studied intensively on various levels. Nathan *et al*. (2008) proposed a general framework for any research conducted in the field of the movement ecology. Authors defined 4 main components, such as internal state of individuals, motion capacity, navigation capacity and the influence of external environmental factors that interact together and lead to the animals' movement. According to the field study, the results could be considered as a contribution to the woodlice motion capacity knowledge, because there were not recorded any internal state indicators, such as oxygen consumption, hemolymph concentration etc and also there were not recorded any environmental factors, such as air humidity or temperature within the study.

Dispersal activity

Several field studies on movement of terrestrial isopods have been conducted during last 50 years. Brereton (1957) studied woodland isopods and changes in their distribution during day and night as well as during seasons. Within other various experiments the horizontal movement of marked animals between trees was observed. The study highlighted the vertical activity on the trees in comparison to the horizontal. Paris & Pitelka (1962) dealt with vagility of *Armadillidium vulgare* within their study on population characteristics. They stated the population was very dispersible in view of the fact, that they released 243 marked animals but only 8 animals were recaptured 24 hour later within a circle area (12.5 m^2) with radius of 2 m. Compared to my results (Tab 4), where the recapture rates were higher, such as 1,000 individuals had been released and 198 individuals were observed 24 h later in experiment 1 and 111 in experiment 2 in area of 36 m$^{2.}$

Paris (1965) studied dispersal activity of 1,000 individuals *Armadillidium vulgare,* labelled by radiophosphorus, in the circular grid of artificial shelters in Californian grassland. The findings of his study were as follows: there were detected individuals in distance of 1 m in 4 min, 3 m in 50 min, maximum dispersal rate was 13 m in 12 hours and maximum distance of 25 m was achieved in the 20th day, and furthermore, author pointed out that the greater dispersal rates were observed in a dry summer season than in rainy winter season. Results observed by Paris (1965) were not surprising, when considering maximum speeds of P*orcellio scaber* examined by Hughes (2008), Schuler *et. al.* (2011) and *Porcellio laevis* examined by Dailey *et al.* (2009), all authors found very similar maximum speeds in range of 0.3-0.8 m/s. Tuck & Hassall (2004) stated in their study on *Armadillidium vulgare* mean speeds 10 times slower 0.003 – 0.005 m/s, these speeds were not measured in the track corridors like did Hughes (2008) and Dailey *et al.* (2009), but in arenas with shelters and food. According to the experimental design of my study, where maximum distance to observe animals was 5.6 m, it was not able to compare exactly the results with Paris (1965). However observed distance 4.4 m in 4 hours (*A. versicolor*) and 5.6 m in 5 hours (*P. scaber*) were consistent with results presented by Paris (1965). And furthermore according to the Paris' findings, it is highly probable, that some individuals achieved higher distances as well.

In the question of extrapolating mean disperse distances, it was recommended by Edney in general (1968) not to infer woodlice behavioural reactions and capability only according to laboratory-based studies, he pointed out that laboratory conditions differ enormously from nature environment, and therefore in the laboratory experiments animals do not have to appear natural behaviour. The fact, that there was conducted a field experiment in my thesis, does not tackle this problem entirely. There should be considered other factors influencing natural behaviour, such as colour marking, which could affected negatively woodlice activity, as was described by Drahokoupilová & Tuf (2012) or significant effect of translocation and handling on movement behaviour, which was described by Heidinger *et. al*. (2009). In the field study on grasshopper by Heidinger *et al.* (2009), there were found significant effects of translocation and handling, such as animals moved longer distances mainly in the 1st day after releasing, decrease in daily turning angles and tend to move more directly after releasing in general. According to their results it was suggested that in the 1st day after releasing animals run fast directly “away” to find suitable environment, unlike usually, when a systematic search (which is based on geometric similarities to a brownian random search) is performed, as was described by Hoffmann (1983) in his study focused on systematic search behaviour of desert isopod *Hemilepistus reaumuri*. Therefore it is highly probable, according to Paris' (1965) results and suggestions of Heidinger *et al.* (2009), that woodlice do not usually move such long distances, as were observed in the study, unless not disturbed enormously.

Vagility

The species vagility comparison was based on mean maximum activity radius of 2 species, which was supposed to be robust enough for statistical analysis (Samietz & Berger 1997). There were not found any significant differences in vagility of 2 species during my study, though there was revealed a slightly higher vagility rate for *A. versicolor* in experiment 2. These results were not consistent with expectations of Dailey *et al.* (2009), who suggested a hypothesis that *Armadillidium vulgare* as a conglobating isopod (Schmalfuss 1984) could rely on passive defence, whereas *Porcellio laevis* was supposed to use an active strategy, such as escape from harsh conditions or predators, and therefore was expected to be a better "runner" than *A. vulgare*.

The hypothesis of higher vagility of *P. scaber* could be consistent with species abundance results of this study. There were observed lower abundances of *P. scaber* compared to *A. versicolor* during both experiments. Such findings could indicate a higher number of *P. scaber* individuals, who had run away from an experimental area and thus were not recorded. When following this idea, there could be considered a hypothesis that decline in *P. scaber* abundance, which was probably caused by migration away from the site, is an indirect evidence of higher vagility of *P. scaber*. If such high vagility was beyond borders of our experimental area, we could collect data, which would not capture a reality, and thus lower measured vagility of *P. scaber* may be a consequence of an undersized dimension of an experimental area.

Sheltering behaviour

Unequal shelter use

Abundances of shelter inhabitants were found not to be even (Tab 5, Tab 8). Since such differences within a small area were also pronounced by Davis & Sutton (1977), Hassall & Dangerfield (1990) and Hornung & Warburg (1996), hypothesis of Den Boer (1961) could be considered. He suggested an idea, based on the field observation of *Porcellio scaber*, that good hiding sites were occupied by numerous individuals regularly every night due to suitable conditions of such shelter and due to searching behaviour of woodlice for exactly such conditions. According to this hypothesis, the empty shelters in my study did not probably offer suitable conditions, when consider also the fact, that shelter had not been discovered by any individual. Hornung & Warburg (1996) also stated in their study conducted in grasslands and forest, that the isopods were not evenly dispersed within a habitat and there was highlighted a patchy distribution influenced by various microclimate conditions of stone shelters, moisture was considered to be an important factor.

The fact that some shelters were stably inhabited by a higher number of individuals (Tab 5, Tab 8) could be influenced besides Den Boer' suggestions (1961) also by recent findings of Devigne *et al*. (2011) and Broly *et al.* (2012). These authors found except environmental factors, also social interaction effects on aggregation behaviour of *P. scaber*, which could influence shelter use abundance. According to conclusions of Devigne *et al*. (2011) and Broly *et al.* (2012), the final location of aggregate under shelter could be considered as a compromise influenced by environmental factors such as air humidity, and also by individual preference and inter-attraction between individuals and current number of individuals in an aggregate. This hypothesis is consistent with olfactory effects of an aggregation pheromone considered by Kuenen & Nooteboom (1963) and proved by Takeda (1980) and Ebisuno *et al*. (1982), who confirmed that aggregation pheromone attracted woodlice individuals of the same species as well as different terrestrial isopods species.

To follow such finding, individuals could tend to join the already inhabited hiding site (Hassall & Tuck 2007), according to a strategy that risk probability of wrong conditions of the site, where many other conspecifics have already aggregated, is supposed to be low. And therefore the shelter, which had offered suitable conditions and had been found, was used throughout a whole monitoring period.

It could be taken into account a possibility of sheltering tenacity, while considering ideas of Devigne *et al*. (2011) and Broly *et al.* (2012), who assumed searching for shelter according to ”sheltermates”. And if there is an evidence of such social behaviour described by (Linsenmair 2007) on desert isopod *Hemilepistus reaumuri*, where sheltering fidelity was proved (Hoffmann 1983). Moreover, shelter fidelity of some crustacean decapods species, was illustrated by Vannini & Cannicci (1995), who studied crabs. This behaviour was not possible to observe on *A. vulgare* and *P. scaber* within this study, according to a fact that both species are very small and continual visual observing was not possible in the grassland, unlike in studies on *H. reaumuri* (Hoffmann 1983; Linsenmair 2007), because body size of *H. reaumuri* is greater, and furthermore the field (desert) is more transparent.

Diurnal activity

According to the differences in sheltering rate, which were significantly influenced by day period (Fig 5, Fig 6), there could be considered a diurnal activity effect, which was studied by Cloudsley-Thompson (1952, 1956), Paris (1963) and Refinetti (2009) on *Armadillidium vulgare* and by Den Boer (1961) on *Porcellio scaber*. All papers agreed the thesis of woodlice' nocturnal foraging activity and sheltering behaviour during day to avoid desiccation. The least sheltered periods in my experiments, were assumed to reflect a higher foraging activity outside the shelters and the most sheltered periods were considered as a period of resting.

As the conclusions of Cloudsley-Thompson (1952, 1956) and Den Boer (1961) were very convincing, the results of experiment 1 revealed contradictions with their findings, because the night period was examined as the most sheltering period for *Porcellio scaber* and also for *Armadillidium versicolor* it was highly sheltered period, even if not the most sheltered one. While considering very short monitoring period (3 nights), there could be noticed an influence of the setting of the releasing time, which was at night in experiment 1. For this reason the individuals, who usually behave actively in the night period, were recorded as sheltering ones, and consequently the results could reflect such coincidence. This problem probably did not affected experiment 2, from 2 reasons. First, monitoring period was longer (7 days). Second, releasing was done in the evening. Nocturnal activity of terrestrial isopods was suggested to be related with a lower evaporation rate affected by lower temperatures and thus higher relative air humidity by Cloudsley-Thompson (1977). Den Boer (1961) stated contrary, the reason of staying out of shelters was an excess water excretion.

High abundances during dusk periods were in compliance with expected diurnal activity (Cloudsley-Thompson 1956, 1977) and it is assumed to illustrate the need to hide during the day to avoid desiccation (Hornung & Warburg 1996). Whereas, in dawn periods, shelters were not inhabited enormously. This happened probably due to morning temperature decrease and thus increase of the relative air humidity, such situation was considered to allow woodlice foraging activity out of shelters.

Where next?

There was a lack of information about terrestrial isopods sheltering tenacity. There have been published some field studies, such as Den Boers' paper focused on field experiments (1961) on *Porcellio scaber* and studies by Hoffmann (1983) and Linsenmair (2007) focused on desert isopods, such as *Hemilepistus reaumuri,* who sheltered in burrows and there was revealed a strong fidelity to the burrows belonging to 1 family. According to his experience, Den Boer (1961) did not believe that *Porcellio scaber* performed shelter fidelity. It was suggested by Paris (1965) to carry out some field study on shelter tenacity. But individual identification appeared to be a crucial factor to success such issues. Up to date, the problem of individual identification within a group of woodlice has not been satisfactory resolved. Despite my former expectations, it was not possible to analyse shelter tenacity, according to the individual identity problem. Even though there were observed shelters with some aggregations, where stable ratio of color-marked individuals was found in following monitoring controls. Until the problem of individual identification is resolved, it seems to be very difficult to conduct studies on shelter fidelity in the real environment.

5. Summary

There was conducted a field study in summer 2011 focused on woodlice behavioural, such as sheltering, locomotion and diurnal activity, on 2 model species *Porcellio scaber* and *Armadillidium versicolor.* Individuals of both species were colour-marked and released into the area with artificial shelters and then monitored for several days. The aim of the thesis was to describe terrestrial isopods' spatial activity and sheltering behaviour features.

The findings of the thesis were as follows:

1. Dispersal ability was detected at least 5.6 m in5 hours (*P. scaber*) and 4.4 m in 4 hours (*A. versicolor*)
2. Vagility was found to be similar for both species (Wilcoxon nonparametric paired test)
3. Time influenced abundance of recaptured animals negatively and shelters were not inhabited equally in time and also not in space.
4. Nocturnal activity of both species was confirmed, according to the significant effect of night period on low sheltering

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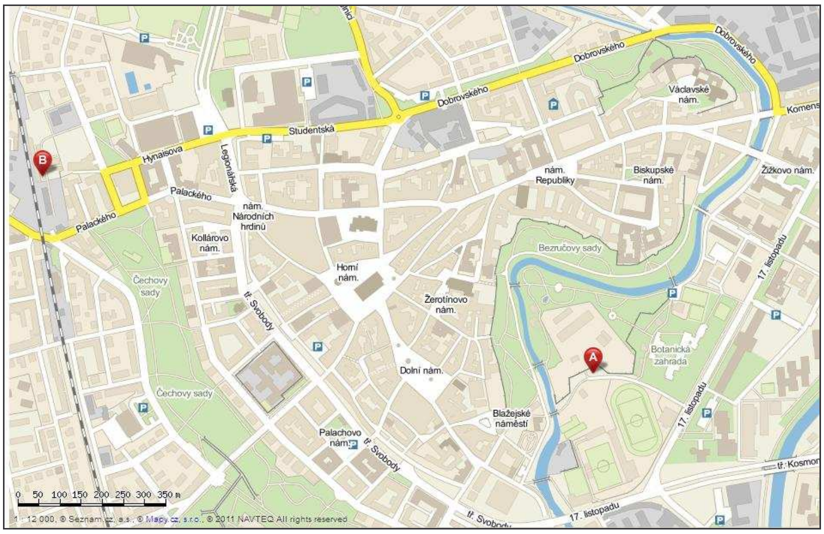
7. Appendices

Appendix 1. Systematic classification and distribution

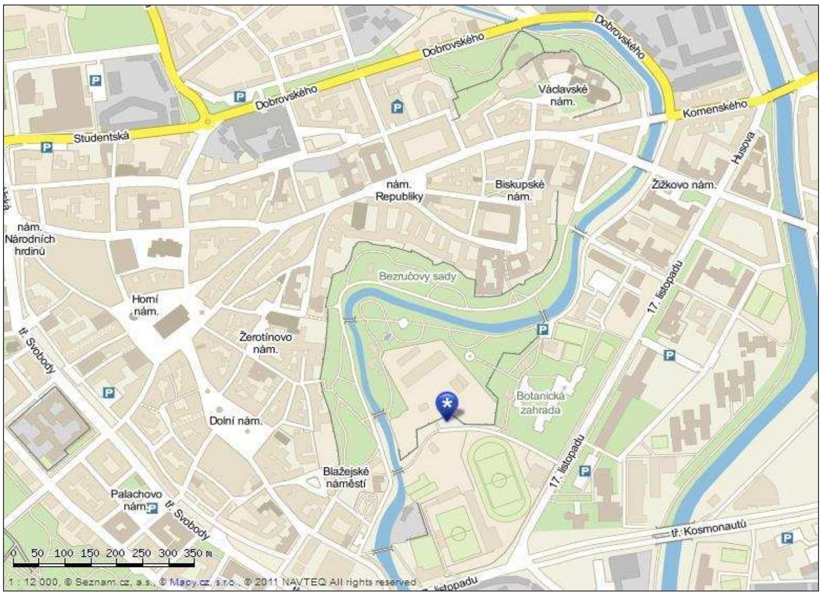
Tab 4. Systematic classification and distribution (Schmalfuss 2008) of species used in the experiment

	Armadillidium versicolor **Stein, 1859**	***Porcellio scaber*** **Latreille, 1804**
Kingdom	*Animalia*	*Animalia*
Phylum	*Arthropoda*	*Arthropoda*
Subphylum	*Crustacea*	*Crustacea*
Class	*Malacostraca*	*Malacostraca*
Order	*Isopoda*	*Isopoda*
Suborder	*Oniscidea*	*Oniscidea*
Family	*Armadillidiidae*	*Porcellionidae*
Genus	*Armadillidium*	*Porcellio*
Species	*Armadillidium versicolor*	*Porcellio scaber*
Distribution	Eastern Europe (Germany, Austria, Czech Republic, Slovakia, Hungary, Albania, Romania, Bulgaria)	Europe except southern parts. Introduced to many parts of the world

Appendix 2. Maps and pictures



Map 1. Collecting localities (A) Korunní pevnůstka fortress, (B) garage area (Mapy.cz, s.r.o. 2013a)



Map 2. Experimental site locality

Fig 8. Grid of artificial brick shelters at the experiment locality Korunní pevnůstka fortress

Appendix 3. Data tables

Tab 5. Total abundance of both species in experiment 1

Monitor. control	**Shelter position**																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Total
25.6. 1:00																	200		200						200						200		200																	1000
25.6. 5:00		2	2	7	1			2	2			3			4	13	4	2	17	13		2	3	1	3	7	2	3	1	2	2	5	24	2	5		1	2			7	1	2		1		1	1	1	196
25.6. 21:00	1		9	13	3	12		6	1	2		12			7	8	7	3	19	22		2	6		18	9	14	1	1		26	1	3	1	12		3	3		1		3	3		5	1	12	2	1	289
26.6. 1:00			3	6	3	13		6		3		17		1	8	4	7	2	13	7				2	13	6	15	5	1		14	1	2	1	8		2	3	1	2			3	1	1		3	2	1	198
26.6. 5:00			2	5	1	1	1	7	1	4		8	2		6	1	7		15	6		2	3		12	3		3	2		15		18	1	7		5	3		1	1		4		1	1	3		1	162
26.6. 21:00	1			1	4	1	4					4	9		5	4	7		14	6		7	4	1	15	1		13	2		21		13		11		2	1		1			3		2	2	7	1	3	179
27.6. 1:00	1			8		1			1			5	2		3	2	2		1	8	1		3	3	6	2		2	1		1		1		3		3						1			1				89
27.6. 5:00	2		2	8	1				1	1		3	3		3	7	1		1	8		1	3		11	1		2	2		9		8		4		1	1					1		1	1	2	1	1	1
28.6. 5:00	1											1				4			1						3					1	8						1						1			1		3		25

Tab 6. *Porcellio scabe*r abundance in experiment 1

Monitor. control	**Shelter position**																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Total
25.6. 1:00																			200												200																			**400**
25.6. 5:00		2	2	7	1			1	2			2				9		1	17	7		1	2		1	3	2	2	1	1	2	2	1	2	2			1				1	1				1			**77**
25.6. 21:00			4	1	1	1		2				2				6	4		18	9			1		1	3		3			21		3	1	5							1	1				3			**91**
26.6. 1:00			1	5	2	3		2		1		4		1	1	3	2	1	11	3							1	2			11	1	1	1	2			2												**61**
26.6. 5:00			1	5		2	1	2	1							1	2		13	1		1									13		2	1	1		1													**48**
26.6. 21:00				9	1		2					2	1		1	4	2		12	1		2									17		2		2		2										1			**61**
27.6. 1:00				6					1			3			1	2			9	1				3					1		8		1				1													**37**
27.6. 5:00	1		1	5					1			1			2	4			9	1		1			1				1		9		2																	**39**
28.6. 5:00	1															4			1						1						3												1							**11**

Tab 7. *Armadillidium versicolor* abundance in experiment 1

Monitor. control	**Shelter position**																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Total
25.6. 1:00																	200								200								200																	**600**
25.6. 5:00								1				1			4	4	4	1		6		1	1	1	29	4		1		1		3	23		3		1	1			7		1		1			1	1	**101**
25.6. 21:00	1		5	3	2	11		4	1	2		1			7	2	3	3	1	13		2	5		17	6	14	7	1		5	1	27		7		3	3		1		2	2		5	1	9	2	1	**180**
26.6. 1:00			2	1	1	1		4		2		13			7	1	5	1	2	4				2	13	6	14	3	1		3		19		6		2	1	1	2			3	1	1		3	2	1	**128**
26.6. 5:00			1		1	8		5		4		8	2		6		5		2	5		1	3		12	3		3	2		2		16		6		4	3		1	1		4		1	1	3		1	**114**
26.6. 21:00	1			1	3	1	2					2	8		4		5		2	5		5	4	1	15	1		13	2		4		11		9			1		1			3		2	2	6	1	3	**118**
27.6. 1:00	1			2		1						2	2		2		2		1	7	1		3		6	2		2			2		9		3		2						1			1				**52**
27.6. 5:00	1		1	3	1					1		2	3		1	3	1		1	7			3		1	1		2	1				6		4		1	1					1		1	1	2	1	1	**52**
28.6. 5:00												1													2					1	5						1									1		3		**14**

Tab 8. Total abundance of both species in experiment 2

Monitor. control	**Shelter position**																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Total
22.9. 19:00																	200		200						200						200		200																	**1**
22.9. 24:00							1			4		1		1	1		2		11	1	1			6	6		1		2		5		5					3	1	1	4	1		1						**59**
23.9. 7:00							1	1		7	1	1			4	1		1	11	2	1		1	13	7				1				2				3	3			1	2	1	1				1	1	**71**
23.9. 19:00	2	2	2				2	1	1	14	5	3		1	7	1		1	11	5	2		3	14	8				1				3	1	1		2	4	1	2	1	4	1	2		1		2		**111**
23.9. 24:00	1				1		2	1		11		1	1	1			1	2	9	2	1			1	3				3						2		4	3				2	1	1				1		**64**
24.9. 7:00					2		1	4		18			1	1	1	1		3	9	2	3			12	4	1			2					1	3	4	3		1		2		3	1						**83**
24.9. 19:00					2		1	3		21				2	3	1	1	4	1	11	2			12	4				2				2	1	3		4	3	2		3	1	3	1						**12**
24.9. 24:00					2			1		5					2			5	7	3	2			13	4	1			2					1	1		4	3	2	1	1	1	1					1		**63**
25.9. 7:00					2					9	1				3	1		4	9	3	6		1	13	8			1	1					1	1		4	4	2		2	1	2					1		**81**
25.9. 19:00					2					1	2	1			3	1		4	9	3	5		1	13	7		1	1	3					2	3		6	3	2	1	2	1	2					2		**9**
25.9. 24:00					2			3		5				1	2	1		4	5	3	6		1	12	4		1	1	2					1	4		4	2	2		4	1	1					1		**73**
26.9. 7:00					2			3		7		1			2	2		4	6	5	5	1	1	14	3	2	1	1	1					3	6		5	4	1		5	3	3	1				1	1	**94**
26.9. 19:00					2			3		8		1		1	2	3		4	6	5	6	1		1	4		1		1			1		2	6		5	2	2	1	6	3	3	2				1	1	**93**
26.9. 24:00					2			1		5					2	1		4	5	6	6			7	4		1					1		2	4		5	1	2	3	3	1	1					2		**7**
27.9. 7:00					2			2	1	5			1		2	2		3	6	5	7			9	4		1							2	4		5	1	3	1	7	1	4					2		**81**
27.9. 19:00				1	2			1							3		2	1	6	5	1			8	1		1		2					2	7		5	2	3	3	6	1	5					2		**71**
28.9. 7:00	1			2	1		1	1		1		2		1	2								3	5			1		1	1				1			5	1					1	1						**32**
29.9. 7:00		1						1				2	1		1		1						3	6			1		1					2			5	2												**28**

Tab 9. *Porcellio scabe*r abundance in experiment 2

Monitor. control	**Shelter position**																																																	Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	
22.9. 19:00																			200												200																			**400**
22.9. 24:00							1										1		10		1								1		5							1												**20**
23.9. 7:00							1					1						1	11	1	1			1					1									1					1					1		**21**
23.9. 19:00		1								1		1			2			1	9	1	1			1					1									1					1			1		1		**23**
23.9. 24:00							1					1						1	7	1				1					1									2					1					1		**17**
24.9. 7:00							1	1										1	7		1			1					1							1	2						2							**18**
24.9. 19:00							1											1	8	9				1					1								1	2					1							**25**
24.9. 24:00																		1	5					2					1								1	3										1		**14**
25.9. 7:00																		1	8					2	1				1								1	3					1							**18**
25.9. 19:00																		1	8					2	1				1								1	3					1					1		**19**
25.9. 24:00																		1	5					2	1				1								1	2												**13**
26.9. 7:00																		1	6					2	1	2								1			1	2				1	1						1	**19**
26.9. 19:00																		1	6					1													1	1				1	1						1	**13**
26.9. 24:00																		1	5					1													1	1												**9**
27.9. 7:00																			6					1													1	1												**9**
27.9. 19:00																			6					1													1	1					1							**10**
28.9. 7:00																																																		**0**
29.9. 7:00																								1													1	1												**3**

Tab 10. *Armadillidium versicolor* abundance in experiment 2

Monitor. control	Shelter position																																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Total
22.9. 19:00																	200								200								200																	**600**
22.9. 24:00										4		1		1	1		1		1	1				6	6		1		1				5					2	1	1	4	1		1						**39**
23.9. 7:00								1		7	1				4	1				1			1	12	7								2				3	2	1		1	2		1				2	1	**50**
23.9. 19:00	2	1	2				2	1	1	13	5	2		1	5	1			2	2	1		3	13	8								3	1	1		2	3	1	2	1	4		2				3		**88**
23.9. 24:00	1				1		1	1		11			1	1			1	1	2	1	1			9	3				2						2		4	1				2		1						**47**
24.9. 7:00					2			3		18			1	1	1	1		2	2	2	2			11	4	1			1					1	3	3	1		1		2		1	1						**65**
24.9. 19:00					2			3		21				2	3	1	1	3	2	2	2			11	4				1				2	1	3		3	1	2		3	1	2	1						**77**
24.9. 24:00					2			1		5					2			4	2	3	2			11	4	1			1					1	1		3		2	1	1	1	1							**49**
25.9. 7:00					2					9	1				3	1		3	1	3	6		1	11	7			1						1	1		3	1	2		2	1	1					2		**63**
25.9. 19:00					2					1	2	1			3	1		3	1	3	5		1	11	6		1	1	2					2	3		5		2	1	2	1	1					1		**62**
25.9. 24:00					2			3		5				1	2	1		3		3	6		1	1	3		1	1	1					1	4		3		2		4	1	1					1		**51**
26.9. 7:00					2			3		7		1			2	2		3		5	5	1	1	12	2		1	1	1					2	6		4	2	1		5	2	2	1				1		**75**
26.9. 19:00					2			3		8		1		1	2	3		3		5	6	1		9	4		1		1			1		2	6		4	1	2	1	6	2	2	2				1		**80**
26.9. 24:00					2			1		5					2	1		3		6	6			6	4		1					1		2	4		4		2	3	3	1	1					3		**61**
27.9. 7:00					2			2	1	5			1		2	2		3		5	7			8	4		1							2	4		4		3	1	7	1	4					3		**72**
27.9. 19:00				1	2			1							3		2	1		5	1			7	1		1		2					2	7		4	1	3	3	6	1	4					3		**61**
28.9. 7:00	1			2	1		1	1		1		2		1	2								3	4			1		1	1				1			4						1	1						**29**
29.9. 7:00		1						1				2	1		1		1						3	5			1		1					2			4	1										1		**25**

Tab 11. Frequency of aggregation size categories in experiment 1

Aggregation categories	Releasing	Monitoring control						
		1	2	3	4	5	6	7
0	44	13	14	15	18	25	19	38
1	0	9	8	10	7	7	13	7
2 - 5	0	18	13	13	12	11	10	3
6 - 10	0	3	7	7	6	6	6	1
11 - 25	0	5	7	4	6	0	1	0
26 and more	5	1	0	0	0	0	0	0

Tab 12. Frequency of aggregation size categories in experiment 2

Aggregation categories	Releasing	Monitoring control																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18
0	44	28	25	16	26	25	24	27	26	23	24	20	20	26	25	26	30	36
1	0	11	14	12	11	9	6	9	9	7	9	10	9	7	6	7	13	7
2 - 5	0	7	6	16	9	12	15	11	9	14	14	15	14	13	14	12	6	5
6 - 10	0	2	2	2	2	1	1	1	4	4	1	3	6	3	4	4	0	1
11 - 25	0	1	2	3	1	2	3	1	1	1	1	1	0	0	0	0	0	0
26 and more	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0