

## Oribatid mites may actively migrate faster and over longer distances than anticipated: experimental evidence for *Damaeus onustus* (Acari: Oribatida)

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### Abstract

The ability of active dispersal of *Damaeus onustus* C. L. Koch, 1844 was studied under laboratory conditions. Six individuals were observed in 15 repetitions, each at least for 30 minutes. The overall time of observation reached 278 minutes. Mites moved actively for several tens of minutes, mostly away from the source of light and heat (negative thermo- and phototaxis). The maximum speed measured reached 3.12 mh<sup>-1</sup>; the average speed was 1.00 mh<sup>-1</sup> with median at 0.86 mh<sup>-1</sup>. The specimens differed mutually, both in maximum and average speed (the latter ranking between 0.49 and 1.82 mh<sup>-1</sup>). During the experiment all individuals were able to reach a distance of at least 10 cm from their starting point, the maximum distance was 28.2 cm. Based on the measured distances it may be assumed that *Damaeus onustus* is able to disperse actively faster and over larger distances than generally anticipated of oribatid mites, particularly in escape from non-favourable conditions.

**Keywords** *oribatid mites* | active migration | speed | dispersal | *Damaeus onustus*

### 1. Introduction

Dispersal of oribatid mites by active migration is considered negligible or very slow (e. g. Behan-Pelletier & Winchester, 1998; Skubala, 2004; Weigmann, 1982), based on observation of their very low mobility. But very limited information from field studies is available to prove this assumption. Berthet (1964) found that the average daily migration distance of 5 different oribatid species was between 0.34 and 4.11 cm, with a maximum reached between 7.5 and 42 cm in a day depending on the species. The results for the same species varied under different conditions, depended on the temperature and humidity and were related to the season of the year. Ojala & Huhta (2001) who observed the active dispersal of 18 oribatid genera from forest soils, concluded that the fastest spreading individuals of the genus *Oppiella*

reached a speed of up to 20 cm per week, and calculated distances that might be potentially covered per year of up to 120 m assuming a yearly activity of 5 months. Recently, Lehmitz et al. (2012) studied active dispersal of oribatid mites both on the surface and below-ground in sophisticated field experiments, using micro-pitfalls and mini-traps. The results from the oribatid species involved varied between 0.3 and 2.1 cm per day.

There is only anecdotic information about the potential ability of oribatid mites to disperse actively, although the oldest information about migration speed obtained under laboratory conditions was presented already by Nicolet (1855). His results suggest that the speed of movement of various species can reach 0.1–5.7 cm per minute. Woodring & Cook (1962) indicated a speed of 2.4 cm min<sup>-1</sup> for *Schelorbitates laevigatus*. Prinzing (2003) assumed an average speed for two oribatid spe-

**Table 1.** Overview of published data on speed of movement of selected oribatid species. Laboratory observations were re-calculated in meters per hour, dispersal measured in field conditions is given in cm per day, as presented by most of cited authors.

species	laboratory speed (mh <sup>-1</sup> )		distance in field (cm/day)		author
	max	average	max	average	
<i>Achipteria coleoprata</i>	1.26	1.08			Wunderle 1992
<i>Achipteria nitens</i>	0.63				Nicolet 1855
<i>Adoristes (poppei)</i>			2.86*	0.59*	Ojala & Huhta 2001
<i>Autogneta longilamellata</i>	0.90	0.84			Wunderle 1992
<i>Camisia horrida</i>	0.05				Nicolet 1855
<i>Carabodes coriaceus</i>	0.36	0.24			Wunderle 1992
<i>Carabodes labyrinthicus</i>	< 5.40				Prinzling 2003
	1.08	0.66			Wunderle 1992
<i>Carabodes (subarcticus)</i>			0.95*	0.09*	Ojala & Huhta 2001
<i>Cepheus cepheiformis</i>	0.45				Nicolet 1855
<i>Cepheus latus</i>	1.08				Nicolet 1855
<i>Ceratoppia bipilis</i>	3.00				Nicolet 1855
<i>Chamobates (schuetzi)</i>			2.86*	1.18*	Ojala & Huhta 2001
<i>Conchogneta (traegardhi)</i>			2.86*	0.47*	Ojala & Huhta 2001
<i>Cyberemaeus cymba</i>	1.14	1.02			Wunderle 1992
	3.40				Nicolet 1855
<i>Damaeus clavipes</i>	3.96	3.24			Wunderle 1992
<i>Damaeus onustus</i>			0.34	8.50	Berthet 1964
<i>Dissorhina ornata</i>	0.90	0.84			Wunderle 1992
<i>Domotorina plantivaga</i>	1.62	1.20			Wunderle 1992
<i>Edwardzetes edwardsi</i>	1.71				Nicolet 1855
<i>Eulohmannia (ribagai)</i>				1.18*	Ojala & Huhta 2001
<i>Eupelops acromios</i>	1.13				Nicolet 1855
<i>Euzetes globulus</i>			0.65	7.50	Berthet 1964
<i>Galumna alata</i>	1.01				Nicolet 1855
<i>Hemileius (initialis)</i>			1.43*	1.18*	Ojala & Huhta 2001
	0.75				Nicolet 1855
<i>Hermannia gibba</i>	0.90	0.72			Wunderle 1992
	0.84				Nicolet 1855
<i>Liacarus coracinus</i>	1.26	1.08			Wunderle 1992
			1.43*	0.68*	Ojala & Huhta 2001
<i>Liacarus nitens</i>	0.51				Nicolet 1855
<i>Nothrus palustris</i>			1.70	11.00	Berthet 1964
<i>Nothrus silvestris</i>				0.79*	Ojala & Huhta 2001
<i>Ommatocephus ocellatus</i>	0.12	0.12			Wunderle 1992
<i>Oppiella (nova)</i>			2.85*	236*	Ojala & Huhta 2001
<i>Oppiella (subpectinata)</i>				0.47*	Ojala & Huhta 2001
<i>Oribatella quadricornuta</i>	2.28	1.92			Wunderle 1992
	1.29				Nicolet 1855
			2.86*	1.18*	Ojala & Huhta 2001
<i>Paleacarus (hystricinus)</i>			0.95*	0.79*	Ojala & Huhta 2001
<i>Parachipteria (punctata)</i>				0.57*	Ojala & Huhta 2001
<i>Pergalumna nervosa</i>	2.22	2.16			Wunderle 1992
<i>Phthiracarus nitens</i>	0.30				Nicolet 1855
<i>Phthiracarus sp.</i>			0.71*	0.18*	Ojala & Huhta 2001
<i>Scutovertex sculptus</i>			min. 2.1		Lehmitz et al. 2012
<i>Schelorbates ascendens</i>	1.80	1.50			Wunderle 1992
<i>Schelorbates laevigatus</i>	1.44				Woodring & Cook, 1962
<i>Schelorbates pallidulus</i>	1.68	1.50			Wunderle 1992
<i>Steganacarus carinatus</i>				1.43*	Ojala & Huhta 2001
			0–4.11	0–21.5	Berthet 1964
<i>Steganacarus magnus</i>	0.60				Nicolet 1855
<i>Suctobelbella spp.</i>				1.18*	Ojala & Huhta 2001
<i>Tectocephus sarekensis</i>			min. 0.3		Lehmitz et al. 2012
			0.57*	0.47*	Ojala & Huhta 2001
<i>Tectocephus velatus</i>	0.24	0.24			Wunderle 1992
<i>Trichoribates incisellus</i>			min. 1.5		Lehmitz et al. 2012
<i>Xenillus discrepans</i>	< 5.40				Prinzling 2003
<i>Xenillus tegeocranus</i>			0.6–3.14	8.5–42.0	Berthet 1964

\* measures originally given in cm per week, here transposed for cm per day

cies being less than  $0.15 \text{ cm s}^{-1}$  (i. e. below  $9 \text{ cm min}^{-1}$ ). The most comprehensive recent information is from 16 oribatid species from a beech-forest in Germany by Wunderle (1992), who documented an average mobility between  $0.2$  and  $5.4 \text{ cm min}^{-1}$  and a maximum between  $0.2$  and  $6.6 \text{ cm min}^{-1}$  depending on the species. Most of the available information by mentioned authors (Tab. 1) was gained from single individuals, with exception of arboricolous species studied by Wunderle (1992), so the individual variability within the species under same or similar conditions is unknown and difficult to judge.

Even less information is available about the frequency and duration of 'active movement' of oribatids, both in field or under laboratory conditions. Measurement and observation of migration behavior of oribatid mites were often restricted to particular situations (e.g. Madge, 1964; 1966; Smrž, 1996; 2005; Wunderle, 1992), but none of the authors measured active movement under varying conditions, ignoring that in certain conditions migration may stop even over a period of a whole day.

The aim of this study is therefore to estimate (a) how fast specimens of the selected oribatid mite species may migrate under controlled conditions, (b) if the tested specimens could migrate only shortly or for longer period and what distance could be theoretically reached in a certain period of time, and (c) to provide information about individual intraspecific variability of migration speed and distance.

## 2. Material and methods

The results presented in this paper deal with one of the largest European oribatid species, *Damaeus onustus* C. L. Koch 1844. Living adult specimens of *Damaeus onustus* were collected from litter and upper soil layer of a forested strip along the former railway at the connection of Tervuren and Wezembeek Oppem, between Astridlaan and Grensstraat, east of Brussels Capital Region/Belgium (GPS  $50^{\circ}49'57.04''$  N,  $4^{\circ}30'42.45''$ ,  $107 \text{ m asl}$ ). The broad-leaved forest consists mostly of mixture of maples, oaks, beeches, wild-cherries and acacias, with admixture of other species. Litter was collected 3 times (18.3.2016, 20.3.2016 and 26.3.2016) and extracted for 2–3 days. Altogether about 5–10 individuals were extracted each time, individuals for experiments were selected randomly from those without visible damages (such as lost leg segments etc.). Altogether 6 different individuals (indicated as A–F) were studied in detail.

Mites were extracted using a modified Berlese-Tullgren apparatus into containers with round cotton

pads saturated with water. During and between the experiments, specimens which were not actually observed were kept either (short-term) in small glass vials with the same arrangements to maintain humidity, or in plastic boxes with water-saturated kitchen-paper covered by paper sheet and fine layer of soil particles sieved from the original sample. Movement of mites was studied as soon as possible, but not later than 48 hours after extraction. The speed of the movement was registered using two different settings: (1) in flat plastic boxes ( $ca 20 \times 14 \text{ cm}^2$ ), with a thick layer of water-saturated kitchen-paper and a cover of paper with  $5 \times 5 \text{ mm}^2$  net pattern (Fig. 1); (2) for longer observations without disturbance, larger ( $ca 35 \times 25 \text{ cm}^2$ ), colour cardboard-paper was used without underlying layer of water-saturated paper (Fig. 2). In both settings, mites were put in the middle of the paper and their movement was observed. The position of the mite after every 30 seconds (or every minute) was marked on the paper by a pencil. The mites were observed until they reached the margins of the available space, for repeated observation they were put again in the middle of paper using a very fine wet brush. To estimate a maximum speed, the longest distance passed in a minute was measured.

The experiments were carried out during evening and night hours (between 9 pm and 2 am), at room temperature ( $21^{\circ}\text{C}$ ), with source of light and heat (table lamp with bulb 40W) located in both settings at a standard place roughly above the upper right corner of the paper, ca. 25 cm above the paper surface.

Immediately after observation, the points indicating the sequential positions of mites were connected. Achieved patterns were analysed, distances measured and evaluated individually as well as for the experimental set. The immobility for more than 1–2 seconds was considered as a stop. Distances were measured in millimetres (individual time segments) and centimetres (overall distance reached), but movement speed is finally transposed and given in  $\text{mh}^{-1}$ .

Each specimen was observed within a single day (in 1 to 4 repetitions), with an overall observation time of at least 30 minutes (30–76 minutes). The six individuals were observed in 4 days for altogether 278 minutes.

Apart of real speed of movements observed as measured distance per each time segment, calculation of 'effective speed' was made. This represents a largest distance reached within any particular time period from the starting point. Given the non-linear movement and frequent changes of direction the effective speed is always lower than overall distance walked by mites.

Distribution of measured values was tested for normality by Shapiro-Wilk test (at  $p=0.01$ ), using QtiPlot software.

### 3. Results

Observed mites were generally moving faster and for longer period as originally expected. Therefore, all observations apart from those of specimen A (fully) and B (second repetition) were made on larger paper, taking into account the relative body size of the observed mites. For specimens A and D there were 4 repetitions, two repetitions for specimens B, E and F, and only one for specimen C (Tab. 2).

#### 3.1. Continuity of movement

All individuals started to move immediately after being released at the starting point. Individuals C, D, E and F moved continuously and without stops throughout the whole observation time. Individual A stopped for 15 sec in one of the four repetitions after 12 minutes of continuous movement. Specimen B stopped movement more often and for periods of 1–2 minutes (5 times), 2–3 minutes (once) and 3–4 minutes (2 times), in the interval

between 13th and 39th minute of a 63-minute observation. During experimental observation (total of 278 minutes), there were only 13 one-minute segments (less than 5% of time) without any movements, all from individual B. For this individual, the proportion of inactivity was about 20% of the observation period.

During the experiments, the other individuals were kept in parallel containers. Even if not followed in detail, they were more or less constantly moving. No stops or phase of immobility were observed during each day of experiments (at least for 80–130 min). Therefore it can be concluded that *Damaeus onustus* is able to move continuously for up to at least 1–2 hours in a given day.

#### 3.2. Direction of movement

Two different directional patterns were observed in the experiments. In a box with a layer of wet paper, mites moved randomly, undirected and changed their direction often (Fig. 1). In a larger area, without humidity management, with a more apparent light (and heat)

**Table 2.** Observed movement speed of *Damaeus onustus*. Different specimens (A–F) were observed in 1–4 repetitions, each in summary for at least 30 minutes. Acronyms for conditions: **l, d** – observation on large paper, in dry conditions; **s, h** – observation on smaller paper, with balanced humidity (see methods for details).

individual	repetition	conditions	time (min)	observed speed (m/hr)				
				minimum	maximum	median	average	SD
A	1	s, h	16	1.53	2.34	1.95	1.94	0.25
	2	s, h	2	2.25	2.28	2.27	2.27	0.02
	3	s, h	13	1.32	2.01	1.92	1.78	0.24
	4	s, h	9	0.27	2.13	1.77	1.56	0.56
	<b>total</b>		<b>40</b>	<b>0.27</b>	<b>2.34</b>	<b>1.95</b>	<b>1.82</b>	<b>0.38</b>
B	1	l, d	63	0	1.11	0.39	0.43	0.33
	2	s, h	13	1.5	3.12	2.28	2.27	0.34
	<b>total</b>		<b>76</b>	<b>0</b>	<b>3.12</b>	<b>0.48</b>	<b>0.74</b>	<b>0.77</b>
C	<b>total</b>	<b>l, d</b>	<b>39</b>	<b>0.12</b>	<b>0.81</b>	<b>0.48</b>	<b>0.49</b>	<b>0.21</b>
D	1	l, d	8	0.87	2.04	1.41	1.40	0.31
	2	l, d	9	1.35	1.86	1.47	1.55	0.17
	3	l, d	9	1.29	1.77	1.5	1.53	0.12
	4	l, d	15	1.02	2.04	1.68	1.66	0.25
	<b>total</b>		<b>41</b>	<b>0.87</b>	<b>2.04</b>	<b>1.5</b>	<b>1.56</b>	<b>0.25</b>
E	1	l, d	13	0.27	1.05	0.72	0.72	0.2
	2	l, d	17	0.45	1.17	0.81	0.8	0.17
	<b>total</b>		<b>30</b>	<b>0.27</b>	<b>1.17</b>	<b>0.78</b>	<b>0.76</b>	<b>0.19</b>
F	1	l, d	22	0.42	1.44	0.83	0.82	0.18
	2	l, d	30	0.63	1.05	0.87	0.86	0.09
	<b>total</b>		<b>52</b>	<b>0.42</b>	<b>1.44</b>	<b>0.86</b>	<b>0.84</b>	<b>0.14</b>
ALL	<b>total</b>		<b>278</b>	<b>0</b>	<b>3.12</b>	<b>0.86</b>	<b>1</b>	<b>0.64</b>

gradient, the mites showed a clear negative photo- and thermotaxis. In most cases the movement was rather straight to the shortest way to escape (Fig. 2). Negative phototaxis was triggered in two individuals by changing the position of light and heat source (after 4 and 11 minutes, respectively, from the beginning of observation). In both cases, the observed specimens changed their direction almost immediately and started to move away from the source, whereby a sharp U-turn was observed (exclamation sign in Fig. 2).

Light and temperature obviously have an impact on the direction and straightness of movement, both being straighter in clearer gradients.

### 3.3. Speed of movement

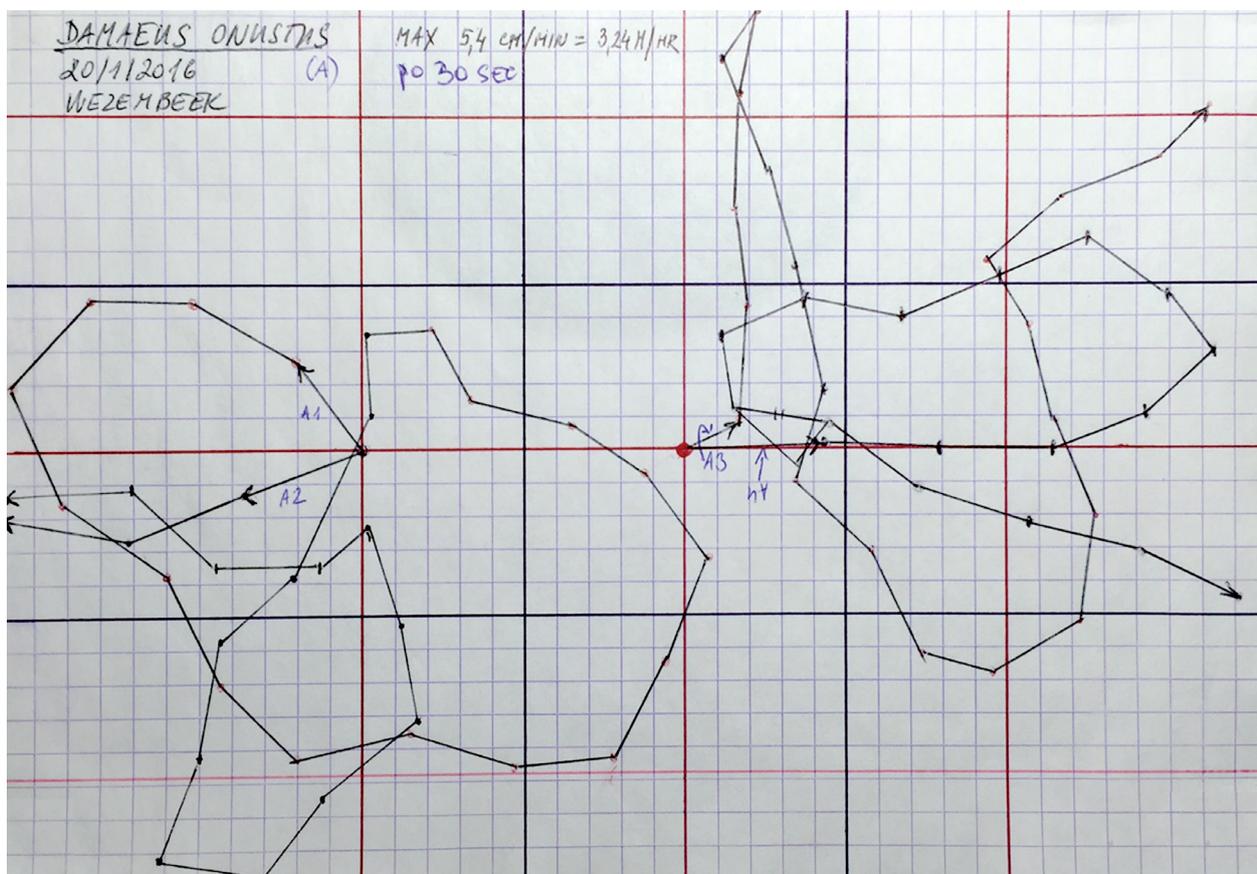
The speed of movement, both maximum and average, varied considerably: within each repetition of the same individual, as well as between the individuals. Results are summarized in Tab. 2.

The maximum speed observed, occurred in specimen B ( $3.12 \text{ mh}^{-1}$ ) which was significantly higher than maximum

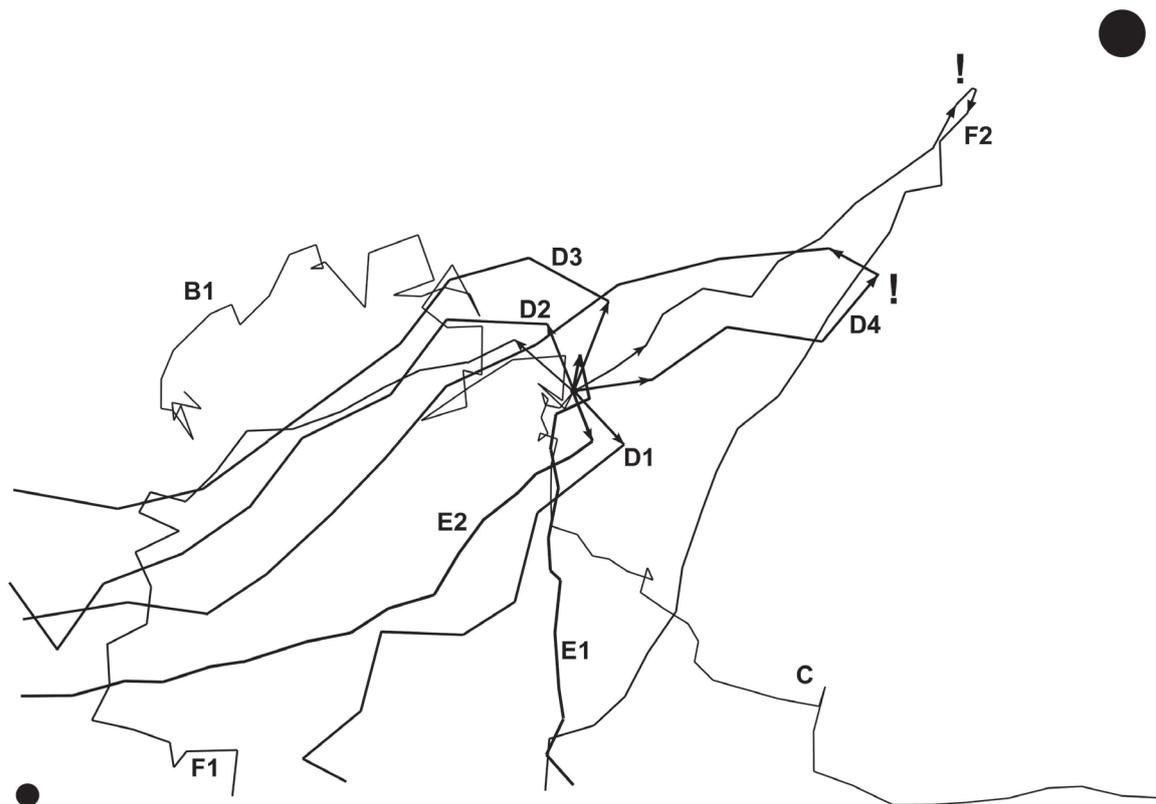
speed of other individuals which ranged between  $2.00 \text{ mh}^{-1}$  in individuals A and D and  $1.00 \text{ mh}^{-1}$  (individual E and F) or even below  $1.00 \text{ mh}^{-1}$  (individual C).

Average speed also differed between individuals, ranging from  $1.82 \text{ mh}^{-1}$  being 4 times higher than the slowest one ( $0.49 \text{ mh}^{-1}$ , individual C). The speed range is indicated in Fig. 3. At least two patterns could be observed with regard to speed: individuals A and D moved with  $1.50$  to  $2.00 \text{ mh}^{-1}$  for most of the time (Fig. 4c), whereas the remaining individuals except B were slower (mostly between  $0.40$  and  $1.00 \text{ mh}^{-1}$ ; see also Tab. 2). In all cases, the speed was rather stable what is demonstrated also by low standard deviation of measured data. Individual B was very slow or immobile for longer periods. Higher standard deviation for this species relate to much increased speed after transfer into an area with balanced humidity (reaching values between  $2$  and  $2.5 \text{ mh}^{-1}$ , see also Fig. 3), also indicated by a higher standard deviation. The mean of all specimens tested reached  $1.00 \text{ mh}^{-1}$  ( $\pm 0.64$ ), with median of  $0.86 \text{ mh}^{-1}$ .

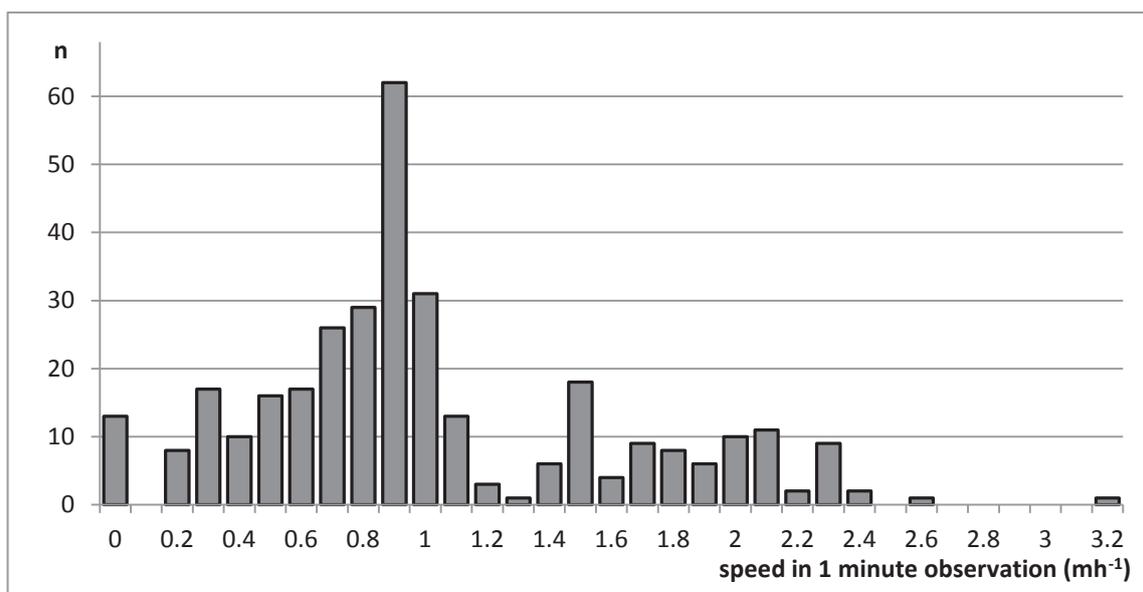
Overall distribution of measured speed within the one minute intervals (Fig. 4) shows a clear peak slightly below  $1.00 \text{ mh}^{-1}$ . The frequency of higher speeds and their variation with abrupt decline after main peak and



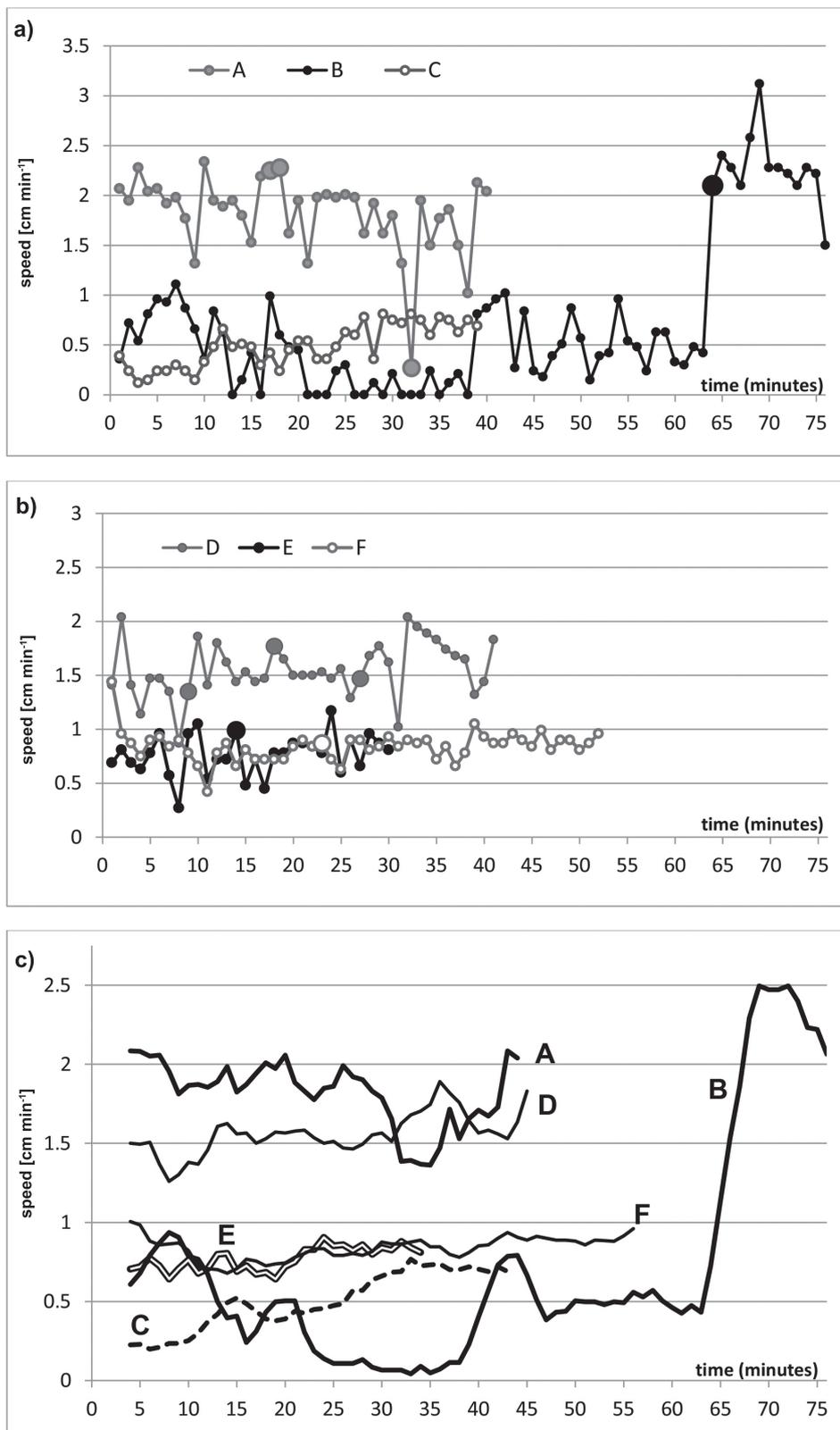
**Figure 1.** Copy of an original record of movement of *Damaeus onustus* (specimen A) on smaller paper with balanced humidity (see methods for details). Repetitions are indicated by A1 to A4, positions were recorded after 30 seconds of movement, for later analysis they were summarized by one minute.



**Figure 2.** Movement of observed specimens of *Damaeus onustus* (B–F) on large paper. Numbers indicate individual repetitions; mites were put on the point in the centre and their movement after each minute marked. Large black dot indicates position of light and heat source, smaller black dot indicates the same in first part of observation of D4 and F2. Exclamation marks indicate the moment when position of light and heat source was changed back to original.



**Figure 3.** Distribution and frequency of measured speeds reached by all observed specimens of *Damaeus onustus* per minute of observation. Classes are given in intervals of 0.1 mh<sup>-1</sup>.



**Figure 4.** Speed of the movement of all observed specimens (A–F) of *Damaeus onustus*, plotted in real distance in centimetres per minute of observation. Above diagrams showing speed (a) of specimens A–C and (b) of specimens D–F. Enlarged dots indicate the transfer of individual to start point after reaching margins of observation area. Diagram below (c) shows running average of measured speed of all specimens over a five minute interval for specimens A–F.

**Table 3.** Effective speed of dispersal and maximally reached distance by *Damaeus onustus* in experiments. For each specimen/repetition combination, the time in which certain distance from starting point (from 2.5 to 25 cm) was reached, and effective speed of dispersal calculated. Time in parentheses indicates the estimated time when given distance would be reached – in case that mites reached the border of observation area. Repetitions with added (a) and (b) indicate part of the movement before (a) and after (b) change of position of light and heat source. Speed is given in  $\text{mh}^{-1}$ , reached distances in centimetres.

individual/ repetition	2.5 cm		5 cm		7.5 cm		10 cm		12.5 cm		15 cm		20 cm		25 cm		maximum distance reached (cm)
	min*	speed**	min	speed	min	speed	min	speed	min	speed	min	speed	min	speed	min	speed	
A1	1	1.50	2	1.50	(12)	0.38	–	–	–	–	–	–	–	–	–	–	6.8
A2	1	1.50	2	1.50	–	–	–	–	–	–	–	–	–	–	–	–	5.6
A3	2	0.75	2	1.50	10	0.45	(11)	0.55	–	–	–	–	–	–	–	–	9.5
A4	1	1.50	2	1.50	3	1.50	–	–	–	–	–	–	–	–	–	–	8.4
B1	6	0.25	15	0.20	38	0.12	47	0.13	52	0.14	–	–	–	–	–	–	12.6
C	11	0.14	14	0.21	21	0.21	25	0.24	29	0.26	32	0.28	38	0.32	–	–	21.9
D1	2	0.75	3	1.00	4	1.13	6	1.00	7	1.07	(9)	1.00	–	–	–	–	14.4
D2	2	0.75	3	1.00	4	1.13	5	1.20	6	1.25	7	1.29	–	–	–	–	18
D3	1	1.50	3	1.00	6	0.75	7	0.86	8	0.94	9	1.00	–	–	–	–	16.3
D4(a)	2	0.75	2	1.50	3	1.50	4	1.50	–	–	–	–	–	–	–	–	–
D4(b)	2	0.75	3	1.00	3	1.50	4	1.50	5	1.50	6	1.50	8	1.50	10	1.50	28.2
E1	5	0.30	7	0.43	9	0.50	11	0.55	14	0.54	–	–	–	–	–	–	12.2
E2	3	0.50	6	0.50	7	0.64	9	0.67	11	0.68	13	0.69	(17)	0.71	–	–	19
F1	2	0.75	4	0.75	6	0.75	7	0.86	10	0.75	16	0.56	–	–	–	–	17.7
F2(a)	2	0.75	4	0.75	6	0.75	8	0.75	10	0.75	12	0.75	–	–	–	–	–
F2(b)	3	0.50	5	0.60	6	0.75	8	0.75	10	0.75	12	0.75	15	0.80	(31)	0.48	24.8
average		0.81		0.93		0.75		0.75		0.78		0.87		0.83		0.99	

\* number in this column indicates in which minute of movement the given distance from starting point was reached by particular specimen

\*\* average speed calculated for a given periode of movement, in  $\text{mh}^{-1}$

other slightly indicated peaks (around 1.50 and 2.00  $\text{mh}^{-1}$ ) suggests potential presence of several speed ‘modes’. The idea is supported by the fact that the distribution of results does not correspond to normal distribution ( $p = 0.01$ ,  $W = 0.7474$ ).

In conclusion, results indicate that *Damaeus onustus* may move with a maximum speed of at least 3.12  $\text{mh}^{-1}$ . The average speed, however, is three times slower.

### 3.4. Effective speed of dispersal

Mites rarely moved straight in one direction, even in the case of negative phototaxis they were escaping in slightly different angles (Fig. 2). Thus, the real distance from starting point is in a given time mostly shorter than the overall distance travelled (Tab. 3). With few exceptions, mites pass distances of up to 5 cm very quickly (usually within 2–4 minutes, Tab. 3), whereas larger distances are passed slower and reached more rarely. Even if there were differences in the observation time between individuals and in some cases animals hit the limit of the observation area, they always had the same space to reach a certain distance. From 16 repetitions, mites reached a distance of 5 cm in all cases, 10 cm in 13 cases, 20 cm in 4 cases and 25 cm only twice. The largest distance measured was 28.2 cm, reached in less than 12 minutes (Fig. 2, Tab. 3). The average speed, in which particular distances were reached, is rather similar (0.75–0.99  $\text{mh}^{-1}$ ; Tab. 3), with an average of 0.82  $\text{mh}^{-1}$ .

## 4. Discussion

Data to compare our results on the speed, continuity and direction of movement are rare. The maximum speed measured here (3.12  $\text{mh}^{-1}$ ) does not differ substantially from that reported by other authors (Wunderle 1992, Nicolet 1855). For *Damaeus clavipes*, species of similar size and life strategy, Wunderle (1992) measured a maximum speed of 6.6  $\text{cm min}^{-1}$  (3.96  $\text{mh}^{-1}$ ). Nicolet (1855) calculated for the same species a maximum of 5.7  $\text{cm min}^{-1}$  (mean 3.42  $\text{mh}^{-1}$ ). In 5 repetitions, Wunderle (1992) found the average speed of *D. clavipes* at a level of 5.4  $\text{cm min}^{-1}$ , corresponding to the results presented here (3.12  $\text{mh}^{-1}$ ). However, only 5 observations (5 one minute segments) on the same individual were used, while our results are compiled from 6 individuals and altogether 278 minutes of observation. The observed speed is, even within a rather small group of individuals, very variable. This means that mites are able to adapt their speed to individual or environmental demands.

Based on the results of this study, which indicate that surface-dwelling oribatid mite *Damaeus onustus* could sustain in continuous movement for at least 1–2 hours and depending on conditions may reach effectively distance of about 0.80 m in one hour, the capability of this species to disperse is potentially much higher than expected. Even when considering not more than 4–5 hours of migration per day and an ‘effective’ speed of movement (0.82  $\text{mh}^{-1}$ ) and migrations restriction (due to seasons) to 5 months of year, an individual of *Damaeus onustus* may theoretically cover a distance up to 400–600 m per year.

It is difficult to judge, to what extent this potential can be realised in field conditions. Mites, particularly if they live under suitable conditions (humidity, food, shelter, etc.), do not necessarily need to move longer distances. Only Berthet (1964) presents migration distance data from a field experiment for *Damaeus onustus*. He found an average daily displacement of only 0.34 cm, with a maximum of 8.5 cm. These values are low compared to their theoretically calculated ability (around 3.20–4.00 m per day), but may result at least partly also from low temperature (5°C). The results of Lehmitz (2012) and Ojala & Huhta (2001), however, also suggest a slower dispersal under field conditions.

Madge (1964) found that individuals of *D. onustus* prefer habitats with higher humidity; this preference is even more pronounced if they are starving. He also found (Madge 1966), that mites tend to move, if on a smooth substrate, while on rough ones they stay for long periods. In the present investigation the influence of substrate texture was not tested, but, as demonstrated on individual B, humidity may have an impact on speed of movement.

The experiments presented above (Berthet, 1964, Madge 1964, Ojala & Huhta 2001, Lehmitz et al. 2012) show the movement of mites within their ordinary habitat. The results indicate the (low) probability that mites will leave relatively good conditions and ‘explore’ new areas, and document – among others – that they may not (re-)invade defaunated or disturbed habitats from suitable habitats easily. Under these conditions it is not surprising that the effective speed of dispersal in the field is comparably very slow.

On the other hand, laboratory conditions, such as in our experiment, rather constitute stress situations (direct exposure to light and heat, absence of food, desiccation), where fast and directed movement may be a prerequisite for survival. The differences in oribatid behaviour under different level of stress may be deducted from observed (at least) two modes of movement: slower ‘walking around’ (between 0.40 and 1.00  $\text{mh}^{-1}$ ) and faster ‘wandering’ (above 2.00  $\text{mh}^{-1}$ ), better suited for larger distances. However, confirmation of these two modes of movement and their relation to environmental conditions

needs further experiments allowing more extensive statistical analysis.

The present data in any case reveals that oribatids may move rather quickly and, when in stress, have the potential to cover larger distances to colonize new habitats or escape from less favourable conditions. This may contribute significantly to active dispersal, colonisation of new habitats and survival of populations, which is in practice relevant e.g. to ecosystem restoration.

## 5. References

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