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MOBILITY, ACTIVITY AND MIGRATION ABILITY OF *STRIGILLARIA CANA* (STYLOMMATOPHORA: CLAUSILIIDAE)

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ABSTRACT: *Strigillaria cana* mobility was observed in natural conditions in lowland mixed forest in NE Poland. Adult individuals cover a mean distance of 164 mm per hour when moving on a tree trunk. Their average speed was 4.76 mm/min and 19 mm/min maximum. *Strigillaria cana* activity depends on humidity. The distance covered by snails and the percentage of active individuals increase at high air humidity. The time of the day (day/night) did not influence *Strigillaria cana* activity. *Strigillaria cana* specimens show limited dispersal. Of 485 observed adults, 59% never changed the tree on which they were present. Specimens that migrate did not move far from their original location, and most of them (86.2%) cover distances of less than 10 m between trees.

KEY WORDS: dispersion; movement; seasonal activity

INTRODUCTION

Land snails are slow organisms with limited mobility. Production of mucus necessary for locomotion takes a lot of energy and makes snails' crawling the most expensive type of movement (DENNY 1980). To reduce that expenditure, snails adapt life strategies minimising a need for locomotion (SPEISER 2001). However, movement is an important aspect of life, used to find food, shelter and breeding partners. It also enables the snails to leave sites with adverse conditions and to reach and colonise new sites. Dispersal influences demographic processes within the population and affects gene flow between populations (SLATKIN 1987). Individual species of snails differ in their ability and tendency for dispersal. Its extent depends both from the snail's ability to change its habitat actively and from passive transport.

The effectiveness of passive transport of land snails (as well as other groups of animals) is evidenced by the rich fauna of oceanic islands (SOLEM 1974), although the conditions favourable for snails: the range of niches and stable climatic conditions also play a significant role for the settlement of these areas (SOLEM 1984). On the other hand, it may seem surprising that on continents, there are small, local populations that are genetically isolated from each other without clear environmental barriers (CAMERON 2013). A species' activity in its natural environment can be one of the many factors influencing the occurrence and overall range of a species, and it is worth paying some attention.

The clausiliid species *Strigillaria cana* was originally described by HELD (1836) in the genus *Clausilia*. Until recently, it was known as *Bulgarica cana*. According to the current taxonomy, it belongs to the Clausiliinae subfamily and the Baleini tribe (BOUCHET et al. 2017, NORDSIECK 2019). However, the genus *Bulgarica* O. Boettger, 1877 was replaced by the earlier genus *Strigillaria* Vest, 1867 (NORDSIECK 2019). *Strigillaria cana* is a central and east European species (LIKHAREV 1962, KERNEY et al. 1983, WELTER-SCHULTES 2012, MARZEC 2017) with well-known biology (MARZEC 2018). It is a long-living species, and its growth in its natural habitat takes more than three years (MARZEC 2018). It inhabits moist deciduous and mixed forests of natural character (LIKHAREV 1962, KERNEY et al. 1983, WIKTOR 2004, HORSÁK et al. 2013), with a strong preference for well-preserved and undisturbed tree stands. It is a strictly dendrophilous species (HORSÁK et al. 2013), living on trunks and in bark crevices of standing or fallen trees (LIKHAREV 1962, KERNEY et al. 1983, SULIKOWSKA-DROZD 2005, HORSÁK et al. 2013). This paper presents the results of a study of *Strigillaria cana* mobility and migration ability in its natural habitat.

RESEARCH AREA

All observations were carried out in the Romincka Forest, NE Poland. It is a compact forest of ca. 360 km^2 situated east of the town of Gołdap (54°18'22"N, 22°18'13"E) on both sides of the Polish–Russian (Kaliningrad Oblast) border. Romincka Forest is a part of the East European Lowland and belongs to the Lithuanian Lakeland macroregion (KONDRACKI 2000). In the geobotanical division of Poland, it belongs to North Section, Augustowski-Suwalski Land. This area is characterised by the most severe climate in the Polish lowlands, with the lowest average annual temperature (6.2 °C) and the shortest growing season (MATUSZKIEWICZ 2007). Among the habitat types of forests, the typical dry-ground forest (*Tilio-Carpinetum*) with a large amount of spruce dominates. There are also many patches of mixed woods and wet or swampy forests. In Romincka Forest, there is a rich land snail fauna (60 species), with 12 clausiliid species (MARZEC 2010). This area is protected as a Natura 2000 site (PLH280005) and the Romincka Forest Landscape Park.

The research polygon (1,600 m^2) was located in the valley of the Duży Budier stream (54°19'33.2"N, 22°41'18.8"E) in the alder-ash forest (*Fraxino-Alnetum*). Alder, at the age of about 60 years, dominates, with hazel as an undergrowth. There were 107 trees on the plot: 57 hazel (trunk diameter 5–20 cm); 34 alders (5–50 cm); 3 birches (25–50 cm); 2 spruces (10–45 cm); 1 oak (50 cm); 1 hawthorn (10 cm); 1 mountain ash (20 cm) and 8 dead trees, still standing (10–40 cm). Ground flora was partly dense with the dominant nettle *Urtica dioica*, but it was much sparser under full shade of trees.

METHODS

Strigillaria cana specimens were marked individually. Three colour stripes (encoded numbers) were painted with nail varnish on the snails' shells (Fig. 1). In 2005–2008, 809 adults were marked, and 485 of them were recaptured. In 2007–2008, one hundred juveniles (at size from 6.8 to 11.3 whorls) were marked, and 46 were recaptured. The current number of whorls was determined and marked at each juvenile's catch. In 2006–2009, regular observations of snails were conducted in the growing season – a minimum of one inspection per month. The snail's number and the tree on which it was found were recorded. Single inspections were also conducted in the years: 2010 (August), 2011 (September) and 2012 (July).

The day-night activity of adult snails was observed from August 31 to September 4, 2006. Observations were conducted every 12 hours (starting at 6.30 a.m. and 6.30 p.m.). Specimens available to the observer (i.e. present on tree trunks to the height of 200 cm from the ground level) were recorded. Only the individuals whose numbers could be read without removing a snail from a tree were recorded. The height on which each snail was found was measured with a measuring tape (accuracy ± 1 cm), from the ground level; additionally, a compass was used to determine the snail's location in the cardinal directions (accuracy ± 30°). The shortest path around the trunk connecting places where a given snail was found before and after twelve hours was treated as the distance covered in that time. When an individual was found in exactly the same place after 12 hours, it was considered inactive during that time. A total of 153 day/night activity data were obtained from 56 individuals observed from 12 hours (1 day/night) to 96 hours (4 days and 4 nights). For simplicity, all observations of each individual were treated as independent.

Speed and mobility during one hour were observed on ten adult snails in the morning hours between July 4–6, 2009. Active individuals (not hidden in shells) were selected for observation among the snails on smooth hazel trunks. Using a pencil, a dot was made on tree bark next to the snail's body, and the observations started. Every 5 minutes, a new dot, representing the snail's current position on the tree, was made. After one hour of observations, all distances covered by the snail were measured with a ruler. The crawling speed was calculated for all 5 minute intervals, during which distances larger than zero were covered.

Between March 2008 and November 2009, I carried out an automatic registration of temperature and humidity in the research area using the HOBO U23-001 recorder with the measurement accuracy for temperature ± 0.2 °C and humidity ± 2.5%. The recorder was placed 10 cm above ground level on a

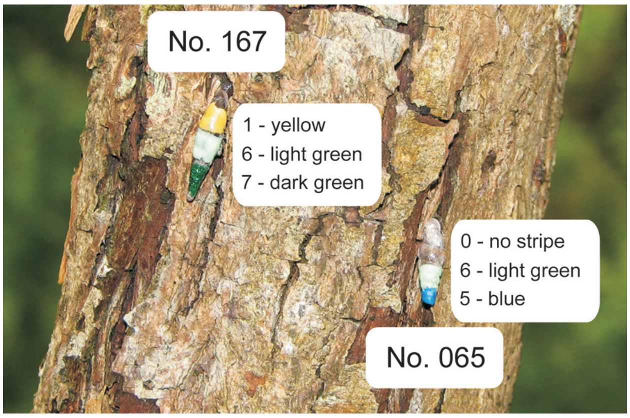


Fig. 1. *Strigillaria cana* specimens marked individually

wooden stake with a roof. Measurements were recorded every hour. HOBOwarePro software was used for data pre-processing.

Only one research activity was carried out outside the main research polygon. In 2008, during the growing season (March–October), I checked the presence of *S. cana* on trees and in litter once a month. On a sample plot (100 m^2) adjacent to the research polygon, I collected all visible clausiliids from the trunks of trees and from a 10-litre sample of litter. I bred all found juveniles in the laboratory until their shell was completed, which allowed for reliable identification of the species.

The following statistical analyses were performed: interquartile range, average values, comparison of average values (Mann-Whitney test), comparison of proportions (Chi-square test), and comparison of covariance (correlation coefficient). For statistical analyses, the PAST program was used (Hammer et al. 2001).

RESULTS

MOBILITY, SPEED

On a tree trunk, active *Strigillaria cana* adults move at a variable pace and sometimes change direction. During one hour, snails covered a mean distance of 164 mm (range 7–572 mm) with an average speed of 4.76 mm/min (range 0.6–19 mm/min) (Fig. 2, Table 1).

DAY–NIGHT ACTIVITY

There was no significant difference between *S. cana* daytime and nocturnal activity. A similar percentage of the observed individuals were active during the day and night (Chi-square test, $\chi^2 = 3.32$, df = 1, p = 0.07). Also, the median distance covered by the active individuals at day and night was identical (Table 2).

Table 1. *Strigillaria cana* mobility on the tree trunk within 1 hour

	Individual (No.)										Mean
	048	166	168	207	261	342	632	690	703	785	
distance covered during one hour [mm]	175	78	235	90	171	7	107	572	20	188	164.3
time of moving [minutes]	40	25	50	25	45	5	30	60	5	60	34.5
mean distance covered in 5 minutes (time of resting excluded) [mm]	21.9	15.6	23.5	18.0	19.0	7.0	17.8	47.7	20.0	15.7	23.81
minimum speed [mm/min]	2.4	0.6	1.0	2.0	1.4	1.4	2.0	2.4	4.0	1.2	
mean speed [mm/min]	4.38	3.12	4.70	3.60	3.80	1.40	3.57	9.53	4.00	3.13	4.76
maximum speed [mm/min]	9.6	5.0	18.0	8.0	8.0	1.4	7.0	19.0	4.0	6.0	

Table 2. Average distances covered by *Strigillaria cana* within 12 hours in various conditions. Medians were compared with the Mann-Whitney test

	time of a day		weather conditions		All observations
	night	day	dry	wet	
no of specimens	81	72	66	87	153
active snails [%]	60.9	50	46.1	64.9	55.2
distance [cm]:					
mean	35.2	25.0	19.5	38.7	30.4
SE	4.07	2.82	2.85	3.72	2.56
min	2	1	1	2	1
max	121	110	109	121	121
median	18	18	10.5	26	18
p (Mann-Whitney test)	0.43		<0.0001		

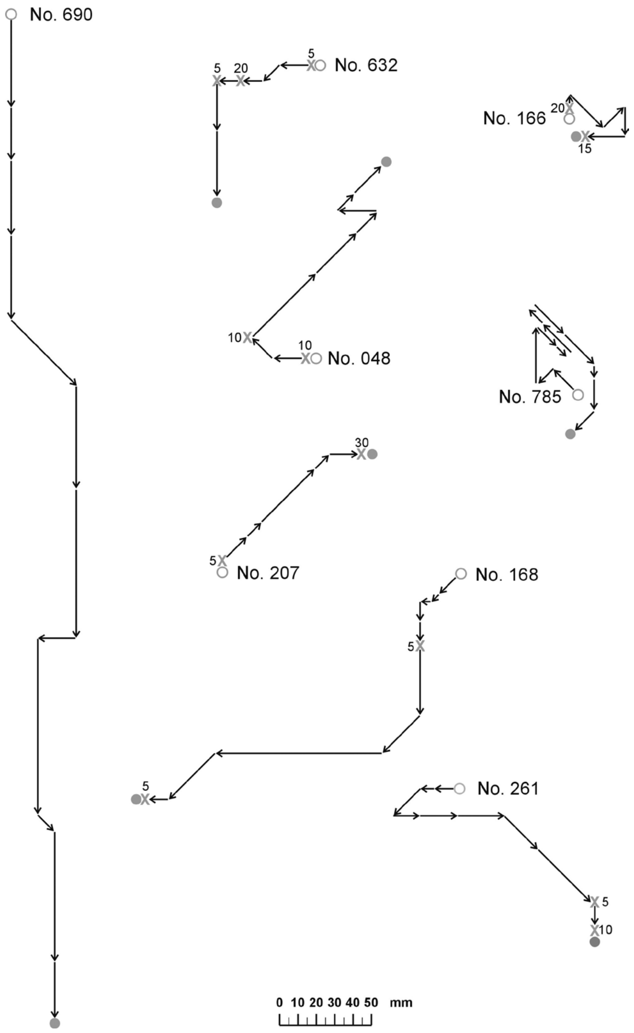


Fig. 2. The route covered in one hour on the tree trunk by *Strigillaria cana* adults individually marked, examples; empty circle – start, full circle – end of observation, X – break, the number at X means break time in minutes, each arrow corresponds to the distance covered in 5 minutes

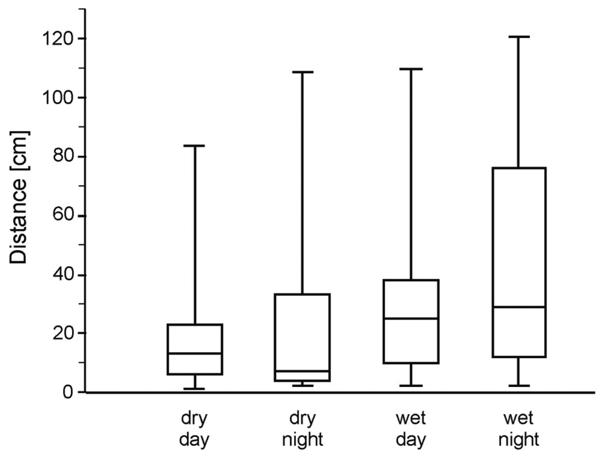
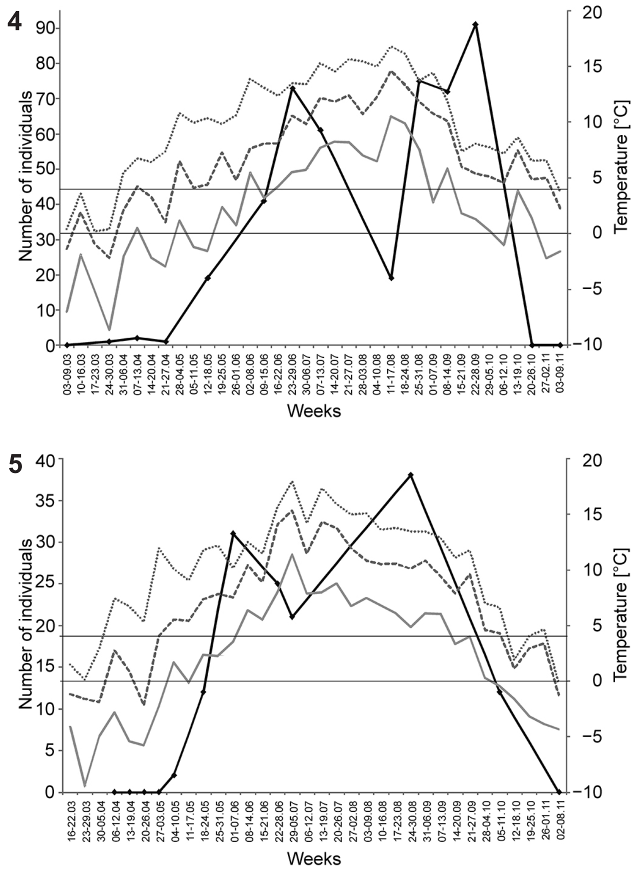


Fig. 3. Distance covered by adult *Strigillaria cana* in 12 hours at different times and conditions; box – interquartile range, horizontal line within box – mean value, vwhiskers – minimum-maximum range

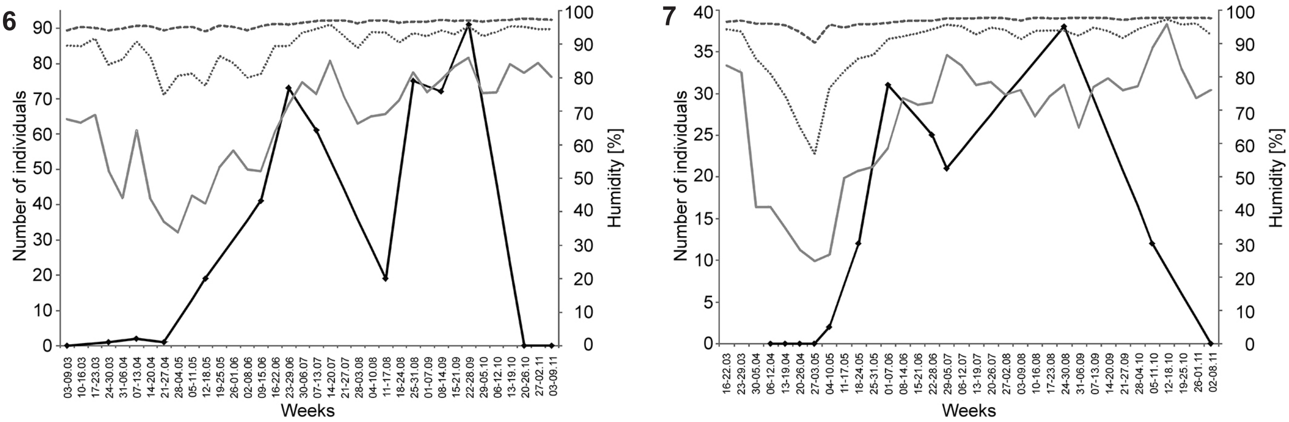
Strigillaria cana activity depends on humidity. On rainy days and nights (wet condition), more snails are active than on days and nights without rain (dry condition) (Chi-square test, $\chi^2 = 9.86$, df = 1, $p < 0.01$). Furthermore, the distances covered by the snails on rainy days and nights are longer (Fig. 3, Table 2). During 12 hours, the active individuals covered the average distance of 30.4 cm (ranging from 1 to 121 cm); mostly those were small distances (Fig. 3).

SEASONAL ACTIVITY

Strigillaria cana is active for six months a year in the studied area: from May to October. Snails started their activity in spring, i.e. they left winter shelters and "appeared" on tree trunks when the average temperature of the coldest 8 hours of the day reached or exceeded 4–5 °C. Short touches of frost that occur in NE Poland even in mid-May did not force the snails to return to winter shelters (Figs 4–5). Whereas in autumn *S. cana* stopped its activity, i.e. "disappeared"



Figs 4–5. Number of *Strigillaria cana* recorded at site with information on the temperature: 4 – the year 2008; 5 – the year 2009. Black line – number of individuals; grey solid line – minimal temperature; grey dashed line – mean temperature of eight coldest hours of the day; grey dotted line – mean daily temperature; horizontal lines mark isotherms of 0 °C and 4 °C



Figs 6–7. Number of *Strigillaria cana* recorded at site with information on the humidity: 6 – the year 2008; 7 – the year 2009. Black line – number of individuals; grey lines – humidity (solid line – minimum, dotted line – mean, dashed line – maximum humidity)

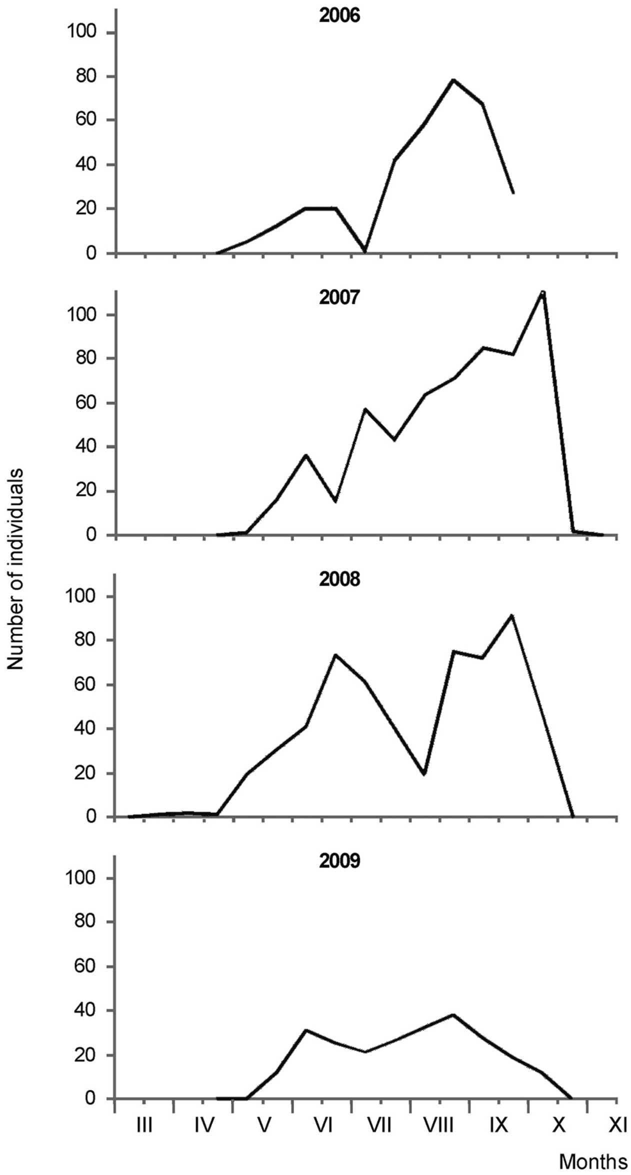


Fig. 8. Number of *Strigillaria cana* individuals observed at the site in consecutive years

from tree trunks and moved to winter shelters at the first frosts. Subsequent warming did not cause snails to resume activity in a given year (Fig. 4). Throughout the year there was high humidity in the research area and no humidity effect on the presence of *S. cana* was observed (Figs 6–7). *S. cana* juveniles are active longer during the year than adults.

There were fluctuations in the number of *S. cana* recorded at the site during each year (Fig. 8). The largest numbers of snails were usually recorded in autumn, and a visible decrease was observed in the summer. Weather conditions had no direct impact on the number of *S. cana* recorded at the site (Table 3).

Both adults and juveniles can stay on tree trunks and in litter (Fig. 9). Adults regularly are present on tree trunks. Juveniles are found irregularly, mostly in very humid places, in clusters of several snails.

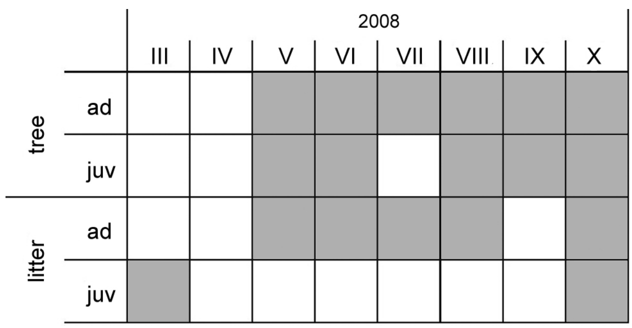


Fig. 9. Adult (ad) and juvenile (juv) *Strigillaria cana* individuals present (grey marks) on trees and litter in the small research area (100 m²) in consecutive months of 2008

DISPERSAL – CHANGE OF SITE (TREE)

Strigillaria cana individuals are not inclined to change the trees on which they are present. Of 485 observed adults, 59% never changed their tree (Table 4). The longest observation time of one individual on the same tree was five years.

Table 3. Impact of the weather condition on the abundance of *Strigillaria cana* at the site during this species activity period, May to September 2008 and 2009. The average values of temperature and air humidity in various time intervals before the control were given; 0 h – means the value of temperature and humidity at the time of control; r – Pearson correlation coefficient, p – the probability of independence

S. cana number at site	Temperature [°C]					Humidity [%]				
	0 h	3 h	12 h	24 h	72 h	0 h	3 h	12 h	24 h	72 h
2	14.41	17.89	13.89	9.82	10.13	78.29	55.69	67.94	77.29	80.62
12	11.90	15.44	13.37	11.40	11.82	89.25	74.09	79.36	83.31	87.61
12	7.44	8.20	7.20	6.92	7.92	97.52	97.56	97.52	97.48	96.75
19	12.20	12.20	8.02	5.72	10.84	59.61	56.50	66.97	74.98	76.12
19	21.41	19.68	14.94	15.48	16.91	71.72	84.08	93.08	94.22	92.76
21	16.01	14.92	15.00	15.83	16.70	97.52	97.46	97.43	97.06	96.12
25	20.15	21.22	17.54	15.75	12.59	88.51	86.12	91.07	91.59	90.61
31	10.74	10.29	7.90	7.43	7.99	84.28	87.04	92.11	93.07	93.66
38	12.36	14.22	12.66	12.26	14.24	97.09	92.64	94.87	96.07	93.81
41	15.15	16.39	13.65	11.93	14.65	70.45	62.12	73.75	78.75	77.66
61	21.29	22.07	20.79	18.45	13.75	89.56	86.64	89.19	91.22	92.55
72	9.31	8.04	7.97	10.17	13.02	80.89	85.69	92.00	92.67	94.59
73	16.34	15.91	11.42	11.42	13.57	74.34	75.29	85.66	84.59	87.53
75	14.00	13.11	11.23	12.01	14.81	85.54	85.74	91.68	93.56	93.70
91	12.10	11.35	5.73	6.37	7.31	92.61	94.77	95.95	94.54	94.60
r	0	−0.18	−0.22	−0.01	0.03	0.06	0.29	0.34	0.26	0.29
p	0.99	0.51	0.42	0.96	0.93	0.82	0.28	0.21	0.35	0.29

Table 4. Tendency of adult *Strigillaria cana* individuals to change trees

Maximum time of observation (years)	Number of individuals	Individuals that never changed their tree		Individuals that changed their tree	
		n	%	n	%
1	143	110	76.9	33	23.1
2	190	112	58.9	78	41.1
3	93	42	45.2	51	54.8
4	46	22	47.8	24	52.2
5	10	2	20.0	8	80.0
6	2	0	0.0	2	100.0
7	1	0	0.0	1	100.0
together	485	288	59.4	197	40.6

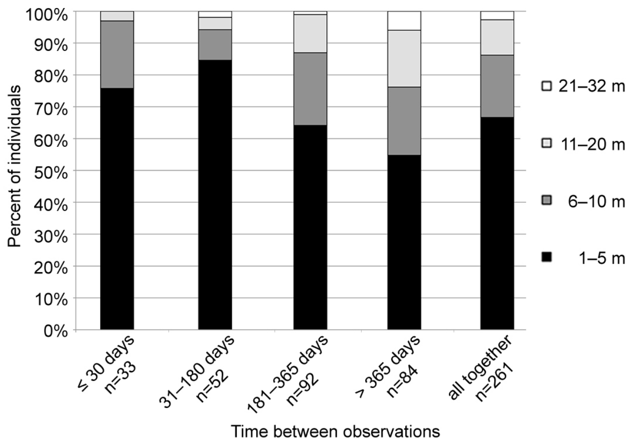


Fig. 10. Migration range. Distances between two consecutive trees (*Strigillaria cana* sites) depending on the time between observations

Specimens that tended to migrate did not move far from their original location. Of all 261 changes of a tree observed, the substantial majority (86.2%) corresponds to distances of up to 10 m between trees (Fig. 10). Snails' migration to trees located 20 m away or more represents only 3.1% of all tree changes (Fig. 11). The average distance between trees for individuals observed precisely after a month was 4.4 m (from 1 to 20 m, n = 31 individuals).

The maximum number of tree changes seen for any individual was six over the whole study (Table 5) and two within any one growing season. In 21 cases, the individuals changed tree, and after some time, returned to the previous one. Such migrations were observed only for two neighbouring trees.

Table 5. Number of tree changes by *Strigillaria cana* adults, observed for a different number of years

Time of observation (years)		Number of individuals	Number of site changes					
			1	2	3	4	5	6
1		33	31	2				
2		80	65	13	2			
3		50	32	14	3	1		
4		23	17	4	1	1		
5		8	5		2			1
6		2	1	1				
7		1			1			
together:	n	197	151	33	10	2	0	1
	%	100	76.6	16.8	5.1	1.0	0.0	0.5

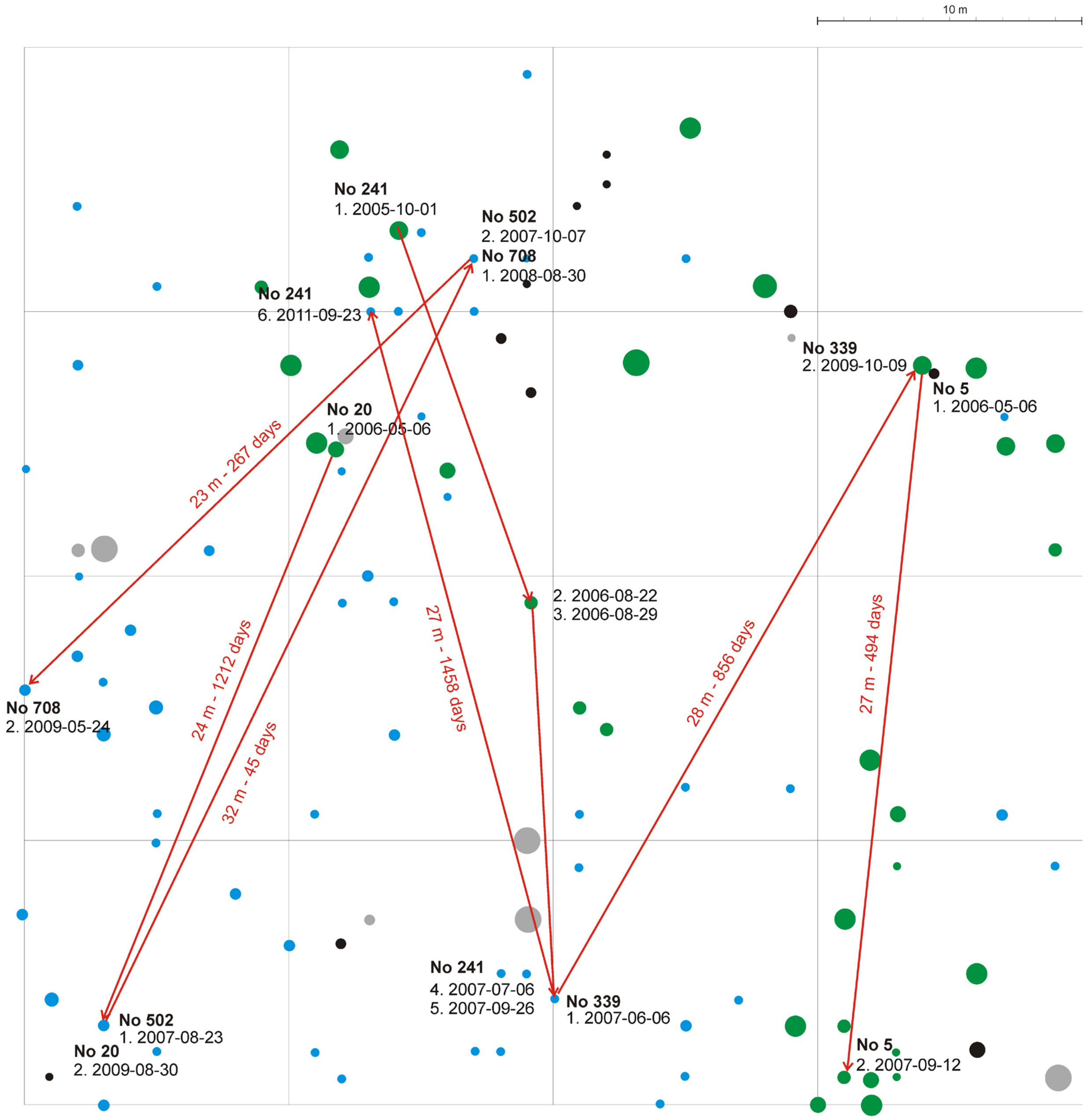


Fig. 11. The largest distances between trees – successive *Strigillaria cana* sites; examples. Numbers and dates indicate subsequent observations of individuals. The scheme of the research area, circles represent trees: green – alder, blue – hazel, grey – others, black – dead tree (standing)

Table 6. Tendency of juvenile *Strigillaria cana* individuals to change trees

Time of observation (years)	Number of individuals	Individuals that never changed their tree		Individuals that changed their tree	
		n	%	n	%
1	29	26	89.7	3	10.3
2	15	12	80.0	3	20.0
3	3	2	66.7	1	33.3
together	47	40	85.1	7	14.9

Juvenile snails also show a low tendency for dispersal, and only 15% of them changed their tree (Table 6). When a juvenile *Strigillaria cana* changed its tree, the new tree was only 1–2 m away from the previous one and was the closest neighbouring tree.

DISCUSSION

MOBILITY, SPEED

Contrary to expectations, *Strigillaria cana* showed high mobility when active. Individuals move in various directions, turn back, left or right (Fig. 2). This means that during an hour, they cover much longer distances than could be determined solely by observing only the starting and the endpoints. And that was the method used to determine this snail activity during 12 hours. As a result, in 12 hours, *S. cana* covered, on average, only twice the distance covered in one hour (data obtained by different methods!). Data on the 12-hour activity rhythm are obviously underestimated, as they assume only a straight linear movement of the snail. Probably, the mobility of other snail species observed during longer intervals is similarly underestimated as most studies on snails' mobility use the method of determining an individual's starting and final location (Baker 1988, Baur & Baur 1988, 1993, 1995, Kleewein 1999, Parmakelis & Mylonas 2004, Popov & Kramarenko 2004, Edworthy et al. 2012). Due to the lack of data, it is impossible to compare *S. cana* mobility with other clausiliids. Among the Helicoidea superfamily, there is a large individual variability in mobility (similar to those observed in *S. cana*): daily covered distances range from a few centimetres to several meters (Baker 1988, Baur & Baur 1993, Kleewein 1999, Popov & Kramarenko 2004). Speeds achieved by many snails in normal environmental conditions are relatively low: about a few centimetres per minute (Solem 1974) and this is also the case for *Strigillaria cana*.

CIRCADIAN RHYTHM

Many land snails, especially slugs, are characterised by a fixed circadian rhythm, with maximum activity during the night or early morning (Rollo 1982, Blanc 1993, Tomiyama & Nakane 1993, Kozłowski 2001). No difference between daytime and nocturnal activity of *Strigillaria cana* was found. Observations were conducted at the end of the summer when days were warm but not hot, and the forest air humidity remained high throughout any one 24 hour period (it was raining every other day). *Strigillaria cana* stay mainly on tree trunks, that is, in the places usually shaded. In such conditions, the day is primarily characterised by the presence of light, and not by the increased temperature and reduced humidity, conditions avoided by snails (Lazaridou-Dimitriadou & Saunders 1986, Wiesenborn 2003). The presence of sunlight itself does not limit *Strigillaria cana* activity. Similarly, no effect of the time of the day on the activity of snails living in the litter, where humidity and temperature conditions are comparatively stable, was observed, e.g. *Punctum pygmaeum* (Baur & Baur 1988). Possibly, during other seasons, *S. cana* activity pattern may be similar to *Cepaea* and *Arianta,* which changed their activity pattern from the daytime to nocturnal with the temperature increase (Cameron 1970).

SEASONAL ACTIVITY

Land snails adapt their activity to regular climatic changes throughout the year to take advantage of favourable conditions and not to expose themselves to unfavourable ones (Cook 2001). *Strigillaria cana* is active approximately in a growing season, like other Central European terrestrial gastropods (Maltz 2003, Szybiak 2010, Myzyk 2011). However, the growing season in the Romincka Forest is shorter than in other lowland parts of Poland (Matuszkiewicz 2007). The activity of *S. cana* throughout the year coincides with the frost-free period (Figs 4–5), which lasts about six months in the study area.

The entry into a state of hibernation (or in summer aestivation) in land snails is probably controlled in two ways: the change in the length of the day triggers physiological processes that prepare the body to rest, and additional environmental factors (e.g. low temperatures, prolonged drought) force it to enter the resting state (Cook 2001). In *Strigillaria cana*, this second factor may be an air temperature drop below 0 °C. Like other terrestrial snails of temperate climate (Myzyk 2011), *S. cana* does not return to activity after starting to rest, even if the factor causing the dormancy has ceased. The conditions needed to resume activity after hibernation vary from species to species: some need rain or dewfall, others need a mechanical disturbance, etc. (Cook 2001). Factors influencing entering (or leaving) hibernation may also differ in one species' populations living in different environments (Iglesias et al. 1996). Temperature probably plays the main role in resuming activity after winter in the *Strigillaria cana* population studied here. As in other land snails (Lazaridou-Dimitriadou & Saunders 1986, Iglesias et al. 1996), *S. cana* juveniles are active longer during the year.

In terrestrial gastropod populations, a seasonal decline in the number of individuals (generally in winter or summer) is associated with an actual decline in numbers or dormancy and hiding (Cook 2001). In the case of *Strigillaria cana*, a long-lived species (Marzec 2018), we deal with the latter situation. This species, even in dry weather, does not leave tree trunks, but hides in the crevices of the bark and under lichens (Urbański 1939). Therefore, changes in *S. cana* abundance during the season were treated as a species activity determinant, not changes in the population size. There was no influence of temperature and air humidity on the activity of *S. cana* expressed in this way in the growing season. A sufficient response to changes in these factors is probably to hide in shells, not move to shelter (the latter reaction takes more time and energy). The decline in the abundance of *S. cana* observed in the summer in the study area (Fig. 8) could be associated with the peak of the breeding period in natural conditions: snails then look for hiding places (e.g. under the bark) suitable for egg laying. As a result, many individuals "disappear" from the trunks and branches of trees on which they usually stay.

The winter shelters of *Strigillaria cana* have not been found. Some forest clausiliids, i.e. *Cochlodina laminata, Ruthenica filograna,* and *Clausilia bidentata,* can overwinter in the litter (Szybiak et al. 2009), while *S. cana* instead seems to stay even in winter on the trees and hibernates hidden deep in crevices and hollows. Such places, inaccessible to the observer, were not searched at any time of the year, as this would involve their destruction. The following observations suggest the possibility of hibernation of *Strigillaria cana* within trees. First, most of the specimens were always found on the same tree for many years. Secondly, adult specimens were found in the litter only when they were also present on trees (even in very early spring), indicating that the snails do not leave shelters in the litter or underground in spring to climb up later on their favourite trees. Juveniles are likely to hibernate in trees and in litter, depending on where the adult lays their eggs: under the bark, in tiny holes, in decaying parts of the trunk, on lobes of bark lying on the ground, etc. Although the most common strategy among land snails is to avoid cold temperatures in winter, many species tolerate partial freezing (Ansart et al. 2001, Ansart & Vernon 2003), including adult and juvenile *S. cana* (Marzec 2018). Shelter in trees, even if not free of frost, seems the most probable site of hibernation.

MIGRATION

Strigillaria cana is a strictly dendrophilous species living under the bark of standing or fallen trees (Horsák et al. 2013). Observation of individually marked specimens showed that *S. cana* spends most of its time on one tree. That is why I considered the migration of this species as a move from one tree to another.

Although the method of snail migration between trees were not the subject of the study, accidental observations allow distinguishing at least two methods. The first way is a crossing to a neighbouring tree moving along boughs. Hazels have expansive canopies and often there is a bridge between them, formed by broken branches resting on two neighbouring trees. *S. cana* was observed on such bridges suspended sufficiently low (so accessible to the observer). The second way involves falling from a tree and actively climbing into another tree. Such falls can happen accidentally when the specimen is pushed by the wind, moving twigs, another animal, etc. Snails may do this also as a reaction to disturbance by a predator (Allen 2004). I have observed an alive snail captured in a dense spider web on a bush under hazel branches, so most probably, this specimen just fell from this hazel. After falling to the ground, the snail can return to the previous tree or select a new one. This may depend on the distance to the last tree, the distance to other trees, and other factors influencing the selection of a tree by the snail. There is also a theoretically possible third way to change the tree. Snails can actively climb down from one tree, cross on the ground, and climb up another. The fact that snail stays for many years at just one tree may suggest that accidental falls can mainly determine the migration of snails between trees. Some individuals changed a tree and then returned to the previous one after some time, which may also confirm the random character of changing the site. On the other hand, the tree parameters may change in time (counted in years), e.g., bark cracking, shading, death of the tree, decomposition of the dead tree, etc. For these reasons, snails may change trees in response to unfavourable conditions.

Strigillaria cana shows a low tendency to migrate. Most individuals never leave their site, and the rest of the snails do not move far away. It is typical for habitat specialists, which are less mobile and less likely to migrate or disperse than generalists (Dahirel et al. 2015). The distribution of distances covered by *S. cana* is skewed – most of the snails cover short distances (Fig. 3). The same applies to the rock-dwelling clausiliid *Albinaria coerulea* (Giokas & Mylonas 2004). Other terrestrial gastropod species show varying tendencies to migrate. It could depend on various factors. Young *Lissachatina fulica* (Tomiyama & Nakane 1993) and *Cornu aspersum* (Dahirel et al. 2016) cover longer distances than adult individuals of these species, but in the case of *Arianta arbustorum* (Baur 1993) or *Chondrina arcadica clienta* (Baur & Baur 1995), age does not influence distance covered. High population density results in increased migration in *Cornu aspersum* (Dahirel et al. 2016) and *Arion ater* (Hamilton & Wellington 1981), but it does not affect the migration of *Ariolimax columbianus* (Hamilton & Wellington 1981) or *Punctum pygmaeum* (Baur & Baur 1988). On the other hand, high density limits the activity of *Cepaea nemoralis* and *C. hortensis* (Cameron & Carter 1979). Snail size affects the migration of *P. pygmaeum* (Baur & Baur 1988) but is of no significance for *A. arbusto-*

rum styriaca (KLEEWEIN 1999). Factors influencing migration may also include the individual character (personality) of particular specimens (DAHIREL et al. 2017) or the site features (BAKER 1988, BAUR 1993, BAUR & BAUR 1995).

The low migration tendency of snails does not always result in poor dispersal to new sites. The invasive *Xeropicta derbentina* spreading in southern Europe does not cover longer distances than other Helicoidea of a similar size. The success of this species results from passive migration (AUBRY et al. 2006). It seems that passive migration could play a key role in reaching new sites by snails. They can be transported by wind (VAGVOLGYI 1975, KIRCHNER et al. 1997), water (BAUR 1993, MIERZWA 2009, OŻGO et al. 2016), animals (KAWAKAMI et al. 2008, MACIOROWSKI et al. 2012, KOLENDA et al. 2017, SIMONOVÁ et al. 2016), or even vehicles (AUBRY et al. 2006). Some clausiliids can also survive passage through a bird's digestive system (SIMONOVÁ et al. 2016) and travel relatively long distances with the host.

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