



Flight performance of *Monochamus sartor* and *Monochamus sutor*, potential vectors of the pine wood nematode

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Abstract

Flight performance of *Monochamus sartor* and *Monochamus sutor*, two potential vectors of the pine wood nematode, *Bursaphelenchus xylophilus* was evaluated in laboratory flight mill tests. Beetles emerging from logs infested in the laboratory and incubated under outdoor conditions as well as field collected beetles were used. The maximum distance flown by *M. sartor* in a single flight was 3,136.7 m. Mean distances (per beetle) per flight ranged from 694.6 m in females to 872.5 m in males for *M. sartor*. In 75% of all individual flights *M. sartor* flew less than 1 km; only 3.7% flew distances longer than 2 km. The mean cumulative distance travelled by *M. sartor* beetles throughout their lifespan was 7.5 km. The smaller *M. sutor* beetles flew faster and longer distances. The maximum distance per flight was 5,556.5 m; mean distances ranged from 1,653.6 m in females to 1178.3 m in males. The number of available laboratory reared beetles was too low for quantification of lifetime flight capacity for *M. sutor*. The findings are compared to published data from *Monochamus galloprovincialis* recorded on the same type of flight mill as well as to field data from mark-release-recapture studies. The high flight capacity of *Monochamus* beetles illustrates the importance of considering dispersal of the vectors when planning control measures against the pine wood nematode.

Key words: dispersal; flight mill; *Monochamus*; phenology; pine wilt disease

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1. Introduction

The pine wood nematode, *Bursaphelenchus xylophilus*, causative agent of the pine wilt disease, is vectored by sawyer beetles of the genus *Monochamus*. Beetles transmit the nematode during feeding on twigs of healthy host trees; native *Monochamus* species are used in areas where the nematode has been introduced. Management of vectors is essential for any management approach against pine wilt disease. Therefore, a better understanding of flight and dispersal capability is important. *B. xylophilus* is native to North America where it is considered a weak pathogen. Since its introduction into Japan in the early 20th century it has been causing major damage in pine forests in Eastern Asia (Zhao et al. 2008). *B. xylophilus* was first detected in Portugal in 1999 (Mota et al. 1999) and spread rapidly over most of the country. Now the whole territory of Portugal is considered demarcated area (EPPO 2011). Four localized outbreaks in Spain are under eradication (EPPO 2014) through rigorous control measures. Based on these experiences, pine wilt disease is considered a major threat for European coniferous forests. *Monochamus galloprovincialis* is the only vector in the infested area in Europe (Sousa et al. 2001). If the nematode will spread to other areas in Europe it is likely that congeners, such as *Monochamus sutor* or *Monochamus sartor*, can function as vectors as well. Efficient traps and lures are available for surveillance and mass trapping of *M. galloprovincialis* (Alvarez et al. 2016; Sanchez-Husillos et al. 2015). These lures are also attractive for *M. sartor* and *M. sutor* (Halbig et al. 2014; Pajares et al. 2016).

The general biology of all European *Monochamus* spp. is similar. Larvae develop under the bark and in the wood of weakened or recently killed conifers. Therefore, they are secondary pest species causing technical damage to the wood. Adult feeding on healthy needles and twigs is primary (Hellrigl 1971). *M. sutor* is widely distributed throughout Europe. It infests *Pinus* spp. in the Pyrenees and in Scandinavia, while Norway spruce, *Picea abies* is the preferred host in Central Europe. The species has been frequently caught in traps in spruce forests in Austria (Hoch et al. 2014). *M. sartor* larvae develop preferentially in the lower part of mature *P. abies*; however, other conifers are accepted as well (Hellrigl 1971; Akbulut & Stamps 2012; Wallin et al. 2013). It occurs less frequently in Austria than *M. sutor* but populations can be high in mature mountainous spruce forests with a significant proportion of fresh dead wood (Hoch et al. 2014; Halbig et al. 2014). *B. xylophilus* infests *Picea* species in its native North American range (Sutherland 2008) and the genus *Picea* is listed as susceptible in the European Union decision on *B. xylophilus* (European Commission 2012). Also if no wilt expression should occur in infected *P. abies* the species will likely function as a reservoir for the nematode. Therefore, management efforts against pine wilt disease must also consider *P. abies* and *Monochamus* species developing in this host.

The spatial spread of pine wilt disease is determined by a combination of long-distance spread, which is mostly mediated by human transport, and short-distance natural dispersal, which is connected to dispersal behavior of the

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vectors (Robinet et al. 2011). Therefore, it is important to have basic data on dispersal capacity of *Monochamus* spp. available for a better understanding and modeling of these processes (Robinet et al. 2013). Flight and dispersal of *M. galloprovincialis* have been thoroughly studied in the laboratory (David et al. 2014) as well as in the field (Gallego et al. 2012; Etxebeste et al. 2016). Application of a spread model indicated that ports in Central and Eastern Europe would facilitate a rapid spread of *B. xylophilus* over Europe in case of incidental introduction (Robinet et al. 2011). Since other *Monochamus* spp. are present in this area as well, it is necessary to gain insight in their flight and dispersal capability to understand the interaction with pine wilt disease in case the nematode switches to these new vector species.

There are different approaches to study dispersal behavior of flying insects. Most often the flight parameters are either derived from laboratory experiments using flight mills or from the field based on mark-release-recapture studies. Both methods have their constraints. When flight distances and speed are recorded on flight mills, these parameters may be underestimated because the insect must accelerate the rotating arm of the flight mill and overcome inertia and mechanical resistance of the device (Taylor et al. 2010). Moreover the insect may be irritated by being tethered to the mill. On the other hand, the lift provided by the arm of the mill may be supportive of flight. Tethered insects may also be more active, because the lack of contact to the ground triggers flight, which is then maintained in the continuous airstream (Edwards 2006). This could lead to overestimation of flight capacity. Nevertheless, flight mill studies can provide benchmarks of intrinsic flight capacity and allow comparison between different physiological states or sexes of insects (David et al. 2014). In mark-release-recapture studies, results are affected by the size of study area (Schneider 2003; Franzen & Nilsson 2007), which will typically lead to underestimation of dispersal capacity.

In this study, we performed laboratory studies on flight performance of emerged and field collected beetles of *M. sartor* and *M. sutor*. The main objective was to produce a set of flight parameters, such as mean flight distance, duration and speed, that is comparable to *M. galloprovincialis* (David et al. 2014) and to detect possible differences in females and males as well as in emerged and field collected beetles. Breeding trials were set up in order to obtain newly emerged beetles but also to better understand the development of *M. sartor* and *M. sutor*. Emergence of *M. sartor* and corresponding temperature data were recorded over four years to calculate the thermal sums at those dates and to possibly detect a temperature threshold triggering emergence.

2. Material and methods

2.1. Insect rearing

In order to have newly emerged beetles for the flight experiments, breeding trials with *M. sartor* and *M. sutor* were set up in the laboratory in July–August 2012. Beetles originated from southern Lower Austria (Austria) and were either collected in the field or emerged from infested *P. abies* logs

brought to the laboratory. In 2013, only *M. sartor* was used for the trials; beetles either emerged from logs from the laboratory rearing or were caught in southern Lower Austria and Styria (Austria). Steel breeding cages with metal gaze (length x width x height: 0.42 × 0.5 × 0.7 m) were provided with *P. abies* logs of 0.5 m length (diameter from 0.09 to 0.22 m) for oviposition and fresh *P. abies* twigs for adult feeding and placed in the laboratory at ambient room temperature (22–27 °C). One male and one female were placed into each cage. Egg depositions (visibly by oviposition scars in the bark made by the female) were counted and marked twice a week; the logs were removed from the cages when the number of oviposition sites exceeded 20. After removal from the cages the logs were stored in the laboratory and watered twice a week to keep them moist. In autumn, all logs were stored in cages outdoors under a roof providing shelter from rain and direct sunlight. Air temperature was recorded hourly by EL-USB-2+ data loggers (Lascar Electronics, UK). Starting in June, the logs were inspected at least two times a week to collect emerged beetles. The logs remained in their outdoor cages after emergence had ceased. Control of emergence and collection of beetles was repeated in spring and summer 2014, 2015 and 2016.

Emerged beetles that were used in the flight mill experiments were reared individually in glass jars (0.5–0.8 liter) covered with metal gaze and provided with fresh spruce twigs for feeding in the laboratory at ambient room temperature. In 2014, some of the tested beetles were allowed to mate and oviposit and were reared like described above. Additionally, beetles for the flight experiments were collected in the field in 2013 and 2014 using multi funnel traps with collecting jars for life trapping (Econex SL, Murcia, Spain) baited with Galloprotect-2D (SEDQ, Barcelona, Spain) and reared in the laboratory as described above.

2.2. Recording flight parameters in flight mill experiments

Flight mill experiments were conducted in three consecutive years, from 2013 to 2015. Tested beetles originated from the above mentioned breeding or were caught in the field in southern Lower Austria, northern Styria or southern Salzburg (Table 1). Two flight mills as described in David et al. (2014) were provided by INRA, BIOGECO (H. Jactel and G. David) to record the beetles' flights: The vertical axis of the flight mill and the horizontal arm (a light carbon rod with a piece of foam glued to the tip) were connected by a ball bearing. A photoelectric sensor (Vishay NY37) was attached to the vertical axis to detect the rotations of the arm; the number of rotations was recorded by a C++ program on a Raspberry pi[®] data logger. Beetles were mounted on the flight mills with a small stripe of thin cardboard that was fixed on their pronotum with contact glue (Pattex Kraftkleber Classic, Henkel AG, Düsseldorf), which could be easily removed from the beetle after the flight session. A small piece of foam was glued on the other end of the cardboard strip to allow fixing it to the flight mill arm with insect pins. Flights were triggered by a slight air flow; beetles that stopped were triggered to start flying again in the same way with a maximum of five

times. Beetles were tested up to three times per week until their death. The length of the elytra was measured after the beetles' death.

Table 1. Overview of *Monochamus* spp. beetles used in flight mill studies in 2013–2015. The specimens either emerged from logs from the laboratory rearing or were collected in the field.

Year	Species	Sex	Type	Number of beetles
2013	<i>M. sutor</i>	f	field	3
2013	<i>M. sutor</i>	m	field	4
2014	<i>M. sartor</i>	f	field	5
2014	<i>M. sartor</i>	f	laboratory	7
2014	<i>M. sartor</i>	m	field	4
2014	<i>M. sartor</i>	m	laboratory	3
2014	<i>M. sutor</i>	f	field	2
2014	<i>M. sutor</i>	m	field	2
2014	<i>M. sutor</i>	m	laboratory	1
2015	<i>M. sartor</i>	f	laboratory	14
2015	<i>M. sartor</i>	m	laboratory	13

2.3 Data analyses

Emergence of beetles from the breeding logs: Thermal sums until emergence of adult beetles in the breeding trials were calculated from January 1 onwards based on hourly recorded temperature data. Since no developmental threshold temperature is known for *M. sartor*, thresholds for the congeneric *M. galloprovincialis* (12.2 °C; Naves & de Sousa 2009) and the spruce bark beetle *Ips typographus* (8.3 °C; Wermelinger & Seifert 1998), which develops in the same habitat as *M. sartor* were tentatively used. The median thermal sum for *M. sartor* to emerge was computed with the calculated thermal sums at the actual dates of emergence for each year.

Flight parameters: For analysis, only flights of a minimum duration of 180 seconds were considered; shorter flights were classified as attempts. Beetles were classified as fliers when they flew for at least 180 seconds twice throughout their lifespan. Every flight was analysed separately even when a beetle flew several times on one day. For each beetle, mean and cumulative flight distance, duration and speed was computed based on all flights during its lifetime. To investigate a possible effect of body size on flight behaviour Pearson's correlation coefficients between elytron length and the various flight parameters were determined.

All statistical analyses and figures were done in R (R Core Team 2014). Because only a low number of *M. sutor* was available and most of them stemmed from trap catches in the field, a detailed analysis of flight parameters was only feasible for *M. sartor*.

3. Results

3.1. Emergence of beetles from the breeding logs

Beetles emerged from the logs from early June to early July (Fig. 1). In the first three years (2013–2015), a period of at least five consecutive days of daily mean air temperature above 20 °C preceded the onset of emergence. In 2016, such period occurred already end of May; emergence started 11 days later. Tentative temperature sums above 8.3 °C and 12.2 °C accumulated until emergence differed between years (Table 2). Of all 124 successfully developed *M. sartor*, 24% emerged in the year following oviposition, 50% in the second

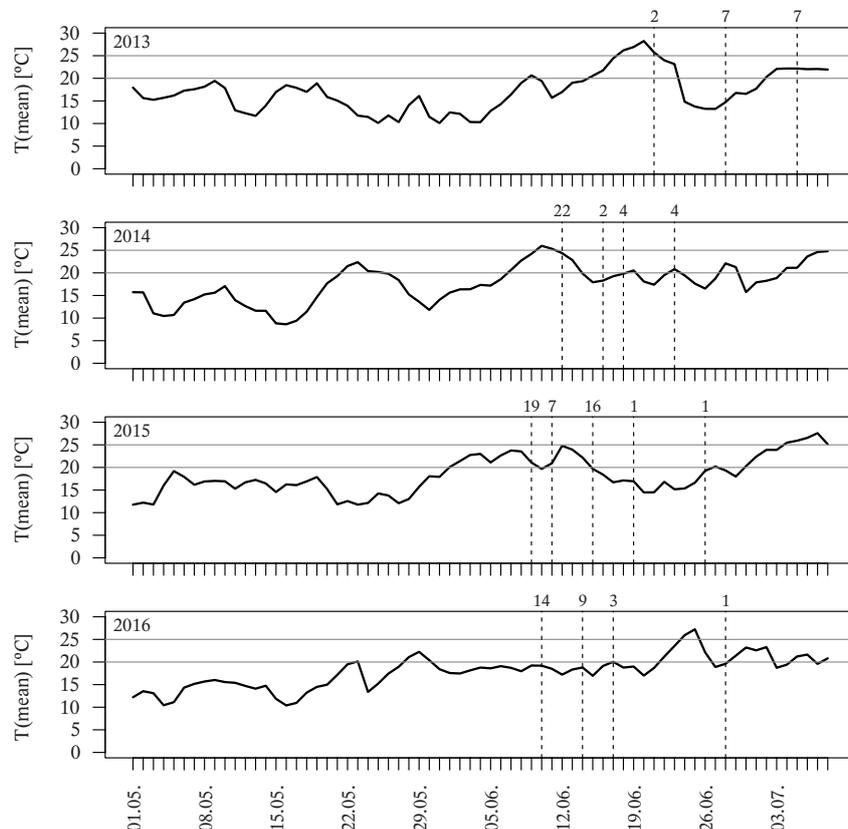


Fig. 1. Daily mean temperature, emergence dates (broken lines) and numbers of emerged *M. sartor* beetles (numbers above broken lines) from 2013 to 2016.

year, and 26% in the third year. 5 larvae which originated from the breeding trial in 2012 were included in this analysis as they would have emerged in 2015; however, those breeding logs were already split for inspection in winter 2014.

Lifetime of emerged beetles differed significantly between sexes: females lived 68 days on average, males 55 days (Mann-Whitney-Test, $p=0.04$).

Table 2. Calculated thermal sums (dd; degree days above 8.3 °C or 12.2 °C thresholds) for *M. sartor* accumulated from January 1 to emergence of beetles from the breeding logs for the first beetle in the season as well as median emergence.

		2013	2014	2015	2016
dd (8.3 °C)	First beetle	565.36	546.67	479.68	454.55
	Median	624.15	546.67	503.66	454.55
dd (12.2 °C)	First beetle	314.3	267.89	243.71	205.78
	Median	346.65	267.89	259.89	205.78

3.2. Flight parameters

In 2014, 33.3% of available *M. sartor* females and 22.2% of *M. sartor* males had to be classified as non-fliers and were excluded from further analyses. In 2015, all beetles were classified as fliers. In both years, all beetles of *M. sartor* classified as fliers flew at least on more than 55% of the days they were tethered to a flight mill. The proportion of beetles flying on particular days within the study period was higher in 2015 than in 2014. Females tested in 2015 showed the highest will-

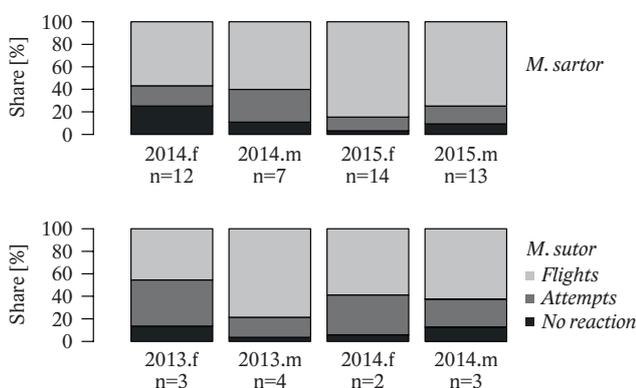
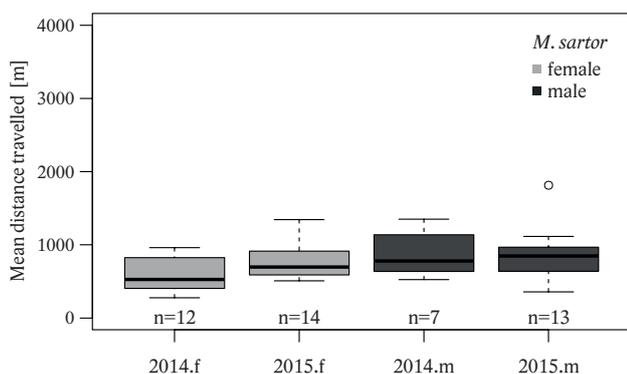


Fig. 2. Percentage of flights, flight attempts and no reaction of *M. sartor* and *M. sutor* that flew at least twice in their lifetime with regard to the days on which they were tested on flight mills. f = females, m = males, n = number of tested beetles.



ingness to fly (84.6%) (Fig. 2). In *M. sutor*, 70% of females and 33.3% of males had to be classified as non-fliers in 2013 as well as 60% of females and 25% of males in 2014; those beetles were also excluded from further analyses. Beetles of *M. sutor* showed a minimum share of flights of 45%; males flew to a higher extent than females in both years. However, numbers of tested beetles were low.

The maximum distance in an individual flight of 5,556.5 m was flown by a field-collected *M. sutor* female in 2013; the maximum distance by *M. sartor* was 3,136.7 m, flown by a female that emerged from the breeding trials in 2015. Mean distances (per beetle) per flight ranged from 694.6 m in females to 872.5 m in males for *M. sartor* and 1,653.6 m in females to 1178.3 m in males for *M. sutor* (Fig. 3). Flight parameters listed in Table 3 did not differ significantly between emerged and field collected females and males of *M. sartor*, except in females where field collected specimens flew on average at significant higher speed than emerged females (Mann-Whitney-Test, $p=0.005$). Thus, field collected and emerged beetles in 2014 were not separated in the analyses, also because of the low number of available beetles in each group. Only emerged beetles were used in 2015.

In nearly 75% of all individual flights females and males of *M. sartor* flew less than 1 km; only 3.7 % flew distances longer than 2 km. With regard to the cumulative distance flown over the whole lifespan, 74.1% of *M. sartor* females and males flew less than 10 km (Fig. 4). The mean cumulative distance was 7.5 km for beetles reared in the laboratory in 2015. Mean duration and mean flight speed in *M. sartor* females and males in 2014 and 2015 are listed in Table 3. Mean flight distance, duration and speed of *M. sartor* did not differ between sexes with one exception; males travelled significantly longer distances than females in 2014 (Student's t-test for homogenous variances: $t=-2.22$; $p=0.04$). The low number of available *M. sutor* did not allow comparisons.

Elytron length showed no influence of distances flown by *M. sartor* in both years (Pearson's $r=0.21$ and -0.11 , respectively).

4. Discussion

Rearing of *M. sartor* test insects in logs kept under outdoor conditions provided the opportunity to collect data on devel-

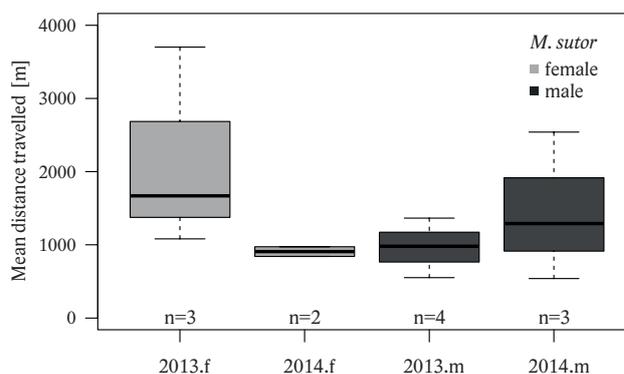


Fig. 3. Boxplots (median, 25% and 75% percentile, circles represent outliers outside 1.5× interquartile range) of mean distances flown in individual flights by each beetle of *M. sartor* and *M. sutor*. f = females, m = males, n = number of tested beetles.

Table 3. Mean distance, duration and speed (\pm standard deviation) of average flight per beetle for *M. sartor* females and males in 2014 and 2015.

	2014		2015	
	Females	Males	Females	Males
Mean distance [m]	600.10 \pm 239.75	886.63 \pm 321.99	775.59 \pm 239.56	864.87 \pm 361.13
Mean duration [s]	877.34 \pm 284.08	1057.73 \pm 289.72	1016.80 \pm 265.38	1089.65 \pm 332.60
Mean flight speed [m/s]	0.69 \pm 0.22	0.91 \pm 0.39	0.75 \pm 0.14	0.78 \pm 0.21
n (no. of beetles)	12	7	14	13

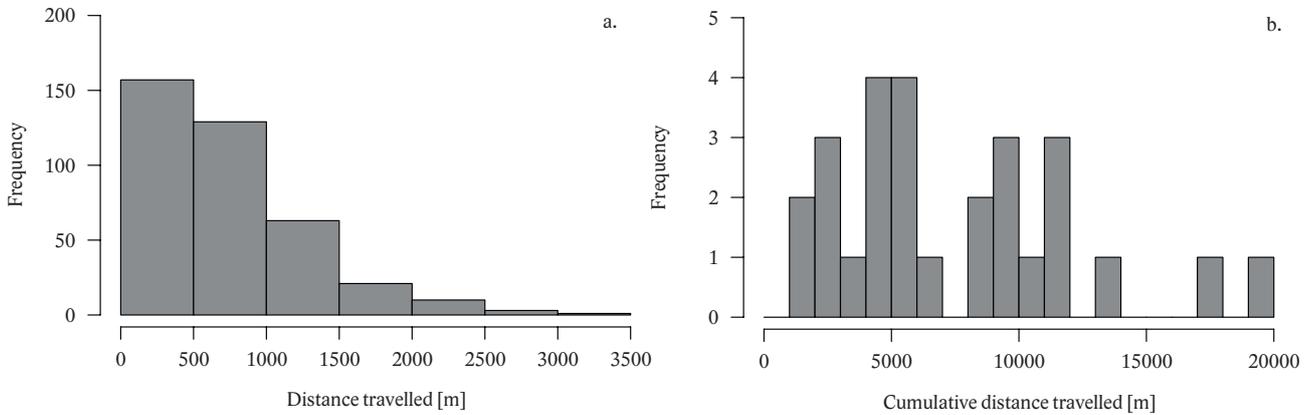


Fig. 4. Histograms of the distances flown by *M. sartor* females and males in 2014 and 2015: (a) all individual flights, (b) cumulative distance for the total lifespan of each beetle.

opment of this species. According to Hellrigl (1971), larval development takes 3.5 to 6 months; the prepupa hibernates and pupation takes place in spring. The pupal stage lasts 2 to 3 weeks. Also immature larvae can overwinter successfully and continue feeding the next spring (Hellrigl 1971). Our observations agree with these findings. Moreover, the data also support a temperature dependent onset of pupation in spring as assumed by Hellrigl (1971). Irrespectively of the time of oviposition in the previous summer (or the year before), beetles emerged during a short period from early June to early July. In three of the four study years, this was preceded by a period of 5 to 8 days with mean temperatures above 20 °C. Accumulated temperature sums before emergence varied between the years so that results do not allow conclusions on a required threshold. There was a trend to lower accumulated temperature sums with increasing number of years spent in the logs. Trap catches in a mountainous spruce forest in Austria at 1240 m elevation yielded the first *M. sartor* in early to mid June in 2013 and 2014. Beetles were caught throughout the summer until mid to late October (Hoch et al. 2014 and unpublished data). The early onset of flight at this high elevation indicates the importance of microclimatic conditions and the effect of solar irradiation on development of the stages inside the wood (which was excluded in the rearing at the institute). The flight period of *M. sutor* was similar according to these trap catches, with a slight tendency to earlier onset of flight. A better knowledge of the flight period of the vectors is of great importance to identify periods of high risk for pine wood nematode transmission.

Monochamus spp. are often regarded as poor flyers mostly based on mark-release-recapture studies and field observation (Akbulut & Stamps 2012). The results of the present study, however, show a high intrinsic flight capacity of *M. sartor* and *M. sutor*. This supports reports from flight

mill studies on *M. carolinensis* (Akbulut & Linit 1999) and *M. galloprovincialis* (David et al. 2014). Mark-release-recapture studies of *M. galloprovincialis* indicate that this flight capacity is also reflected in remarkable dispersal of individual beetles (Gallego et al. 2012; Etxebeste et al. 2016).

Flight parameters for *M. sutor* are similar to those measured for *M. galloprovincialis* on the same type of flight mill. Mean distances of individual flights were 1.0 km and 1.3 km for female and male *M. galloprovincialis* (David et al. 2014). Also the flight speed was very similar at ca. 1.3 m/s. Both species are of similar size; body length ranges from 16 to 23 mm in *M. sutor* and 11 to 24 mm in *M. galloprovincialis* (Wallin et al. 2013). The larger *M. sartor* (24 to 34 mm; Wallin et al. 2013) flew at lower mean speed and distance. Males tend to have slightly higher flight capability; however, differences were rarely statistically significant. The beetles can travel remarkable distances in individual flights: maximum recorded distances were 3.1 km for *M. sartor* and 5.6 km for *M. sutor*, which is less than for 8.5 km for *M. galloprovincialis* (David et al. 2014). David et al. (2014) report an average lifetime flight distance of 16 km (total of all flights) for *M. galloprovincialis*, more than twice the value reported in this study for *M. sartor*. However, care has to be taken when comparing the two species as *M. sartor* were tested in a lower number of flight sessions than *M. galloprovincialis* in the study by David et al. (2014). Therefore, we likely underestimate the lifetime flight capacity of *M. sartor*. The low number of *M. sutor* in our experiments and their origin mostly from field catches do not allow analysis of lifetime flight capacity for this species.

It is of interest to compare flight parameters from the laboratory to dispersal data measured in mark-release-recapture studies in the field. Maximum recorded distances of 5.3 km (Etxebeste et al. 2016) and 8.3 km (Gallego et al. 2012) show a remarkable dispersal capacity for *M. gallopro-*

vincialis, which corresponds to flight distances recorded on flight mills. However, it was only a small portion that was recaptured in the most distant traps. Analysis with a diffusion model showed that only 20% of the beetles travel > 1000 m while 50% recapture would be expected at ca. 500 m (Etxebeeste et al. 2016). The type of vegetation has an influence; Gallego et al. (2012) report that beetles would readily fly to a trap 2 km away from the release site when no trees were in between. A small mark-release-recapture experiment in Austria recorded mean distances from release to recapture site of 155 m for *M. sartor* and 182 for *M. sutor*. Beetles crossed mature spruce stands, groups of trees killed by bark beetles as well as open areas on their way to the trap. The maximum distance of 387 m for *M. sutor* represented also the maximum distance of a trap to the release point (Halbig et al. 2014). Apparently, the scale of the experiment in steep terrain limited the recorded distances in this case. Based on the flight mill data, *M. sutor* may show a similar dispersal like *M. galloprovincialis*. For *M. sartor*, a shorter range of dispersal can be expected.

5. Conclusions

European legislation gives guidelines for eradication measures in case *B. xylophilus* infection is found in a tree. One central measure is a clear cut of all susceptible hosts in a radius of 500 m around an infested tree (European Commission 2012). This strategy will likely remove infested trees at an early stage of introduction of *B. xylophilus*. However, as indicated by this and other studies presented in this paper it will not be sufficient to prevent *Monochamus* beetles from dispersing from the treated area to adjacent forests. Both tested species, *M. sartor* and *M. sutor* will, like *M. galloprovincialis*, easily be able to travel a distance of 500 m. Therefore, additional measures like intensive trapping are necessary to prevent vectors from escaping. Dispersal capacity must also be taken into account when designing surveillance programs at potential ports of entry for *B. xylophilus*.

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