

The Impact of Environmental Factors on the Efficacy of Chemical Communication in the Burying Beetle (Coleoptera: Silphidae)

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Abstract

There is growing evidence that a wide range of insect sex pheromones are condition dependent and play a fundamental role in mate choice. However, the effectiveness of pheromonal communication might not only depend on internal factors of the sender, but also on attributes of the microhabitat, in which the signaler chooses to emit its chemical signal. For example, the degree of anthropogenic land use might affect how successful the signal is transmitted, as land use has been shown to affect animal communities and the complexity of biotic interactions. To test the hypothesis that parameters of the microenvironment determine males' ability to attract females via their sex pheromone, we used the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae) as our model system. We exposed 144 males across differently managed forest stands and analyzed the impact of 29 environmental parameters. Our data revealed that human land use intensity had no effect on a male's attractiveness. However, the harvested tree biomass positively affected the proportion of competitors attracted. Furthermore, we found that soil characteristics were important factors determining the amount and body size of females a male was able to attract. Consequently, we present evidence that the environmental context of a signaling male influences the effectiveness of chemical signaling either because it affects the transmission process or the prevailing abundance of potential signal receivers. Thus, our results demonstrate that males need to make careful decisions about the location where they emit their pheromone, as this choice of microhabitat has an impact on their fitness.

Key words: sex pheromone, mate choice, forest management, signal efficacy, land-use intensity

Insects employ a diverse array of mate finding tactics (Choe and Crespi 1997, Shuker and Simmons 2014). Males and females of some species just move around to find a suitable mating partner. Others use acoustic, olfactory or visual signals to attract potential mates from a distance. How successful individuals are in attracting mates depend on many intrinsic and extrinsic factors. Especially when signals are involved in mate choice and costly to be produced, there are usually condition-dependent and the quality or quantity of signaling is, for example, affected by the nutritional state, degree of parasitism, age or body size of an individual (Zahavi 1977, Andersson 1994, Johnstone 1995, Rowe and Houle 1996). Environmental parameters, however, can also impact the amount of mates attracted, either because they affect the efficacy of signal transmission and detection or because they influence the local abundance of signal receivers, i.e., potential mating partners (Endler and Basolo 1998, Bradbury and Vehrencamp 2011). Hence, individuals have to make careful

decisions about the location where they emit their signals, as these decisions might profoundly affect their mating success.

In general, the effectiveness of a signal is expected to depend on a complex interaction between the characteristics of the signal itself and the environmental conditions under which signaling occurs (Endler 1992, Fleishman 2000, Bradbury and Vehrencamp 2011). The efficacy of visual signals, for example, can be influenced by lighting conditions. (Milinski and Bakker 1990; Bennett et al. 1996, 1997; Seehausen and van Alphen 1998; Loyau et al. 2007; Chapman et al. 2009) or by the colors of the visual background. Several bird species, for example, have been shown to enhance the contrast of their visual signal against the background by either actively choosing suitable locations or behaviorally modifying the existing visual background (Théry and Vehrencamp 1995, Heindl and Winkler 2003, Uy and Endler 2004, Endler and Day 2006, Olea et al. 2010, Sicsú et al. 2013). In addition to visual signaling, acoustic

communication systems are also influenced by human-generated habitat modification (Rabin and Greene 2002). Anthropogenic noise can disturb communication systems in marine mammals (Wartzok et al. 2003, Tyack 2008) and has also been shown to have an impact on the performance of mate attraction and territorial songs in birds (Slabbekoorn and Peet 2003, Brumm 2004, Slabbekoorn and den Boer-Visser 2006, Fuller et al. 2007, Slabbekoorn and Ripmeester 2008, Templeton et al. 2016), amphibians (Sun and Narins 2005), and insects (Lampe et al. 2012, Shieh et al. 2012, Orci et al. 2016). Human-generated seismic noise can even have a negative effect on acoustic communication systems during parental care, thereby leading to reduced brood sizes (Phillips et al. 2020).

The effectiveness of chemical signals may also highly depend on environmental factors and the local conditions in which they are emitted (Wyatt 2014, Boullis et al. 2016, Henneken and Jones 2017, Groot and Zizzari 2019). For example, a study in rock lizards, *Iberolacerta cyreni*, demonstrated that high temperature profoundly reduced the efficacy of male scent marks and, therefore, had an impact on their attractiveness to females (Martín and López 2013). The likely explanation for this finding is that the environmental temperature largely affects the stability and persistence of scent marks and other less volatile pheromones. Furthermore, numerous pest management studies have explored the effects of environmental conditions and trap locations on pheromone trap catches of several invasive insect species. These studies found, for example, that temperature, wind speed and relative humidity affect the amount of caught animals (Kaae and Shorey 1973, Linn et al. 1988, Adams et al. 1995, Östrand et al. 2001, Tinzaara et al. 2005). In addition, several studies demonstrated that the placement of traps at different heights and habitat types, ranging from wooded to open field conditions, affects pheromone trap catches of various beetle (Lindgren et al. 1983, Francese et al. 2008, Dodds et al. 2010, Dodds 2011, Reddy et al. 2011) and moth species (Sharma et al. 1971, Hirano 1976, Swailes and Struble 1979, Hanula et al. 1984, Krishnananda and Satyanarayana 1985, Athanassiou et al. 2004, Sarzynski and Liburd 2004, Athanassiou et al. 2007, Kong et al. 2014).

Human management activities and the type of land-use are particularly diverse in European cultural landscapes and their quantitative intensities are strongly variable (Herzog et al. 2006, Reidsma et al. 2006, Stoate et al. 2009). Changes in environmental conditions attributable to variable land use intensity have been shown to affect animal communities and the complexity of biotic interactions profoundly (Dirzo et al. 2014, Birkhofer et al. 2015, Ceballos et al. 2015, Newbold et al. 2015, Simons et al. 2015, Chisté et al. 2016, Gossner et al. 2016, Birkhofer et al. 2017, Frank et al. 2017, Seibold et al. 2019). Although some of the mechanisms behind these effects have been uncovered, it is currently underexplored whether differences in land-use type and intensity can have an impact on the effectiveness of sexual signals and, therefore, influence the number of successful matings and biodiversity (Tuomainen and Candolin 2011). In our study, we examined whether land-use intensification and other biotic and abiotic environmental factors influence a male's ability to attract females via chemical signaling. As we analyzed the impact of overall 29 environmental parameters, we provide an in-depth study of how the effectiveness of chemical signaling depends on the environment.

We used the burying beetle, *Nicrophorus vespilloides* (Coleoptera: Silphidae), as our model organism. Burying beetles provide elaborate bi-parental care in the form of defending and feeding their young on small vertebrate carcasses that they bury as a food resource for their developing larvae (Pukowski 1933, Trumbo 1990b, Eggert and Müller 1997, Scott 1998, Royle and Hopwood 2017). To obtain a female, males actively search for a carcass to which females will also

be attracted. After finding and securing a carcass suitable for reproduction, male burying beetles often emit a species-specific sex pheromone to increase their chances of attracting females from a distance (Eggert and Müller 1989a,b, 1992). However, males employ an alternative mate-finding tactic by emitting the sex pheromone daily in the absence of a carcass (Müller and Eggert 1987, Eggert and Müller 1989c, Eggert 1992, Beeler et al. 1999, Chemnitz et al. 2015, Mulrey et al. 2015). During the day, males usually use first the search tactic and later on, if they were not successful in finding or securing a carcass, they start to employ the chemical signaling tactic (Eggert 1992). Although males primarily attract females by means of their sex pheromone, some males also respond to the signal, albeit in smaller numbers (approx. sex ratio 1: 3.5) and also other *Nicrophorus* species are occasionally attracted (Müller and Eggert 1987; Haberer et al. 2008, 2011; Chemnitz et al. 2015). An attracted congeneric beetle might benefit from the possible detection or take-over of a carrion resource and conspecific males from the opportunity to mate with surplus females that the pheromone emitter attracts (Müller and Eggert 1987). Once attracted, females copulate with males, also in the absence of a carcass (Eggert and Müller 1989b, Eggert 1992).

The male sex pheromone of *N. vespilloides* consists of two substances, ethyl 4-methyl heptanoate (EMH) and (*E*)-geranylacetone (GA) (Haberer et al. 2008, 2017; Chemnitz et al. 2015, 2017a). Our recent study has shown that the same males that emitted a higher quantity of their sex pheromone in the laboratory are able to attract more females under field conditions (Chemnitz et al. 2017a). Moreover, the sex pheromone provides information about various aspects of an individual's condition and has been found to be dependent on internal factors such as the actual nutritional state, age, body size, and parasite load (Chemnitz et al. 2015, 2017b, 2018). Furthermore, males that have reproduced on a carcass are afterward able to produce a higher amount of their sex pheromone and attract more females than males that had not the opportunity to breed (Chemnitz et al. 2017b). Having established that the effectiveness of chemical signaling depends on various intrinsic factors, we aimed to analyze in the current study whether the success of males in attracting females via their pheromone is also dependent on environmental factors. Males have to fly through the forest to search for a carcass. If they are not able to find a suitable carrion resource, they need to make decisions about the location where they want to emit their pheromone. Parameters of the signaling microenvironment might determine their mating success. To test this hypothesis, we have conducted a field experiment, thereby exposing laboratory-reared calling *N. vespilloides* males across 24 differently managed forest stands in the south of Germany and assessing the amount of the attracted *Nicrophorus* beetles and the amount and body size of the attracted *N. vespilloides* females. We hypothesized that the environmental context and the forest management intensity influences a male's ability to attract females. We used beetles that were reared and maintained under the same condition in the lab instead of wild beetles to minimize variation in attractiveness due to differences in body condition.

Materials and Methods

Study species

Experimental *N. vespilloides* beetles used in this study were the fifth-generation offspring of beetles collected from carrion-baited pitfall traps in a deciduous forest in Ulm, Germany (48° 25' N, 9° 57' E) in 2015. All beetles were reared under standardized conditions, i.e., a male and a female were provided with a mouse carcass

(20 g ± 4) in temperature-controlled incubators at 20°C for reproduction. Prior to the experiment, beetles were maintained in temperature-controlled incubators at 20°C with a 16:8 (L:D) h cycle and housed in small plastic containers (10.0 × 10.0 × 6.5 cm) filled with moist peat. Males were fed decapitated mealworms (*Tenebrio*) twice a week. The day prior to the experiment, all males were transferred to 0.2 liter plastic containers (see description below), which were used during the field experiment, and fed mealworms once. Experimental males were between 20 and 35 d of age.

Study site and experimental setup

We conducted our study in the Biosphere Reserve Schwäbische Alb, Germany (48°20'60.0"N to 48°32'3.7"N; 9°12'13.0"E to 9°34'48.9"E) within the framework of the Biodiversity Exploratories project (<http://www.biodiversity-exploratories.de>; Fischer et al. 2010) during August 2016. Experiments were performed in 24 square-shaped experimental forest plots (each 100 × 100 m) that were selected based on stratified random sampling, with strata representing different land use intensities and several other different abiotic factors such as soil type and soil temperature (Fischer et al. 2010). In each transect along the margin, we established three pitfall traps that were located in the south, west and north of each plot.

Experimental males ($n = 144$) served as bait and were placed in small plastic containers half-filled with moist peat and hanging above the opening of the traps (Chemnitz et al. 2015). The lid and the upper part of the containers were perforated to allow pheromone dispersal. Beneath the container, we placed two plastic cups that were stacked one in the other, with the inner cup being filled with an odorless soapy solution to reduce surface tension. To protect the traps against precipitation, we placed rain covers above them. In general, our experimental design ensured that a female's mate choice was only based on a male's long-range sex pheromone and was not affected by visual cues or contact pheromones (Chemnitz et al. 2015, 2017a,b). Although experimental males were all reared under the same laboratory conditions, they might still have differed in their body condition and quality, which could affect pheromone emission (Chemnitz et al. 2015, 2017a). As the aim of our study was to determine whether environmental parameters influenced a male's attractiveness, irrespective of any intrinsic effects, we controlled for the latter by exposing overall six different males per plot. The first three males per plot were exposed in the field for three consecutive days and the second three males for two consecutive days. In general, males were only exposed on days on which the daytime temperature was above 13°C and on days without precipitation. After the exposure events, traps were emptied and the trap catches were brought into the laboratory. The caught beetles were identified and sexed and the body size of *N. vespilloides* females was determined by measuring the mean pronotum width.

Environmental variables

We analyzed a total of 29 biotic and abiotic environmental variables (Supp Table 1 [online only]). All variables and their respective values were known from basic plot inventories within the Biodiversity Exploratories (basic data regarding, for example, soil type, soil composition, climate, vertical structure, and management; e.g., Fischer et al. 2010, Hessenmöller et al. 2011, Schall and Ammer 2013, Lange et al. 2014). All soil types were determined in a soil inventory by Fischer et al. (2010) and described according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2006). We considered soil parameters such as soil type, soil temperature, soil moisture, and soil pH as being important variables for our

analyses, because the soil type is known to be an important factor in determining the local abundance of carrion beetles, especially burying beetles (Pukowski 1933, Scott 1998, Jakubec and Ruzicka 2015). The forest management intensity was quantified by using the developed silvicultural management intensity indicator (SMI), which combines three main characteristics of a given stand: stand age, tree species and aboveground, living and dead wooden biomass (Schall and Ammer 2013). For land-use characterization, we also used the forest management intensity index (ForMI). The ForMI is the sum of three components: the proportion of harvested tree volume, the proportion of tree species that are not part of the natural forest community, and the proportion of dead wood showing signs of saw cuts (Kahl and Bauhus 2014). Since all components are calculated as proportions, they are dimensionless.

Statistics

Statistical analyses were performed by using R version 3.1.2 (R Core Team 2014). Since we exposed, on each plot, the same number of males for exactly the same amount of time, we were able to pool all trapped beetles per plot. Consequently, we obtained one data point for each plot representing a value of males' mate attraction success on a specific plot. To quantify the relative importance of the effect of environmental variables (see Supp Table 1 [online only]) on 1) the total abundance of burying beetles, 2) the total abundance of *N. vespilloides* beetles, and 3) the total abundance of *N. vespilloides* females attracted, we used the Random Forest Approach (randomForest function in the MASS package; Breiman et al. 1984, Breiman 2001, Poggio and Gimona 2015). This procedure allowed us to extract the seven most important environmental variables across all 29 analyses variables (Supp Table 1 [online only]) used in this study. In the majority of models (with the exception when body size was used as response variable), the factors soil temperatures at 5 cm and at 10 cm below ground were extracted as the most important factors. As those two variables correlated significantly, we omitted the factor soil temperature at 10 cm below ground due to redundancy. Afterward, we applied a GLM with a quasi-Poisson error structure (due to overdispersion) with the six (in the case of body size seven) variables derived from Random Forest. The SMI and ForMI were run in a separate model by using GLMs with a quasi-Poisson error structure. To assess the relative importance of the environmental variables on the mean body size of *N. vespilloides* females, we performed the Random Forest Approach and subsequently GLMs with Gaussian error structure. For all models, statistical significance of fixed effects was based on F-statistics. In addition to the null hypothesis significance testing approach, we adopted an information-theoretic approach to extract the best and most parsimonious model. In the case of body size as response variable, Akaike's Information Criterion adjusted for small sample sizes (AICc) and AICc weights (w) was used to assess the relative strength of support for models, in the case of the amount of attracted beetles, we used Quasi-AIC (QAIC).

Results

Overall, during the five trapping days, the 144 experimental males attracted 455 *Nicrophorus* beetles of two different species, *N. vespilloides* ($n = 319$), of which 299 were females and 20 were males, and *N. investigator* ($n = 136$), of which 69 were females and 67 were males. There was a significant correlation between the total amount of attracted *N. vespilloides* and *N. investigator* beetles (Pearson correlation, $r = 0.65$, $P < 0.01$). Regarding the amount of

attracted *N. vespilloides* beetles, there was large variation between plots, ranging from 0 to 24 attracted individuals (median = 5.5; first quartile = 2.25; third quartile = 10).

The simplified model, containing the six most important predictor variables extracted by the Random Forest approach (Table 1), explained overall 58.7% of the variation in the total amount of attracted *Nicrophorus* beetles. From this overall six predicted variables, only the soil temperature at 5 cm underground (Fig. 1A; Table 1) and the proportion of harvested tree biomass (Fig. 1B; Table 1) significantly influenced the total amount of attracted *Nicrophorus* beetles. The model containing the variables soil temperature and the proportion of harvested tree biomass was also the model with the lowest QAIC (Supp Table 2 [online only]). There was no significant influence of the silvicultural management intensity (SMI; quasi-Poisson GLM, $F_{1,22} = 1.21$, $P = 0.28$) and the forest management intensity (ForMI; quasi-Poisson GLM, $F_{1,22} = 1.04$, $P = 0.32$) on the amount of attracted *Nicrophorus* beetles.

Regarding the amount of attracted *N. vespilloides* beetles, the simplified model explained 56.0% of the variation (Table 2). The total amount of attracted *N. vespilloides* beetles was influenced by the soil temperature at 5 cm underground (Table 2). The model containing soil temperature as sole variable was also the best supported one with the lowest QAIC (Supp Table 2 [online only]). The SMI (quasi-Poisson GLM, $F_{1,22} = 0.07$, $P = 0.80$) and the ForMI (quasi-Poisson GLM, $F_{1,22} = 0.04$, $P = 0.85$) had no significant influence on the amount of attracted *N. vespilloides* individuals.

Since the pheromone emitting males only attracted overall 20 con-sexuals, it is not surprising that the simplified model for attracted female *N. vespilloides* (Table 3) is not much different from the model for the total amount of *N. vespilloides* individuals. The simplified model explained 53.7% of the variation in the amount of attracted female *N. vespilloides* (Table 3). The amount of attracted females was also influenced by the soil temperature at 5 cm underground (Fig. 2; Table 3) and the model containing soil temperature as sole variable was also the best supported one with the lowest QAIC (Supp Table 2 [online only]). The other important parameter extracted by the Random Forest approach were all related to soil characteristics and included pH, clay content, medium silt, and medium sand content (Table 3). There was also no significant effect of the SMI (quasi-Poisson GLM, $F_{1,22} = 0.04$, $P = 0.84$) and the ForMI (quasi-Poisson GLM, $F_{1,22} = 0.03$, $P = 0.88$) on the amount of attracted *N. vespilloides* females.

The simplified model regarding the body size of the attracted *N. vespilloides* females only explained 35.7% of the variance (Table 4). There was no significant effect of any of the predicted variables of the simplified model (Table 4). However, based on AICc,

Table 1. Results of quasi-Poisson GLM examining the effects of six environmental variables of the simplified model on the amount of attracted *Nicrophorus* beetles

<i>Nicrophorus</i> beetles			
Fixed effects	Estimate (SE)	F	P
Soil temperature at 5 cm underground	0.43 (0.12)	13.44	0.002
pH	0.021 (0.15)	0.020	0.89
Harvested tree biomass	1.24 (0.56)	4.85	0.042
Clay	0.0029 (0.0048)	0.36	0.56
Medium silt	0.0012 (0.0063)	0.034	0.86
Coarse silt	0.0034 (0.0046)	0.54	0.47

Significant *P*-values are given in bold. R^2 of the simplified model: 0.59.

the model containing fine silt was better supported than the null model (Supp Table 2 [online only]). In fact, when testing this parameter separately, the fine silt content of soil had a positive impact on the body size of attracted females (Gaussian GLM, $F_{1,22} = 4.87$, $P = 0.038$; Fig. 3). In general, body size varied immensely between females and ranged from a pronotum width of 3.87 to 6.10 mm (mean \pm SD: 5.01 ± 0.41).

Discussion

In insects, a variety of sex pheromones have been found to be condition-dependent and play an essential role in mate choice (Steiger and Stökl 2014). However, local differences in the environmental conditions of the habitat can also influence the transmission of male courtship signals (Endler 1992, Bradbury and Vehrencamp 2011) or the number of signal receivers and may, therefore, impact the attraction success of a pheromone-emitting male. In the current study, we have tested whether the environmental context and forest management activities affect the amount of mates a male burying beetle is able to attract by means of chemical signaling. Although we analyzed overall 29 habitat parameters, we found that very few of them influenced a pheromone-emitting male's effectiveness to attract females. In particular, our results showed that soil temperature had an impact on the amount of attracted *N. vespilloides* females, whereas different land-use and management intensities had no effect on a male's ability to attract potential mating partners. Furthermore, the body size of attracted females, an important fitness parameter in burying beetles (Otronen 1988, Trumbo 1990a, Creighton 2005, Steiger 2013, Hopwood et al. 2014), was positively affected by the fine silt content of the soil.

Environmental factors can influence the structure of the forest resulting in considerable variation in the vegetation cover (open or closed) and complexity. Like other members of the genus, male *N. vespilloides* attract conspecific females by using long-range sex pheromones (Pukowski 1933, Haberer et al. 2008). Differences in the vegetation cover and complexity can affect wind speed and the degree of mechanically generated turbulences and thus the range and the precision of the pheromone plume (Sharov et al. 1997, Sauer and Karg 1998, Strand et al. 2009). Hence, suitable environmental and atmospheric conditions can enable males to spread their pheromone plume over a long distance and/or to emit a precise pheromone plume (plume of narrow width with high pheromone concentration) to attract a large amount of beetles (Fares et al. 1980, Elkinton et al. 1984, Byers 2008). In addition, stand density and other vegetation parameters might influence the population density of beetles and thus the number of potential signal receivers. Therefore, males that emit their pheromone in a microhabitat supporting a high abundance of burying beetles might be able to attract more females than males calling in an undesirable habitat. Consequently, factors influencing the transmission of the signal and the population density should be important determinants of the amount of females attracted, rendering the choice of the signaling site crucial for males. However, we have found no effect of forest type, stand density, or vegetation diversity on the amount of attracted beetles. A large-scale carrion study by von Hoermann et al. (2018), of which a part was conducted at the same location as our study, analyzes whether vegetation characteristics affected the abundance of carrion beetles attracted to piglet cadavers. They did not find any effect of forest vegetation on beetle abundance, a result that is consistent with our finding.

In addition to differences in vegetation, different habitat types exhibit temporal and spatial differences in soil properties and composition. In our study, we found that the soil characteristics of the

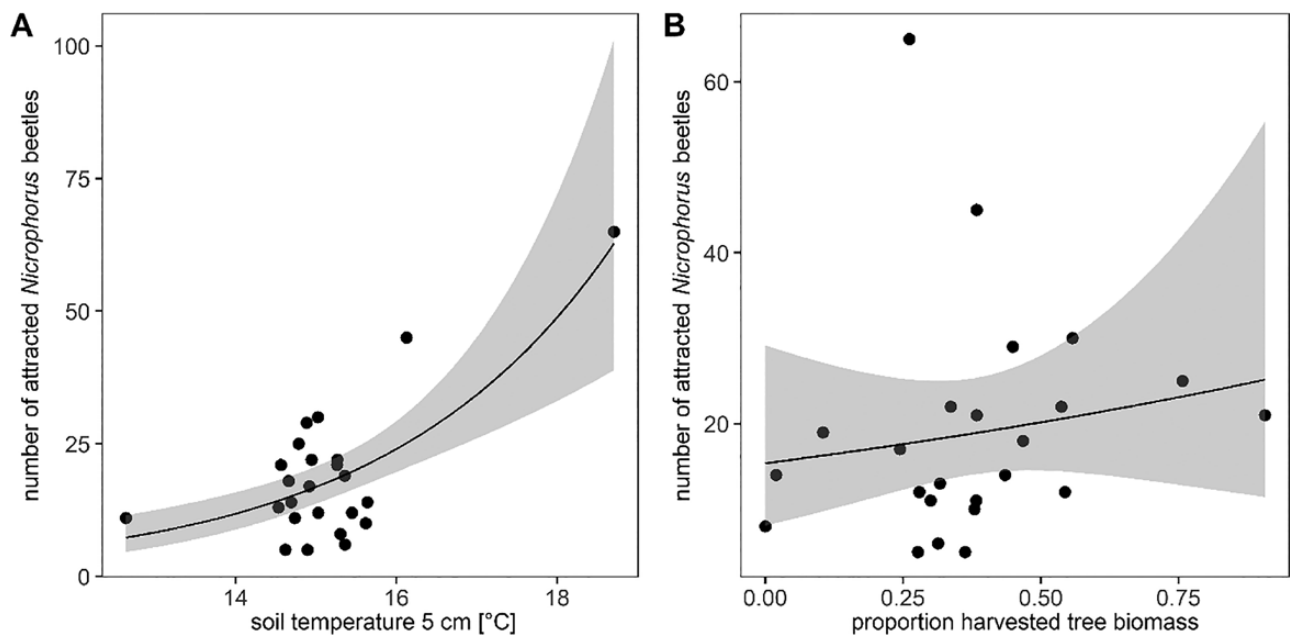


Fig. 1. Effect of (A) the soil temperature at 5 cm underground (°C) and (B) the proportion of harvested tree biomass on the amount of attracted *Nicrophorus* beetles. Experimental males were exposed in the field for 3 d during the first exposure event and for 2 d during the second event. The shaded regions show the 95% confidence interval.

Table 2. Results of quasi-Poisson GLM examining the effects of six environmental variables of the simplified model on the amount of attracted *N. vespilloides* beetles

<i>N. vespilloides</i>			
Fixed effects	Estimate (SE)	<i>F</i>	<i>P</i>
Soil temperature at 5 cm underground	0.42 (0.13)	11.12	0.005
pH	0.12 (0.16)	0.59	0.45
Clay	-0.0059 (0.0073)	0.69	0.43
Medium silt	-0.0056 (0.0098)	0.63	0.57
Coarse silt	-0.0057 (0.0072)	0.87	0.44
Medium sand	-0.0025 (0.013)	0.035	0.85

Significant *P*-values are given in bold. R^2 of the simplified model: 0.56.

environment influenced the amount and size of attracted females. We could show specifically that higher soil temperatures had a positive effect on the amount of attracted *Nicrophorus* beetles including potential mating partners and that the fine silt content of the soil affected positively the body size and, therefore, the quality (Steiger 2013) of attracted females. As has been known for a long time, soil parameters are very important habitat characteristics for burying beetles (Pukowski 1933, Scott 1998, Jakubec and Ruzicka 2015). This might be because burying beetles reproduce on small vertebrate carcasses that they bury in the soil as a food resource for their developing larvae, which pupate and enclose in the soil. Scott (1998) proposed that it is easier for the beetles to dig in damp soil that is rich in organic material. Moreover, some soils are assumed to be better able to maintain a stable environment in terms of moisture and temperature, both of which are beneficial for the reproduction of the beetles (Novák 1961, 1962). Laboratory experiments have shown that burying beetles are able to distinguish among different soil types and to choose the best substrate for digging (Muths 1991). A further

study has found a higher abundance of silphid beetles on loose soils that might be particularly suitable for digging (von Hoermann et al. 2018). In addition, the development of larvae should be strongly dependent on soil temperature, as burying beetles lay their eggs directly into the soil. It might, therefore, be possible that the beetles require a specific temperature for optimal development. In fact, a recent study found evidence that temperature has an effect on offspring number and fitness in *N. vespilloides* (Grew et al. 2019). Although soil temperature might influence pheromone transmission, it more probably has an effect on the prevailing number or activity of beetles and, therefore, males choosing to call on sites with warmer soil can attract more females.

Climatic conditions are major environmental factors influencing species abundance and richness. All levels of biodiversity, ranging from organisms to ecosystems, are expected to be affected by several environmental components influenced by climate change (Parmesan 2006, Bellard et al. 2012). In a previous study, we found that daytime temperature affected the amount of beetles that a male was able to attract: the higher the daytime temperature was, the lower was the amount of attracted beetles (Chemnitz et al. 2017a). In our current study, daytime temperature did not affect the amount of beetles attracted. This result was, however, not unexpected, as daytime temperature did not exhibit much variation between the five trapping days and ranged only between 15 and 17°C (measured at 10 cm above ground).

Anthropogenic disturbances and land use are other important factors that are known to influence habitat type and the environment (Sala et al. 2000, Foley et al. 2005, Goudie 2013). Depending on the various landowners and regulations, the forest management and, thus, the level of disturbance differs substantially. Land-use intensity and the consequential environmental changes of a given habitat may influence beetle communities directly by reducing their population size or indirectly by affecting habitat heterogeneity, habitat availability, or prey (and consequently carcass) availability (Lange et al. 2014). Indeed, carabid, staphylinid, and dung beetle communities

Table 3. Results of quasi-Poisson GLM examining the effects of six environmental variables of the simplified model on the amount of attracted *N. vespilloides* females

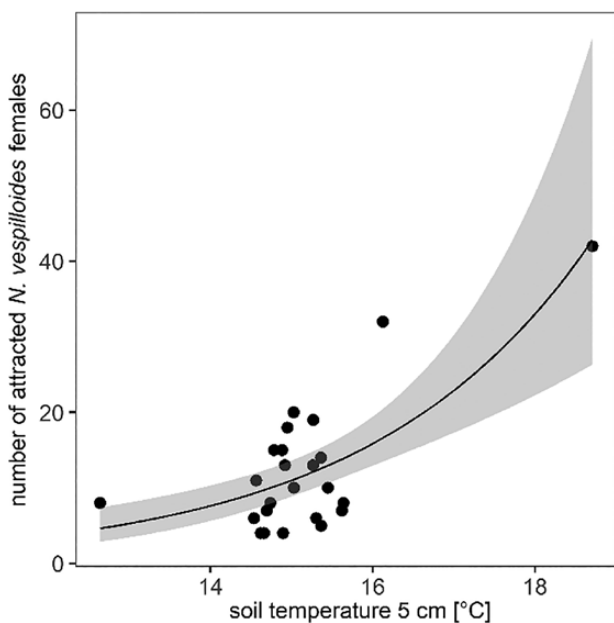
<i>N. vespilloides</i> females			
Fixed effects	Estimate (SE)	F	P
Soil temperature at 5 cm underground	0.42 (0.14)	10.22	0.005
pH	0.11 (0.16)	0.48	0.50
Clay	-0.0053 (0.007)	0.51	0.49
Medium silt	-0.0049 (0.010)	0.23	0.63
Coarse silt	-0.0052 (0.0076)	0.48	0.50
Medium sand	-0.0002 (0.014)	0.0003	0.99

Significant *P*-values are given in bold. R^2 of the simplified model: 0.54.

Table 4. Results of quasi-Poisson GLM examining the effects of seven environmental variables of the simplified model on the body size of attracted *N. vespilloides* females

Body size <i>N. vespilloides</i> females			
Fixed effects	Estimate (SE)	F	P
Soil temperature at 5 cm underground	0.064 (0.0039)	2.73	0.12
pH	0.047 (0.042)	1.25	0.28
Number of herbs	-0.00007 (0.0003)	0.05	0.82
Clay	0.00036 (0.0016)	0.10	0.76
Fine silt	0.0029 (0.0018)	2.59	0.13
Medium silt	0.00083 (0.0018)	0.19	0.66
Coarse silt	-0.00007 (0.0014)	0.003	0.96

Significant *P*-values are given in bold. R^2 of the simplified model: 0.36.

**Fig. 2.** The relationship between the soil temperature at 5 cm underground (°C) and the amount of attracted *N. vespilloides* females. Experimental males were exposed in the field for 3 d during the first exposure event and for 2 d during the second event. The shaded regions show the 95% confidence interval. Even when the two “outliers” are removed, the effect remains significant.

have all been documented to be affected by human management activities, although both negative and positive effects have been reported (du Bus de Warnaffe and Lebrun 2004, Vanbergen et al. 2005, Niemelä et al. 2007, Fuller et al. 2008, da Silva et al. 2008, Barragán et al. 2011, Lange et al. 2014, Frank et al. 2017, von Hoermann et al. 2020). In our current study, we did not reveal any negative effects of forest management activities on the amount of attracted beetles, which means that neither the emission nor the transmission of the sex pheromone is considerably impaired, nor is there an influence on the prevailing abundance of beetles. Von Hoermann et al. (2018) have similarly determined no effect of land-use intensity on the abundance and diversity of the two burying beetle species *N. vespilloides* and *N. investigator* Zetterstedt (Coleoptera: Silphidae). They have observed, however, an effect on the species *N. humator* Gleditsch (Coleoptera: Silphidae), with a lower abundance of the beetles in

locations with higher forest utilization. In our study, *N. vespilloides* males did not attract *N. humator* individuals, presumably, as they are less common at the study location than the other two species (von Hoermann et al. 2018).

Interestingly, males attracted 299 females and only 20 males in the current study. Thus, males were able to attract 15 times more females than males, a result that is different from those of the other studies (Müller and Eggert 1987, Eggert and Müller 1989b) and from our previous studies in which the sex ratio was not as biased towards females (Chemnitz et al. 2015, 2017a, b). Furthermore, we found in the current study that calling males attracted a considerable number of individuals of the congeneric burying beetle *N. investigator*. Past and recent investigations have also shown that calling male *N. vespilloides* attract members of other congeneric species (Müller and Eggert 1987; Haberer et al. 2008, 2011). However, as expected, males attracted significantly more conspecifics than *N. investigator* beetles, and in *N. vespilloides*, the sex ratio was shifted towards females, whereas in *N. investigator* the sex ratio was 1:1. Müller and Eggert (1987) assumed that the response of larger congeners to the pheromone emission of smaller species is adaptive. If the pheromone emitter is in the possession of a carcass, it can be taken over by members of larger species, irrespective of their sex. The attracted *N. investigator* is both larger than and competitively superior to *N. vespilloides* (Pukowski 1933, Otronen 1988). In general, male *N. vespilloides* would benefit from calling at locations where they can attract more conspecific females than conspecific males or congeneric beetles. In fact, our data revealed that the harvested tree volume correlated positively with the amount of attracted *Nicrophorus* beetles, but there was no effect on the amount of conspecific females. When specifically testing for an effect of harvested tree biomass on the ratio of potential mating partners to potential competitors, i.e., *N. vespilloides* males and *N. investigator* beetles, it becomes apparent that this factor has a negative effect (binomial GLM, $F_{1,22} = 16.96$, $P < 0.001$). The harvest of living trees is certainly a core activity of forest management. Unfortunately, we can currently only speculate why it favors the attraction of competitors via pheromonal signaling. It might be possible that anthropogenic disturbance caused by logging activities has a negative impact on scavengers and carrion dwelling arthropods other than burying beetles. This scenario would lead to a higher abundance of available carcasses, which in turn might positively affect the population density of the competitive superior *N. investigator*. We advocate that more research should be conducted to understand the impact of logging on burying beetle communities.

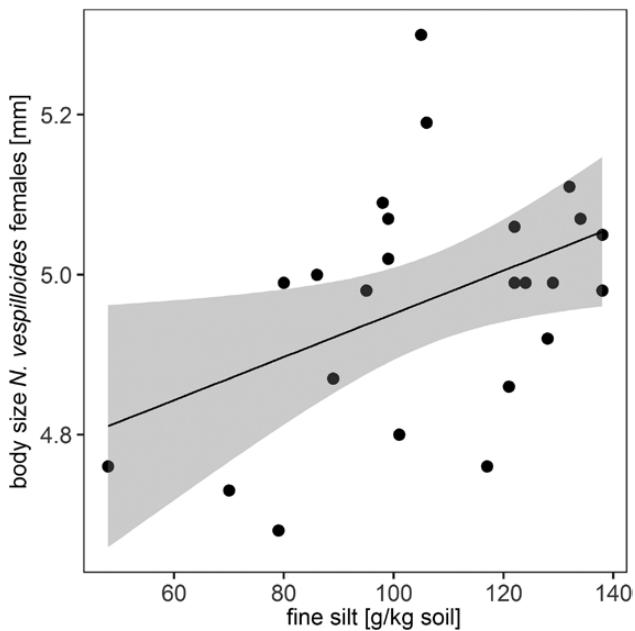


Fig. 3. The relationship between the fine silt content of the soil and the body size of attracted *N. vespilloides* females. Experimental males were exposed in the field for 3 d during the first exposure event and for 2 d during the second event. The shaded regions show the 95% confidence interval.

Collectively, our study examining 144 exposed pheromone-emitting *N. vespilloides* males across differently managed forest stands demonstrates that forest soil characteristics are important factors determining the amount and size of females a male is able to attract. Our results specifically show that males that call at a place with higher soil temperatures attract more females. Thus, we have found evidence that not only internal factors (Chemnitz et al. 2015), but also the environmental context of a calling male influences his “attractiveness” to females and, therefore, his fitness; however, we currently do not know whether the soil temperature directly affects pheromone transmission or rather the prevailing abundance of potential signal receivers. Irrespective of the exact mechanism, our results suggest that male *N. vespilloides* would benefit by actively choosing sites with warmer soil temperature when calling for females. However, we also have to emphasize that the majority of our tested environmental data, including forest management intensity, had no impact on the amount of attracted mating partners. Our results, therefore, indicate that communication via volatile long-range pheromones is rather robust to environmental changes and might be a successful signaling strategy in a variable environment. Furthermore, our study suggests that *N. vespilloides* abundance is quite stable across different habitats and environmental conditions. The reason for the success of this species might lie in its elaborate parenting behavior. Parental care has been shown to buffer against environmental variation and alleviate or remove environmental hazards (Smiseth et al. 2012, Grew et al. 2019). Hence, species exhibiting parental care, such as burying beetles, are able to actively create a stable micro-environment in which offspring can thrive.

The current study focused on pheromone emission in a burying beetle. We believe that the exposure of other pheromone-emitting insects would be a fruitful avenue for future studies, which might provide further insights into the way in which habitat choice and anthropogenic-induced environmental changes affects the efficacy of chemical signaling.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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Data Availability Statement

The data from this study are available as supplementary material.

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