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The relationship between *Nemozoma elongatum* (Coleoptera: Trogossitidae) and its primary bark-beetle prey-species

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Abstract

Key message *Nemozoma elongatum* (Linnaeus, 1761) shows a positive response to artificially produced lures targeting its two main prey species, *Pityogenes chalcographus* (Linnaeus, 1761) and *Taphrorychus bicolor* (Herbst, 1793), with a preference for *P. chalcographus*. We do not recommend using these lures in traps because they could unintentionally capture *N. elongatum*. However, these lures could potentially aid in controlling target pests by leveraging allochthonous kairomones to attract predators to areas with higher pest densities.

Context *Nemozoma elongatum* in Central Europe primarily preys on *P. chalcographus* and *T. bicolor*, but it can target nearly 40 species of bark beetles. While it responds well to the aggregation pheromone of *P. chalcographus*, its response to artificial lures for *T. bicolor* is unknown.

Aims The study aimed to confirm if *N. elongatum* beetles react in the same way to a lure containing bicolorin and Chalcoprax® and if their response to the prey abundance of *P. chalcographus* parallels the response observed in *T. bicolor*.

Methods During 2022, three Theysohn® pheromone traps were set with Beech Bark Beetle Lure®, containing bicolorin, and one trap with Chalcoprax® in mature beech stands at 11 study sites across the Czech Republic. To study the dependence of the numbers of *N. elongatum* captured, GLMMs were used to analyze the following variables: both lures, abundance of prey species, abundance of beech, age of beech, altitude, presence of adjacent non-forest areas (such as a freshly exposed edge of a beech forest), and the distances to the nearest spruce forest and the nearest clear-cut area.

Results *N. elongatum* prefers *P. chalcographus* as its primary prey, as indicated by its response to the tested lures. Its abundance is dependent on the presence of *T. bicolor* and *P. chalcographus*.

Conclusion *N. elongatum* is a prey opportunist that responds to bark beetle aggregation pheromones, as confirmed for several species. It is frequently caught in traps with Chalcoprax® and bicolorin, the pheromone of *T. bicolor*. Although more commonly attracted to Chalcoprax®, indicating a preference for *P. chalcographus*, *N. elongatum* may consume other species given its attraction to volatile compounds from host trees.

Keywords Beech bark beetle, Bicolorin, Chalcogran, *Pityogenes chalcographus*, Six-toothed spruce bark beetle, *Taphrorychus bicolor*

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1 Introduction

Predators of bark and wood-boring beetles operate within a tri-trophic interaction. They take advantage of prey cues that the prey use to localize their habitat and intercept the pheromones they utilize for intra-specific communication (Vet and Dicke 1992; Hulcr et al. 2006). Predators often exploit components of their prey's chemical signaling systems to locate and capture them. Some pheromone components provide an advantage to the predator and are referred to as kairomones (Schlee 1992; Howse et al. 1998). It has been suggested that there are at least two fundamental predatory strategies for ensuring an expanded range of bark beetles: a "general strategy," demonstrated by various species of clerids (such as *Thanasimus* spp. and *Enoclerus lecontei* (Wolcott, 1910)), and a "specialized strategy," apparently exhibited by trogossitid beetles (such as *Temnochila chlorodia* Mannerheim, 1843 and *Nemozoma elongatum* (Linnaeus, 1761)).

N. elongatum was considered a specialized predator preying upon bark beetle species associated with the chalcogran-producing bark beetles of the genus *Pityogenes* (Heuer and Vité 1984; Kohnle and Vité 1984). Despite this, *N. elongatum* is a generalist and is found under the bark of various woody species, both deciduous and coniferous, and among various bark beetle species (Kleine 1909; Escherich 1923). It may have nearly 40 species of bark beetles as prey (Wigger 1993). However, the primary prey in Central Europe includes the bark beetle *Pityogenes chalcographus* (Linnaeus, 1761), which infests spruce, and the bark beetle *Taphrorychus bicolor* (Herbst, 1793), which primarily lives on beech (Horion 1960; Dippel 1996).

P. chalcographus can be captured using pheromone traps, and this method has been used since the 1980s to monitor and control *P. chalcographus* populations, as this beetle occasionally causes economic damage (Escherich 1923; Hedgren 2004). However, it was soon discovered that these traps also captured predator species, revealing a significant flaw in Integrated Pest Management. *N. elongatum* was found in large numbers, especially in traps baited with Chalcoprax (Dippel 1991; Baier 1994; Wigger 1993; Zahradník 1995; Zahradník and Zahradníková 2020). This species can constitute up to 60% of all predators caught in these traps (Zumr 1988).

The population of *T. bicolor* sometimes increases due to wind-thrown material (Petercord 2006) or the decline of beech forests (e.g., Lakatos and Molnár 2009), causing concern among foresters and managers (Turek 2019; Paj 2021). An artificial pheromone dispenser, known as "Beech Bark Beetle Lure®," containing the aggregation pheromone bicolorin (Kohnle et al. 1987), has been developed for monitoring and is currently in use (Nikolov et al. 2023). *N. elongatum* has also been found in these traps (personal observation), which is understandable as *T. bicolor* is its prey (Horion 1960) and is expected to respond to its aggregation pheromone.

Trapping predators in pheromone traps can have adverse effects, but the impact on predator populations and their prey is still debatable. Some authors have evaluated the adverse effects of pheromone traps using a simple calculation based on the lifespan (4–5 months), fertility (60 eggs), and predation rates of adults (one *P. chalcographus* beetle) and larvae (30 *P. chalcographus* larvae) (Baier 1991, 1994). As a result, capturing one fertilized female *N. elongatum* can save nearly 2000 specimens of *P. chalcographus* (excluding mortality) (Zahradník and Zahradníková 2020). Due to this level of predation, other authors also consider *N. elongatum* larvae to be effective bark beetle antagonists (Baier 1994; Dippel 1996). Given its efficiency as a predator, more methods to attract *N. elongatum* should be developed to reduce bark beetle populations through biological control.

The main objectives of this study were to determine whether *N. elongatum* responds to industrially produced "Beech Bark Beetle Lure®" and whether the capture rates of *N. elongatum* beetles are affected by the type of pheromone bait used to target two potential prey species. We also wanted to determine if the response of *N. elongatum* to the prey abundance of *P. chalcographus* parallels the response observed in *T. bicolor* (Harz and Topp 1999). Additionally, we hypothesized that the abundance of *N. elongatum* may be influenced by variables related to the abundance of host trees for both prey species, like other bark beetle predator species such as *Thanasimus formicarius* (Linnaeus, 1758) in spruce stands (see Vanická et al. 2020).

2 Material and methods

2.1 Study sites and sampling

Four Theysohn® traps were placed on wooden frames in mature beech stands at 11 study sites across the Czech Republic (Table 1), covering both the Carpathicum (three sites) and Hercynicum (eight sites) regions. The center of each trap was set at a height of 1.3 m, spaced 20 m apart directly within the beech forests. Lures were initially placed into traps in early April 2022, replaced every eight weeks, and the traps were emptied every one or two weeks until the end of September 2022. Samples were cleaned of debris and non-target organisms to ensure the most accurate estimate of *T. bicolor* and *P. chalcographus* beetle counts. High numbers of trap catches were quantified using a graduated cylinder, with 1 ml representing 440 *T. bicolor* individuals (Holuša et al. 2025) and 550 *P. chalcographus* individuals (Zahradník and Zahradníková 2020). Low trap catches were counted individually. *N.*

Table 1 Variables of the 11 beech stands studied in the Czech Republic in 2022, where three Theysohn® traps baited with bicolorin and one trap baited with Chalcoprax® were placed

Study site	Latitude	Latitude	Altitude (m a.s.l.)	Sampling plot area (ha)	Percentage of beech	Buffer 500 (ha)	Buffer 1000 (ha)	Buffer 5000 (ha)	Adjacent beech area (ha)	Age	Forest openness (%)	Adjacent open area	Presence of exposed edge of beech forest	Nearest spruce forest (m)	Nearest clear-cut area with spruce branches (m)	Commercial versus old-growth forests	Number of trap sampling	Number of samplings used for determination of sex ratio
Dobříš	49.812452	14.107444	590	46.6	5	5.36	12.94	210.13	10	Overmature	14.87	Absence	Absence	140	260	Old-growth	40	12
Hejnice	50.880843	15.182433	375	4.9	5	0.79	43.30	2435.93	1	Overmature	41.17	Presence	Absence	600	800	Commercial	52	1
Jirkov	50.541449	13.483799	360	136.74	50	9.25	101.49	1501.18	1000	Premature	12.23	Absence	Absence	1200	1600	Old-growth	36	15
Korunní	50.334305	13.081835	470	5.9	100	49.38	219.61	2570.99	100	Mature	42.04	Absence	Presence	205	760	Commercial	32	16
Kristiánov	50.766807	15.071423	380	50.5	50	0.00	1.99	918.93	10	Mature	6.92	Presence	Absence	170	1700	Commercial	52	11
Lázně Kynžvart	50.003505	12.649779	740	40.72	100	34.96	111.32	807.24	10	Overmature	7.85	Absence	Absence	200	1480	Commercial	28	5
Liberec	50.776831	15.079482	390	2.7	50	2.43	31.04	1167.14	1	Overmature	53.67	Presence	Absence	560	630	Commercial	52	2
Obřany Mt	49.373114	17.725295	530	20	100	53.84	187.60	2870.84	1000	Premature	17.19	Presence	Presence	80	220	Commercial	32	11
Podhradní Lhota	49.408774	17.777045	720	122.4	100	43.76	147.32	1933.99	1000	Premature	8.81	Absence	Presence	240	120	Old-growth	32	7
Smrdutá Mt	49.371462	17.752075	580	6.5	90	63.59	230.87	3562.95	1000	Mature	4.82	Absence	Presence	240	300	Old-growth	32	5
Těchlovice	50.680420	14.227411	510	40.8	100	70.88	218.50	1076.07	1000	Mature	10.27	Absence	Presence	130	620	Commercial	52	15

elongatum individuals were also counted individually. The sex ratio of *N. elongatum* was determined for samples with over 10 individuals, with the sex determined through dissection of the genitalia from the last abdominal segment (see Kolibáč 2014).

2.2 Used lures

Three pheromone traps were baited with Beech Bark Beetle Lure®, containing bicolorin (AlphaScents), and one trap with Chalcoprax® [chalcogran 2.15% w/w (Safety Data Sheets)]. We used an unbalanced design because the response of *N. elongatum* to chalcogran is well-known, while our primary interest was in its response to bicolorin. To confirm the actual composition of the two baits used, chemical analyses were conducted.

For the separation, detection, and identification of lure compounds, we used a comprehensive two-dimensional gas chromatographic-mass spectrometric system, Pegasus 4D (LECO, St. Joseph, MI, USA), employing an Agilent 7890B gas chromatograph. Separation was performed on an HP-5MS UI capillary column (30 m, 0.25 mm i.d., 0.25 µm film thickness) coupled to a VF-17MS column (1.2 m, 0.1 mm i.d., 0.1 µm film thickness) via a consumable-free modulator. Both columns were from Agilent (USA). Lures were taken from freshly opened pouches, inserted into clean 5 L jars, and sealed. Samples were incubated for 10 min, and volatile compounds were extracted for 5 min at room temperature onto an SPME fiber (Supelco). The collected volatiles were desorbed into a split/splitless injector (split 10:1) at 275°C. The GC oven temperature program was as follows: 40°C for 2 min, then ramped at a rate of 10°C/min to 100°C, followed by 5°C/min to 320°C, and held at this temperature for 3 min. The second-dimension oven and modulator had an offset of 5°C and 15°C, respectively, with a modulation period of 5 s. The total GC run time was 55 min, including a 700 s solvent delay. Ions (ionization energy at 70 eV) were collected in a mass range of 35–500 Da with a frequency of 100 Hz. Compounds were identified by their specific mass spectra.

2.3 Used variables

The main variables we studied included the abundance of prey species, precisely the number of captured *P. chalcographus* and *T. bicolor* individuals during each sampling event, as well as the type of lure used (Chalcoprax®, further Chalcoprax, or with Beech Bark Beetle Lure®, further bicolorin). Additionally, environmental variables such as the abundance of the host tree species of *T. bicolor* (beech), its age, and study site altitude were considered in the analysis. The availability of host tree species was assessed at three levels: (i) the area of the homogeneous forest studied (sampling plot area) and percentage of beech; (ii) the areas of the adjacent beech forests located within buffer zones of 500, 1000, and 5000 m around the study sites using biotope mapping results of the Czech Republic (Härtel et al. 2009). Only the category of beech forest was evaluated. All spatial analyses were conducted using ArcGISPro 10.1 (ESRI, 2022); (iii) the total area of continuous beech forest to which the site belongs (adjacent beech area), which was defined by treeless woodland, forests of other tree species, and distinguished from young forests. A semi-logarithmic scale was used (1 indicating less than 1 ha of beech forest, 10 indicating up to 10 ha, 100 indicating up to 100 ha, 1000 indicating up to 1000 ha, and 10,000 indicating up to 10,000 ha of beech forest).

The age of the forest was divided into three categories: premature (forests under 100 years old), mature (101–150 years old), and overmature (151 years and older). The forest openness was evaluated by taking photos of the sky from the ground at eleven locations 20 m apart, covering an area of approximately 200 m^2 in July 2022. The images were then analyzed using ImageJ software (v.1.47) to determine the percentage of white (visible sky) and black (canopy covers) pixels.

The study utilized the following landscape variables: (i) The presence or absence of adjacent non-forest areas, such as meadows or agricultural land, representing permanent non-forest areas maintained by agricultural practices; (ii) The presence or absence of a freshly exposed edge of a beech forest stand; and (iii) The distance to the nearest spruce forest and the nearest clear-cut area with spruce branches from logging in 2021–2022 was measured as an environmental variable.

The category of "commercial vs. old-growth forests" is defined as the complexity of forest ecosystems based on human intervention. Managed forests were those actively influenced by human activities such as logging, planting, or other forest management practices. These interventions often simplified the structure and composition of the forest. On the other hand, old-growth forests were relatively untouched by modern human activities, allowing them to maintain their natural complexity, including the diverse tree age structure of forests and abundant deadwood. Old-growth forests were represented by areas under protection.

2.4 Data analysis

A Bayesian method was applied to evaluate how key abiotic characteristics of the forest influence beetle abundance. Utilizing the "brm" function from the well-known "brms" package in R (Bürkner 2017), we built Bayesian regression models based on our dataset. The model accounted for variability across trap IDs by nesting trap ID within the sampling study site as a variable with a random intercept effect. Poisson distributions were selected as priors to account for parameter uncertainty, while a non-informative distribution was used for the response variable.

Four chains were run to ensure proper convergence and mixing of the Markov Chain Monte Carlo (MCMC) process, each with 2,000 iterations. The scale reduction factor (SRF), also known as the "Gelman-Rubin statistic" (R-hat), was monitored to check for convergence, with SRF values below 1.2 indicating successful convergence within each chain.

In addition, multicollinearity's negative effect in selecting relevant variables (Cade 2015) was evaluated. Therefore, the final model was also checked for multicollinearity by calculating the variance inflation factor for each explanatory variable by using "vif" function (Fox and Weisberg 2019). The explanatory variables of the final model had a "vif" of less than two. We removed from the model both perfectly linearly correlated explanatory variables (forest age, forest openness, and presence of exposed edge of beech forest) and those that increased the multicollinearity of the model (all buffer zones and adjacent beech area). Before analyzing data, numerical explanatory variables were standardized to zero mean and unit variance. The chi-squared test was also applied to compare whether males and females had balanced abundance captured in both bark beetle traps.

3 Results

3.1 Flight activities of *Taphrorychus bicolor*, *Pityogenes chalcographus*, and *Nemozoma elongatum*

During the study, a total of 5737 *N. elongatum* individuals, 166,411 *T. bicolor* individuals, and 17,597 *P. chalcographus* individuals were captured. *T. bicolor* was first captured in traps on April 27th. The highest number of beetles per trap per collection was observed in May and June, with slightly lower numbers in July and very low ones in August and early September. In contrast, captures of *P. chalcographus* in pheromone traps began in May, with higher numbers in June and July. The numbers gradually decreased in August, and only a few individuals were captured in early September 2022. *N. elongatum* was most abundantly captured in May, with lower numbers in June and even fewer in July. There were only a few captures in August and September, with the last few individuals caught in early September (Fig. 1).

3.2 Trap catches and sex ratio of *Nemozoma elongatum*

Comprehensive two-dimensional gas chromatographic records confirmed that each commercial lure, containing either the functional compound bicolorin (Beech Bark Beetle Lure®) or chalcogran (Chalcoprax®), did not contain even trace amounts of the functional compound of the other lure (Fig. 2).

In the samples used to determine the sex ratio, 181 females and 859 males were found. We had 501 males and 129 females in three traps using bicolorin, while one Chalcoprax®-baited trap contained 358 males and 52 females of *N. elongatum*. In individual traps baited with bicolorin, we captured 6 to 931 *N. elongatum* beetles, while traps baited with Chalcoprax® captured 9 to 473 *N. elongatum* beetles. In the bicolorin captures, this accounted for 0.1% to 15% of the total catch, whereas in

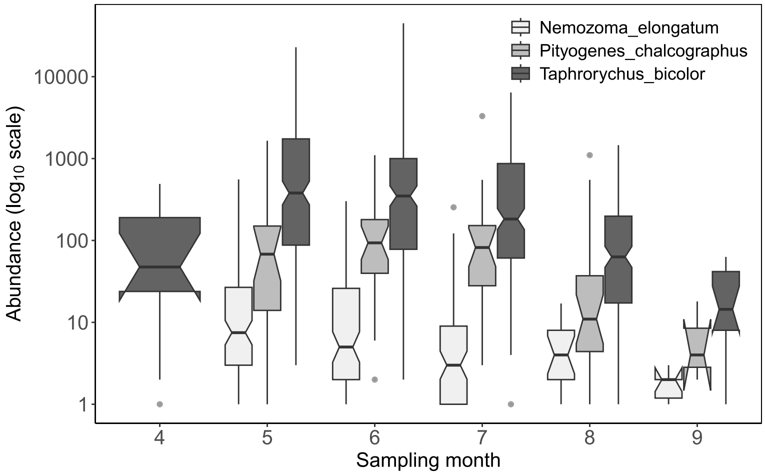

Fig. 1 Log-transformed numbers of beetles (*Nemozoma elongatum*, *Pityogenes chalcographus,* and *Taphrorychus bicolor*) captured in pheromone traps baited with bicolorin and Chalcoprax per trap and collection at 11 sites in the Czech Republic from April to September 2022. The bold horizontal bar within the box represents the median. The bottom and top of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points, while the dots represent outliers. The notches indicate confidence intervals; if the notches of two plots do not overlap, it provides strong evidence that the medians are significantly different

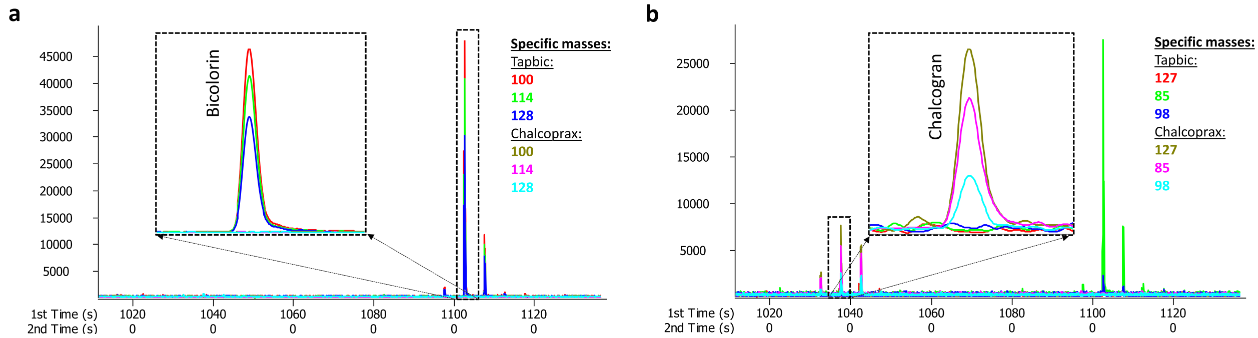

Fig. 2 Overlaid chromatographic records of volatiles emitted by commercial lures with extracted specific masses for detected functional compounds, bicolorin (m/z 100. 114 and 128) (**a**) and chalcogran (m/z 127. 85 and 98) (**b**). In each chromatogram, the base modulation of the pheromone compound is zoomed in to prove that in another dispenser, even no traces of the selected compound are present

the Chalcoprax® captures, it accounted for 0.4% to 75% (Table 2).

The average number of beetles captured was higher for Chalcoprax than for bicolorin ($\mu = 20.7$, SE = 4.154 vs. $\mu = 8.0$, SE = 1.211). Additionally, we observed that more males ($\mu = 8.7$ and 8.0, SE = 0.07) than females ($\mu = 1.3$ and 2.0, SE = 0.06) were captured on both baits ($\chi^2 = 442$, df = 1, p-value < 0.0001; $\chi^2 = 228.38$, df = 1, p-value < 0.0001). Our analysis indicated a clear relationship between sex and lure. The data also showed that female trapping on Chalcoprax was significantly lower than on bicolorin (Fisher's exact test: odds ratio (95% CI) = 1.772 (1.236–2.566), p-value < 0.01) (Fig. 3). The number of females in the catches gradually decreased from April to September (Fig. 4).

3.3 Variables influencing the abundance of *Nemozoma elongatum* in traps

Only a few environmental variables had a significant effect on the number of captured *N. elongatum* (Fig. 5). The abundance of *N. elongatum* in the traps was most strongly declined when the distance to clear-cuts in spruce forests increased (see Table 3, Figs. 5 and 6). The second strongest factor was the sampling plot area, specifically the size of the homogeneous forest segment at the study site, which has a positive effect on the abundance of *N. elongatum* (Table 3, Figs. 6 and 7). Additionally, the abundance of *N. elongatum* was positively influenced by the number of both prey species, with more *T. bicolor* and *P. chalcographus* (Table 3, Fig. 5) captured. More individuals of *N. elongatum* were captured on Chalcoprax bait than on bicolorin (Table 3, Fig. 5).

Table 2 Average number of *Taphrorychus bicolor* and *Nemozoma elongatum* captured from three traps baited with bicolorin, and the number of *Pityogenes chalcographus* and *Nemozoma elongatum* captured from a trap baited with Chalcoprax® at 11 sites in beech forests in the Czech Republic in 2022

Lure	**Bicolorin**			**Chalcoprax**		
Study site	***Taphrorychus bicolor***	***Nemozoma elongatum***	**Percentage of *N. elongatum***	***Pityogenes chalcographus***	***Nemozoma elongatum***	**Percentage of *N. elongatum***
Dobříš	19,183.0	98.7	0.1	1938.0	65.0	3.2
Hejnice	7402.3	9.0	0.1	7379.0	27.0	0.4
Jirkov	3078.7	144.7	4.5	99.0	309.0	75.7
Korunní	2912.0	506.3	14.8	2139.0	226.0	9.6
Kristiánov	2697.3	116.3	4.1	1007.0	83.0	7.6
Lázně Kynžvart	1293.7	23.0	1.7	408.0	255.0	38.5
Liberec	932.0	22.7	2.4	2106.0	66.0	3.0
Obřany Mt	6727.7	81.0	1.2	352.0	9.0	2.5
Podhradní Lhota	3232.3	195.0	5.7	311.0	473.0	60.3
Smrdutá Mt	3365.0	29.7	0.9	1252.0	67.0	5.1
Těchlovice	4646.3	83.0	1.8	606.0	217.0	26.4

Also shown is the percentage share of *Nemozoma elongatum* relative to the total number of prey and predators

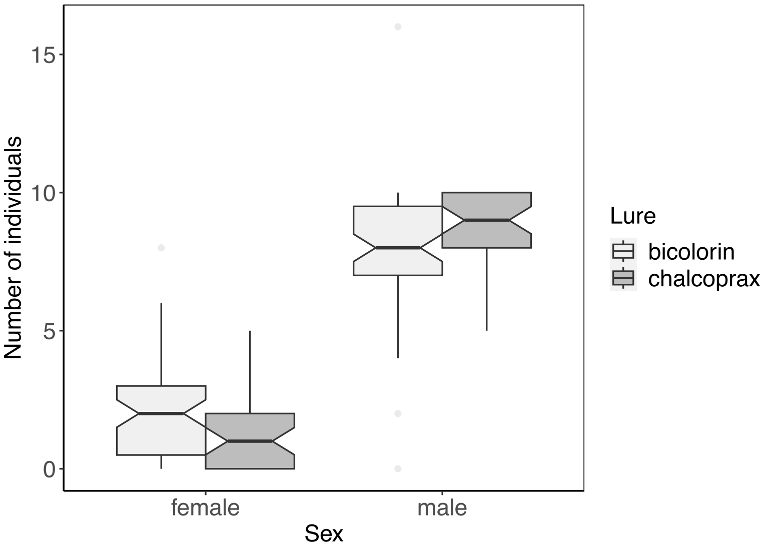

Fig. 3 Number of males and females of *Nemozoma elongatum* captured in pheromone traps baited with bicolorin and Chalcoprax® per trap and control at 11 sites in the Czech Republic in 2022. The bold horizontal bar within the box represents the median. The bottom and top of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points, while the dots represent outliers. The notches indicate confidence intervals; if the notches of two plots do not overlap, it provides strong evidence that the medians are significantly different

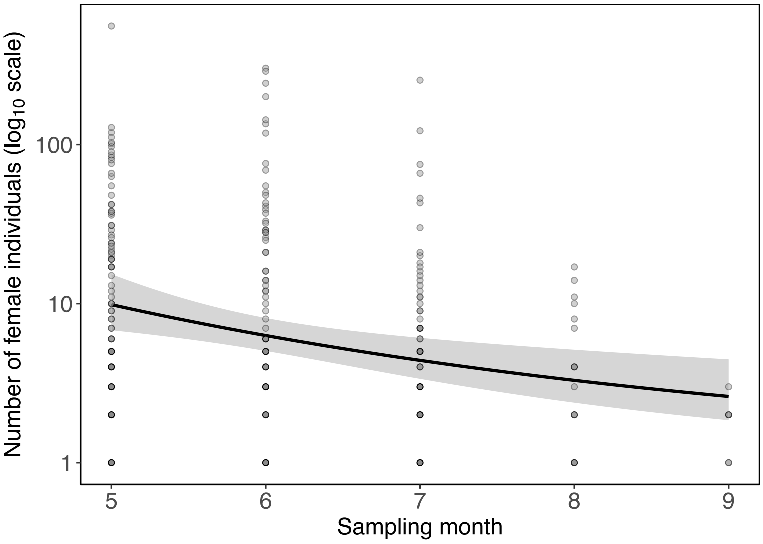

Fig. 4 Log-transformed counts of female *Nemozoma elongatum* captured per trap collection in pheromone traps baited with bicolorin and Chalcoprax at 11 sites in the Czech Republic from April to September 2022. A regression curve with a marked 95% confidence interval was fitted by a generalized linear model with negative binomial error distribution and link function log

The trap catches of *N. elongatum* consistently increased with the rising number of captured *T. bicolor* throughout the entire season and in May (Fig. 8). However, the relationship between *N. elongatum* and the abundance of captured *P. chalcographus* differed. Initially, the population of *N. elongatum* increased with the abundance of captured *P. chalcographus* throughout the vegetative season but later decreased. Nevertheless, when considering only the captures in May, there was a significant positive influence, with the population of *N. elongatum* showing a slight but significant increase with the number of *P. chalcographus* captured (Fig. 9).

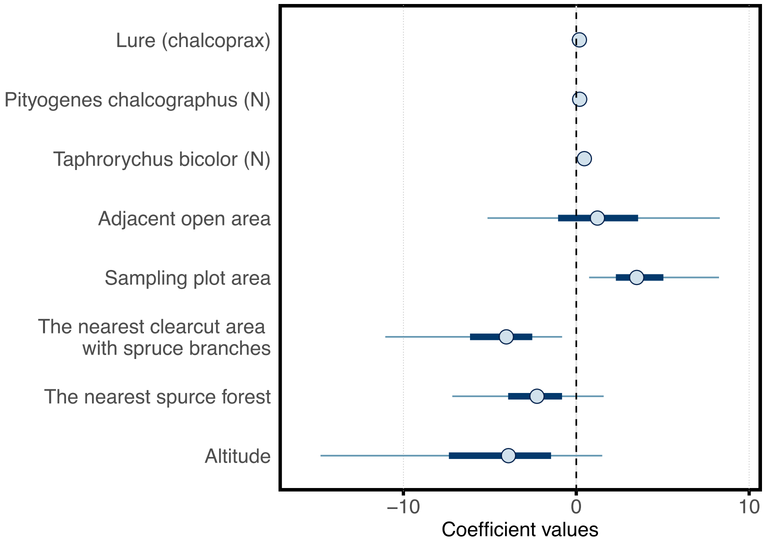

Fig. 5 The interval plot displays the posterior distribution of the coefficients, illustrating the effect size of each environmental variable, as well as the abundance of both bark beetle species and lure at 11 sites in the Czech Republic in 2022 on *Nemozoma elongatum* abundance estimates derived from MCMC samples. The plot shows the estimated median value of the coefficients' posterior distribution (represented by a blue circle), along with the Bayesian highest density credible intervals (depicted as a dark blue line) and the Bayesian 95% prediction intervals (shown as a light blue line). An explanatory variable has a significant impact on the dependent variable if zero is not part of the highest density interval (dark blue)

Table 3 Posterior summary table of the Bayesian model analyzing the association between forest characteristics, the abundance of *Taphrorychus bicolor* and *Pityogenes chalcographus*, and the dependent variable *Nemozoma elongatum* abundance

Variable	Effect size	Est. error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	−2.088	2.795	−8.731	2.184	1.004	1374	1043
Lure (Chalcoprax®)	0.182	0.073	0.04	0.328	1.001	7253	5843
Sampling plot area	3.924	2.581	0.249	9.919	1.003	1399	962
Altitude	−5.015	5.698	−18.554	2.666	1.003	1520	1051
The nearest spruce forest	−2.52	2.841	−8.909	2.387	1.003	1533	1355
The nearest clearcut area with spruce branches	−4.853	3.717	−13.603	−0.226	1.004	1519	1036
Abundance of *Pityogenes chalcographus*	0.196	0.03	0.138	0.253	1.001	7567	5946
Abundance of *Taphrorychus bicolor*	0.467	0.084	0.302	0.632	1.001	6286	5468
Adjacent non-forest areas	1.386	4.435	−6.923	9.992	1.002	1741	2111

Explanatory variables whose confidence intervals do not include zero have a significant impact on the dependent variable

4 Discussion

N. elongatum was captured in traps baited with both bicolorin and Chalcoprax and placed in mature beech forests at eleven sites in the Czech Republic in 2022. Beetles were more abundant in traps baited with Chalcoprax than with bicolorin. The number of *N. elongatum* captured was lower with distance from the nearest clearcuts in the spruce forest, with this relationship being the strongest. Moreover, the numbers of *N. elongatum* captured increased as the sampling plot area increased, and these numbers were positively correlated with both numbers of *T. bicolor* and *P. chalcographus* captured.

4.1 Flight activity of *Nemozoma elongatum*

T. bicolor flies earlier because it lives in beech forests which are warmer and receive more light in April compared to spruce forests during the same time (Wigger 1996a). As a result, *N. elongatum* and *P. chalcographus* appear later. *T. bicolor* and *P. chalcographus* potentially may complete two generations per year at mid-elevations. The mature generation breeds from April to July, while the offspring generation begins in August and September. The broods may not fully mature before winter, and individuals can overwinter at different stages (larva, pupa, or young/callow beetle) within the breeding systems (Pfeffer

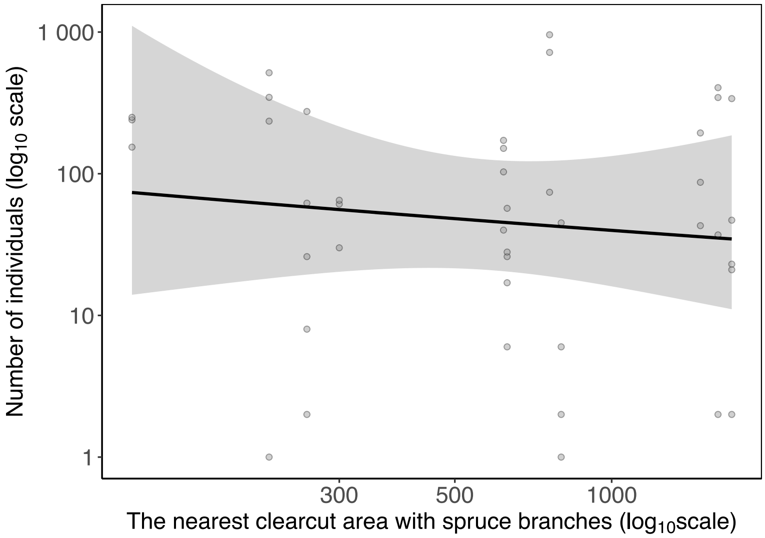

Fig. 6 Dependence of the number of captured *Nemozoma elongatum* individuals on the distance from clear-cuts in spruce forests to pheromone traps baited with bicolorin and Chalcoprax® at 11 sites in the Czech Republic in 2022. A regression curve with a marked 95% confidence interval was fitted by a generalized linear model with negative binomial error distribution and link function log

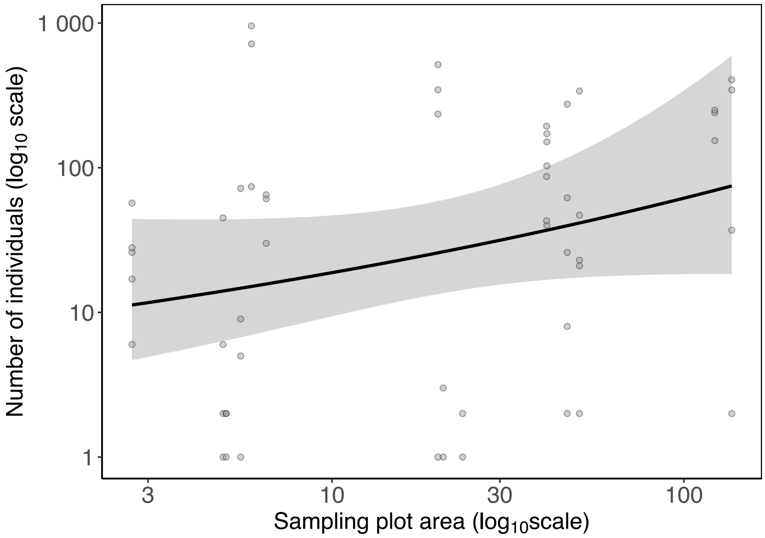

Fig. 7 Dependence of the abundance of *Nemozoma elongatum* captured in pheromone traps baited with bicolorin and Chalcoprax® at sites in the Czech Republic in 2022 on the size of the homogeneous sampling plot area in which the traps were placed. A regression curve with a marked 95% confidence interval was fitted by a generalized linear model with negative binomial error distribution and link function log

1955; Ogris et al. 2020). As a result, the two generations are sometimes difficult to differentiate based on trap catch data due to their widely separated development. In contrast, *N. elongatum* has only one generation per year (Dippel 1994). As found in our study, *N. elongatum* was also captured by other authors from May to September, but the number of individuals caught from July onwards was low and decreased until September (Hellrigl and Schwenke 1985; Baader and Vité 1986; Vaupel et al. 1987; Roediger 1988; Wigger 1996a). Adults *N. elongatum* become active in early spring (Baier 1991) as they search for food, such as bark beetles in gallery systems (Heuer and Vité 1984; Baier 1991). The lifespan of *N. elongatum* is 3–5 months, which covers almost the entire growing season (Dippel 1996). We hypothesize that later in the year, *N. elongatum* is less likely to be caught in pheromone traps because they exhibit thigmotactic responses at short distances, climb into the entrance holes of bark

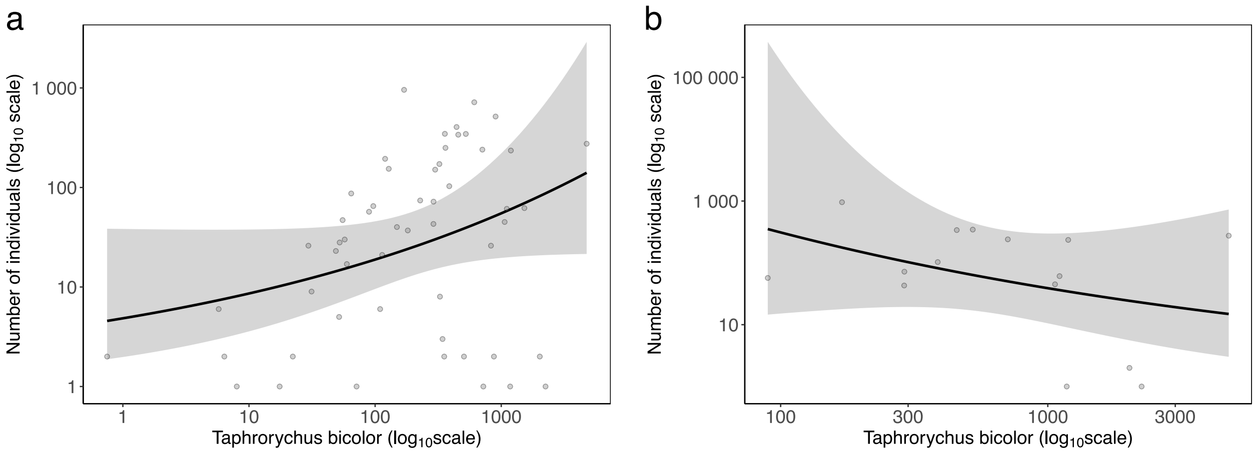

Fig. 8 Dependence of the log-transformed abundance of *Nemozoma elongatum* on the abundance of its prey, *Taphrorychus bicolor*, captured in pheromone traps baited with bicolorin for the entire season (**a**) and in May (**b**) at sites in the Czech Republic in 2022. Regression curves with a marked 95% confidence interval were fitted by a generalized linear model with negative binomial error distribution and link function log

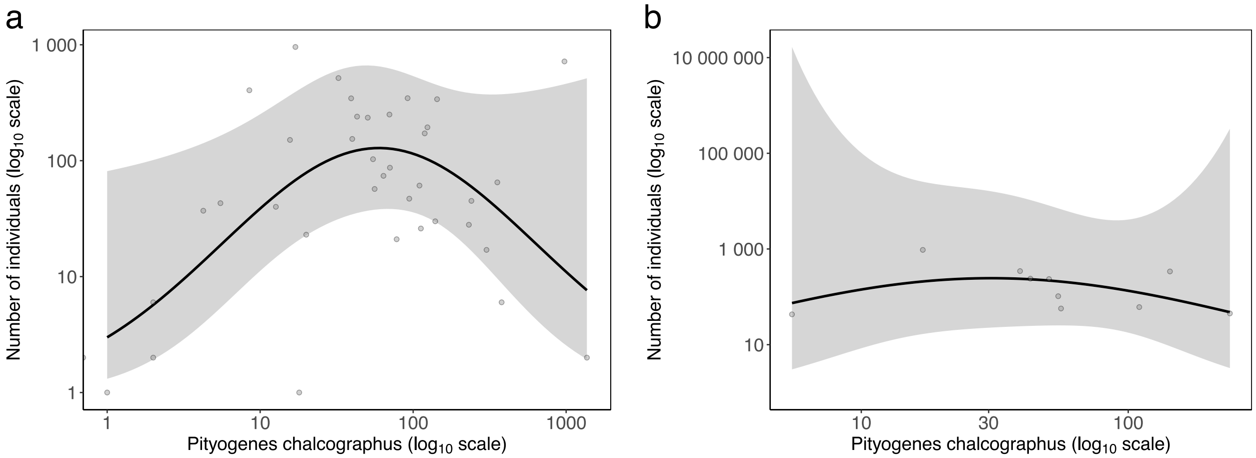

Fig. 9 Dependence of the log-transformed abundance of *Nemozoma elongatum* on the abundance of its prey, *Pityogenes chalcographus*, captured in pheromone traps baited with Chalcoprax® for the entire season (**a**) and in May (**b**) in the Czech Republic in 2022. Regression curves with a marked 95% confidence interval were fitted by a generalized linear model with negative binomial error distribution and link function log

beetles (Heuer and Vité 1984), and no longer fly. Having consumed all larvae of bark beetle, the hatched *N. elongatum* larvae also emerge from the gallery system in search of more food (Baier 1991), specifically to occupy new bark beetle tunnel systems. Female of *N. elongatum* lay eggs for approximately 2 months until late summer (Baier 1991), and the larvae that hatch later will find the bark beetles of the following generation. Even adult bark beetles are suitable preys for *N. elongatum* larvae, but they can only hunt directly in gallery systems because they do not have a grasping front pair of legs (Baier 1991; Wigger 1996a). Field studies have shown that after oviposition in late April or May, most offspring of *N. elongatum* overwinter in the third larval stage (Dippel 1994). However, at several study sites, higher beetle catches were recorded in July and August, corresponding to a new filial generation that has undergone a developmental period of 110 days (Dippel 1994).

4.2 Sex ratio of *Nemozoma elongatum*

Analysis of the genitalia of captured *N. elongatum* showed that more males than females were captured in traps using both baits, bicolorin, and Chalcoprax. The reason for this result is unclear, but both sexes are attracted to bark beetle kairomones (see Baier 1991; Mizell III et al. 1984). We did not find any studies that examined whether male and female predators of bark beetles respond differently to kairomones.

One potential explanation is that males are more active and actively search for individual bark beetle gallery systems that females may already occupy (Wigger 1996a). Consequently, males may be more mobile and repeatedly search for *P. chalcographus* gallery systems using the scent of kairomones while looking for females inside the gallery system. Conversely, the female may no longer search for a new gallery system for a longer period once it lays eggs. Therefore, we speculate that males respond better to pheromones.

Another potential reason for the low number of females captured in traps could be that egg-laying females cannot fly during oviposition due to the enlarged ovaries, which occupy substantial space, and underdeveloped flight muscles. This phenomenon of muscle degeneration is common among insects transitioning from dispersal to reproduction, as resources such as proteins from flight muscles are reallocated to egg production and other reproductive functions (Johnson 1957). It has been observed in several bark beetle species, where flight muscles degenerate and regenerate following the initiation of gallery construction (Chapman 1956; Borden and Slater 1969; Langor 1987; Robertson 1998). Therefore, a higher proportion of *N. elongatum* females is likely to swarm in the spring after hibernation. Although the extent of this process in bark beetle predators has been less thoroughly studied, it is plausible that similar physiological mechanisms are at play, especially in species requiring rapid shifts from dispersal to predation or reproduction.

4.3 Olfactory responses and predatory behavior of *Nemozoma elongatum* towards bark beetle species

Adults of *N. elongatum* respond to pheromones from both main prey species, i.e., *T. bicolor* and *P. chalcographus*. However, more *N. elongatum* beetles in the same habitat were caught with Chalcoprax than with bicolorin, suggesting that *P. chalcographus* is the primary prey of *N. elongatum*, as previously reported by Dippel (1996). Although the reaction of *N. elongatum* to bicolorin has not been experimentally confirmed and was only reported in a patent (Zuhlke and Müller 2007), they have listed a response to chalcogran (ethyl-1,6-dioxaspiro[4.4] nonane) + methylbutenol or methylbutinol + methyl (2E,4Z)-2,4-decadienoate (Chalcoprax) (e.g. Achtnicht 2008), cis-verbenol + grandisol, i.e., the pheromone of *Pityophthorus pityographus* (Ratzeburg, 1837) (Francke et al. 1987) and vittatol, i.e., the pheromone of *Pteleobius vittatus* (Fabricius, 1787) (Klimitzek et al. 1989). This is, therefore, the first published evidence of *N. elongatum*'s response to bicolorin.

N. elongatum exhibits thigmotactic responses (Heuer and Vite 1984). It enters bark beetle gallery systems, feeding on adult bark beetles and laying eggs in the corridors. The hatched larvae then burrow through bark beetle corridors and gradually feed on prey larvae (Baier 1991). This behavior explains the wide prey spectrum (Kleine 1909; Nikitsky 1974; Nass 1993 in Wigger 1996b), including olfactorily indifferent bark beetles colonizing the same host as the primary prey (Heuer and Vite 1984).

Wigger (1993) described the significant role of pheromone components in *N. elongatum*. Research has proven that the species responds to the pheromones of at least five bark beetle species (see above), indicating that it is likely responsive to a broad spectrum of bark beetle pheromones. Wehnert and Müller (2012) confirmed its reaction to cis-verbenol, and it is possible that *N. elongatum* also responds to the pheromones of *Ips typographus* (Linnaeus, 1758), as more individuals were captured using Pheroprax® than pure cis-verbenol (Wehnert and Müller 2012). However, considering that *I. typographus* is larger than *P. chalcographus* or *T. bicolor*, it is improbable to be the primary species in their diet. Therefore, it is evident that the addition of Chalcoprax to Pheroprax enhanced the response (Wigger 1993).

Wigger (1993) reported that the catches of *N. elongatum* in ethanol and Linoprax® baited traps increased only after adding Chalcoprax. However, *N. elongatum* could probably respond to pure ethanol or α-pinene, similar to the North American trogossitid *Temnoscheila virescens* Fabricius, 1801 (Miller 2023). Like Wigger (1993) findings, *T. virescens* showed higher catches when combining lures releasing pine host kairomones (ethanol + α-pinene) with lures releasing bark beetle pheromones (ipsenol + ipsdienol) (Miller and Asaro 2023). The ability to eavesdrop on bark beetle pheromones could further enhance the likelihood of predators finding prey, especially for species that need to locate larvae of bark and woodboring beetles promptly for their larvae to feed on (Miller et al. 2023).

The ability to switch target prey in response to prey availability is an important trait for generalist predators (Brin and Bouget 2018). *N. elongatum* is undoubtedly a generalist. However, most of the existing scientific literature has focused on the intensity of consumption of larvae and pupae of *P. chalcographus* (Baier 1991, 1994; Dippel 1991, 1996), which has created the impression that it is a specialist on this prey (Sakamoto 2007). The preference for *P. chalcographus* as prey is evidenced not only by the higher catches of the predator with Chalcoprax but also by the fact that fewer *N. elongatum* were caught when clear-cuts in spruce forests with remaining branches, where *P. chalcographus* proliferates, were farther away. Higher numbers of *N. elongatum* flew from these areas into pheromone traps.

4.4 Quantitative response of *Nemozoma elongatum* to prey abundance

A positive correlation was found between the number of *N. elongatum* individuals trapped and the numbers of both prey species, *T. bicolor* and *P. chalcographus*. Throughout the season, responses from all catches vary. This indicates better synchronization with the development of *T. bicolor* as both the full-season and May dependencies increase. Conversely, minimal synchronization is observed with *P. chalcographus*, likely because the filial generation of *P. chalcographus* in traps tends to be more numerous (e.g., Galko et al. 2017), whereas *N. elongatum* catches decrease. However, if we compare only May catches, the period when all three species emerge from overwintering parental generation, the numbers characterize the population densities of all three species at the site, and the dependence on both prey species is linear. This indicates that the abundance of *N. elongatum* depends on the population densities of both prey species, expressed by the number of overwintering beetles caught in a linear relationship. If there was an influence, the response would have to be diametrically different (Lacitignola et al. 2016).

The populations of *N. elongatum* and *T. bicolor* show a clear linear increase, as indicated by simple experiments (Harz and Topp 1999). The numerical response of *N. elongatum* to the abundance of *P. chalcographus* is evident from Wigger's (1996b) three-year observations, indicating that *N. elongatum* predators are not significantly reducing the population density of *T. bicolor* (see also Harz and Topp 1999) or *P. chalcographus*. While studies on the feeding habits of adults and larvae, as well as the high abundance of *N. elongatum*, suggest that this predator may have a significant negative impact on the reproduction of *P. chalcographus* (Baier 1994; Dippel 1996), this fact is confirmed, even though observations are limited only to a few cases. Unsuccessful colonization of *T. bicolor* resulted in male mortality (approximately 1/5) due to sap exuding (90%) and predators (10%), with only one case of *N. elongatum* predation (10%). At the same time, the rest flew elsewhere (4/5) (Zach et al. 2002).

4.5 Bark beetles and predator trap capture ratio

When using individual traps baited with bicolorin, 6 to 931 *N. elongatum* individuals were trapped, representing 0.1% to 15% of the total catch. Captures of this species on traps baited with *P. chalcographus* lures were as high as one-fifth (Wigger 1996b). Still, the average capture ratio is significantly lower at only 0.1–2.1% (Wigger 1996b). However, when trapped in a habitat unrelated to the bark beetle species, such as *P. chalcographus* in beech forests, the proportion of *N. elongatum* may be high (see Table 3) because *P. chalcographus* flies from a distance. Previous research by Wigger (1993) showed percentages varying significantly from 0.4 to 79% (Wigger 1993). Therefore, evaluating the proportion of *N. elongatum* trapped relative to the species in whose habitat or forest the traps were installed is essential.

4.6 Implication for pest management

Although *N. elongatum* does not significantly suppress the populations of its prey, its response to the pheromones of its prey can be exploited as "allochthonous kairomones" (see Wehnert and Müller 2012). By strategically placing pheromones, we could increase the population of *N. elongatum* in specific areas without increasing pest populations. There is an advantage in the case of *N. elongatum* since its two main prey species inhabit diametrically different trees. Thus, in monospecific managed commercial forests, it is potentially useful to attract *N. elongatum* with bicolorin to areas in spruce forests with epidemic levels of *P. chalcographus*, and conversely with Chalcoprax in beech forests.

However, to assess *N. elongatum* potential for management purposes, it will be important to study whether we can indeed increase the population of *N. elongatum* locally and, subsequently, whether predation has an impact on different prey species and in various types of environments. Furthermore, the artificial spatial concentration of the predator using allochthonous kairomones could negatively affect the reproductive performance of *N. elongatum* itself, as larvae may become cannibalistic at high local densities (Baier 1991). Therefore, the spatially limited application of allochthonous kairomones to attract predators and control bark beetle outbreaks could result in reduced predator populations the following year due to excessive cannibalism.

5 Conclusion

N. elongatum is a prey opportunist that responds to the aggregation pheromones of bark beetles, as confirmed for several bark beetle species. *N. elongatum* is caught in large numbers in traps with Chalcoprax, as has long been known. Still, it is also attracted to traps lured with bicolorin, the aggregation pheromone of *T. bicolor*. Although it is caught more frequently with Chalcoprax, suggesting a preference for *P. chalcographus*, it may also consume various other species. This is because *N. elongatum* is attracted to the volatile compounds emitted by the host trees of bark beetles and moves thigmotactically across the trees, occupying galleries of different bark beetle species. Consequently, effectively trapping it during the season or luring it elsewhere is not feasible.

We believe that *N. elongatum* may not significantly affect the prey population numbers, as both the predator and the prey populations are increasing. Asynchrony of development time, voltinism, and differences in spring swarming behavior between prey (*P. chalcographus* and *T. bicolor*) and predator may be the main reasons why the generalist predator *N. elongatum* principally fails to control outbreaking (escaping) prey populations (because of widespread drought stress, abiotic disturbances (wind and snow damage) and/or surplus supply of food resources (logging residues).

However, there is potential to use Chalcoprax as an "allochthonous kairomone" in beech forests. Conversely, bicolorin could be used to increase *N. elongatum* abundance in spruce thickets. However, this issue necessitates further investigation and meticulous field experiments to ensure a comprehensive understanding.

Pheromone traps with bicolorin capture tens to hundreds of *N. elongatum*, making up to 5% of the total catch. The impact of trapping on the *N. elongatum* population is expected to be minimal. Generally, pheromone traps should not be used to control both species, *T. bicolor* and *P. chalcographus*, as both species are very abundant, and these traps cannot effectively control their populations. The use of bicolorin is recommended only for monitoring. For this purpose, it is sufficient to prepare beech trapping branches and check for the presence of *T. bicolor*.

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Authors' contributions

Conceptualization: Jaroslav Holuša, Tomáš Fiala; methodology: Jaroslav Holuša, Karolina Resnerová; formal analysis and investigation: Jaroslav Holuša, Karolina Resnerová, Barbora Dvořáková, Jan Šipoš, Jaromír Hradecký, Tomáš Fiala; writing—original draft preparation: Jaroslav Holuša, Karolina Resnerová, Barbora Dvořáková, Jan Šipoš, Jaromír Hradecký, Tomáš Fiala; writing—review and editing: Jaroslav Holuša, Karolina Resnerová, Barbora Dvořáková, Jan Šipoš, Jaromír Hradecký, Tomáš Fiala; Resources: Jaroslav Holuša; Supervision: Jaroslav Holuša. The authors read and approved the final manuscript.

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Data availability

The datasets generated during and/or analyzed during the current study are available here https://doi.org/10.5281/zenodo.14543665.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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