EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **122**: 184–188, 2025
doi: 10.14411/eje.2025.023
ORIGINAL ARTICLE

Effect of local and exotic origin of Asteraceae seeds on their consumption by ground beetles (Coleoptera: Carabidae)

Alois HONĚK[1], Zdenka MARTINKOVÁ[1] and Stano PEKÁR[2]

[1] Czech Agrifood Research Center, Drnovska 507, 161 00 Praha 6, Czech Republic; e-mails: alois.honek@carc.cz, zdenka.martinkova@carc.cz

[2] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic; e-mail: pekar@sci.muni.cz

Key words. *Pseudoophonus rufipes*, *Harpalus affinis*, enemy escape hypothesis, seed preference

Abstract. Prior familiarity of carabid beetle populations with seeds of a plant species might result in a preference for locally available species, either due to evolutionary adaptation or learning. Rejection of exotic species might favor the survival of the exotic species due to enemy release. In adults of two Carabidae species, *Pseudoophonus rufipes* (DeGeer) and *Harpalus affinis* (Schrank), we investigated the consumption of seeds of the local (growing inside the distribution range of experimental carabid individuals) Asteraceae species *Taraxacum officinale* and *Crepis biennis*, and the exotic (growing outside this area) Asteraceae species *Adenostyles alliariae* and *Homogyne alpina*. We assumed that the seeds of the exotic species would be consumed less than the seeds of the local species because the seeds of exotic species are not typically found within the range of the tested carabid populations and therefore may be preferred less than the seeds of local species. The seeds of both exotic species were consumed less than the seeds of the preferred local species, *T. officinale*, but were consumed more than the seeds of the rejected local species, *C. biennis*. Both carabid species preferred *A. alliariae* seeds over *H. alpina* seeds. No difference was observed between the preferences of the mobile and well-flying species *P. rufipes* and the sedentary and rarely flying *H. affinis*. The study did not demonstrate the hypothesized preference of the two tested beetle species for the seeds of locally available plant species.

INTRODUCTION

The predation of seeds by ground beetles (Carabidae) has been studied in detail (Kulkarni et al., 2015). The intensity of seed predation for a particular plant species varies and depends on both the species of plant and species of carabids. Seed consumption depends on several factors, particularly seed size (Honek et al., 2003, 2007), and the mechanical (Fofová et al., 2020) and chemical (Kulkarni et al., 2017) properties of the seeds. One factor that has not yet been investigated in relation to seed consumption is the familiarity of the carabid population with the seed species. Like other post-dispersal seed predators, carabids may exhibit different preferences for seeds of plant species with which they come into contact in the local outdoors versus those from species that these predators cannot encounter because these plants grow in other geographic areas. In this work, the seeds of herb species growing in the area from which the carabid populations used as predators originate are designated “local,” the seeds of herb species growing outside this area – which these carabid populations could not encounter – are designated “exotic.” We therefore tested the hypothesis that one factor influencing seed consumption is the correspondence between the geographic origin of the carabid population being tested and that of the geographic origin of the plant species providing the tested seeds. This may result from coevolution of the carabid population and local herb flora or from experience with the taste of food during the ontogenetic development of the experimental animals before the start of the experiment. Experimental animals were presented with either seeds from plant species growing at the location where the tested carabid population was collected (hereafter, “seeds of local plant species”) or seeds from plant species growing outside the distribution area of the tested carabid species (hereafter, “seeds of exotic plant species”).

Rejection of seeds of exotic species may contribute to their high invasive capacity by releasing them from seed predation pressure imposed by herbivores in their area of origin. This expectation is formulated and predicted by the enemy-release hypothesis (Castells et al., 2013). However, the contrary situation can also occur: seeds of exotic species might be preferred because they are attractive and new to local predators. Exotic seed species then will be preferred over local seed species. These rare cases, referred to as “new association,” have been observed in pre-dispersal seed predators (Cogni, 2010).

In accordance with the enemy-release hypothesis, we assumed that seeds of exotic species would be consumed reluctantly, i.e., less than seeds of the rejected local *Asteraceae* species, *C. biennis*. Predation on these two species truly reflects the range of acceptance of local seeds by carabid beetles. In contrast, if there was no difference in preference for local and exotic seed species, the consumption of exotic species would fall within the range observed for local seed species. That is, the exotic seed species would be consumed less than the preferred *T. officinale* and more than the rejected *C. biennis*. This could occur if carabids do not perceive a fundamental difference between the properties of local and exotic seed species. A third possibility may also emerge in the experiments – that ground beetles would consume exotic seed species more than preferred local seed species. This case then would be a "new association" (sensu Cogni, 2010) between carabid preference and seed qualities. We studied these predictions using two abundant local seed-eating carabids, seeds of two abundant local *Asteraceae* species – one preferred and one rejected – and seeds from two exotic *Asteraceae* species.

MATERIAL AND METHODS

Carabids

We tested the seed preferences of two seed-eating species of Carabidae (Coleoptera), *Harpalus affinis* (Schrank) and *Pseudoophonus rufipes* (DeGeer). Both species belong to the tribe Harpalini and are eager seed consumers that prefer seeds as their food. Although both carabid species prefer similar species of seeds (Honek et al., 2003; Saska et al., 2019), *P. rufipes* has higher consumption, likely due to its larger body mass (dry mass 31.3 mg) than *H. affinis* (14.1 mg) (Jorgensen & Toft, 1997; Honek et al., 2007). Both species are common in dry to moderately moist, unshaded habitats such as fields, meadows, ruderals, and forest edges (Hurka, 1996). They live in lowland and submontane regions (Hurka, 1996), avoiding alpine habitats (Obenberger, 1952). *Pseudophonus rufipes* is a good nocturnal flier (Honek & Pulpan, 1983; Zhang et al., 1997; Šustek, 1999), whereas *H. affinis* rarely flies (Holliday & Hagley, 1978).

The beetles used in the experiments were collected from fields surrounding the grounds of the Czech Agrifood Research Centre (formerly Crop Research Institute) in Praha – Ruzyně (50.09°N, 14.30°E), Czech Republic. The carabids were collected using pitfall traps that were exposed in the field for 3 days. The captured beetles were then stored for 3 days in 0.5 L plastic bottles filled with moist filter paper at a temperature of 5–7°C. This storage method prevented cannibalism and standardized hunger levels.

Seeds

Carabids were fed seeds from four herb species belonging to the Asteraceae family, which are similar in shape, mass, and size. The seeds were collected at the time of dispersal and stored in dry conditions at room temperature until the experiment commenced. The thousand-seed mass was determined before the experiment; seed dimensions were obtained from Bojňanský & Fargašová (2007), and seed volume was calculated as that of a rotational ellipsoid. The two local seed species, abundant at the location where the experimental carabid beetles were sampled, were *Taraxacum officinale* Weber in Wiggers (seeds collected on 29.4.2008, seed mass = 0.599 mg, volume = 2.95 mm^3) and *Crepis biennis* (L.) (seeds collected on 14.5.2008, 0.798 mg, 2.20 mm^3). Both species are common in meadows, lawns, ridges, and similar habitats (Kubát et al., 2002). Seeds of both species were sampled in Praha – Ruzyně (50.08°N, 14.30°E, altitude 340 m a.s.l.). The carabid specimens used in the experiments could have prior exposure to these local species.

Exotic species, growing only in areas outside the territory where the experimental carabids were sampled, included *Adenostyles alliariae* (Gouan) Kemer (seeds collected on 1.10.2008 in La Berarde, France, 44.93°N, 6.30°E, altitude 1750 m a.s.l., seed mass = 1.158 mg, volume = 3.00 mm^3) and *Homogyne alpina* (L.) Cass. (seeds collected on 6.8.2008 near Leoben, Austria, 47.35°N, 15.21°E, altitude = 1350 m a.s.l., seed mass = 1.138 mg, volume = 3.00 mm^3). Populations of both exotic herb species nearest to the origin of the carabid populations are found in subalpine and alpine areas, at a minimum of 80 km from where the experimental carabids were collected (Slavík & Štěpánková, 2004). Hence, the carabid specimens used in the experiment did not have prior exposure to these exotic species, which precludes them from having learned to eat these species.

Experimental design

Preference experiments were conducted in cylindrical plastic arenas (9 cm in diameter, 7 cm deep) covered with a flat plastic lid irregularly perforated with holes of 1 mm diameter (Fig. 1). The arenas were filled to a depth of 1 cm with sieved soil that contained no local seeds. The seeds were provided by thirty small crown bottle cups, 2 cm in diameter and 0.5 cm deep, which were filled with white plasticine (Jovi® Barcelona). The seeds were gently pressed into the plasticine surface to ensure that their access to the carabids was not affected.

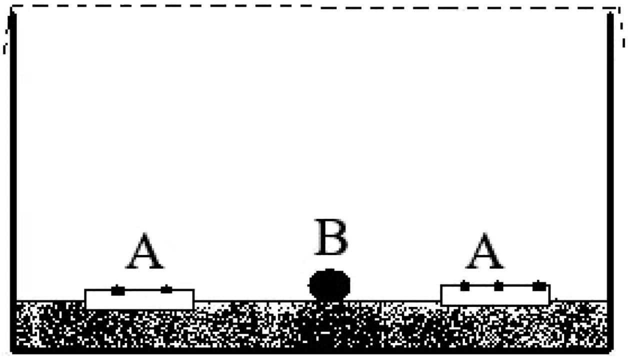

Fig. 1. Schematic representation of an arena in which seeds were presented for predation. The illustration shows a plastic arena covered with a lid perforated with 1 mm diameter holes and filled to a depth of 1 cm with sieved soil. A – crown bottle cups filled with white plasticine, with seeds pressed into the surface of the plasticine. B – a piece of moistened cotton.

The multi-choice experiment consisted of 20 replicates (20 arenas) for the species *P. rufipes* and 20 replicates (20 arenas) for the species *H. affinis*, where each replicate represents one carabid individual given a choice between the seeds of all four plant species. The dual-choice experiments included six experiments, each consisting of 20 replicates (arenas) containing two cups: one with a local seed species and one with an exotic seed species. Each experiment featured one of all six possible local × exotic seed combinations. The experiments were conducted at 25°C under natural photoperiod conditions. The multi-choice experiment lasted four days, from August 3 to August 7, 2009, and the dual-choice experiments lasted four days, from August 31 to September 4, 2009.

The sex of the beetles was determined, and only males were used in the experiments. This was because, in both species of carabids, females represented only 10% of the collected population.

Using both sexes could influence seed consumption, and controlling for this effect would be difficult. One beetle was placed into each arena, and the soil was moistened with 2 ml of tap water. During the experiment, the beetles consumed no food except for the experimental seeds. Water was provided on a piece of moistened cotton. The number of seeds consumed was counted twice daily, at 08:00 and 20:00 h. Cups with fewer than 15 seeds remaining were replaced with new cups containing 30 seeds, ensuring continuous access to all seed species throughout the experiment.

Statistical analysis

As in all experiments, a certain type of randomized complete block design (where the arena was a block) was used. The data were analyzed with methods that can handle correlated data arising from such a design (Zuur et al., 2009; Pekár & Brabec, 2018). Specifically, we used generalized estimating equations (GEE) from the *geepack* package (Yan & Fine, 2004) in the R environment (R Core Team, 2023). GEE is an extension of GLM for correlated data, which uses a marginal approach in the model. The response variables were counts of consumed seeds, so in all analyses, we used Poisson errors with a logarithmic link function and an exchangeable (or compound symmetry) working correlation structure. In the multiple-choice experiments, the linear predictor included an interaction between the two carabid species and the seed species as explanatory variables. In the two-choice experiments, the linear predictor included only seed species. Post hoc comparisons were performed based on treatment contrasts.

RESULTS

Multiple-choice experiment

The number of consumed seeds varied significantly between carabid species, with the larger *P. rufipes* (Fig. 1A) consuming more seeds than the smaller *H. affinis* (Fig. 1B) (GEE-p, $\chi^2_3 = 60.2$, $P < 0.0001$). As expected, consumption also varied by seed species, both in *P. rufipes* (GEE-p, $\chi^2_3 = 316$, $P = 0.014$) and *H. affinis* (GEE-p, $\chi^2_3 = 174.7$, $P < 0.001$), being highest for the preferred local seed *T. officinale* and lowest for the rejected local species *C. biennis*. The consumption of seeds of exotic species was intermediate.

For *P. rufipes* (Fig. 1A), the consumption of *T. officinale* seeds was significantly greater than that of *A. alliariae* seeds (contrast, $P < 0.0001$) and *H. alpina* seeds (contrast, $P < 0.0001$). The consumption of *C. biennis* seeds was significantly lower (contrast, $P < 0.0001$) than that of *A. alliariae* seeds, but it was not significantly lower (contrast, $P > 0.05$) than that of *H. alpina* seeds.

For *H. affinis* (Fig. 1B), the consumption of *T. officinale* seeds was significantly greater than that of *A. alliariae* seeds (contrast, $P < 0.0001$) and *H. alpina* seeds (contrast, $P < 0.0001$). The consumption of *C. biennis* seeds was significantly lower (contrast, $P < 0.01$) than that of *H. alpina* seeds, but it was not significantly lower than that of *A. alliariae* seeds (contrast, $P > 0.05$).

Both carabid species consumed the seeds in significantly different frequencies (GEE-p, $\chi^2_3 = 10.6$, $P = 0.014$).

Dual-choice experiments

In *P. rufipes* (Table 1), the consumption of seeds of the preferred local species *T. officinale* was significantly greater than that of the rejected local species *C. biennis* (GEE-p, $\chi^2_1 = 606$, $P < 0.001$), and the two exotic species *A. alliariae* (GEE-p, $\chi^2_1 = 368$, $P < 0.001$) and *H. alpina* (GEE-p, $\chi^2_1 = 250$, $P < 0.001$). The consumption of seeds of the rejected local species *C. biennis* was significantly smaller than that of both exotic species, *A. alliariae* (GEE-p, $\chi^2_1 = 445$, $P < 0.001$) and *H. alpina* (GEE-p, $\chi^2_1 = 140$, $P < 0.001$). Among the exotic species, the consumption of seeds of *A. alliariae* was significantly higher than that of *H. alpina* (GEE-p, $\chi^2_1 = 20.9$, $P < 0.001$).

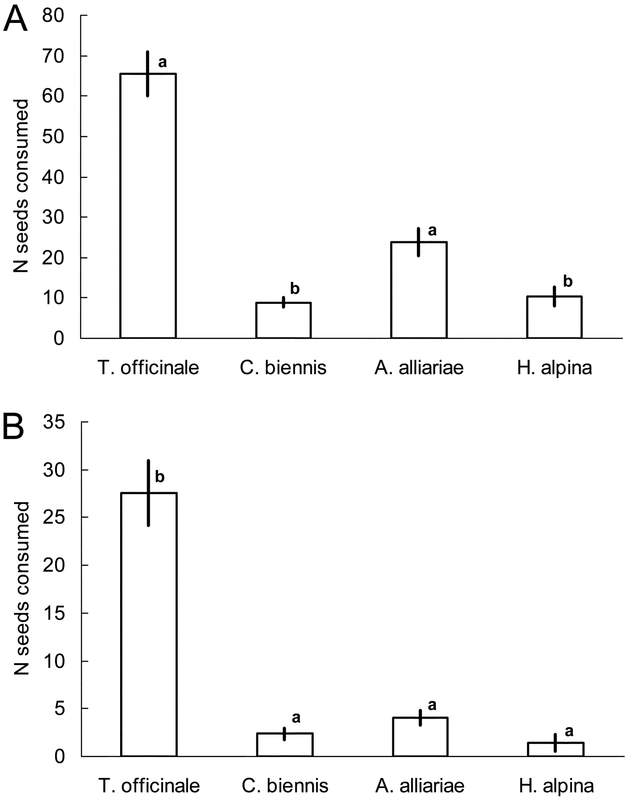

Fig. 2. Empirical number of seeds (± SE) consumed in a multiple-choice experiment by (A) *Pseudoophonus rufipes* and (B) *Harpalus affinis*. Different letters above columns indicate significant differences.

DISCUSSION

Geographical differences in seed species preferences can significantly influence the consumption by pre-dispersal predators. There are notable interspecific differences in seed consumption when predators prefer local over exot-

Table 1. Dual-choice experiments with *Pseudoophonus rufipes*. Each experiment (E) represents one of six possible pairwise combinations of seed species, with N denoting the number of replicates. The seed species and the empirical average number of seeds (X) ± standard error (SE) consumed over 4 days are provided.

E	N	Seed species	X ± SE	Seed species	X±SE
1	20	*T. officinale*	82.7 ± 4.89	*C. biennis*	9.3 ± 0.86
2	20	*T. officinale*	91.1 ± 5.35	*A. alliariae*	23.6 ± 1.97
3	20	*T. officinale*	88.8 ± 4.23	*H. alpina*	10.5 ± 1.63
4	19	*C. biennis*	9.5 ± 1.25	*A. alliariae*	95.8 ± 5.08
5	20	*C. biennis*	8.9 ± 1.64	*H. alpina*	46.2 ± 5.65
6	20	*A. alliariae*	63.15 ± 6.18	*H. alpina*	26.15 ± 4.74

ic species (Moreira et al., 2020; Sun et al., 2022). At the intraspecific level, resistance to predation varies among geographic populations of one plant species (Bogdziewicz et al., 2019). The causes of differences in seed consumption may be chemical (Hornoy et al., 2012; Moreira et al., 2020) or morphological (Bogdziewicz et al., 2019) variations between geographic populations of seeds. Whether preferences for seed species result from coevolution of the carabid population and the local herb flora (i.e., innate preferences) or from experience with the taste of suitable food during ontogenetic development (i.e., learned preferences) requires further study.

The geographic origin of seeds also influences interspecific differences in preference among post-dispersal seed predators. Seeds of plant species introduced from exotic areas are generally less protected from predation than those from native species within the predator's region, meaning local seeds are eaten more than exotic seeds (Fenner & Lee, 2001; Castells et al., 2013). However, this general pattern has not been confirmed in all cases (Blaney & Kotanen, 2001). In the present study, exotic seeds were consumed less than preferred local seeds but more than rejected local seeds. The difference in consumption between exotic seeds and non-preferred local seeds was smaller than the difference between exotic and preferred local seeds. While exotic seeds were not preferred, our results contradict the assumption that seeds of exotic species are entirely protected from predation.

Our findings are valuable because they compare the consumption of local and exotic seeds within the same plant family (Asteraceae), which are similar in shape and size. This similarity likely reduced the influence of morphological and taxonomic differences that could negatively affect the palatability of exotic seeds.

The hypothesis that local seeds would be eaten more than exotic seeds was not confirmed for the studied Asteraceae species. The intensity of consumption of exotic seeds (*A. alliariae* and *H. alpina*) was within the range observed for local species, and the enemy-release hypothesis (Wolfe, 2002) was not supported.

This negative result can be explained by two reasons. First, there is a broad range of suitability for seed predation within local species. The local seeds included both the highly preferred *T. officinale* and the highly rejected *C. biennis*. These represent extreme cases of preference and avoidance in Carabidae (Saska et al., 2019). Consequently, preferences for exotic seeds are likely to fall somewhere between these extremes. Second, the weight, size, and shape of local and exotic seeds did not differ significantly. The mechanical properties and chemical composition of the cotyledons probably differed little between local and exotic species, not enough to be perceived by carabids and thus not to induce a clear preference for local seeds.

For seeds of taxonomically related *Asteraceae* species with similar shape and size, we did not observe an effect of seed origin on the intensity of carabid predation, contrary to what the "enemy-release hypothesis" would predict – namely, a greater preference for seeds of native species (known to predators) than for seeds of exotic species (less known). While predation intensity differed, preferences for native and exotic seeds were not clearly distinguishable.

ACKNOWLEDGEMENTS. We thank L. Kreslová, H. Uhlířová and H. Smutná for their excellent technical assistance. A.H. and Z.M. were supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0423. Additionally, we appreciate AJE (American Journal Experts) for English language editing.

REFERENCES

Blaney C.S. & Kotanen P.M. 2001: Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. — *Can. J. Bot.* **79**: 284–292.

Bogdziewicz M., Espelta J.M., Bonal R. & Abaevi V.D. 2019: Tolerance to seed predation mediated by seed size increases at lower latitudes in a Mediterranean oak. — *Ann. Bot.* **123**: 707–714.

Bojňanský V. & Fargašová A. 2007: *Atlas of Seeds and Fruits of Central and East-European Flora.* Springer, Dordrecht, 1046 pp.

Castells E., Morante M., Blanco-Moreno J.M., Sans X., Vilatersana R. & Blasco-Moreno A. 2013: Reduced seed predation after invasion supports enemy release in a broad biogeographical survey. — *Oecologia* **173**: 1397–1409.

Cogni R. 2010: Resistance to plant invasion? A native specialist herbivore shows preference for and higher fitness on an introduced host. — *Biotropica* **42**: 188–193.

Fenner M. & Lee W.G. 2001: Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. — *N. Zeal. J. Ecol.* **25**: 95–99.

Fofová H., Cavar-Zeljkovic S., Honek A., Martinkova Z., Tarkowski P. & Saska P. 2020: Which seed properties determine the preferences of carabid beetle seed predators? — *Insects* **11**: 757, 13 pp.

Holliday N.J. & Hagley E.A.C. 1978: Occurrence and activity of ground beetles (Coleoptera: Carabidae) in a pest management apple orchard. — *Can. Entomol.* **110**: 113–119.

Honek A. & Pulpan J. 1983: The flight of Carabidae (Coleoptera) to a light trap. — *Věst. Čs. Spol. Zool.* **47**: 13–26.

Honek A., Martinkova Z. & Jarosik V. 2003: Ground beetles (Carabidae) as seed predators. — *Eur. J. Entomol.* **100**: 531–544.

Honek A., Martinkova Z., Saska P. & Pekar S. 2007: Size and taxonomic constraints on seed consumption by adult Carabidae (Coleoptera). — *Basic Appl. Ecol.* **11**: 1–11.

Hornoy B., Atlan A., Tarayre M., Dugravot S. & Wink M. 2012: Alkaloid concentration of the invasive plant species *Ulex europaeus* in relation to geographic origin and herbivory. — *Naturwissenschaften* **99**: 883–892.

Hurka K. 1996: *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlin, 565 pp.

Jorgensen H.B. & Toft S. 1997: Food preference, diet dependent fecundity and larval development in *Harpalus rufipes* (Coleoptera: Carabidae). — *Pedobiologia* **41**: 307–315.

Kubát K., Hrouda L., Chrtek J., Kaplan Z., Kirschner J. & Štěpánek J. 2002: *Klíč ke květeně České republiky (Key to the Flora of the Czech Republic)*. Academia, Praha, 928 pp.

Kulkarni S.S., Dosdall L.M. & Willenborg C.J. 2015: The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: A review. — *Weed Sci.* **63**: 355–376.

Kulkarni S.S., Dosdall L.M., Spence J.R. & Willenborg C.J. 2017: Seed detection and discrimination by ground beetles

(Coleoptera: Carabidae) are associated with olfactory cues. — *PLoS ONE* **12**(1): e0170593, 11 pp.

Moreira X., Abdala-Roberts L., Bruun H.H., Covelo F., DeFrenne P., Galmán A., Gaytán A., Jaatinen R., Pulkkinen P., TenHoopen J.P.J.G. et al. 2020: Latitudinal variation in seed predation correlates with latitudinal variation in seed defensive and nutritional traits in a widespread oak species. — *Ann. Bot.* **125**: 881–890.

Obenberger J. 1952: *Krkonoše a jejich zvířena* (*The fauna of Giant Mountains*). Přírodovědecké nakladatelství, Praha, 292 pp.

Pekár S. & Brabec M. 2018: Generalized estimating equations: A pragmatic and flexible approach to the marginal GLM modelling of correlated data in the behavioural sciences. — *Ethology* **124**: 86–93.

R Core Team 2023: *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/

Saska P., Honek A. & Martinkova Z. 2019: Preferences of carabid beetles (Coleoptera: Carabidae) for herbaceous seeds. — *Acta Zool. Acad. Sci. Hung*. **65**: 55–74.

Slavík B. & Štěpánková J. 2004: *Květena České republiky 7* (*Flora of the Czech Republic 7*). Academia, Praha, 767 pp.

Sun X., Li H., Zhang A., Hirka A., Csoka G., Pearse I.S., Holyoak M. & Xiao Z. 2022: An intercontinental comparison of insect seed predation between introduced and native oaks. — *Integrat. Zool.* **17**: 217–230.

Šustek Z. 1999: Light attraction of carabid beetles and their survival in the city centre. — *Biologia* **54**: 539–551.

Wolfe L.M. 2002: Why alien invaders succeed: support for the escape-from-enemy hypothesis. — *Am. Nat.* **160**: 705–711.

Yan J. & Fine J.P. 2004: Estimating equations for association structures. — *Statist. Med.* **23**: 859–880.

Zhang J., Drummond F.A., Liebman M. & Hartke A. 1997: Phenology and dispersal of *Harpalus rufipes* DeGeer (Coleoptera: Carabidae) in agroecosystems in Maine. — *J. Agric. Entomol.* **14**: 171–186.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. & Smith G. 2009: *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, 574 pp.

Received April 1, 2025; revised and accepted July 18, 2025