Acta Zoologica Academiae Scientiarum Hungaricae 65(4), pp. 335–348, 2019
DOI: 10.17109/AZH.65.4.335.2019

HABITAT USE OF AN ENDANGERED BEETLE *CARABUS HUNGARICUS* ASSESSED VIA RADIO TELEMETRY

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Carabus hungaricus is an endangered habitat specialist of tall-grass steppe occurring in the Pannonian region. In this study, we used radio telemetry to examine whether habitat type (different habitat patches in steppe mosaic), sex, time of day, temperature and air pressure affect the activity of this species. During the reproductive period of *C. hungaricus* in October 2017, we equipped ten individuals, five males, and five females, with small 0.3 g VHF transmitters and tracked them for seven consecutive days. The average speed of tagged individuals was 1.29 m/h for the fastest individual and 0.21 m/h for the slowest one. The shape of trajectories indicated random walk; only in few cases did beetles cover larger distances between two tracking sessions. Habitat type significantly affected beetle movement; the average speed was higher in grassy patches and common juniper stands, while it decreased in mosses and litter under shrubs. Although there was no effect of sex, time of day, or air pressure on beetles' activity, the temperature had a positive effect on movement. Beetles' movement patterns indicated preferred patches within the assumed optimal habitat. The availability of suitable patches within steppe mosaic can be therefore crucial for the persistence of this species.

Keywords: Natura 2000, insect movement, PicoPip radio-transmitters, steppe mosaic, temperature, *Carabus hungaricus*

INTRODUCTION

Movement behaviour is a crucial aspect of the ecology of a species and determines its occurrence in the environment (Allen & Singh 2016). Whereas dispersal is essential to colonize new suitable habitats at landscape/regional scales (Bowler & Benton 2005), different behavioural patterns occur at smaller local scales, influencing spillover between neighbouring habitats (i.e. asymmetric movement of individuals from one habitat patch to another) or fine-scale movements within the particular habitat (Wallin & Ekbom 1988, Tscharntke *et al.* 2005). However, a habitat perceived uniform by the human observer does not necessarily represent relevant within-habitat heterogeneity to a particular insect species (Nève de Mévergnies & Baguette 1990, Charrier *et al.* 1997). This can be especially true for insects with special fine-scale habitat requirements which, however, still can be partially unfolded (Negro *et al.* 2017). When such species also have limited dispersal capacity, they can be threatened by habitat fragmentation, alteration or loss (Ewers & Didham 2006).

Scale-dependent movements of the ground beetles (Coleoptera: Carabidae, hereafter carabids) have already been the focus of ecological studies. Carabids are often used as good indicators of habitat quality (Lövei & Sunderland 1996) because their distribution and movement activity can be affected by various biotic (e.g. sex, breeding season, food distribution) and abiotic (e.g. temperature, humidity, light intensity) factors (e.g. Thiele 1977, Butterfield 1997, Turin *et al.* 2003, Kádár *et al.* 2017, Wehnert & Wagner 2019). Carabid responses to suitable or adverse environmental conditions are manifested in changes in between- and within-habitat utilization (Riecken & Raths 1996, Tuf *et al.* 2012, Kádár *et al.* 2017, Martin-Chave *et al.* 2018). Two different patterns of individual movement can be described: a random walk and lower average speed may suggest preferred habitat and satisfactory prey availability, while a faster, directed movement is an efficient strategy to escape adverse sites or for dispersal of individuals (i.e. migration, Baars 1979, Niehues *et al.* 1996, Růžičková & Veselý 2018).

Movement behaviour of carabids has traditionally been investigated with mark-recapture combined with pitfall trapping of living individuals (Grüm 1971, Rijnsdorp 1980, Nève de Mévergnies & Baguette 1990, Althoff *et al.* 1994, Skłodowski 1999, Matern *et al.* 2007, Volf *et al.* 2018, Wehnert & Wagner 2019). However, obtaining movement data by pitfall trapping has limitations due to its dependence on ground-dwelling activity of the beetles. This could lead to uncertainties between observed (i.e. recorded distance and time between consecutive catches of the same individual) and real, fine-scale trajectory of movement. Consequently, this could lead to bias in registering important behavioural patterns, such as feeding, mating and habitat utilization. One possibility to overcome this problem is direct, continuous observation of an individual in the field. It requires, however, intensive field effort and observing time is often limited (Drees *et al.* 2008). Telemetric approaches may be a promising solution. Radio telemetry is a rapidly developing method, which allows the tracking of large insects, including carabids under natural conditions (Kissling *et al.* 2014). The genus *Carabus* is suitable for radio-tracking due to size and body mass (large-bodied species weigh approximately 1g), so these species can carry even the relatively heavy active transmitters. Although the majority of studies have been done on common European species, including *C. auratus* L., 1760 (Reike 2004), *C. coriaceus* L., 1758 (Riecken & Ries 1992, Riecken & Raths 1996, 2000), *C. hortensis* L., 1758 (Reike 2004), *C. monilis* F., 1792 (Riecken & Ries 1992, Riecken & Raths 2000), *C. nemoralis* O. F. Müller, 1764 (Deichsel 2007), and *C. ullrichii* Germar, 1824 (Růžičková & Veselý 2016, 2018), there are only few papers focusing on threatened species or those with high conservation potential (Negro *et al.* 2008, 2017). Nevertheless, there is a growing use radio telemetry for assessing habitat use of endangered species with disjunctive distribution ranges and special habitat requirements, such as the wetland specialist *C. clathratus* L., 1761 (Jopp 2003) or the endemic habitat specialist of western Italian Alps, *C. olympiae* Sella, 1855 (Negro *et al.* 2008, 2017). Movement patterns provide direct clues for understanding species-habitat interactions and may, therefore, improve species conservation (Allen & Singh 2016).

In this study, we focused on another habitat specialist, *Carabus hungaricus* Fabricius, 1792 that inhabits dry calcareous and sandy grasslands in the Pannonian Basin. The species is highly threatened by habitat loss and fragmentation, and is listed in EU legislation as a typical invertebrate species of Pannonian steppe. Previous research revealed its macro-scale habitat requirements and population structure, size, and between- and within-year dynamic (Pokluda *et al.* 2012, Bérces & Elek 2013). Dispersal abilities and potential barriers to dispersal are also known (Elek *et al.* 2014). These population-level studies leave movement activity at individual-scale unknown, although the understanding of spatio-temporal ecology of *C. hungaricus* is important for developing effective conservation actions.

This lack of knowledge prompted us to explore fine-scale movement patterns of this species in its typical habitat, a tall-grass steppe in Hungary. Since the steppe consists of a microhabitat mosaic of grasses, mosses, bushes, trees, and patches with bare sandy soil, it can be presumed that the utilization of particular patches by the species may vary. Moreover, sex and abiotic factors, such as temperature, humidity, and time of day might also play a role in activity and movement pattern as it was documented for other carabids, (Thiele 1977, Butterfield 1997, Tuf *et al.* 2012, Růžičková & Veselý 2016, 2018) but not for this species (Turin *et al.* 2003). Therefore using radio telemetry, we aimed to clarify the following questions:

(1) How the individuals of *C. hungaricus* utilize the different microhabitat patches of the Pannonian tall-grass steppe vegetation?

(2) Is there any sex-specific difference in movement activity, average speed or detected trajectories?

(3) How the most cardinal environmental conditions, such as temperature, humidity, time of day and air pressure, can affect these measured movement components?

MATERIAL AND METHODS

Study area

Live specimens were collected approximately 50 km southeast of Budapest near the village of Táborfalva, central Hungary. The typical habitat for *C. hungaricus* in this region is the Pannonian sandy grassland (*Festucetum vaginatae*) which covers a total area of 980 ha, approximately 6 km long and 2 km wide (GPS: 47.1048N, 19.3975E). The area is a part of 'Turjánvidék' Natura 2000 site, established to protect valuable and threatened habitats and species, among them the plant species *Iris arenaria* and *Colchicum arenarium*. This site is used as a military training area without any agricultural activity. The average annual rainfall is 520–540 mm with an average yearly temperature of 10.3 °C (min. –17 °C, max. +34 °C, Dövényi *et al.* 2010). The landscape is formed by a mosaic of 1–5 m tall dunes covered with tall-grass vegetation, dominated by *Stipa borystenica*, *Chrysopogon gryllus* and *Festuca vaginata*, together with sporadically scattered shrubs of *Crategus* sp., *Juniperus communis*, and *Berberis vulgaris*. Additionally, the ground is covered by various species of mosses and lichens or remained bare.

Study species

Carabus hungaricus is a medium-sized (22–28 mm) black-coloured ground beetle with dull elytra. It cannot fly due to the reduction of hind wings (Turin *et al.* 2003). Its main activity period is in autumn (September–October) when it reproduces and another, smaller activity peak occurs in the first half of June when the tenerals emerge (Bérces & Elek 2013). Unlike the majority of *Carabus* species, *C. hungaricus* prefers open habitats, and as a dry grassland specialist, it is typical for the Pannonian and steppic biogeographical regions. The species is strictly protected by local legislation or Red-listed in several countries, including Austria (Zulka 2014); the Czech Republic (Veselý *et al.* 2017); Hungary, Moldova (Neculiseanu *et al.* 1992), Slovakia (Holecová & Franc 2001), and Russia (Iliashenko & Iliashenko 2000). In the Pannonian Basin, its populations inhabit sandy grasslands, extending from Serbia in the south, throughout the sandy areas along the Danube River, all the way to Austria and southern part of the Czech Republic to the north. In Hungary, which is the last stronghold of *C. hungaricus*, the most numerous populations inhabit lowland sandy steppes and the largest population has estimated 3,000–8,000 individuals (Bérces *et al.* 2018). This species has been monitored since 2005 by the Duna–Ipoly National Park Directorate to enhance the nature conservation status of the species as a part of the implementation of EU Habitats Directive (92/43/EC).

Radio-tracking and environmental variables

For tracking, we used ten live individuals (five males and five females) captured by unbaited pitfall traps. Using a cyanoacrylate gel glue, we attached small transmitters to the top of beetles' elytra. These PicoPip radio-transmitters (weight 0.3 g, 8 × 5 × 4 mm, 10-day battery life-span, manufactured by Biotrack Ltd., Wareham, UK) had the specific frequencies between 150–151 MHz and 5 cm long antenna directed backward (Fig. 1). The mass of the transmitters varied between 34.5–49.2% of beetle body mass. After mounting the transmitters, beetles were kept separately in plastic boxes for the first few hours until the adhesive completely dried. Afterward, the tagged beetles were released in the study area approximately 5 m apart from each other to avoid mutual interferences and were tracked over seven consecutive days during *C. hungaricus*'s reproduction period at the beginning of October 2017. Using Sika hand-held receiver (Biotrack Ltd.) and Yagi directional antenna, we were able to detect the transmitter signal from about 120 m. Tagged individuals were directly tracked, thus we started the search at the point (fix), where the beetle was found during the previous tracking session, and we followed the signal until we reached the source of the signal with an accuracy of up to 50 cm. At this stage, we stopped localizing the individual due to the risk of trampling because tracked beetles were often hidden under grass, moss or litter. At least four tracking sessions were made every day. For each fix, we recorded GPS coordinates, distance covered between two consecutive tracking sessions to avoid possible GPS errors at small scales, daytime, and type of habitat. Other environmental data, i.e. air temperature, humidity, and changes in air pressure (i.e. variables which can bias the movement of beetles), were obtained from the closest meteorological station operated by National Meteorological Service of Hungary (https://www.met.hu/). At the end of radio-tracking period, we recaptured all specimens and retrieved their transmitters. Then, the beetles were released at original capture locations.

Data analyses

Since the beetles' positions were not recorded at regular time intervals, first we calculated the average speed per hour for each fix as a covered distance divided by given time period. Then, we used the random forest algorithm (the *cforest* function from the 'party' package, Strobl *et al.* 2008) to test the predictive power of the measured variables. Due to the strong negative correlation of air temperature and humidity (Pearson r = -0,796), only the temperature was used for further analysis. To analyse the beetles' movement activity (the average speed per hour) in relation to biotic and abiotic factors, linear mixed models were used. In these models, the response variable was square-root transformed to acquire normal distribution. Habitat (categorical variable with four levels: grass, mosses, leaf litter and bare ground under common juniper stands), sex (categorical), temperature (continuous), air pressure (continuous), and time of day (categorical, two levels: day and night) were used as fixed effects; individual ID as a random effect. For the analysis, we created a full model which contained all explanatory variables, including their interaction with sex. Subsequently, non-significant variables and interactions were gradually removed from the model in a backward selection. We used the *lme* function from the 'nlme' package (Pinheiro *et al.* 2017). As post hoc comparisons of pairwise differences, we used the *glht* function from the 'multcomp' package (Hothorn *et al.* 2008) with Tukey contrasts for multiple comparisons of means (Bretz *et al.* 2010). All analyses given above were conducted in R 3.4.1 (R Core Team 2017).

Fig. 1. Male of *C. hungaricus* with fixed radio-transmitter (photo: Sándor Bérces).

RESULTS

In total, we recorded 309 fixes, 168 were active (i.e. with movement activity) and 141 were stationary. Concerning habitat types, 24 fixes were recorded in leaf litter, 17 in the ground under common juniper stands, 55 in mosses, and 213 in grassy patches. The most active individual covered a total distance of 102.93 m, the slowest one 19.09 m (both individuals were females). The average speed was 1.29 m/h for the fastest beetle and 0.21 m/h for the slowest one, respectively (Table 1). In a few cases, the tracked beetles stayed at the same spot for one or two days. The visual inspection of the shape of recorded trajectories showed that the beetles mostly randomly walked around; only in a few cases did they cover larger distances (Fig. 2). Different habitat patches significantly affected (χ^2 = 15.801, d.f. = 3, P = 0.001) walking speed, which was higher in grass and under common juniper stands, than in mosses and leaf litter under shrubs (Fig. 3a). Sex had no effect on movement activity. Regarding the environmental variables, only temperature (χ2 = 9.177, d.f. = 1, P = 0.002) had a positive effect (Fig. 3b). We found no effect neither of the time of day nor of air pressure.

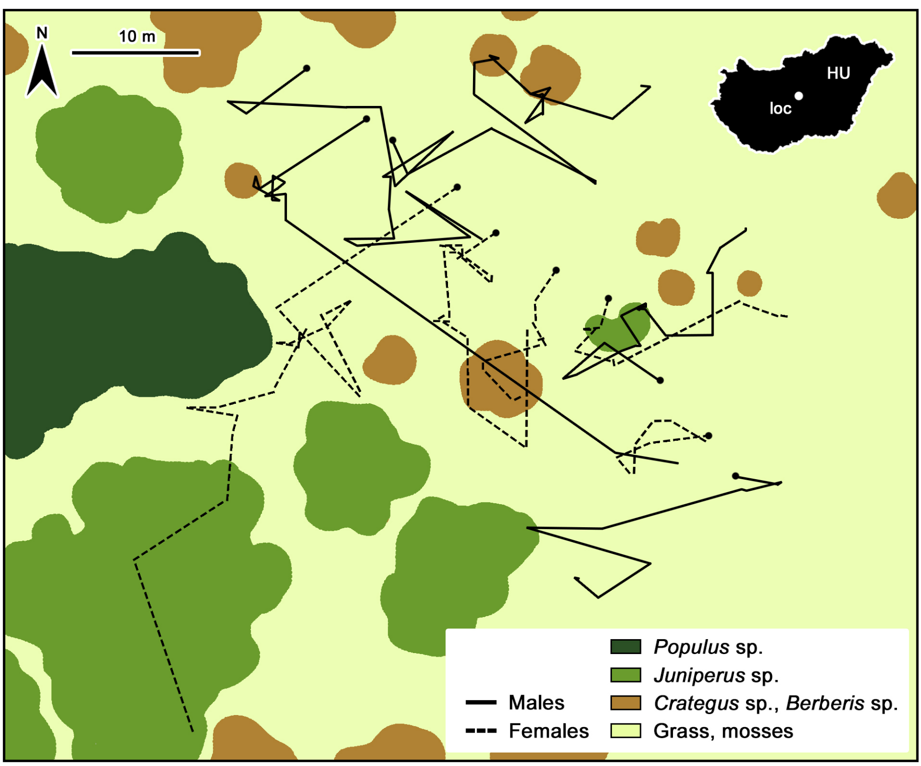

Fig. 2. Movement patterns of all tracked individuals, black dots represent releasing points. In the inserted map of Hungary, "loc" indicates the position of study site.

Table 1. Movement characteristics of radio-tracked individuals: total covered distances and the average speed per hour. Fix_{act} = number of fixes with activity, Fix_{pass} = number of fixes without activity.

No. of individual	Sex	Total distance (m)	Average speed±SD (m/h)	Fix_{act}	Fix_{pass}
1	male	77.45	0.83±1.3	15	13
2	male	64.11	0.57±1.1	13	16
3	male	101.65	1.29±2.2	23	11
4	female	102.93	0.93±1.6	20	16
5	female	54.10	0.67±1.5	23	11
6	female	19.09	0.21±0.4	15	14
7	female	26.90	0.42±1.0	12	16
8	male	51.62	0.62±0.9	26	7
9	female	20.55	0.26±0.6	10	18
10	male	42.94	0.52±1.2	11	19

DISCUSSION

Daily displacement

Individuals of *C. hungaricus* frequently move and active beetles may disperse >1 km within one season (Elek *et al.* 2014). The same study estimated the daily displacement ranging from 8.4 to 20.3 m/day, depending on the study site, sampling design, and spatial arrangement of microhabitats. Here, we recorded similar values (5–31 m/day) using radio-tracking. It seems that *C. hungaricus* is slightly more active than the other *Carabus* species in open habitats, such as

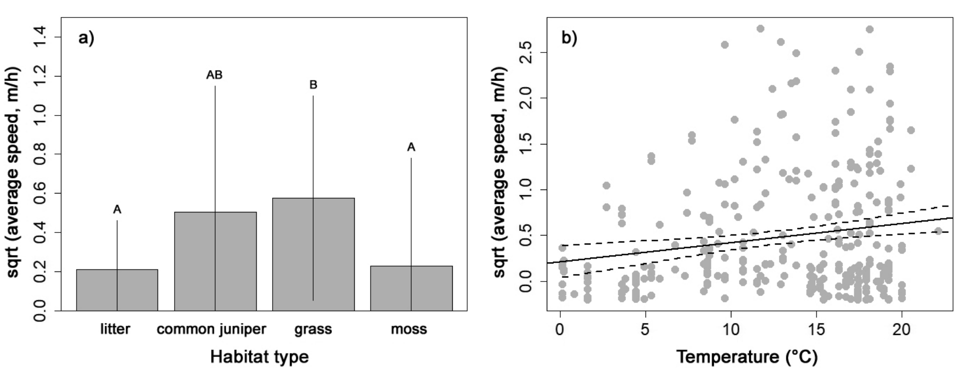

Fig. 3. Responses of the movement activity of *C. hungaricus* to habitat type (a) and temperature (b). Error lines (a) and dashed lines (b) represent 95% confidence interval and capital letters at the bottom of bars indicate significant differences according to Tukey contrasts for multiple comparisons of means.

meadows and fallow lands. For instance, the similar-sized *C. nemoralis* walks only with an average speed of 2.6 m/day (Deichsel 2007), while the much larger *C. clathratus* covers 2.5 m/day (Jopp 2003). For *C. coriaceus*, the speed varies between 2.26–7.32 m/day and for *C. monilis*, it is 9.9 m/day (Riecken & Raths 1996, 2000). The speed of *C. auratus* was estimated by different methods and ranged from 4.3–15.0 m/day (Niehues *et al.* 1996, Reike 2004). *C. hungaricus* can be faster than the other carabids, possibly due to different open habitats and density of vegetation at ground level which can impede the movements of carabids (Mauremooto *et al.* 1995, Szyszko *et al.* 2004, Ranjha & Irmler 2014). Whereas hay meadows are often overgrown by dense tussock grasses, our grassland was a habitat mosaic with bare soil patches that tagged beetles crossed faster. It is important to note that all above mentioned speed values do not represent the maximal reachable speed of species because the time when the tracked individual is inactive is included in the calculations. As previously recorded (Baars 1979, Niehues *et al.* 1996, Riecken & Raths 1996, Růžičková & Veselý 2016, 2018), tagged individuals could stop for several hours or a day, without any movement. The reason for such behaviour still remains unexplored.

Habitat use

The visual inspection of movement patterns (i.e. shapes of recorded trajectories) revealed that the predominance of the random walk might suggest overall suitability of the studied steppe habitat since the directed movement was rare. However, when the average speed is considered, the differences in microhabitat utilization appeared. The tracked individuals were faster in grass and under common juniper stands, while their average speed decreased in mosses, lichens, and leaf litter under *Berberis* and *Crategus* shrubs. Patches, where the average speed was lower, can be considered as favourable due to higher availability of shelter; they may act as oviposition sites due to their relatively stable humidity (Baars 1979, Rijnsdorp 1980). Adult carabids can be highly mobile at small spatial scales (Jopp & Reuter 2005), but other developmental stages are less vagile. Eggs, larvae and pupae are more sensitive to adverse environmental conditions and disturbances than adults and their movement is limited, so they can not simply escape from unfavourable sites. The choice of suitable habitat patches by adults can be therefore the key to persistence of these more threatened life stages (Lövei & Sunderland 1996, Wehnert & Wagner 2019). Our results correspond with previous findings that *C. hungaricus* prefers relatively humid patches with litter in xeric grasslands and tall-grass ruderal vegetation nearby (Čížek *et al.* 2012). The average speed on bare ground under common juniper stands and in grassy parches was higher suggesting the unsuitability of these patches or better permeability.

No sex-specific movement

Previous research revealed that males were more active during the breeding season than females (based on male/female ratio of catches, Bérces & Elek 2013), our radio-tracking, however, found no difference in sex-specific movement patterns: males and females were equally active. Higher male activity exists in several other *Carabus* species (Drees & Huk 2000, Szyszko *et al.* 2004, Kádár *et al.* 2015). These studies used pitfall traps where males could be positively attracted by pheromones to traps containing females (Luff 1986, Baumgartner 2000), creating a bias. Radio-tracking is not influenced by this pheromone-luring effect and showed no differences in walking speed between sexes in several *Carabus* species (Riecken & Raths 1996, Negro *et al.* 2008, Růžičková & Veselý 2018).

Environmental factors affecting movement activity

Although circadian activity patterns in carabids differ considerably between habitat types (forest species tend to be nocturnal whereas grassland species are usually diurnal: Greenslade 1964, Thiele 1977), we found no effect of time of day on the movement activity of *C. hungaricus* during its reproduction period. The dark colour of the species might suggest a nocturnal activity (Lövei & Sunderland 1996), however, no other information about the circadian activity of *C. hungaricus* is available to this date. Since some nocturnal *Carabus* species had a certain degree of daytime activity during their breeding period (Thiele & Weber 1968), it is possible that outside the breeding season, the circadian activity of *C. hungaricus* is different.

The temperature had a positive effect on the activity of *C. hungaricus,* which is not particularly surprising since carabids are ectotherms. Tagged beetles, however, were active even around temperatures near 0°C. As Jaskuła and Soszyńska-Maj (2011) reported, several species of the family Carabidae (adults as well as larvae) can be active also during winter. *C. hungaricus* seems to be a temperature tolerant species because active beetles were observed on the soil surface during sunny days in December (Bérces, unpublished data). Less tolerant is the species at the other end, because it aestivates during the hottest summer days in July (Bérces & Elek 2013). The majority of *Carabus* species has an optimal temperature range when they are active and this optimum can be sex-specific, such as in *C. ullrichii* (Růžičková & Veselý 2018) or *C. granulatus* (Drees & Huk 2000). Temperature plays an important role also in the life history because it can accelerate the maturation of gonads (Sota 1987) or trigger of oogenesis (Althoff *et al.* 1994). Although a previous study reported that females of *C. hungaricus* preferred drier and warmer sites than males (Pokluda *et al.* 2012), our data did not support this conclusion.

Air pressure did not affect the movement activity of tracked *C. hungaricus* individuals. It seems that other environmental factors are more important predictors for species activity than air mass changes. Another explanation might be in the short time tracking period (one week) when the weather was relatively stable without strong changes in front system. In general, the impact of changes in air pressure on activity of carabids is still unexplored and studies focused on this topic are almost missing. Only Kádár and Szentkirályi (1992) found significant effects of cold and warm weather fronts on the flight activity of carabids. For ground-dwelling movement, however, no information exists. Therefore, the link between changes in air-masses and behavioural patterns of carabids, as well as other insects, should be considered in further studies alongside the long-term monitoring.

CONCLUSION

Our radio telemetry recording the fine-scale movement and habitat use of *C. hungaricus* showed that the preferred habitat type was not equally utilized by the species. The availability of suitable patches for various requirements, from feeding to larval development, within habitat mosaic can be crucial for species persistence. For the conservation of *C. hungaricus* in our study site, the steppe should be maintained open and patchy at the fine-scale; thus not only grass but scattered bushes and mosses are required. Such habitat mosaic can be maintained by a low grazing pressure (0.1 livestock unit per ha, only a few months of grazing during the season) alternating with years of non-grazing. Mowing, if necessary, should be targeted to eliminate succession. The connectivity of these patches at landscape/regional scale might be achieved by adjacent set-aside fields because *C. hungaricus* can penetrate such non-crop habitats (Pokluda *et al.* 2012). Our study showed that movement patterns may be an effective tool for habitat use assessment. Future research should be therefore focused on a detailed description of covered trajectories as a proxy for the individual-level response to habitat management.

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Acknowledgements – We are grateful to Annamária Csóka for support within the Turjánvidék Life project (no. LIFE10NAT/HU/000020), György Verő and Ármin Csipak for field assistance and Zoltán Elek and two anonymous reviewers for constructive comments on previous versions of this manuscript.

REFERENCES

Allen, A. M. & Singh, N. J. (2016): Linking movement ecology with wildlife management and conservation. – *Frontiers in Ecology and Evolution* **3**: 1–13. https://doi.org/10.3389/fevo.2015.00155

Althoff, G. H., Hockmann, P., Klenner, M., Nieheus, F. J. & Weber, F. (1994): Dependence of running activity and net reproduction in Carabus auronitens on temperature. Pp. 95–100. *In:* Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J. P. (eds): *Carabid beetles: ecology and evolution*. – Springer, Dordrecht.

Baars, M. A. (1979): Patterns of movement of radioactive carabid beetles. – *Oecologia* **44**: 125–140. https://doi.org/10.1007/BF00346411

Baumgartner, R. (2000): Sexual attraction in Carabus auronitens F.: males lured by females. Pp: 139–145. *In:* Brandmayr, P., Lövei, G., Brandmayr, T. Z., Casale, A. & Vigna-Taglianti, A. (eds): *Natural history and applied ecology of carabid beetles.* – Pensoft, Sofia.

Bérces, S., Csóka, A. & Elek, Z. (2018): Befolyásolja-e a kísérleti elrendezés a magyar futrinka (Carabus hungaricus) populációjának becsült paramétereit? Módszertani esettanulmány a táborfalvai hosszú távú fogás-jelölés-visszafogás kutatásokról. Pp. 679–696. *In:* Korda, M. (ed.): *Természetvédelem és kutatás a Turjánvidék északi részén*. – Rosalia, Duna–Ipoly Nemzeti Park Igazgatóság, Budapest. [in Hungarian]

Bérces, S. & Elek, Z. (2013): Overlapping generations can balance the fluctuations in the activity patterns of an endangered ground beetle species: long-term monitoring of Carabus hungaricus in Hungary. – *Insect Conservation and Diversity* **6**: 290–299. https://doi.org/10.1111/j.1752-4598.2012.00218.x

Bowler, D. E. & Benton, T. G. (2005): Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biological Reviews* **80**: 205–225. https://doi.org/10.1017/S1464793104006645

Bretz, F., Hothorn, T. & Westfall, P. (2010): *Multiple Comparisons Using R.* – CRC Press, Boca Raton, 208 pp.

Butterfield, J. (1997): Carabid community succession during the forestry cycle in conifer plantations. – *Ecography* **20**: 614–625. https://doi.org/10.1111/j.1600-0587.1997.tb00430.x

Charrier, S., Petit, S. & Burel, F. (1997): Movements of Abax parallelepipedus (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. – *Agriculture, Ecosystems & Environment* **61**: 133–144. https://doi.org/10.1016/S0167-8809(96)01101-2

Čížek, L., Hauck, D. & Pokluda, P. (2012): Contrasting needs of grassland dwellers: habitat preferences of endangered steppe beetles (Coleoptera). – *Journal of Insect Conservation* **16**: 281–293. https://doi.org/10.1007/s10841-011-9415-6

Deichsel, R. (2007): *Habitatfragmentierung in der urbanen Landschaft – Konsequenzen für die Biodiversität und Mobilität epigäischer Käfer (Coleoptera: Carabidae und Staphylinidae) am Beispiel Berliner Waldfragmente*. – Ph.D. Thesis, Freien Universität Berlin.

Dövényi, Z., Ambrózy, P., Juhász, Á., Marosi, S., Mezősi, G., Michalkó, G., Somogyi, S., Szalai, Z. & Tiner, T. (2010): *Magyarország kistájainak katasztere.* – MTA Földrajztudományi Kutatóintézet, Budapest. [in Hungarian]

Drees, C. & Huk, T. (2000): Sexual differences in locomotory activity of the ground beetle Carabus granulatus L. Pp. 133–138. *In:* Brandmayr, P., Lövei, G. L., Brandmayr, T. Z., Casale, A. & Vigna-Taglianti, A. (eds): *Natural history and applied ecology of carabid beetles*. – Pensoft, Sofia.

Drees, C., Matern, A. & Assmann, T. (2008): Behavioural patterns of nocturnal carabid beetles determined by direct observations under red-light conditions. Pp. 20–24. *In:* Penev, L., Erwin, T. & Assmann, T. (eds): *Back to the roots and back to the future? Towards a new synthesis between taxonomic, ecological and biogeographical approaches in Carabidology*. – Pensoft, Sofia.

Elek, Z., Drag, L., Pokluda, P., Čížek, L. & Bérces, S. (2014): Dispersal of individuals of the flightless grassland ground beetle, Carabus hungaricus (Coleoptera: Carabidae), in three populations and what they tell us about mobility estimates based on mark–recapture. – *European Journal of Entomology* **111**: 663–668. https://doi.org/10.14411/eje.2014.080

Ewers, R. M. & Didham, R. K. (2006): Confounding factors in the detection of species responses to habitat fragmentation. – *Biological Reviews* **81**: 117–142. https://doi.org/10.1017/S1464793105006949

Greenslade, P. J. M. (1964): The distribution, dispersal and size of a population of Nebria brevicollis (F.), with comparative studies on three other Carabidae. – *The Journal of Animal Ecology* **33**: 311–333. https://doi.org/10.2307/2633

Grüm, L. (1971): Spatial differentiation of the Carabus L. (Carabidae, Coleoptera) mobility. – *Ekologia Polska* **19**: 1–34. https://doi.org/10.1007/BF00380922

Holecová, M. & Franc, V. (2001): Červený (ekosozologický) zoznam chrobákov (Coleoptera) Slovenska. Pp. 111–128. *In:* Baláž, D., Marhold, K. & Urban, P. (eds): *Červený zoznam rastlín a živočíchov Slovenska*. – Ochrana prírody, Štátna ochrana prírody Slovenskej republiky, Banská Bystrica. [in Slovak]

Hothorn, T., Bretz, F., Westfall, P. & Heiberger, R. M. (2008): Multcomp: Simultaneous inference in general parametric models. – *Biometrical Journal* **50**: 346–363. https://doi.org/10.1002/bimj.200810425

Iliashenko, V. Y. & Iliashenko, E. I. (2000): *Krasnaya kniga Rossii: pravovye akty*. – State committee of the Russian Federation for Environmental Protection, Moscow. [in Russian]

Jaskuła, R. & Soszyńska-Maj, A. (2011): What do we know about winter active ground beetles (Coleoptera, Carabidae) in Central and Northern Europe? – *ZooKeys* **100**: 517–532. https://doi.org/10.3897/zookeys.100.1543

Jopp, F. (2003): *Empirische Analysen und Modellierungen des Ausbreitungsverhaltens von Wirbellosen aus einem Niedermoor*. – Ph.D. Thesis, Freien Universität Berlin.

Jopp, F. & Reuter, H. (2005): Dispersal of carabid beetles – emergence of distribution patterns. – *Ecological Modelling* **186**: 389–405. https://doi.org/10.1016/j.ecolmodel.2005.02.009

Kádár, F., Andorkó, R. & Elek, Z. (2017): Reproductive characteristic and habitat selection of Carabus ullrichii (Coleoptera: Carabidae) in woodland habitats in Hungary. – *Acta Zoologica Academiae Scientiarum Hungaricae* **63**: 343–354. https://doi.org//10.17109/AZH.63.3.343.2017

Kádár, F., Fazekas, J. P., Sárospataki, M. & Lövei, G. L. (2015): Seasonal dynamics, age structure and reproduction of four Carabus species (Coleoptera: Carabidae) living in forested landscapes in Hungary. – *Acta Zoologica Academiae Scientiarum Hungaricae* **61**: 57–72. https://doi.org/10.17109/AZH.61.1.57.2015

Kádár, F. & Szentkirályi, F. (1992): Influences of weather fronts on the flight activity of ground beetles (Coleoptera, Carabidae). Pp. 500–503. *In:* Zombori, L. & Vásárhelyi, T. (eds): *Proceedings of the Fourth European Congress of Entomology and the XIII. Internationale Symposium für die Entomofaunistik Mitteleuropas.* – Hungarian Natural History Museum, Budapest.

Kissling, W. D., Pattemore, D. E. & Hagen, M. (2014): Challenges and prospects in the telemetry of insects. – *Biological Reviews* **89**: 511–530. https://doi.org/10.1111/brv.12065

Lövei, G. L. & Sunderland, K. D. (1996): Ecology and behavior of ground beetles (Coleoptera: Carabidae). – *Annual Review of Entomology* **41**: 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311

Luff, M. L. (1986): Aggregation of some Carabidae in pitfall traps. Pp. 386–397. *In:* den Boer, P. J., Luff, M. L., Mossakowski, D. & Weber, F. (eds): *Carabid beetles: Their adaptations and dynamics.* – Fischer, Stuttgart.

Martin-Chave, A., Béral, C., Mazzia, C. & Capowiez, Y. (2018): Agroforestry impacts the seasonal and diurnal activity of dominant predatory arthropods in organic vegetable crops. – *Agroforestry Systems* 1–17. https://doi.org/10.1007/s10457-018-0309-4

Matern, A., Drees, C., Meyer, H. & Assmann, T. (2007): Population ecology of the rare carabid beetle Carabus variolosus (Coleoptera: Carabidae) in north-west Germany. – *Journal of Insect Conservation* **12**: 591–601. https://doi.org/10.1007/s10841-007-9096-3

Mauremooto, J. R., Wratten, S. D., Worner, S. P. & Fry, G. L. A. (1995): Permeability of hedgerows to predatory carabid beetles. – *Agriculture, Ecosystems & Environment* **52**: 141–148. https://doi.org/10.1016/0167-8809(94)00548-S

Neculiseanu, Z. Z., Stratan, V. S., Vereşciaghin, B. V. & Ostaficiuc, V. G. (1992): *Insectele rare şi pe cale de dispariţie din Moldova*. – Ştiinţa, Chişinău. [in Romanian]

Negro, M., Casale, A., Migliore, L., Palestrini, C. & Rolando, A. (2008): Habitat use and movement patterns in the endangered ground beetle species, Carabus olympiae (Coleoptera: Carabidae). – *European Journal of Entomology* **105**: 105–112. https://doi.org/10.14411/eje.2008.015

Negro, M., Caprio, E., Leo, K., Maritano, U., Roggero, A., Vacchiano, G., Palestrini, C. & Rolando, A. (2017): The effect of forest management on endangered insects assessed by radio-tracking: The case of the ground beetle Carabus olympiae in European beech Fagus sylvatica stands. – *Forest Ecology and Management* **406**: 125–137. https://doi.org/10.1016/j.foreco.2017.09.065

Nève de Mévergnies, G. & Baguette, M. (1990): Spatial behaviour and microhabitat preferences of Carabus auronitens and Carabus problematicus (Coleoptera, Carabidae). – *Acta Oecologica* **11**: 327–336.

Niehues, F. J., Hockmann, P. & Weber, F. (1996): Genetics and dynamics of a Carabus auronitens metapopulation in the Westphalian Lowlands (Coleoptera, Carabidae). – *Annales Zoologici Fennici* **33**: 85–96.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2017): *nlme: Linear and Nonlinear Mixed Effects Models.* https://CRAN.R-project.org/package=nlme

Pokluda, P., Hauck, D. & Čížek, L. (2012): Importance of marginal habitats for grassland diversity: fallows and overgrown tall-grass steppe as key habitats of endangered ground-beetle Carabus hungaricus. – *Insect Conservation and Diversity* **5**: 27–36. https://doi.org/10.1111/j.1752-4598.2011.00146.x

R Core Team (2017): *R: A language and environment for statistical computing.* – R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Ranjha, M. H. & Irmler, U. (2014): Movement of carabids from grassy strips to crop land in organic agriculture. – *Journal of Insect Conservation* **18**: 457–467. https://doi.org/10.1007/s10841-014-9657-1

Riecken, U. & Raths, U. (1996): Use of radio telemetry for studying dispersal and habitat use of Carabus coriaceus L. – *Annales Zoologici Fennici* **33**: 109–116.

Riecken, U. & Raths, U. (2000): Radio-telemetrische Untersuchungen zum Raum-Zeit-Verhalten von Laufkäfern am Beispiel von Carabus coriaceus Linné, 1758 und C. monilis Fabricius, 1792. – *Angewandte Carabidologie* **2**: 49–58.

Riecken, U. & Ries, U. (1992): Untersuchung zur raumnutzung von laufkäfer (Col.: Carabidae) mittels radio-telemetrie. Methodenentwicklung und erste freilandversuche. – *Zeitschrift für Ökologie und Naturschutz* **1**: 147–149.

Reike, H.-P. (2004): *Untersuchungen zum Raum-Zeit-Muster epigäischer Carabidae an der Wald-Offenland-Grenze*. – Forstwissenschaftliche Beiträge Tharandt, Ulmer, Stuttgart.

Rijnsdorp, A. D. (1980): Pattern of movement in and dispersal from a dutch forest of Carabus problematicus Hbst. (Coleoptera, Carabidae). – *Oecologia* **45**: 274–281. https://doi.org/10.1007/BF00346470

Růžičková, J. & Veselý, M. (2016): Using radio telemetry to track ground beetles: Movement of Carabus ullrichii. – *Biologia* **71**: 924–930. https://doi.org/10.1515/biolog-2016-0108

Růžičková, J. & Veselý, M. (2018): Movement activity and habitat use of Carabus ullrichii (Coleoptera: Carabidae): The forest edge as a mating site? – *Entomological Science* **21**: 76–83. https://doi.org/10.1111/ens.12286

Sota, T. (1987): Mortality pattern and age structure in two carabid populations with different seasonal life cycles. – *Researches on Population Ecology* **29**: 237–254. https://doi.org/10.1007/BF02538889

Skłodowski, J. (1999): Movement of selected carabids species (Col. Carabidae) through a pine forest-fallow ecotone. – *Folia Forestalia Polonica* **41**: 6–23.

Strobl, C., Boulesteix, A., Kneib, T., Augustin, T. & Zeileis, A. (2008): *Conditional variable importance for random forests.* http://www.biomedcentral.com/1471-2105/9/307

Szyszko, J., Gryuntal, S. & Schwerk, A. (2004): Differences in locomotory activity between male and female Carabus hortensis (Coleoptera: Carabidae) in a pine forest and a beech forest in relation to feeding state. – *Environmental Entomology* **33**: 1442–1446. https://doi.org/10.1603/0046-225X-33.5.1442

Tscharntke, T., Rand, T. A. & Bianchi, F. J. (2005): The landscape context of trophic interactions: insect spillover across the crop—noncrop interface. – *Annales Zoologici Fennici* **42**: 421–432.

Thiele, H. U. (1977): *Carabid beetles in their environments*. – Springer, Berlin, 369 pp. https://doi.org/10.1007/978-3-642-81154-8

Thiele, H. U. & Weber, F. (1968): The diurnal activity of carabid beetles. – *Oecologia* **1**: 315–355.

Tuf, I. H., Dedek, P. & Veselý, M. (2012): Does the diurnal activity pattern of carabid beetles depend on season, ground temperature and habitat? – *Archives of Biological Sciences* **64**: 721–732. https://doi.org/10.2298/ABS1202721T

Turin, H., Penev, L. & Casale, A. (2003): *The genus Carabus in Europe. A synthesis*. – Pensoft, Sofia–Moscow–Leiden, 511 pp.

Veselý, P., Moravec, P. & Stanovský, J. (2017): Carabidae. Pp. 295–301. *In:* Hejda, R., Farkač, J. & Chobot K. (eds): *Red list of threatened species of the Czech Republic: Invertebrates.* – Příroda, Nature Conservation Agency of the Czech Republic, Praha.

Volf, M., Holec, M., Holcová, D., Jaroš, P., Hejda, R., Drag, L., Blízek, J., Šebek, P. & Čížek, L. (2018): Microhabitat mosaics are key to the survival of an endangered ground beetle (Carabus nitens) in its post–industrial refugia. – *Journal of Insect Conservation* **22**: 321–328. https://doi.org/10.1007/s10841-018-0064-x

Wallin, H. & Ekbom, B. (1988): Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: A field tracing study. – *Oecologia* **77**: 39–43. https://doi.org/10.1007/BF00380922

Wehnert, A. & Wagner, S. (2019): Niche partitioning in carabids: single-tree admixtures matter. – *Insect Conservation and Diversity* **12**: 131–146. https://doi.org/10.1111/icad.12321

Zulka, K. P. (2014): *Priorisierung österreichischer Tierarten und Lebensräume für Naturschutzmassnahmen*. Umweltbundesamt GmbH, Wien, 122 pp.

Received May 24, 2019, accepted August 28, 2019, published November 22, 2019