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, Sklodowski 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. ulrichii 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 (Jöpp 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).

![Male of C. hungaricus with fixed radio-transmitter](image). 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 ($\chi^2 = 15.801$, 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 ($\chi^2 = 9.177$, 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.](image-url)


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

| No. of individual | Sex | Total distance (m) | Average speed±SD (m/h) | Fix$_{\text{act}}$ | Fix$_{\text{pass}}$ |
|-------------------|-----|--------------------|------------------------|----------------|------------------|
| 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](image-url)  
**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 (Mau-remooto 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 Jaskula 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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