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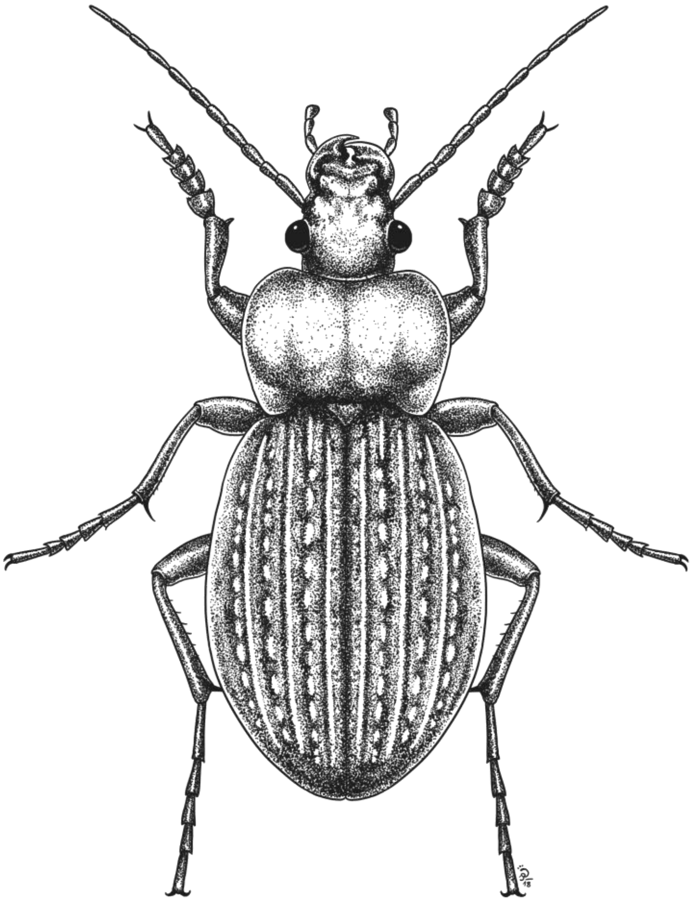
Radio telemetry of ground beetles: Habitat use and movement activity of *Carabus ullrichii*



Ph.D. thesis

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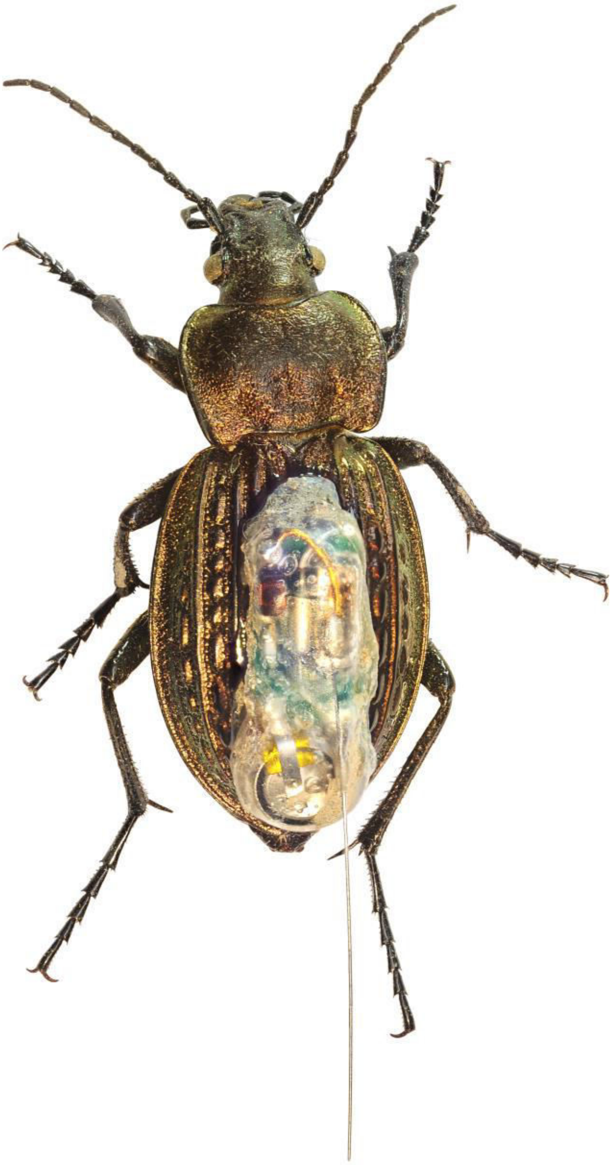
Photo of *Carabus ullrichii* on the next page by Michal Hykel



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Olomouc, 15th June, 2018

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Jana Růžičková

Abstract

Despite the fact that landscape fragmentation significantly affects movement and habitat use of many insect species, it is still relatively unknown how these species utilize particular habitats. This is especially true for species that are not restricted only to single habitat, but use various habitats with different environmental conditions during their life cycles. In this thesis, I therefore focused on such species, *Carabus ullrichii*, a robust, large ground beetle, occupying various habitats from deciduous forests to meadows and arable fields, with questions of how the species utilizes particular habitats based on its movement patterns, sex, and average speed and also which environmental factors affect its movements. Radio telemetry, an advanced method, was used for tracking movement behavior of beetles. Tracking the movements of *C. ullrichii* in different habitats revealed that its activity was affected by temperature and time of the day. In addition, the circadian activity of this species likely varies between geographical localities and habitats. Whereas forest beetles might be rather dusk and night-active, meadow and field inhabitants were active not only in the night-time but also in the day-time. Movement of ground beetles is usually composed by two different patterns: random walk with small distances covered in different directions and directed movement which is characterized by long covered distances in the same direction. In the case of *C. ullrichii,* where individuals moved at the border of two different habitats, forest and meadow, radio-tracked individuals preferred the forest environment based on the increasing tendency to random walk. Males were able to walk as fast as females, but they were more associated with forest edge than females that moved further into forest and meadow interior. Likely, the inner edge of the forest could serve as a mating site where males wait for new females, while fertilized females dispersed into the surroundings.

Keywords: carabids, circadian activity, habitat preferences, movement patterns, radio telemetry.

Abstrakt

I když pokračující fragmentace prostředí výrazně ovlivňuje pohyb a možnosti druhů využívat určitý typ prostředí, stále není v mnoha případech přesně známo, jak konkrétně jsou tato stanoviště využívána. To platí zejména pro druhy, které nejsou vázány jenom na jeden typ prostředí, ale během svého životního cyklu využívají vícero stanovišť s různými podmínkami. Takovým druhem je i relativně velký střevlík Ulrichův (*Carabus ullrichii*), který se vyskytuje jak v lesích, tak na otevřených stanovištích jako jsou louky a pole. V této práci jsem se zaměřila na to, jak střevlík Ulrichův využívá konkrétní typy stanovišť podle tvaru trajektorie jeho pohybu, pohlaví a průměrné rychlosti. Pro sledování pohybové aktivity brouků byla využita radiotelemetrie, moderní metoda umožňující v současnosti i sledovaní větších druhů hmyzu. Z výsledků vyplývá, že pohybová aktivita studovaného druhu byla ovlivněna teplotou a denní dobou, avšak je možné, že odpověď druhu se může lišit v závislosti na lokalitě a stanovišti. Zatímco brouci pohybující se v lese byli spíše soumrační až noční, jedinci z otevřených ploch byli aktivní jak v noci, tak ve dne. Pohyb střevlíků se dělí na dvě složky: první, tzv. *random walk,* se vyznačuje krátkými uraženými vzdálenostmi s častým střídáním směru, zatímco pro druhý, tzv. *directed movement*, jsou typické dlouhé vzdálenosti ve stejném směru. Na základě porovnání trajektorií sledovaných jedinců na rozhraní louky a lesa, bylo zjištěno, že brouci více preferovali les. Dále, že samci byli stejně rychlí jako samice, ale více se zdržovali na vnitřním okraji lesa, na rozdíl od samic, které vstupovaly hlouběji do lesa či louky. Pravděpodobně lesní okraj slouží jako místo k rozmnožování, kdy se samice pro spáření rozptylují do okolí, zatímco samci zůstávají na okraji a čekají na další samice.

Klíčová slova: denní aktivita, pohyb, radiotelemetrie, střevlíkovití, využívaní habitatu.

Content

1. Introduction

In recent decades, landscape fragmentation has become an important issue in conservation biology because of human activities, especially in densely populated parts of Europe (Saunders et al. 1991, Fahrig 2003). It is a landscape phenomenon which occurs when habitat loss reaches a point at which habitat continuity is broken (Opdam & Wiens 2002). This process results in the division of large, continuous habitats into smaller, isolated habitat fragments (Saunders et al. 1991, Ewers & Didham 2005). A direct reduction of habitat area leads to a creation of new edges, and some of the habitat fragments are therefore altered by external conditions which dramatically differ from those prevailing in an interior. At large scale, the spatial arrangement of the remaining habitat fragments, together with shape complexity, edges permeability, and patches isolation, and thus overall landscape matrix quality and structure is important in determining the abundance and composition of species within fragments (Ewers & Didham 2005) as well as dispersal of species between fragments (Franklin 1993, Gustafson & Gardner 1996, Collinge & Palmer 2002). Unsuitable structural characteristic of landscape matrix can significantly restrict movement of animals within their distribution ranges (Hanski & Ovaskainen 2000). However, dispersal is essential for colonization of new suitable habitats, population dynamics and gene flow between populations which help species to cope with environmental changes and local extinction processes (Den Boer 1990, Clobert et al. 2004, Bowler & Benton 2005). Among animal taxa, insects are one of the most threatened groups which are negatively affected by landscape fragmentation; their overall decline has been documented regardless habitats (Benton et al. 2002, Hallmann et al. 2017).

Ground beetles (Coleoptera: Carabidae, hereafter carabids) are often used as good indicators of environmental changes in the continuously fragmenting landscape due to their sensitiveness to habitat alterations and disturbances (Altieri 1999). They are generally influenced by various environmental parameters, both biotic and abiotic, at different spatial scales depending on their ability to disperse in landscape matrix (Thiele 1977, Altieri 1999, Bianchi et al. 2006). In agricultural lands, carabids play an important role as predators of pest (Kromp 1999, Gagic et al. 2017) and with more than 40,000 described species, they are one of the most species-rich coleopteran families and one of the best-known insect groups in the Northern hemisphere (Lövei & Sunderland 1996).

European species of large carabids of genus *Carabus* are brachypterous or micropterous with only a few existing exceptions of flying species (Turin et al. 2003). Due to their inability to fly, landscape fragmentation is a more serious threat for their dispersal than for flying carabid species. Some of these *Carabus* species are already threatened because their distribution ranges are reduced or scattered (Turin et al. 2003, Matern et al. 2008, Pokluda et al. 2012, Elek et al. 2014, Volf et al. 2018). Their dispersal power and ability to colonize new habitats is rather low. For instance, long term study of dispersal power of *Carabus hortensis* Linnaeus, 1758 revealed that this species disperses with average speed 127 m per year with low variation between years (Völler et al. 2018). Moreover, several studies concluded that even narrow strips of unsuitable habitats and linear structures as roads might pose as a barrier and thus restrict species dispersal (Mader et al. 1990, Niehues et al. 1996, Yamada et al. 2010, Matern et al. 2011, Pokluda et al. 2012). Therefore, the knowledge of species' movement behavior, such as dispersal power and/or willingness to cross specific habitats, could help to understand causes and consequences of dispersal and movement behavior which is vital for predicting species' responses to environmental changes (e.g. Negro et al. 2008, Elek et al. 2014, Völler et al. 2018, Volf et al. 2018).

1.1. Movement activity of ground beetles: key factors and patterns

Abiotic factors, such as light, temperature, and humidity, play a fundamental role in regulation of movement behavior and daily or annual rhythms of carabids as well as other insects (Thiele & Weber 1968, Thiele 1977, Turin et al. 2003). Responses to these factors are species-specific, influenced by breeding period and can even differ not only among populations of the same species but even on individual level (Thiele 1977, Atienza et al. 1996, Tuf et al. 2012). For instance, individuals of *Carabus auratus* Linnaeus, 1761 from the same population exhibited different types of diurnal activities, when some were nocturnal and some diurnal or even indifferent to light conditions (Thiele & Weber 1964).

In predatory species, movement can be affected by morphological and physiological adaptations as well as by the distribution and availability of food resources (Thiele 1977, Wallin & Ekbom 1994). Previous studies revealed that foraging beetles move significantly differently than satiated individuals. Moreover, movement in areas with higher abundance of prey was more torturous with reduced speed (Baars 1979, Wallin &

Ekbom 1994, Szyszko et al. 2004). Also, searching for mates during breeding period significantly affects movement activity (Szyszko et al. 2004, Kagawa & Maeto 2009) and consequently results in species-specific time-activity peaks (Thiele 1977). At sex level, it could be presumed that males actively look for females during breeding period, and females are more active after mating due to search for suitable oviposition sites (Kagawa & Maeto 2009). At species level, Larsson (1939) described two annual rhythms of ground beetles based on their seasonal peaks of activity: Adults of *autumn breeders* are active during breeding period in summer and autumn and overwinter as larvae or adults (some species live for more than one year). On the other hand, *spring breeders* lay eggs in spring and early summer, larvae appear in summer and freshly emerged adults occur in autumn with or without small peak of activity before overwintering. Additionally, some species have flexible reproductive period (Thiele 1977).

Regardless the basic motivation of individuals in the movement studies, in general, we distinguish two different patterns of movement behavior of ground beetles: random walk and directed movement (Baars 1979). Random walk is fuzzy search characterized by short distances covered by beetles and high turning tendency in random directions. It is likely a result of frequent encounters with potential prey and mates as well as a spatially restricted area. Directed movement is systematic walk with large distances covered in more or less the same direction. In open habitats near forest edges, the dark silhouette of woodland can help the beetles in orientation (Thiele 1977, Niehues et al. 1996). Directed movement is an efficient strategy to escape from or avoid adverse sites, or it facilitates dispersion of individuals (Fig. 1). Individuals do not show this behavior synchronously and ratio of random walk and directed movement varies between habitats, suggesting different intra-specific habitat use. For instance, the predominance of random walk may suggest preferred habitat with suitable environmental conditions, prey availability, and help to avoid predators such as insectivorous rodents (Baars 1979, Wallin & Ekbom 1988, Niehues et al. 1996, Riecken & Raths 1996).

1.2. Methods of studying movement behavior of carabids

Movement patterns, habitat use, and diurnal activity of ground beetles were studied for many years with different approaches and techniques, from pitfall trapping and individual marking to technically advanced and challenged telemetric methods. All these approaches

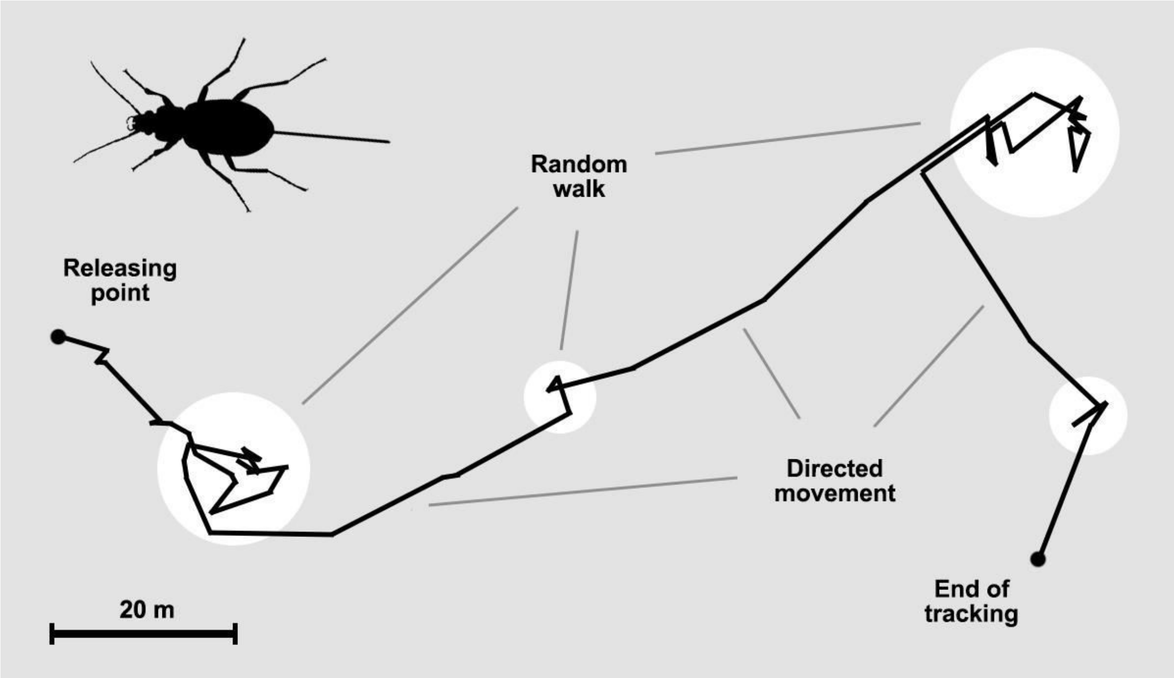

Figure 1: Two patterns of carabid movement: random walk (white circles) is characterized by small distances covered per day in random directions, whereas large distances covered per day in one direction are typical for the directed movement. Total covered distance: 280 m in 16 days, source: Appendix II.

request different level of sampling effort and each has its own special advantages as well as limitations.

Pitfall trapping is the most traditional sampling method for studying biology and ecology of ground beetles. Unbaited pitfall traps without the killing agent are usually arranged according to square designs or parallel transects and checked every few hours. Captured living beetles are individually marked (e.g. painted marks, cuts or numerical is engraved code in the elytra) and released. This method usually requires high sampling effort, but enables to catch and mark a large number of individuals (Rijndorp 1980, Althoff 1994, Skłodowski 1999, 2008, Kagawa & Maeto 2009, Yamada et al. 2010, Bérces & Elek 2013, Elek et al. 2014, Ranjha & Irmler 2014). More frequent checks and/or specific trap modifications allow separating catches from different time of the day and thus studying species' diurnal activity patterns (Luff 1978, Tuf et al. 2012). Other modifications involve enclosure designs with pitfall traps arranged to the circle at the inner edge of the fence or some other barrier to avoid escaping from the experimental area. Beetles are released in the center of the enclosure and the time and directions of their movement are recorded (Niehues et al. 1996).

However, obtaining movement data by pitfall trapping has certain limitations, such as dependency on ground surface activity of beetles. This could lead to some uncertainties between observed (i.e. distance and time between consecutive catches of same individual) and real movement patterns. This represents a problem because some important behavioral traits, such as actual habitat use may be masked. Drees et al. (2008) therefore introduced an easy-to-use method of continuous **direct observation** of nocturnal beetles under red light (590-680 nm, low sensitivity of carabids above 550 nm is known: Hasselmann 1962) in their natural habitat. Beetles marked by white dots were directly observed by the researcher for several hours during night from sufficient distance to avoid any disturbances and position of individuals was recorded at regular time intervals.

The radioactive technique is based on labeling beetles by **paint with radioactive isotope** (^{192}Ir). This isotope emits a considerable amount of gamma rays that can be detected by scintillation detector at a distance of several meters (Baars 1979). However, author stated that no more than 10 beetles is possible to track simultaneously due to large covered distances of labeled beetles and thus high searching effort. Besides, even though adult insects are much less sensitive to radiation than vertebrates (Baars 1979), within few weeks most of the tracked beetles died due to radiation.

The next two methods are telemetric and operates with active or passive transmitters (also referred as tags), which are attached to the tracked individuals. First, **harmonic radar** includes large ground-based radar station or lighter handheld radar, which serve as transmitting and receiving units. Tracked beetles are marked by small passive tags that radiate transmission at exactly half of the wavelength of the original wave emitted by harmonic radar. The energy for tag functioning is delivered by radar (no battery is required for tags) and extreme miniaturization is therefore possible (Riley et al. 1996). These very small tags include only a wire and a diode and thus weight only few milligrams. This allows tracking even very small and light insect species, such as butterflies, beetles, bumblebees and bees, without any obvious effect on their behavior (Riley et al. 1996, Kissling et al. 2014). However, the high length of the wire for achieving sufficient range of the signal may be limiting for some species. Moreover, passive tags do not have unique signals and tracked individuals therefore can not be individually identified when they are tracked simultaneously. Also water, high humidity or dense vegetation and rugged surface fade the signal and can reduce detection ranges (Lövei et al. 1997, Kissling et al. 2014). Nevertheless, in case of carabids, harmonic radar was successfully used to study ecology and biology of several carabid species (e.g. Wallin & Ekbom 1988, Niehues et al. 1996, Lövei et al. 1997, O'Neal et al. 2004, Szyszko et al. 2004, 2005).

Second, **radio telemetry** was for a long time used only to study movement behavior of vertebrates (for the first time in LeMunyan et al. 1959) due to heavy active (i.e. battery powered) transmitters attached to animals. Nevertheless, recent continued advances in technology allowed developing transmitters that are small enough to track also large insect species, such as large *Carabus* species, under field conditions. This method involves three primary components: (i) active transmitters which are attached to the insect (consisted of a transmitting unit, a battery and an emitting antenna), (ii) a receiving antenna system, and (iii) a receiver. Transmitters emit signal in the very high (specific, and known) frequency and the later two components detect and process emitted radio signal (see Fig 2).

Undisputable advantage of this technique is the possibility to track and locate a tagged individual at any time and thus get accurate and detailed documentation of individual movement and microhabitat preferences (Kissling et al. 2014). It enables to track each individual separately because each tag has a specific unique frequency. Moreover, radio-tracking allows localizing tracked individual very accurately, in the case of insects to centimeters. However, the emitting antenna's length affects the detectability of emitted signal, when shorter emitting antenna significantly decreases signal range and increases overall searching time. Similarly, as in the harmonic radar system, heavy rain and dense vegetation can reduce detectability or interfere with the signal and thus it is sometimes difficult to distinguish reflections from the original signal (Riecken & Raths 1996). For insects in general, the most limiting factor for radio telemetry use is the weight of the tags (Kissling et al. 2014).

Currently, the mass of the lightest commercially produced transmitters is less than 0.5 g, (0.22 g, model LB-2X, 8 × 4 × 2.8 mm, Holohil Systems Ltd., Canada, and 0.29 g, PicoPip, 13 × 5 × 3 mm, Biotrack Ltd., UK). There is a trade-off between transmitters' weight versus power (i.e. signal range) and battery life (Wikelski et al. 2007). For instance, the battery's life-span is one to three weeks for the smallest tags mentioned above. Heavier transmitter will provide longer battery life, but for many insect groups, including ground beetles, it is too heavy and therefore unusable in field research. Due to the tag's mass, insects are not used for a recently relatively common method of tracking larger animals - GPS technology which allows positioning according to geographic coordinates with the help of satellites systems (Kissling et al. 2014).

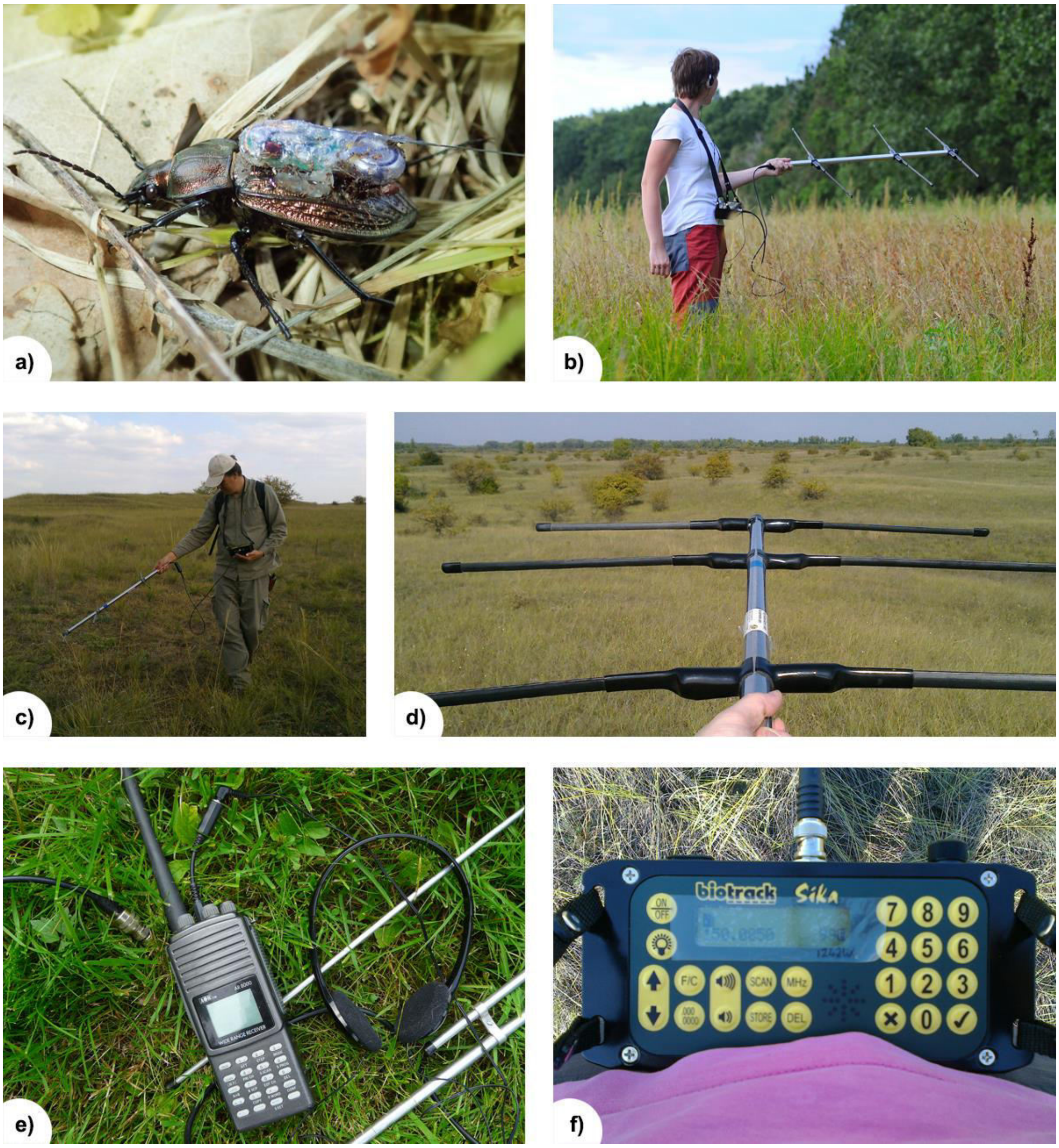

Figure 2: Principal components of radio telemetry. An active transmitter (tag) attached to a ground beetle by glue (a) consists of a transmitting unit, an emitting antenna and a power source, i.e. battery. Tag emits regular pulses of fixed very high frequency, usually in MHz, which is unique for each tag. The signal of the tag is detected by hand-held receiving antenna system, such as multiple parallel elements compiled in a line (Yagi, b, d) or a short dipole antenna (e), and processed by a receiver (e, f). During tracking, the tracking person sets the tag frequency into receiver and sweeps the receiving antenna from side-to-side to determine the direction of the strongest signal (b, c).

Photos: Milan Veselý (a), Michal Hykel (b), Jana Růžičková (c-f).

The first radio telemetry study on insects was conducted in the late 1980s on aquatic, stream-dwelling dobsonfly larvae *Protohermes grandis* (Hayashi & Nakane 1988, 1989). Since then, and especially in recent decade, there has been a substantial increase in such studies. Large species of various insect taxa, such as dragonflies (Wikelski et al. 2006, Levett & Walls 2011, Moskowitz & May 2017), orthopterans (Lorch et al. 2000, 2005, Watts & Thornburrow 2011), hymenopterans (Pasquet et al. 2008, Hagen et al. 2011, Kissling et al. 2014), butterflies (Liégeois et al. 2016) and beetles (Rink & Sinsch 2007, Hedin et al. 2008, Svensson et al. 2011, Chiari et al. 2013, McCullough 2013, Hamidi et al. 2017, Tini et al. 2017, 2018, Drag & Čížek 2018), were used as model organisms. In the contrast to vertebrates, there is no radio-tracking "4% rule" in insects, i.e. the tag mass should not exceed 4% of the body mass of the tracked individual. The tag/body mass ratio is approximately 20–30% in most of the studies tracking insect (Kissling et al. 2014). However, e.g. at bumblebees the tag may be as heavy as body itself (Hagen et al. 2011; Fig. 3). Although bumblebees can carry heavy loads such as nectars and pollen, the additional weight may likely affect the energy expenditure and movement activity of tagged individuals. Up to date, only one study tested the impact of transmitters on insect behavior (Hamidi et al. 2017) and revealed that the presence of tags negatively affected flying activity and burrowing behavior of *Rhynchophorus ferrugineus* (Olivier, 1790) (Coleoptera: Dryophthoridae). Therefore, more studies on energy cost and behavioral influence in long term are needed.

Among ground beetles, species of the genus *Carabus* are ideal for radio-tracking because they are large and also relatively heavy with body mass approximately 1g (Riecken & Raths 1996, Negro et al. 2008, 2017). To date, only three species were radio-tracked: *Carabus coriaceus* Linnaeus, 1758 (body mass: 1.37–1.79 g, tag mass: 0.6–0.7 g, tag/body mass ratio: 34–51%, Riecken & Raths 1996), *Carabus olympiae* Sella, 1855 (0.75 g, 0.3 g, 40%, Negro et al. 2008, 2017) and *Carabus ullrichii* Germar, 1824 (0.7-1.5 g, 0.3 g, 20–42%, Appendix I and II of this thesis), but it can be assumed that ecology of more *Carabus* species, especially habitat specialists such as *Carabus hungaricus* Fabricius, 1792, will be studied by this technique (Bérces, personal communication). As stated before, genus *Carabus* includes mostly flightless species (Turin et al. 2003). Therefore, their radio-tracking is limited only to ground level and used transmitters do not affect the flying activity which could make a problem in other insect groups (Hamidi et al. 2017). The localization of tagged beetles is based on direct tracking, when the searching starts at the point (often referred as fix), where individuals were found in the previous tracking session. Then the researcher walks in the direction of the loudest signal to get close to the tagged beetle. At the point of 0.5 m distance from the expected signal source, the localization is stopped due to risk of stepping on the individual (Riecken & Raths 1996). Other option for finding tagged individuals is triangulation. It is usually used in cases when tagged individuals are somewhere in the inaccessible terrain or for avoiding disturbing the animal (White & Garrott 1990, Kenward 2000). During triangulation, the signal source is determined from different directions around tagged individual and current position is calculated based on angles recorded. This approach is mostly used for flying insect species

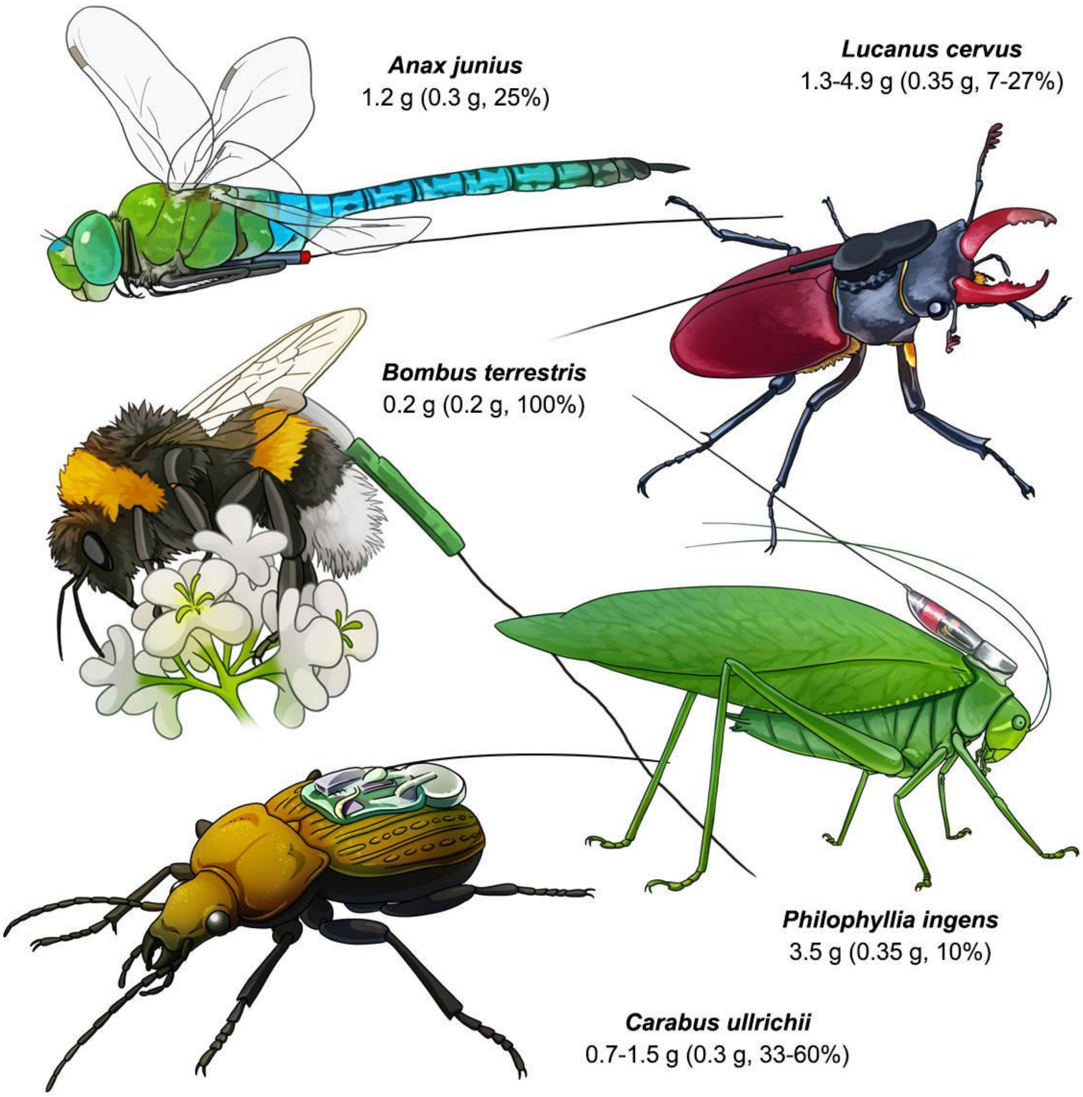

Figure 3: Examples of insect species used for radio telemetry studies. Under the scientific name, body weight and transmitter weight with tag/body mass ratio (in parentheses) are stated according to Wikelski et al. (2006), Rink & Sinsch (2007), Hagen et al. (2011), Kissling et al. (2014) and Appendix I and II.

with great dispersal (Rink & Sinsch 2007, Levett & Walls 2011, Moskowitz & May 2017, Tini et al. 2017, 2018).

Most insect radio telemetry studies have focused on habitat use and movement patterns, including quantification of movement paths and distances (Riecken & Raths 1996, Negro et al. 2008, Pasquet et al. 2008, Hagen et al. 2011, Watts & Thornburrow 2011), habitat selection (Rink & Sinsch 2007, Negro et al. 2008, Tini et al. 2017, 2018, Drag & Čížek 2018), and size of home ranges (Moskowitz & May 2017), as well as on foraging behavior (Hayashi & Nakane 1988, 1989), activity patterns (Riecken & Raths 1996), migrations (Wikelski et al. 2006), and even on evolutional aspects (Kelly et al. 2008). Such data are fundamental for basic and applied biodiversity science, such as species conservation, pest control, and habitat management. However, broader generalization of movement behavior and space utilization across species, functional groups and habitats is limited due to relatively low number of radio-tracked studies and some aspects are still neglected or poorly studied, such as intraspecific variability between sexes, ages, and individuals (Kissling et al. 2014).

1.3. Thesis focus

Some ground beetles, as well as other insect species, are not restricted to a single habitat, but use various habitat types during their life cycle. However, their habitat requirements are often unknown or based only on a particular life stage, although knowledge of specific utilization of occupied habitats and factors affecting species' movement in particular environment is crucial for their persistence (e.g. Dennis & Sparks 2006, Dennis 2012, Chiari et al. 2013, Tini et al. 2017, 2018, Hykel et al. 2018).

This thesis focuses on **movement activity and habitat use of *Carabus ullrichii,*** ubiquitous carabid species that occurs in various types of habitats from deciduous forests to open and semi-open habitats, such as arable fields and meadows. However, its utilization of particular habitat is still unknown, even it can be presumed that *C. ullrichii* likely shows some intraspecific variability in its activity due to different environmental condition in utilized habitats. Therefore, we studied species-specific and sex-specific movement activity in different habitats using radio-telemetry. In the first part of this thesis (**Appendix I**), we tested the suitability of radio telemetry as an advanced method for monitoring activity of this species, for the first time quantified the species-specific movement, and studied how daytime and temperature affect movement activity of individuals occurring in a foothill orchard. In the second part (**Appendix II**) we focused on a lowland population from a boundary between a floodplain forest and a meadow during *C. ullrichii's* reproductive period in late spring and early summer. Since these two habitats naturally differ in their environmental conditions (i.e. abiotic factors and density of ground vegetation), it can be presumed that these differences could affect beetles' movement. Similarly, sex-specific resource requirements during breeding season may indicate different habitat utilization. In the last part (**Appendix III**) the usage of radio-telemetry in entomology including its advantages, limitations, and prospects for future research is summarized.

Overall, this thesis is focused on four questions:

(i) Is the radio telemetry a suitable method for tracking *C. ullrichii*? This method was used only on a handful of carabid species (see above) and therefore some information on potential limitations of this method could be still overlooked.

(ii) What is the average speed of target species in particular habitat?

(iii) Do abiotic factors affect movement activity of the species and if yes, which ones and how?

(iv) Is the shape of the movement trajectory affected by specific habitat use in relation to reproductive behavior of *C. ullrichii*? These questions presume that average distances covered per particular time unit and prevalence of movement pattern (i.e. random walk and directed movement) may show variability between habitats and sexes due to different microclimatic conditions and physiological requirements and therefore suggesting different habitat utilization.

2. Materials and methods

2.1. Model species

Being locally highly abundant species, *Carabus ullrichii* is 22–33 mm long, robust, convex ground beetle with shiny cupreous coloration and three rows of conspicuously elevated elytral tubercles. Its antennae and legs are always black (Hůrka 1996, Fig. 4a). Distributional range extends from south-western Germany to western Ukraine, Romania, and Bulgaria and currently four subspecies are recognized: *C. u. ullrichii, fastuosus, rhilensis* and *arrogans* (Turin et al. 2003, Fig 4b). This species inhabits various types of deciduous forests (Kleinert 1983, Andorkó & Kádár 2006, Máthé 2006, Kádár et al. 2017) as well as open or semi-open habitats, such as meadows, arable fields, fallow lands, gardens, and orchards from lowlands to foothills (Hůrka 1996, Veselý & Šarapatka 2008, Deuschle & Glück 2009, Huidu 2011). As a typical spring breeder, *C. ullrichii* overwinters as adult and reproduce in spring (from late April to June). Its larvae occur during summer, freshly emerged adults appear during the second half of August and are active till October, when they start the hibernation (Turin et al. 2003). The species reproduces only once per season with relatively low fecundity and its generations do not overlap (Kádár et al. 2017).

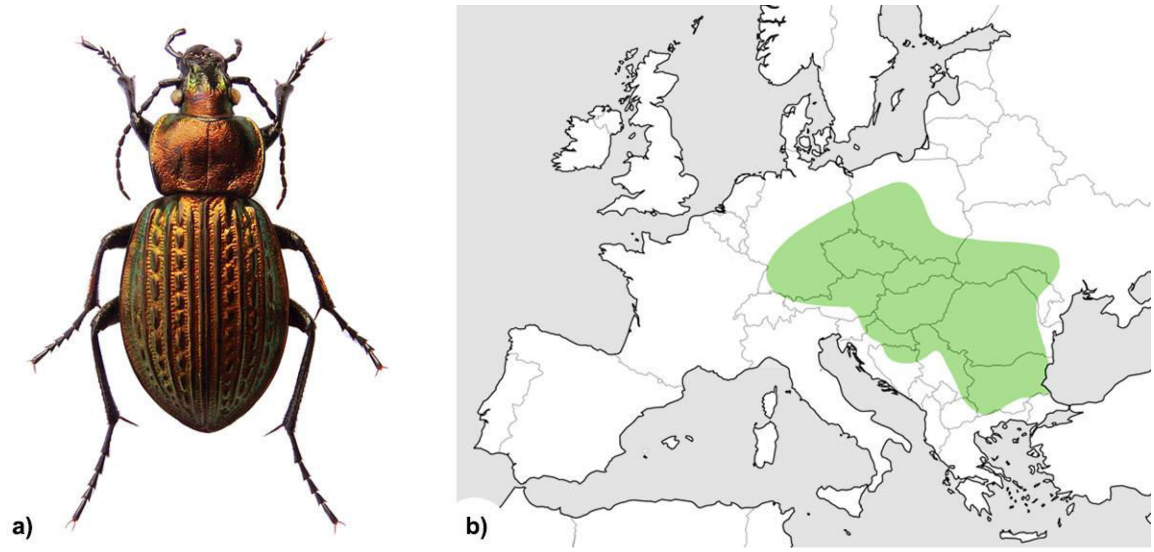

Figure 4: Female of *Carabus ullrichii* (a) and distribution range of the species (b) according to Turin et al. (2003).

2.2. Study sites

We studied movement patters of two different populations of *C. ullrichii* in the Czech Republic: first in foothills (**Appendix I**) and second in lowlands (**Appendix II**). Previous field surveys have shown that this species is one of the most common ground beetles with spring peak of activity that occurs in both study sites.

First, rural landscape was located in foothills of the Beskidy Mountains, north-eastern Moravia, the Czech Republic (cadastral territory of village Jarcová, Vsetín district, 49°25'28"N 17°57'11"E, approximately 380 m a.s.l.). The study site was 15 years old orchard with scattered *Prunus spinosa* and small groups of other tree species, such as *Betula pendula* and *Picea abies*, and relatively dense tussocks of various grasses with common meadow dicots, such as *Ajuga reptans*, *Taraxacum officinale*, *Trifolium pretense*, and *Leucanthemum vulgare* in the herbal layer (Fig. 5a).

Second, lowland population was located in a floodplain of the Morava River in Litovelské Pomoraví Protected Landscape Area near town Litovel (Olomouc district, Central Moravia, CZ, 49°41'38"N 17°06'14"E, approximately 230 m a.s.l.). The study site covers border (hereafter also as ecotone) between two different habitats without a wide gradual transition zone between them: hay meadow with predominance of dense tussocks of various grasses (Fig. 5b), and floodplain forest of various age structures with mixed patches of full and partly open tree canopy cover dominated by *Fraxinus excelsior* and *Tilia cordata,* and by *Galium aparine*, *Urtica dioica,* and *Allium ursinum* in the sparse herbal layer (Fig. 5c).

2.3. Data sampling and analyses

All beetles used for radio-tracking in **Appendix I and II** were captured by pitfall traps positioned across study sites during its activity peak in late spring in the second half of May and consequent radio-tracking was conducted in the begging of June. Each trap was consisted of two plastic cups inserted into each other, baited with cat food, and checked every 12 hours to avoid damage of beetles. Before all radio-tracking experiments, captured individuals were kept separately in plastic boxes for few days in the room temperature and fed every two days by mealworms *at libitum*.

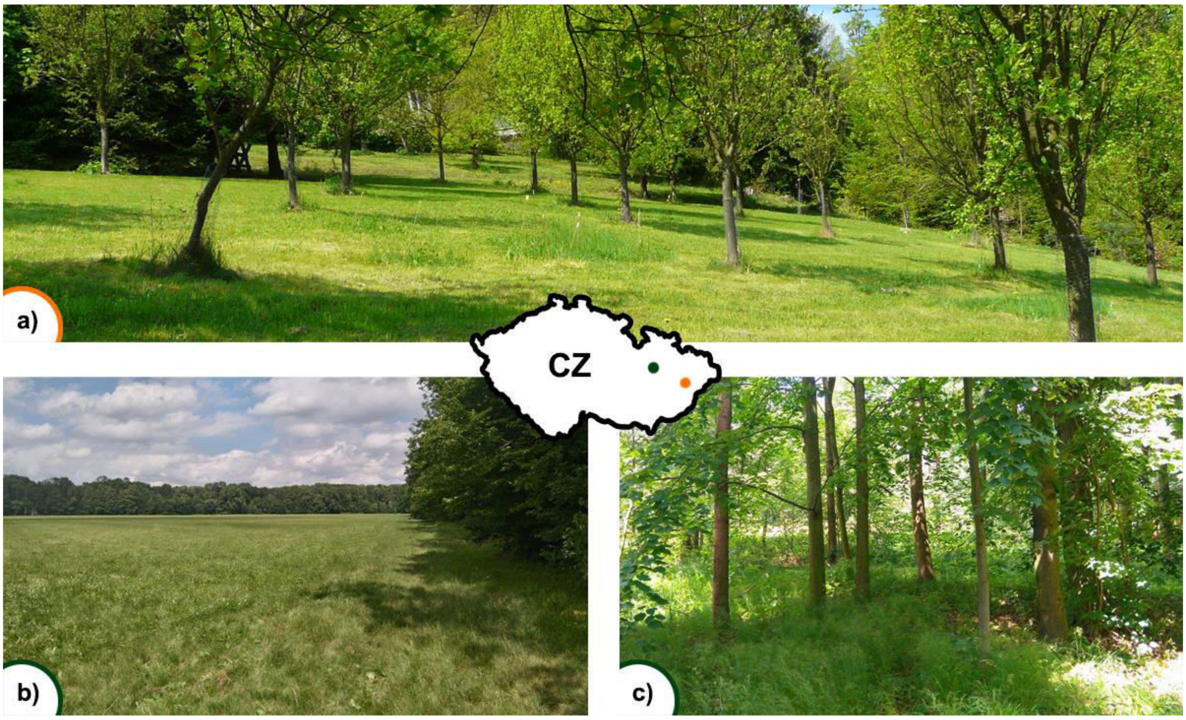

Figure 5: Study sites. Orchard (a), meadow (b) and floodplain forest (c), habitats where *C. ullrichii* was radio tracked. Orange and dark green edges of labels correspond with study site positions in the map of the Czech Republic.

We used PicoPip transmitters (weight 0.3 g, 13 × 5 × 3 mm, Biotrack Ltd., Wareham, UK) with specific frequencies between 173–174 MHz. One day before experiments, beetles were equipped by transmitters attached to the top of their elytra by cyanoacrylate glue (liquid or gel), sometimes also with silicone putty to asses the most suitable adhesive material for attaching transmitters. Short emitting antenna (25 mm) was directed backwards and the battery, as the heaviest part, was located at the back of the transmitter (Fig. 6). Tags themselves can be customized during production and thus the position of the battery can be in the front, back or at the center of the transmitter. Therefore, the center of gravity may change and could bias the body's balance. In cases when battery is centered, the transmitter is several millimeters higher than in other cases, so it could restrict beetles' movement in narrow habitats, such as dense grassy vegetations (Bérces, personal communication). In the first study (**Appendix I**), we tracked relatively low number of beetles (4 individuals, 3 females and 1 male) only to test feasibility of radio-tracking. Beetles were released at the center of the studied area approximately 5 m apart to avoid mutual interference, and tracked every 3 hours for 10 consecutive days. Since our methodological approach seemed to be ideal for tracking beetles, we conducted second study (**Appendix II**) with more individuals and in different habitats. We released 21 beetles (11 females and 10 males) at the forest-meadow ecotone and tracked for 16 days.

For radio-tracking, we used AR8000 (AOR Ltd.) and Sika (Biotrack Ltd.) hand-held receivers with Yagi directional receiving antenna and 20 cm dipole receiving antenna for short distances. Since distances covered by ground beetles could be small (only tens of centimeters) in 3 h periods, dipole antenna could process and determine signal source more precisely than Yagi antenna. Each tracking session started at the point of previous fix of tracked individuals. We used the direct tracking method, i.e. walking in the direction of the loudest signal to get close to the tagged beetle to the point of 0.5 m distance from expected signal source. At each fix, we recorded distance covered by tracked individual from the last tracking session and main environmental variables potentially influencing the movement of large ground beetles: temperature, humidity on the ground level, time of the day (light condition), and type of habitat. For the recording of the trajectory of each individual, we used two different methods to assess better precision in small scales. The first one was based on a GPS system where each fix was recorded by GPS coordinates (**Appendix I**). Second approach involved GPS system only for coordinates of starting fixes and the rest of the trajectory was recorded by covered distance and the direction (azimuth) between consecutive fixes (**Appendix II**).

To test the influence of environmental factors and sex on the movement activity of *C. ullrichii*, we used generalized linear models with negative binomial error distribution. Movement trajectories made by tracked beetles were projected into the map to characterize beetles' movement patterns in the studied habitats. For detailed description of data analyses see **Appendix I and II**.

Figure 6: Female (left) and male (right) of *Carabus ullrichii* with fixed radio transmitters.

3. Results and discussion

3.1. Radio-tracking

We proved that radio-telemetry is a suitable method for tracking ground beetles' movement. Since the majority of *Carabus* species is unable to fly, transmitters could be simply attached to the beetles' elytra. Our experiments with various types of adhesive materials for attaching transmitters revealed that cyanoacrylate glue gel was easier to apply and less disturbing for individuals during handling than a combination of relatively fragile glue and elastic silicone putty, which required more time to dry out. We did not observe any limitations of movement behavior: beetles were not only able to move several meters within three hours in densely overgrown and narrow habitat but were also observed during feeding on earthworms or digging into soil (**Appendix I and II**). Similarly, Negro et al. (2008) reported several observations of tagged *C. olympiae* eating snails and copulating with untagged partners and concluded that radio-tracking likely did not substantially reduce foraging and mating success in short time period. However, it is possible that attached transmitter increases the overall energy expenditure of its host and negatively affects its fitness in longer term, but so far no studies on this topic exist.

Based on the quality and signal's range, it was also possible to determine whether the tracked beetle was burrowed in the soil or remains on the ground surface. Since there was no available information on movement ability of *C. ullrichii* and detectability of transmitters' signal was usually shorter than 60 m (its quality depended on the terrain and vegetation density), we expected that three hours interval between tracking sessions could be an acceptable compromise between the time invested by the researcher for tracking the individuals and the distance they could possibly cover. This prediction showed to be right and beetles never moved out of the signal range. Sometimes, distances covered by ground beetles were short (tens of centimeters to several meters) in relatively short time period (hours to days), therefore using GPS for fixes positioning might not be appropriate due to large error of GPS system at small spatial scales (**Appendix I**). Likely, more accurate approach of fixes positioning involved GPS only for recording coordinates of starting fixes and then all following fixes were marked by colored sticks embedded in ground. Trajectory of tracked individuals was then recorded by covered distance and the direction between consecutive fixes (**Appendix II**).

3.2. The speed of *Carabus ullrichii*

The average speed of movement of C. *ullrichii* varied between individuals, but comparing sexes, there was no significant difference between males and females. The range of speed was very variable. It could be very low (a few centimeters), to several meters per 3-hour period regardless habitat. In orchard, the range of the average speed was 0.2–1.7 m per 3 h period depending on individual (**Appendix I**). In second study (**Appendix II**), the speed was 0.14–3.18 m per 3 h for males and 0.04–3.07 m for females. These results were similar to speed of other large carabids where individuals were able to walk for several meters per day. For instance, the known values of speed are 2.26–7.32 m per day for *C. coriaceus* in a meadow and 2.01–22.16 m per day for the same species in a forest (Riecken & Raths 1996), 9.3–15.0 m per day for *Carabus auronitens* Fabricius, 1792 in fallow land (Niehues et al. 1996), and 1.4–32.4 m per day for *C. olympiae* in a forest (Negro et al. 2018). Ranjha and Irmler (2014) concluded that the speed of ground beetles in general was positively correlated with body size. However, it is also affected by habitat requirements, when strictly woodland species walked slower than habitat generalists (Brouwers & Newton 2009). In contrast, Firle et al. (1998) argued that the distances covered by an individual depended on the availability of prey and not body size, with decreasing speed in higher prey densities. Since we found that average speed of *C. ullrichii* was lower in the forest than in the meadow, we can presume that forest likely provide better opportunities for foraging than meadow in concordance with prey availability hypothesis of Firle et al. (1998).

The highest speeds per 3 h recorded in orchard were 6.0 m for males and 14.1 m for females, in the forest 20.1 m for males and 19.6 m for females and in the meadow 7.5 m for males and 17.6 m for females (**Appendix I and II**). It seems that vegetation thickness at the ground level might affect speed of walk. Dense tussocks did not appear to serve as a barrier for movement, but could reduce the highest speed of beetles in the meadow while in the forest relatively sparse herbal layer enabled beetles to move faster. Other studies also supported these findings that beetles could run faster in habitats with higher proportion of bare soil (Mauremooto et al. 1995, Ranjha & Irmler 2014).

In several cases, we found beetles of both sexes stayed at the same spot for several tracking sessions and sat in self-dug holes irrespective of climatic and microhabitat conditions (**Appendix I and II**). After several hours or even days, they all left their holes and continued in movement activity. This behavior was directly (Baars 1979) or indirectly

(Niehues et al. 1996, Riecken & Raths 1996) mentioned also in previous studies. We can assume that females may stay at one spot for longer time period due to oviposition (Thiele 1977). However, we recorded this behavior in both females and males. Baars (1979) observed that this inactivity shows no correlation to reproductive behavior of adult carabids. After a disturbance, beetles left their holes, but did not walk substantial distances in the next days. However, the real explanation of this phenomenon is still unknown. Beetles could likely either rest, being satiated, or wait for more suitable environmental conditions for activity.

3.3. Abiotic factors affecting movement activity

Since insects are ectotherms, the positive relationship between movement activity and temperature is not surprising. Carabids have various preferences toward different temperatures based on their life history. Finding patches with suitable temperature is crucial for acceleration of maturation of the sexual glands (Sota 1986). Moreover, daily mean temperature may determine the timing of reproduction, as was reported for the spring breeder *C. auronitens* (Alhoff et al. 1994). We found that temperature-dependent movement of *C. ullrichii* varied between sexes in lowlands (**Appendix II**), where males were active at temperatures around 15°C, while females showed no temperature preference. It seems to be counterintuitive because temperature should affect females more than males due to the physiological differences in their breeding behavior (Atienza et al. 1996). In June, females of *C. ullrichii* were in reproductive or even post-reproductive period. In this part of the breeding season, females likely looked for enough of prey to refill the energy costs of reproduction, than for sites with suitable temperature for development of their ovaries and eggs. Due to the low number of radio-tracked individuals in orchard, we could not support this sex-specific temperature dependency in foothills, although we found activity peak around 15°C for this species (**Appendix I**).

The distribution of circadian activity patterns differed considerably between the habitat types. Ground beetles inhabiting forest and with large body (i.e. body length > 10 cm) seem to be more nocturnal than small species of open habitats (Thiele 1977, Luff 1978, Lövei & Sunderland 1996). Based on our findings, circadian activity of *C. ullrichii* varied between localities and habitats. Whereas forest beetles were more active during night with the activity peak in the first few hours after sunset (as was also reported for some other *Carabus* species; Thiele 1977, Szyszko et al. 2005) beetles inhabiting open habitats were active regardless of the light conditions. During midday, temperature in open habitats became unsuitable for beetles, so they try to escape or hide (Thiele 1977). Although the predominance of nocturnal activity in the forest was likely connected to higher moisture requirements, we found no effect of humidity on movement activity (**Appendix II**). Likely, even the minimal humidity of soil surface or leaf litter was enough to resist desiccation of beetle's body (Althoff et al. 1994).

3.4. Habitat use and sex-specific movement patterns

In its whole distribution range, *C. ullrichii* occurs in various habitat types (Andorkó & Kádár 2006, Máthé 2006, Deuschle & Glück 2009, Huidu 2011, Kádár et al. 2017). For instance, it inhabits both wet and dry forests in Slovakia (Kleinert 1983). In Hungary, *C. ullrichii* selects habitats according to the light intensity with preference of open oak forests, but it can also use beech forest and its transition zones (Kádár et al. 2017). In the Czech Republic, the species is also reported from arable fields and fallow lands (Hůrka 1996, Veselý & Šarapatka 2008). Thus, it can be assumed that its habitat use may vary depending on the geographical position. At the forest-meadow ecotone (**Appendix II**), beetles of both sexes mostly moved at the forest's inner edge or its interior and showed random walk pattern alternated with directed movement. On the other hand, if any individual (only females, see below) reached the meadow, its movement was almost direct without any random walk patterns or stops and their average speed was significantly higher than their movement in the forest. Foraging for prey and seeking for mates resulted in area-restricted search and higher tendency to random walk (Wallin & Ekbom 1988). Movement behavior of *C. ullrichii* suggested that floodplain forest and its ecotone provided more suitable resources than meadow. In comparison with tracked individuals from orchard (**Appendix I**), it was likely that habitat preferences of this species may vary between localities. Beetles from orchard in foothills seemed to prefer open habitats, whereas lowland individuals favored forest habitats.

Females more often penetrated forest or meadow interiors at greater distances. Males were able to walk as fast as females, but they were more associated with the forest, where they walked close and parallel to the forest's inner edge and rarely entered the meadow (**Appendix II,** Fig. 7). These sex-specific movement patters suggested that males

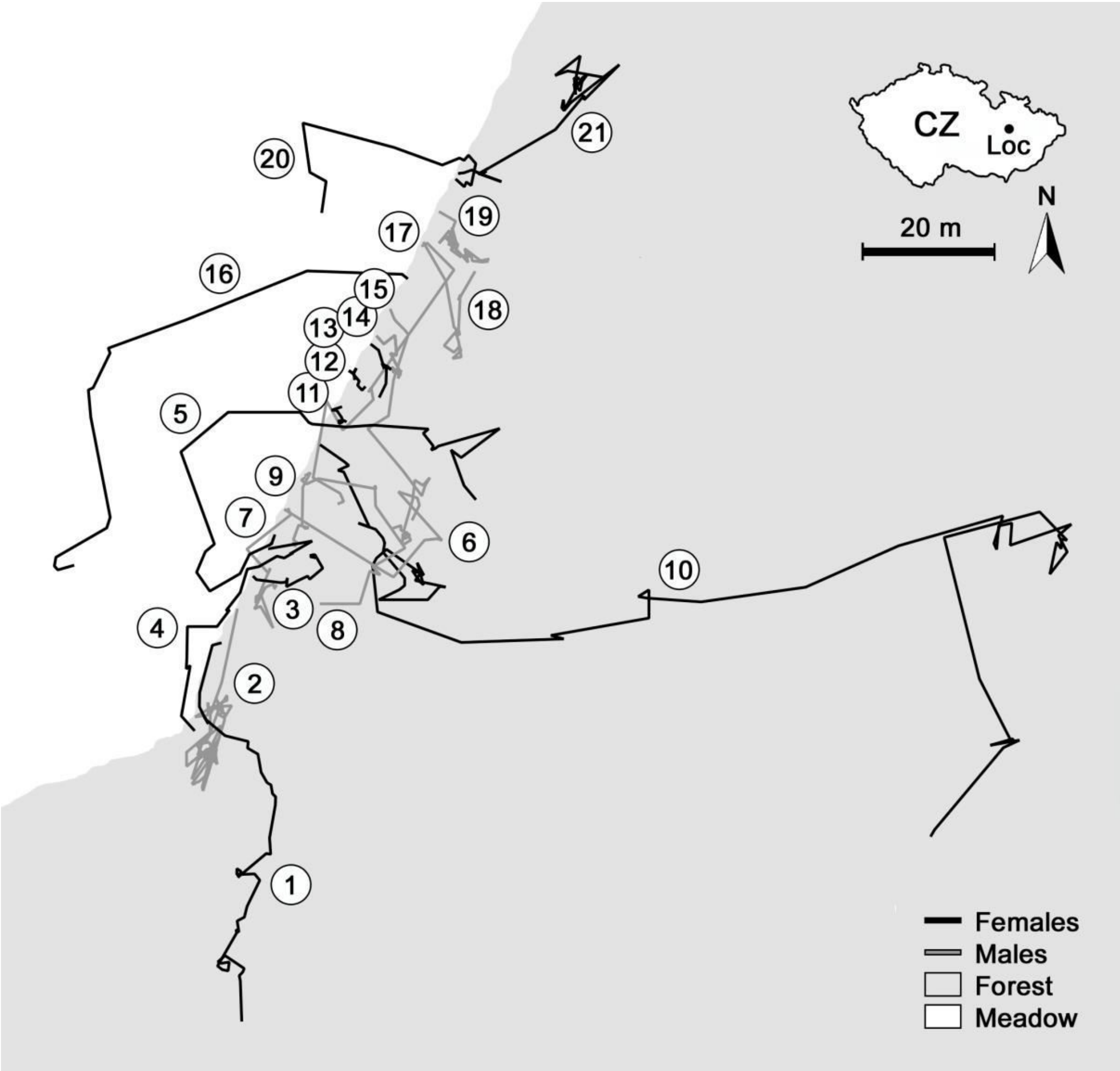

Figure 7: Movement patterns of all 21 tracked individuals at meadow-forest transition from Appendix II.

waited for females and mated with them at the ecotone. After mating, fertilized females dispersed into surrounding forest and looked for suitable oviposition sites and for prey to support reproduction. Only females walked further into the meadow: it is likely that females utilized open habitats for dispersal to other suitable habitats as Rijnsdorp (1980) proposed for forest species *Carabus problematicus* Herbst, 1786 in the meadow. Similar sex-specific movement behavior at the border of two different habitats as in *C. ullrichii* was observed in *Carabus yaconinus* Bates, 1873 in the mixed farmland-woodland landscape (Kagawa & Maeto 2009). Adults were most abundant at the edge of the forest and their numbers gradually decreased when entering into the woodland. Females were collected within the forest and neighboring orchards more frequently than males. Very similar "border" preference showed *C. ullrichii*. Thus, it could be considered to be an ecotone specialist, as was formerly reported for some other *Carabus* species (namely *Carabus arvensis* Herbst, 1784*, C. coriaceus,* and *Carabus nemoralis* Müller, 1764) based on their frequent movement patterns along forest edges (Riecken & Raths 1996, Skłodowski 1999, 2008). It seems that ecotones are important sites for *C. ullrichii* as well as other large carabids and therefore the function of habitat transitions in landscape matrix should not be underestimated, especially when patches with suitable environmental condition are already fragmented.

4. Conclusions and future research

Fragmented landscape has significant impact on movement of many species due to changes in borders, size and spatial distribution of suitable habitat fragments within landscape matrix. For ground beetles, movement to different habitats and adjustment of the circadian activity are two strategies for avoiding adverse environmental conditions. Nevertheless within one species, these patterns may vary in time, space and between sexes according to their physiological requirements and reproduction period. Using ecotones as mating sites may be temporary advantageous because likely it is easier to find a mate there than in the habitat interior. Suitable edges however may rapidly change their position due to ongoing fragmentation and thus the species may not respond flexibly and its occurrence may be negatively affected. Similarly, if isolation of habitat fragments reaches the point in which the species can not cover the distance between suitable patches, its dispersal will be restricted and limited to few close fragments.

These conclusions are based on only limited number of individuals of target species. Therefore, it is possible that in other parts of the range, species response to environmental conditions may vary due to different habitat preferences of individuals. Further research should focus on other habitats (e.g. arable fields), as well as on different habitat transitions and its permeability (e.g. field-forest border), and management (e.g. different types of forestry). It can be assumed that a large number of studies on radio telemetry of carabids will be published in near future. This technique does not depend on the running activity of tagged individual and allows instant tracking at any time (i.e. regardless movement or inactivity of the individual). Foraging success and position of mating and oviposition sites as a basic traits of habitat use are easier to study by telemetry than by pitfall trapping, especially in carabids. Nevertheless, more attention should be given to methodology of radio-tracking, especially to assessing the impact of the transmitter on energy expenditure of its host in longer time period, including basic measurements of condition before and after tracking, laboratory experiments and field observations.

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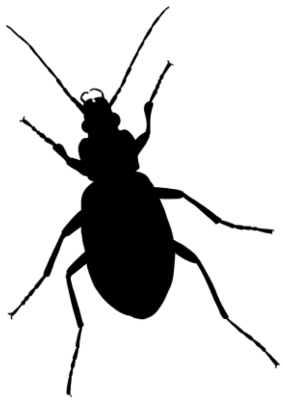
Appendices

Appendix I: Růžičková J. & Veselý M. (2016): Using radio telemetry to track ground beetles: Movement of *Carabus ullrichii*. Biologia 71(8): 924–930.

Appendix II: 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.

Appendix III: Růžičková J. & Veselý M. (2016): Využití radiotelemetrie v entomologii / Usage of Radiotelemetry in Entomology. Živa 6: 314–315. (In Czech with English abstract.)

Appendix I



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Using radio telemetry to track ground beetles: Movement of *Carabus ullrichii*

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Abstract: Radio telemetry is an advanced method for studying movement behaviour which is one of the keys to understanding species ecology and biology. Using this method we studied the movement of *Carabus ullrichii* Germar, 1824, a large and apterous ground beetle species. Four individuals (one male, three females) were equipped with 0.28 g transmitters and radio-tracked for 10 days in three hour intervals in mosaic rural area; meadow and orchard. We found that maximum distance covered by an individual during this period was 120.9 m and *C. ullrichii* travelling speed in such habitat ranged from 1.69 to 13.43 m per day. Our preliminary results indicate that diurnal activity of this species is not affected by light conditions but by temperature. Beetles were most active at temperatures 15.0–17.4 °C. Here we provide the first study of the movement ability of this species.

Key words: carabid beetles; *Carabus ullrichii*; radio-tracking; telemetry; movement

Introduction

Understanding of population dynamics and species interactions is the great challenge of modern ecology (Kareiva 1990). Colonization of new habitats and gene flow between populations plays a vital role in population persistence. Recently landscape fragmentation, as a result of human activities, has restricted connectivity of many animal populations and has increased extinction risk (Kromp 1999; Holland & Luff 2000). Thus, fragmentation is a serious problem especially for small invertebrate species with low dispersal ability (Kotze et al. 2011; Bérces & Elek 2013). Therefore studying insect movement and dispersal behaviour is one of the main issues facing the conservation of species and their environment (Ranius 2006; Brouwers & Newton 2009).

For many years the only applicable methods for studying movement, dispersal and habitat preferences of epigeic arthropods was through grids of pitfall traps on sampling plots or enclosure experiments. Spatial movements of ground beetles are usually studied by capture-mark-recapture methods, but this approach suggests high sampling effort (Lys & Nentwig 1991; Kennedy 1994; Kawaga & Maeto 2009; Ranjha & Irmler 2014). However, these techniques do not provide accurate or detailed documentation of individual movements, which is important to obtain better picture of individual behaviour and microhabitat preferences.

Baars (1979) introduced tracking of two carabid species labeled by radioactive Iridium isotope and tracked by scintillation detector; however, there was a considerable loss of the labeled beetles and most of them died within seven weeks due to radiation effects. Another possibility is to use harmonic radar with passive tags. These tags only contain a diode and a wire so they are light (6–20 mg) and can be carried by small and flying insects such as bees or butterflies without influencing their behaviour (Kissling et al. 2014). However, diodes are passive and do not have unique signals, therefore the number of simultaneously tracked individuals is limited. Moreover, this technique requires a powerful and expensive radar device. Inspite of these disadvantages, harmonic radar was successfully used to study ecology and biology of several carabid species (e.g., Wallin & Ekbom 1988; Niehues et al. 1996; Lövei et al. 1997; Szyszko et al. 2004, 2005).

Radio telemetry is often and widely used method for studying movement behaviour of large-bodied animals (White & Garrott 1990; Kenward 2000). However, radio telemetry is still quite uncommon in invertebrates due to technical parameters of radio transmitters (battery capacity, size and weight) and species biology (Kissling et al. 2014). Nevertheless, recently developed active battery powered radio transmitters are smaller, lighter and can be used to track insects in natural conditions; e.g., beetles (Rink & Sinsch 2007; Hedin 2008; Svensson et al. 2011; Chiari et al. 2013), dragonflies, (Wikelski et al. 2006; Levett & Walls 2011), crickets (Lorch et al. 2005; Watts & Thornburrow 2011) and bees (Pasquet et al. 2008; Hagen et al. 2011).

Currently, only three studies used radio telemetry with active transmitters for studying dispersal, movement behaviour, speed, diurnal activity and habitat use of carabid species. Moreover, these studies have fo-

Fig. 1. Female of *Carabus ullrichii* with fixed radio-trasmitter (0.28 g) at the top of elytrae with 25 mm short antena directed backwards.

cused on only two species of ground beetles, *Carabus coriaceus* L., 1758, the largest carabid species in Central Europe (Riecken & Ries 1992; Riecken & Raths 1996) and *Carabus olympiae* Sella, 1855, an endangered species from western Italian Alps (Negro et al. 2008).

In this paper we present the first prelimitary results of movement pattern of *Carabus ullrichii* Germar, 1824. We tested the application of radio telemetry as advanced method for monitoring acitivity of this species and quantification of species-specific movement. We also studied how the distances covered by beetles are influenced by daytime period and temperature, which are assumed to be important factors affecting the movement of large ground beetles (e.g., Thiele 1977; Turin et al. 2003).

Material and methods

The movement of *C. ullrichii* was studied in May and June 2015 in the foothills of the Beskydy Mountains in the northeast of the Czech Republic, in the village Jarcová (49.4245° N, 17.9533° E, 380 m a.s.l). The study area (0.7 ha) is a typical rural area with a mosaic of meadow and orchads. Moreover, previous investigations have shown that *C. ullrichii* is one the most common species of genus at this locality.

Carabus ullrichii is an apterous, wide and robust, 22–33 mm long beetle of cupreous colouration and tuberculate elytral intervals. The species is widely distributed in Central and Eastern Europe (Hůrka 1996; Turin et al. 2003). This species is typical spring breeder with overwintering adults and summer larvae and has only one reproductive period with peak of activity in early summer, with non-overlapping generations (Andorkó 2014). Immature males and females are active from August to Semptember. *Carabus ullrichii* is a forest species locally, but not obligatorily subdominant to dominant in deciduous forests of normal and humid hydrical series in the oak and beech-oak vegetation tiers (Zlatník 1976). Recedent to subdominant in oak-beech vegetation tier, reaching to the beech vegetation tier, exceptionally even to the beech-fire tier. It escapes the forests of the oligotrophic series, well prospering in the mesotrohpic, eutrophic nitrophilous and basic trophical series. Species also penetrates to secondary habitats, in dependence on increasing continuity and density of wooden vegetation and decreasing distance from the potential immigration sources. In the existing landscape structure of Central Europe it escapes intensively managed fields and some meadows.

To collect bettles, we used two 0.5 litre plastic cups inserted into each other as pitfall traps (Thiele 1977; Kromp 1999), which were baited with few pieces of cat food. Live beetles collected in these traps were kept in the laboratory for 7–10 days in separate boxes and fed mealworms and cat food every two days at libitum. Six beetles (four females, two males) were tagged using 0.28 g PicoPip transmitters (13 × 5 × 3 mm; Biotrack Ltd., Wareham, United Kingdom, www.biotrack.co.uk). We used cyanoacrylate glue and silicone putty for attaching and fixing radio-tags at the top of elytrae with short antena directed backwards (Fig. 1). These tags had a 25 mm long antenna and unique individual frequencies. One day after tagging, the beetles were released at 18:00 in central part of the study area in meadow, about 4 m from each other to avoid mutual interference and located every three hours (at 0:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00 and 21:00) for 10 following days. Nonetheless, two of the six transmitters (one female and one male) stopped emitting signal after a few hours and therefore were excluded from the study. The remaining tags had a battery life span between 16–23 days.

For tracking, we used the AR8000 hand-held receivers (AOR Ltd. 1994) with Yagi directional antenna and 20 cm dipole antenna for short distances. The radio signals from these tags were strong enough to be detected from 60 m. After approaching within 2 m of an individual we switched the Yagi antenna to short dipole antenna, which better locate the trasmitter signal range to 10–40 cm. At this point we stopped localising the specimen due to risk of stepping on it. Coordinates of each position (fixes) were plotted on the map and identified using Garmin GPS (Oregon 550t). Coloured stick was also driven into a soil, one for each fix, to avoid potential GPS measurement errors. Distances between the points were measured by a measuring tape. Distances shorter than 0.5 m were considered as fixes with no activity. Finally, air temperature at 2 m above the ground level was recorded every 3 hours at each fix together with locating the beetles. If any individual approached the border of research area, beyond that we would not be able to track it, we cap-

Table 1. Individual body weight without fixed transsmiter, ratio of body mass and tag mass, total distance in m, mean distance ± SD in m covered by radio-tracked beetles in 24 h period and maximum distance per 24 and 3 hours in meters.

No.	Sex	Initial body weight (g)	Body and tag mass ratio (%)	Total distance	Mean distance in 24 h period	Max (24 h)	Max (3 h)
1	f	1.21	23.1	79.8	7.98 ± 5.5	16.5	10.4
2	m	0.92	30.4	16.6	1.69 ± 3.7	11.6	6.0
3	f	1.34	20.9	120.9	13.43 ± 6.0	22.3	14.1
4	f	1.08	25.9	111.6	11.16 ± 10.9	29.3	13.0

tured the specimen and released it at the point of the first fix. As the intention of study was to measure species-specific movements and not habitat preferences, we expected that beetle relocation should not affect the individual activity. At the end of sampling period, we recaptured all specimens and retrieved their transmitters and then released all the beetles at their original capture locations. Because some tags were still generating pulses after removing from beetles, we also tested the life span and quality of signal to battery discharge.

Patterns of individual movements were visualised in QGIS 2.8 Wien (QGIS Development Team 2015). GPS coordinates of all fixes were projected into orthophotography map sourced by Czech Office for Surveying, Mapping and Cadastre (www.geoportal.cuzk.cz).

For statistical analysis three hours periods were classed into four groups representing different light conditions of the day: mornings with fixes between 6:00 and 9:00, midday with fixes between 12:00 and 15:00, evening with fixes between 18:00 and 21:00 and night with fixes between 0:00 and 3:00. Similarly movement activity (covered linear distances) and temperature were divided in six respectively eleven categories with units 2.5 m for linear distance and 2.5 °C for temperature. Covered linear distances per three hours and day (consecutive 24 hours) are presented as minimum – maximum value followed by the average ± standart deviation in parentheses. Differences in movement (number of three hour periods in specific distance category between individuals) in various times of day were tested with separate one-way ANOVA tests. To test the temperature influence on covered distance, we used generalized linear mixed models (GLMMs) with negative binomial error distribution and log link. In the GLMMs, temperature category was a fixed effect and individuals were a mixed effect. For the analysis, we used the *glmer.nb* function from the lme4 package (Bates et al. 2014). For post-hoc comparisons between temperature categories, we used the *glht* function from the multcomp package (Hothorn et al. 2008) with Tukey's pairwise multiple comparisons of means (Bretz et al. 2010). Analyses were conducted in R 3.2.2 (R Development Core Team 2015).

Results

From May 28 to June 7, 2015 (Table 1, Fig. 2) we collected 313 fixes in total. Radio-tracking period was 9–10 days depending on signal quality of tags. The battery life span was 18–31 days. The mass of transmitters varied from 20.9–30.4% of beetle body mass. Radio-tagging apparently did not disturb or limit ground beetles, as we observed them eating earthworms ($n = 2$), found them digged into soil or caught their signal coming out of the mousehole ($n = 3$).

Total distances covered by single individual ranged from 16.6 to 120.9 m in meadow habitat. Due to low number of individuals we did not compare the differences between sexes. Individuals were able to walk for several meters per 3 hour intervals, maximum distance reached in three hours interval was 14.1 m (in morning). Average linear distance per three hours interval varied between 0–6 (0.2 ± 0.9) m for the least active specimen and 0–14.1 (1.7 ± 2.8) m for the most active specimen. Per day the range varied between 0–11.6 (1.7 ± 3.7) m and 4.7–22.3 (13.4 ± 6.0) m. Movement activity did not differ by light condition (Fig. 3), however it was significantly affected by temperature (GLMM: $\chi^2 = 37.026$, df = 10, $P < 0.001$). Beetles were most active at temperatures 15.0–17.4 °C. With increasing and decreasing temperature decline also the activity of beetles. Below 5 °C, no movement was recorded (Fig. 4).

Discussion

Our goal in this field survey was to study movement ability of *C. ullrichii* which we plan to use as a model species in future ecological studies. We also tested the use of radio telemetry as a method for tracking individuals of this species. In last two decades the availability of small and light radio transmitters allows researchers to track small-bodied animals (Kissling et al. 2014). So far, radio-tracking was used only in two ground beetle species; 32–42 mm long *C. coriaceus* (tag mass 34–51%) (Riecken & Ries 1992; Riecken & Raths 1996) and smaller (18–38 mm) *C. olympiae* with tag mass approximately 40% of the average individual mass (Negro et al. 2008). We have verified that radio telemetry is a suitable method for monitoring smaller carabids such as *C. ullrichii* (tag mass 21–30%).

As there was no information on movement ability of *C. ullrichii* available, we expected the three hours interval between checks to be an acceptable compromise between the time invested by researcher for tracking the individuals and the distance they could possibly cover. This prediction showed to be right and beetles never escaped out of the transmitter signal range during the period.

The speed of *C. ullrichii* ranged from 1.69 to 13.43 m day^{-1} in meadow and orchard which is similar to speed of other large carabid species. The known values of speed are 2.26–7.32 m day^{-1} for *C. coriaceus* in meadow (Riecken & Raths 1996); 9.3–15.0 m day^{-1} for *C. auronitens* F., 1792 in fallow land (Niehues et al. 1996); 4.1 m per 12 h period for *C. olympiae* in shrub-

Fig. 2. Movement pattern of four specimens of *C. ullrichii*. The size of points represent the number of three hour periods with no activity (the smallest points = zero periods with no activity, the largest points = more than 10 periods with no activity). Starting points are outlined in black, black line represents the border of study area.

bery (Negro et al. 2008) and 6 m h^{-1} for *C. nemoralis* Müller, 1764 in set-aside areas and 2 m h^{-1} in semi-natural habitats (Kennedy 1994).

The habitat in which we tracked *C. ullrichii* was mostly short grass meadow with solitary trees or small groups of trees. Tag fixed at the top of elytra apparently could limit beetles to move across narrow microhabitats. However, based on similar movement distances observed in other radio-tracked carabids mentioned above we assume that transmitters did not substantively affected *C. ullrichii* movement. Furthermore, during our research individuals were not only able to move several meters within three hours in densely overgrown habitat but were also observed during feeding or digging into soil.

Carabid activity rhythm depends on many factors like sex, breeding season, habitat or geographic range (Szyszko 2004; Tuf et al. 2012). Body size of ground beetles is positively correlated with movement range (Ranjha & Irmler 2014) and strictly woodland species move much more slowly than generalist species (Brouwers & Newton 2008). By contrast, Firle et al. (1998) argued that the distances covered by individual depend on the availability of prey, but do not correlate with body size. According to literature (Luff 1978; Lövei & Sunderland 1996; Hůrka 2005; Negro et al. 2008), woodland and large ground beetles (body length > 10 mm) are mostly animals with night activity whereas field and small species are rather diurnal. However, radio-tracked *C. coriaceus* showed both nocturnal and diurnal activity with greater distances covered at night (Riecken & Raths 1996). Individuals of *C. auratus* within one population can have different life cycles, some are nocturnal, some diurnal and others are indifferent (Thiele 1977). Similarly our results showed that *C. ullrichii* is not typical nocturnal species. Although, the longest lin-

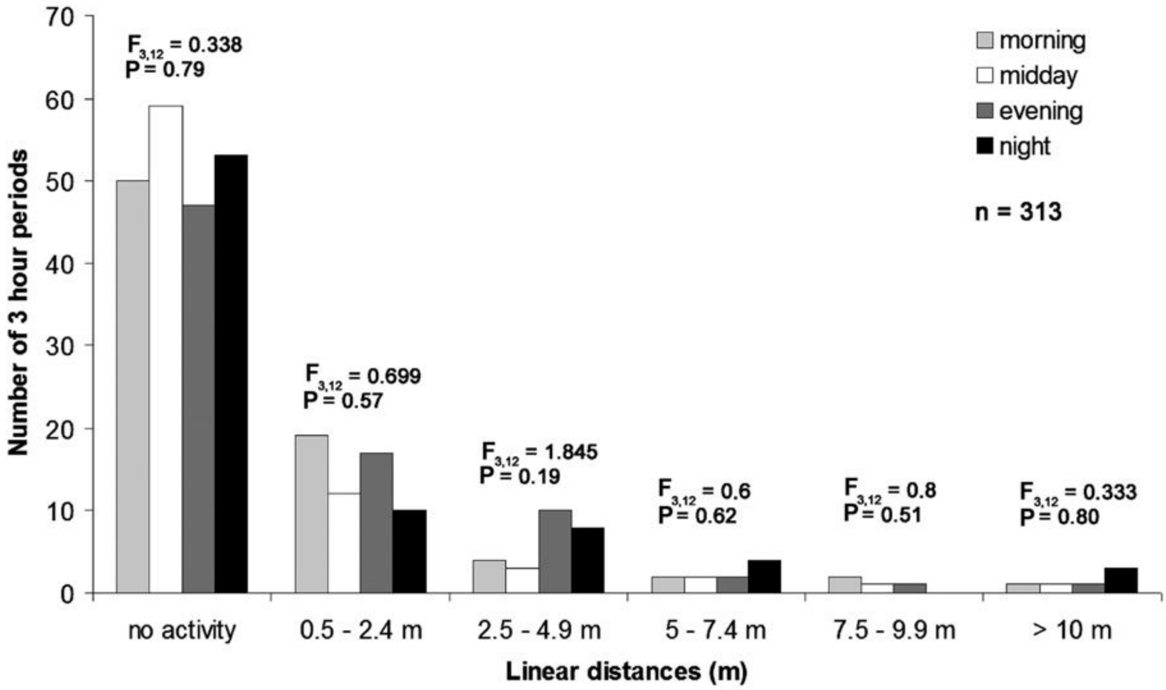

Fig. 3. Linear distances covered by *C. ullrichii* in different light conditions. For each distance class differences between daytimes were tested via one-way Anova. n = number of distances measured.

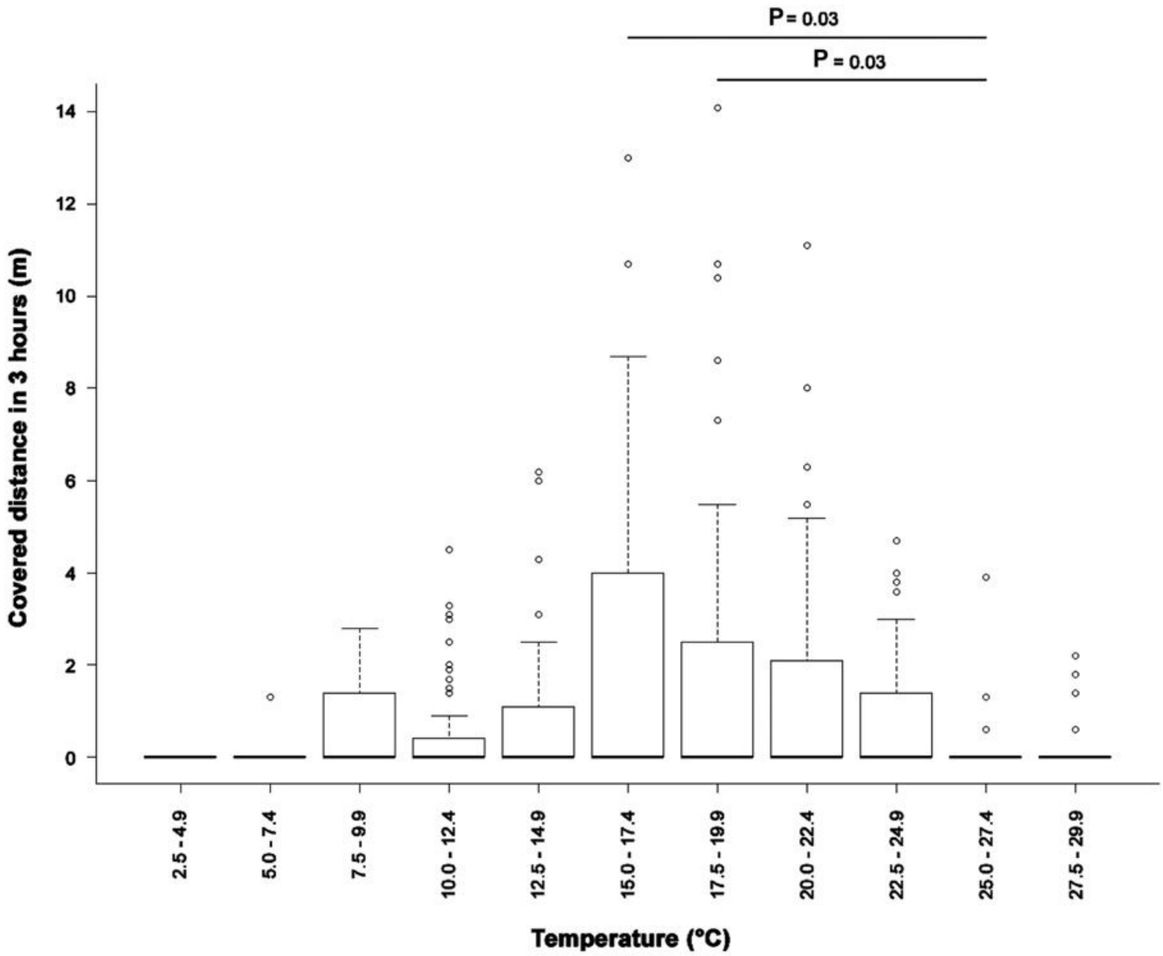

Fig. 4. Distances covered by individuals of *C. ullrichii* within three hours intervals in different temperature classes followed by straight lines of Tukey's pairwise multiple comparisons of means.

ear distances (more than 10 m) per three hour period were mostly covered in the night, the maximum distance per three hour walked by one individual was covered in morning hours.

Most of ground beetles are predators which play an important role in ground ecosystem. Movement behaviour is connected with starving; movement of beetles thus can be an indicator of habitat quality (Szyszko et al. 2004). On the other hand, harmonic radar study by Wallin & Ekbom (1988) showed no differences between movements of starving and ad libitum fed beetles (*Pterostichus melanarius* Illiger, 1798 and *P. niger* Schaller, 1783).

Thiele (1977) pointed out a temperature influence on habitat choice. His laboratory experiments on *Abax* species, *Nebria brevicollis* (F., 1792) and *Poecilus cupreus* (L., 1758) showed similar prefered temperature curves with activity peaks between 15–20 ℃. Some species have a preference toward different temperatures in relation to their reproduction biology; higher temperatures accelerated the maturation of the sexual glands (Tuf et al. 2012). Forest species appear to be more dependent upon the dark contition whereas the temprerature is more important for field species (Thiele 1977). Here we show that temperature had an influence on activity of *C. ullrichii.* In this study beetles moved mostly in meadow and under trees in orchard considered here as open habitat. It could be an explanation of temperature influence on species-specific movement.

Movement behaviour is an important aspect of organismal biology and in insects there is still lack of knowledge. Understanding factors that influence species behaviour including movement enable us to create favourable conditions for persistence of insect populations and technological developments provide new opportunities and methods. Our study illustrates the feasibility of radio-telemetry for tracking large epigeic ground beetles.

Movement activity of *C. ullrichii* seems to be indifferent to light conditions but temperature affected. Nevertheless, we are indeed awared that to generalise our results these trends need to be investigated in further research with much wider data set.

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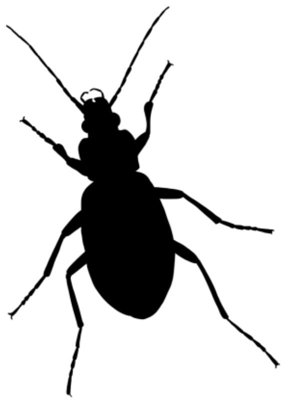
Appendix II



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ORIGINAL ARTICLE

Movement activity and habitat use of *Carabus ullrichii* (Coleoptera: Carabidae): The forest edge as a mating site?

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Abstract

Some carabid species are not restricted to a single habitat only, but use various types of habitats. In these species, relatively little is known about the utilization of occupied habitats and factors affecting their movement within these habitats. In this study, we focus on the movement activity of ubiquitous *Carabus ullrichii* during its reproductive period at the border of two types of habitats, a meadow and a forest. We tracked 21 adult individuals using radio telemetry and recorded in total 1,687 position fixes. Movement activity was associated with the type of habitat and specific environmental conditions such as time of the day and air temperature. Both sexes activated preferably at dusk and during the night, although males were most active at temperatures around 15°C, while females showed no preference for temperature. Males were able to walk as fast as females, but they were more associated with forest edge. We assume that the inner edge of the forest could be used as a mating site and after mating males stay there and wait for new females with which to mate, while fertilized females disperse into the surroundings. They moved further into the closed forest where they were likely looking for oviposition sites and food resources to support reproduction. Exclusively females were recorded to visit the meadow at a greater distance from the forest edge and their movements there were almost always direct.

Key words: carabids, dispersal, movement behavior, radio telemetry, reproduction.

INTRODUCTION

Movement and dispersal of animals have consequences not only for species fitness but also for population dynamics. In addition, the colonization of new suitable habitats and gene flow within populations are crucial for species persistence (Clobert *et al.* 2004; Bowler & Benton 2005). In the last few decades, movement of animal species has often become limited as a result of human activities and connectivity of populations is currently restricted due to landscape fragmentation (Saunders *et al.* 1991; Hanski & Ovaskainen 2000). This can be a significant threat especially for invertebrates with low dispersal ability such as flightless beetles of the genus *Carabus* Linnaeus (Turin *et al.* 2003; Ewers & Didham 2006). For these ground-dwellers, even small patches of unfavorable habitats or linear structures, such as roads, may pose a barrier (Mader *et al.* 1990; Niehues *et al.* 1996; Yamada *et al.* 2010; Matern *et al.* 2011). Therefore, the knowledge of their movement behavior (e.g. quantification of speed or willingness to cross specific habitats) and of its causes and consequences is vital for predicting a species response to environmental changes (e.g. Negro *et al.* 2008; Elek *et al.* 2014).

Movement behavior of *Carabus* species, as well as of other ground beetles, is primarily regulated by endogenous physiological factors. However, it also may be significantly affected by abiotic environmental conditions, particularly by light, temperature, and humidity (Thiele & Weber 1968; Thiele 1977; Turin *et al.* 2003). Nevertheless, response to these factors could be strongly influenced by breeding period and may differ among species, or even within the populations of the same species (Thiele 1977; Atienza *et al.* 1996; Tuf *et al.* 2012). In general, carabid movement is usually composed of two patterns: random walk with small

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distances covered per day in random directions and directed movement with large distances covered per day (e.g. Niehues *et al.* 1996; Riecken & Raths 1996). While random walk is most likely the result of frequent encounters with food resources or mate-seeking, directed movement is an efficient strategy for escaping from adverse sites or for dispersal (Baars 1979; Wallin & Ekbom 1988). These movement patterns may vary between habitats, suggesting different habitat preferences and utilizations (Wallin & Ekbom 1988; Niehues *et al.* 1996).

The ground beetle *Carabus ullrichii* Germar, 1824 is an abundant species occurring in various types of habitats from fields to forests (e.g. Hůrka 1996; Turin *et al.* 2003; Deuschle & Glück 2009). However, very little is known about the usage of habitats occupied by this species and factors affecting its movement within the habitats. In this study, we used radio telemetry to investigate a movement activity of *C. ullrichii* during its reproductive period in late spring and early summer at the border of two different habitats, a meadow and a forest. These habitats naturally differ in their environmental conditions, and it can be assumed that these differences could affect movement of beetles. Similarly, sex-specific resource requirements during breeding season may indicate different habitat utilization. Therefore, we tried to answer following questions: (i) which abiotic factors affect movement activity of the species?; and (ii) is the shape of movement trajectory, which reflects prevailing pattern of movement (i.e. random walk or directed movement), movement direction and the time spent in a particular environment, affected by specific habitat use in relation to reproductive behavior?

MATERIALS AND METHODS

Target species

Carabus ullrichii is a 22–33 mm long, robust beetle with cupreous coloration, occurs in Central and Eastern Europe from south-western Germany to western Ukraine, Romania, and Bulgaria, being abundant throughout the range (Turin *et al.* 2003). This species inhabits various types of deciduous forests (Andorkó & Kádár 2006; Máthé 2006; Andorkó 2014) as well as open or semi-open habitats such as meadows, fields, gardens, and orchards from lowlands to foothills (Hůrka 1996; Deuschle & Glück 2009; Huidu 2011; Růžičková & Veselý 2016). *Carabus ullrichii* is a typical spring breeder with overwintering adults, spring reproduction, and summer larvae. Adult beetles occur from March to September, the fresh imagoes appear during the second half of August, and they are active till hibernation (Turin *et al.* 2003). As it reproduces only once per season with relatively low fecundity and its generations do not overlap (Andorkó 2014), all individuals included in this study belonged to the same age cohort.

Study site

The study was conducted in the floodplain of the Morava River in Litovelské Pomoraví Protected Landscape Area near town Litovel (Central Moravia, Czech Republic, 49°41′38″N 17°6′14″E, approximately 230 m a.s.l.). The study site covers two different habitats: (i) floodplain forest of various age structures dominated by *Fraxinus excelsior* and *Tilia cordata* with mixed patches of full and partly open tree canopy cover and by *Galium aparine*, *Urtica dioica* and *Allium ursinum* in the sparse herbal layer; and (ii) hay meadow with predominance of dense tussocks of various grasses. The border between these two habitats is very abrupt without a wide gradual transition zone.

Data sampling

We collected adult individuals of *C. ullrichii* during their main activity and reproductive period in May and June, 2016 using baited pitfall traps positioned across the study site. To avoid a bias of possible individual preferences for certain habitat, we placed the traps at the border of the forest and the meadow. Each trap consisted of two 0.5-liter plastic cups telescoped to make extraction easier and baited with cat food placed in a plastic bottle lid at the bottom. We checked them every 12 h to avoid damage of beetles. Before the in-situ experiment, we kept captured beetles *ex situ* in separate boxes at the room temperature and we fed them every two days with mealworms *ad libitum.*

Radio telemetry is a widely used method for studying the movement behavior of vertebrates. In the last two decades, transmitter sizes have become small enough to allow also tracking of large insect species under natural field conditions. Undisputable advantage of this method is the possibility to track and locate a tagged individual at any time (Kissling *et al.* 2014). In the previous study, we found that radio telemetry is a suitable method for monitoring movements of our model species (Růžičková & Veselý 2016). Therefore, we used the same PicoPip transmitters (weight 0.3 g, volume of 13 × 5 × 3 mm; Biotrack Ltd., Wareham, UK) with specific frequencies between 173–174 MHz in this study. One day before the beginning of the experiment, we attached the tag with short antenna directed backwards at the top of beetle's elytra by cyanoacrylate glue gel (Fig. 1). In total, we tagged 21 individuals, 10 males and 11 females. The mass of tags was approximately 33% of the initial body weight of tracked males (median 0.9 g, range: 0.7–1.2 g) and 27% of the body weight of females (median 1.1 g, range: 0.8–1.5 g). We released beetles at the border between the habitats at 12:00 Central European Summer Time (CEST) on 31 May 2016, 5 m apart from each other to avoid mutual interference. We then located individuals every 3 h until signal loss (but not later than June 16, 2016).

For radio-tracking, we used the Sika hand-held receiver (Biotrack Ltd.) with Yagi directional antenna and 20 cm dipole antenna for short distances. We were able to detect the transmitter signal from a distance of 60 m. During every tracking session, we started searching for tagged individual at the point (fix), where it was found in the previous session. First, we walked in the direction of the bearing of the signal to get close to the tagged beetle. At the point of 0.5 m distance to expected signal source, we stopped localizing the individual due to risk of stepping on it. Based on the quality and range of the signal, we were also able to determine whether the tracked beetle was in the soil or on the ground surface. We recorded GPS coordinates of the starting fixes and then marked all following fixes by colored sticks hammered into the ground. When the distance covered between two tracking sessions was shorter than 0.5 m, it was considered as a fix with no activity. At each fix, we recorded the type of habitat (forest or meadow), temperature and relative humidity at the ground level, and the distance covered and the direction (azimuth) between consecutive fixes.

Data analyses

We classified the 3-h observation periods into four categories representing different parts of the day: fixes at

Figure 1 Female of *Carabus ullrichii* with a fixed radio-transmitter.

3:00 were classified as dawn, fixes between 6:00 and 18:00 as day, fixes at 21:00 as dusk, and fixes between dusk and dawn were assigned as night. To test the influence of sex, environmental factors (type of habitat, temperature, and relative humidity) and the part of day on the movement of *C. ullrichii*, i.e. the covered distance per 3-h period (response variable), we used generalized linear mixed models (GLMMs) with negative binomial error distribution. Due to the presence of large numbers of zero values in the covered distances, we used ($x + c$) transformation, where x is the response variable and c was 1/2 of the smallest, non-zero value. In the GLMMs, temperature, daytime, humidity, and sex were fixed effects and individual was a mixed effect. For the analysis, we used the *glmer.nb* function from the 'lme4' package (Bates *et al.* 2015). As post-hoc comparisons of pairwise differences between the mean covered distances in different daytime classes 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). To find a preferred direction of movement of tracked beetles, we used Rao's spacing test (*rao.spacing.test* function) from the "circular" package (Agostinelli & Lund 2013) and tested a uniformity of displacement's directions (azimuths) between fixes. All analyses were conducted in R 3.2.2 (R Core Team 2015). Movement trajectories made by tracked beetles we visualized in QGIS 2.8 Wien (QGIS Development Team 2015) by Azimuth and Distance Plugin (De Paulo *et al.* 2016) to characterize beetles' movement patterns in the studied habitats.

RESULTS

We recorded a total of 1,687 fixes; 475 (28%) with movement activity (222 for males and 253 for females) and 1,212 (72%) with no activity (567 for males and 645 for females). The shortest tracked period obtained from a single individual had 13 fixes, while the longest tracking period contained 127 fixes. The shortest total distance covered by a single beetle was 5.6 m (in 125 fixes), and the longest one was 280.1 m (in 127 fixes), both for females. Movement characteristics of all tagged individuals in detail provides Table 1. Median of distances covered per 3-h interval was 0.45 m (range: 0.14–3.18 m) for males and 0.95 m (0.04–3.07 m) for females. The highest speed recorded was 20.1 m per 3 h for males and 19.6 m per 3 h for females, both in the forest. In the meadow, the highest speed recorded was much lower: 7.5 m per 3 h for males and 17.6 m per 3 h for females.

Table 1 Movement characteristics of radio-tracked individuals: total covered distances, mean speeds in 3-h observation periods and mean directional vectors

No. of individual	Sex	Total distance (m)	Mean speed per 3 h (m)	Mean vector (°)	Fix_{act}	Fix_{pass}
1	f	79.3	0.62	174.2	45	82
2	m	140.5	1.29	159.2*	63	46
3	f	17.7	0.16	88.8	16	94
4	f	47.2	1.18	205.8*	18	22
5	f	97.4	1.25	117.3	26	52
6	m	41.3	3.18	111.4	10	3
7	m	35.0	0.33	123.9	17	88
8	m	39.0	1.95	183.9	12	8
9	m	14.3	0.14	168.7	10	89
10	f	280.1	2.21	145.3	64	63
11	f	5.6	0.04	102.9	9	116
12	f	7.0	0.06	119.4	9	118
13	f	11.2	0.80	173.9	7	7
14	m	15.8	0.15	202.0	13	92
15	m	53.9	0.49	177.5	26	84
16	f	79.7	3.07	209.7	14	12
17	m	55.1	2.90	169.3	11	8
18	m	40.6	0.41	120.6	24	75
19	m	44.4	0.40	238.0	36	74
20	f	44.5	0.95	240.2	13	34
21	f	79.5	1.03	67.9	32	45

Values marked by asterisk indicate non-random displacement of directions based on Rao's spacing test ($P < 0.05$). Fix_{act} = number of fixes with activity, Fix_{pass} = number of fixes without activity.

The movement activity (i.e. covered distance per 3 h) of *C. ullrichii* was significantly affected by temperature ($\chi^2 = 33.863$, df = 1, $P < 0.001$), the part of day ($\chi^2 = 31.455$, df = 3, $P < 0.001$), and the type of habitat ($\chi^2 = 48.083$, df = 1, $P < 0.001$). The effect of temperature was sex-specific (sex-temperature interaction: $\chi^2 = 5.646$, df = 1, $P = 0.018$). Males were most active at 15°C, while females had no visible activity peak (Fig. 2). Beetles were most active at dusk and night (Fig. 3a), with no significant difference in the diel activity between the sexes (sex-daytime interaction: $\chi^2 = 4.324$, df = 3, $P = 0.229$). Humidity had no significant effect on the movement activity ($\chi^2 = 0.208$, df = 1, $P = 0.648$).

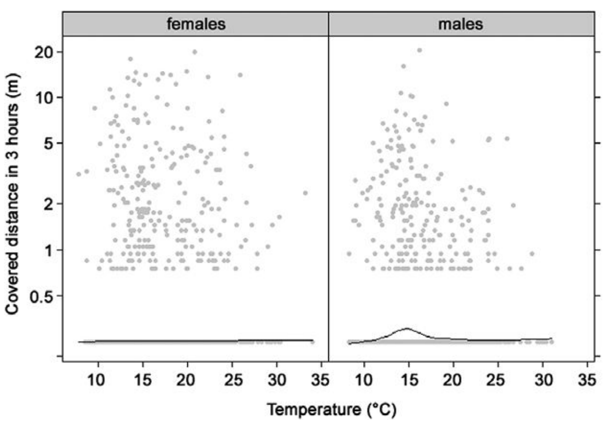

Figure 2 The effect of temperature on movement activity of females and males. Each symbol represents a single fix, and black smooth curve is fitted Loess curve.

Although all individuals were released at the border of the habitats, most of them moved towards the interior of the forest and showed patterns of random walk alternating with directed movement (Fig. 4a). In this habitat, some individuals (regardless of sex) were able to stay at the same spot for three or four days hiding in leaf litter or burrowing into the soil. Individuals having dispersed towards meadows showed movements without random walk and stops, and when compared with movements in the forest, their mean speed per 3 h was significantly higher (Fig. 3b). While females penetrated the meadow and the forest at greater distances, males rarely entered the meadow and walked closer and parallel to the forest edge. Except for two individuals, no prevailing walking directions were detected (Table 1). Mean directional vectors of all studied individuals ranged from 67.9° to 240.2° (northeast – southwest), which corresponds with the position of the forest (Fig. 4b).

DISCUSSION

Using radio telemetry, we found that the movement activity of *C. ullrichii* was associated with the type of habitat, specific environmental conditions such as temperature and the part of day. In ectotherms, the relation

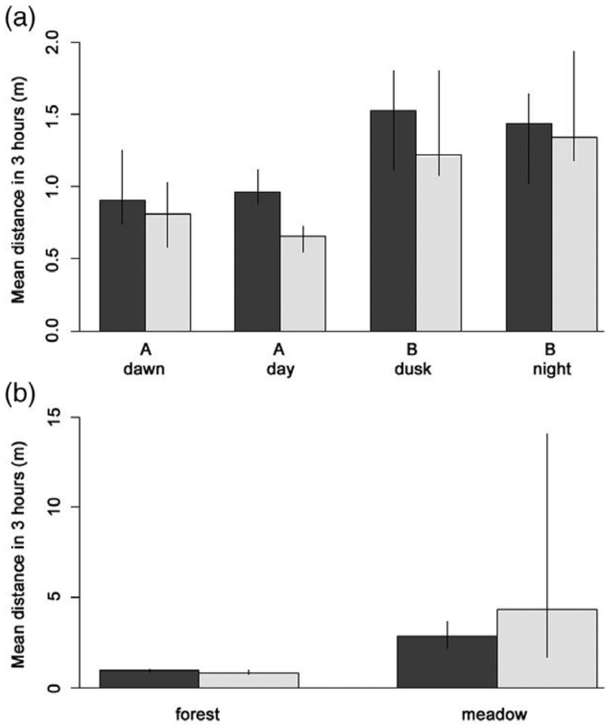

Figure 3 The mean covered distance (m) of females (dark bars) and males (light bars) per 3-h period during (a) each part of the day and (b) in different habitats; error lines represent 95% CIs. Capital letters above daytime labels indicate significant differences in the mean covered distance among different times of a day, based on the post-hoc Tukey's pairwise multiple comparisons of the means.

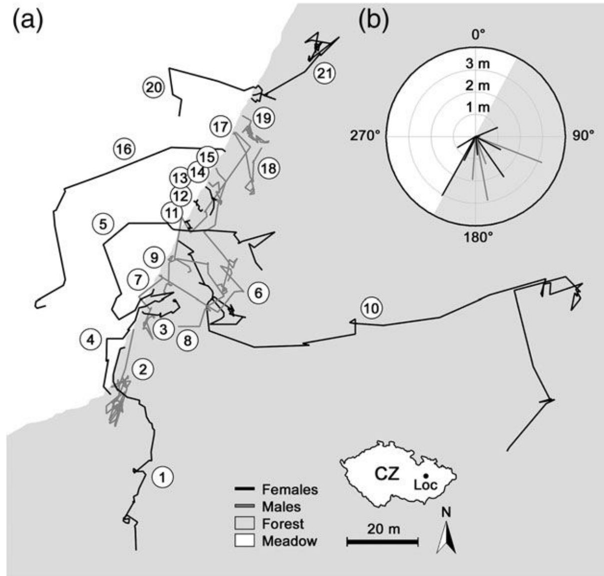

Figure 4 (a) Movement patterns and (b) mean directional vectors of all tracked individuals. Numbers next to the trajectories in (a) correspond with the numbers of individuals presented in Table 1. The length of each vector in (b) represents the mean speed per 3 h. In the inserted map of the Czech Republic (CZ), "Loc" indicates the position of study site.

between activity and temperature is not particularly surprising (e.g. Atienza *et al.* 1996; Honěk 1997). *Carabus* species have preferences towards different temperatures depending on their reproduction biology, because temperature accelerates or suppresses the maturation of the sexual glands (Sota 1986). For instance, Althoff *et al.* (1994) reported that mean daily temperature in May determined the timing of reproduction in the spring breeder *Carabus auronitens* Fabricius, 1792. In *C. ullrichii*, the effect of temperature differed between sexes; males were most active at temperature around 15°C, while females showed no preferred temperature. This is counterintuitive, as temperature is expected to have a greater effect on females due to physiological differences inherent in the breeding behavior (Atienza *et al.* 1996). During our field work conducted in late May and June the majority of radio-tracked females were in reproductive or even post reproductive period. In this time, it is likely more important for them to find enough food to refill the energy costs of reproduction (Kagawa & Maeto 2009) than to search for sites suitable in temperature for the development of their ovaries and/or eggs.

Adults of *C. ullrichii* were more active during the dusk and in the early night hours. Thiele (1977) and Szyszko *et al.* (2005) also reported that some other *Carabus* species tend to be active in early hours after sunset. In general, woodland-dwelling and/or large carabids are mostly nocturnal, whereas small, open-habitat species are mainly diurnal, although exceptions exist (Lövei & Sunderland 1996; Riecken & Raths 1996). Our previous study indicated that circadian activity of *C. ullrichii* individuals from meadow and orchard was not affected by light conditions (Růžičková & Veselý 2016). Compared to our recent findings, it is likely that *C. ullrichii* circadian activity varies between populations, geographical localities, and habitats. Whereas forest populations might be rather night-active as in the general pattern of circadian activity of carabids mentioned above, meadow and field inhabitants are active not only in the nighttime but also in the daytime. During midday, the temperature conditions in open habitats become unsuitable for beetles and they try to escape or hide from such conditions (Thiele 1977). However, we did not observe any influence of relative humidity at the ground level on the movement activity. Likely, even the minimal humidity of leaf litter and soil surface is high enough to resist desiccation of beetle's body (Althoff *et al.* 1994).

It is often reported that *C. ullrichii* occurs in various types of habitats from deciduous forests to arable lands (e.g. Hůrka 1996; Deuschle & Glück 2009; Andorkó 2014), but relatively little is known about specific habitat utilization. Our results showed that vegetation structure at the ground level did not affect the mean speed but the maximum speed of movement. In the meadow, dense tussocks did not appear to act as barriers, but rather reduced the maximum speed of walk, while relatively sparse herbal layer inside the forest enabled individuals to walk quicker. These findings are in agreement with studies obtained from other types of habitats such as grass, hedgerows, and crop lands, where beetles can sprint faster in habitats showing higher proportion of bare soil (Mauremooto *et al.* 1995; Ranjha & Irmler 2014).

Ground beetles are predators foraging for prey by exploring, and thus exhibit an increased turning frequency leading to an area-restricted search in sites with high prey density (Wallin & Ekbom 1988). In *C. ullrichii,* the higher tendency to random walk in the forest suggests that this type of habitat provides more suitable conditions for foraging than the meadow, where the movement was almost exclusively direct. In addition, only females were detected to penetrate the meadow at a greater distance from the forest edge. It is likely that females utilize open habitats for dispersal as proposed by Rijnsdorp (1980). Females were also able to walk further into the forest interior than males, likely seeking favorable oviposition sites and searching for food resources to support reproduction (Kagawa & Maeto 2009). Although males were able to walk as fast as females, they spent most of the time at the forest inner edge or in nearby forest. Similar sex-specific movement patterns between forest and orchard were observed in *Carabus yaconinus* Bates, 1873 (Kagawa & Maeto 2009). The inner edge of the forest could be used as a mating site: after mating, fertilized females disperse into surroundings, while males wait there to mate with newly arriving females. Occasionally, individuals of both sexes stayed at a spot for several fixes irrespective of climatic and microhabitat conditions. This behavior was indirectly mentioned also in other studies on movement patterns of *Carabus* species, using different tracking techniques (Niehues *et al.* 1996; Riecken & Raths 1996), but without explanations of this phenomenon. Likely, beetles could either rest, being satiated, or wait for more suitable conditions (temperature, day time, etc.). Preferences of *C. ullrichii* for the forest edge may also raise the question of whether the species should be considered as an "ecotone" specialist as was formerly reported by Skłodowski (1999, 2008) and Riecken and Raths (1996) for some *Carabus* species based on their parallel movement patterns to the forest edge.

In conclusion, the movement to different habitats and adjustment of the circadian activity are two strategies for avoiding adverse environmental conditions. Nevertheless, these patterns may vary in time, space and between sexes according to their physiological requirements and reproductive conditions (Atienza *et al.* 1996). In *C. ullrichii*, the movement activity depends not only on abiotic factors of environment but it is also associated with reproductive behavior. After mating, females move actively looking for suitable oviposition sites or food resources especially in the forest interior, while males move only at the forest inner edge.

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Appendix III

Abstract: It is not so long ago that the use of radio telemetry for studying animal biology and ecology was only applicable to vertebrates. However, recently developed radio transmitters are smaller and lighter, which opens up new opportunities for using this method to track insects in natural conditions. In this article, we provide short overview of using radio telemetry in insect studies and describe its advantages and limitations. As an example of insect tracking, we present our first study on the movement activity of the ground beetle *Carabus ullrichii*.

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Využití radiotelemetrie v entomologii

Radiotelemetrie představuje technologii pro dálkový přenos dat za použití radiového signálu. Nachází široké uplatnění v mnoha oborech lidské činnosti od kosmonautiky, meteorologie, vojenství až po biologii. Od 60. let minulého stol. byla použita v celé škále zoologických studií, a to hlavně u obratlovců. Jde o unikátní způsob, jak se o životních strategiích živočichů dozvědět více, protože řadu druhů lze ve volné přírodě jen velmi těžko přímo sledovat. Navíc technologický pokrok otevírá v současnosti možnost využití i v entomologii.

Radiotelemetrie pracuje s aktivními vysílači (transmittery neboli tagy) s vlastním zdrojem energie, které se připevní na živočicha. Jsou zality do ochranného obalu z plastu, aby citlivé součástky odolaly nepříznivým vlivům prostředí. Vysílačky vydávají vlastní radiový signál (pulzy) o velmi vysoké frekvenci, obvykle mezi 30–300 MHz. Signál je pomocí externí antény zachycen přijímačem, který má u sebe výzkumník (obr. 1). Každá vysílačka používá jedinečnou frekvenci, není proto problém sledovat více jedinců současně. Stačí jen správně naladit přijímač. Síla a směr signálu určí polohu sledovaného zvířete vůči pozorovateli, případně i to, zda se jedinec pohybuje, nebo ne. Ze získaných dat můžeme zjistit celou řadu životních charakteristik zkoumaného druhu – polohu hnízda, úkrytu či nory, velikost domovského okrsku, pohybovou a denní aktivitu nebo migrační schopnosti. Sofistikovanější vysílačky zaznamenávají dokonce tepovou frekvenci, tělesnou teplotu a polohu těla.

Kvůli hmotnosti vysílaček byla radiotelemetrie po desetiletí doménou zejména zoologů zkoumajících větší druhy obratlovců, jako jsou šelmy nebo kopytníci (např. Živa 2013, 5: 234–237), někteří hlodavci, větší ptáci a další. Nicméně v posledních letech technický rozvoj umožňuje výrobu stále menších a lehčích vysílaček, což nejen rozšiřuje spektrum studovaných obratlovců např. o menší ptáky nebo plazy (viz Živa 2008, 3: 131–133), ale pozornost se obrací i na bezobratlé. Tím se otevírají nové možnosti využití radiotelemetrie také mezi entomology, kteří si totiž donedávna museli (a často stále musejí) vystačit při studiu biologie a ekologie hmyzu s různými druhy pastí spojenými s mnoha metodickými limity (někdy opomíjenými, Živa 2015, 6: 304–306), odchytáváním a značením jedinců (tzv. capture-mark-recapture) nebo přímým pozorováním.

Vysílačku můžeme na zkoumaného jedince připevnit několika způsoby, záleží na velikosti zvířete a způsobu jeho života. U obratlovců se nejčastěji používají popruhy, ušní známky, obojky nebo implantáty. Další možností je nalepení vysílačky přímo na tělo, což představuje v podstatě jediné východisko u bezobratlých – pevná kutikula k tomu i přímo vybízí (obr. 3).

U vysílačky rozhoduje hmotnost baterie, která určuje její životnost. A zde narážíme na největší problém využitelnosti radiotelemetrie při studiu bezobratlých. Větší hmotnost vysílačky sice zajistí delší výdrž, avšak pro většinu hmyzích druhů bude příliš těžká a v praktickém výzkumu tudíž nepoužitelná. Kvůli hmotnosti se zatím u bezobratlých nepoužívá ani dnes už běžná metoda sledování větších zvířat – GPS technologie, umožňující určení polohy podle geografických souřadnic za pomoci družice. Proto je potřeba drobný hmyz soustavně sledovat v jeho prostředí a ne prostřednictvím počítače z pohodlné pracovny. V současné době mají nejmenší komerčně vyráběné vysílačky s velikostí pouhých 5 × 12 × 1,5 mm hmotnost zhruba 0,2 g a jejich životnost se pohybuje kolem 7 dnů. Tyto nejmenší vysílačky se dají použít např. pro čmeláky. Při výzkumu hmyzu mají většinou hmotnost do 1 g. U obratlovců bývá pravidlem, že hmotnost připevněného vysílače by neměla překročit 4 % tělesné hmotnosti zvířete. U zástupců hmyzí říše bývá tento poměr vyšší a kolísá od 6 % (u velkých druhů brouků) až do 100 % (u čmeláků). Nabízí se otázka, do jaké míry připevněná vysílačka ovlivní život jedince. Je pravděpodobné, že může mít vliv na chování, energetické nároky nebo metabolismus nositele v kratším či delším časovém horizontu. Např. vysílačkou zatížený čmelák zemní méně létá a více odpočívá. Na druhou stranu pohyblivost kobylky *Anabrus simplex* s vysílačkou a bez ní se významněji neliší. Avšak počet studií v této oblasti bádání je zatím velmi omezený, a proto bude třeba provést rozsáhlejší experimenty.

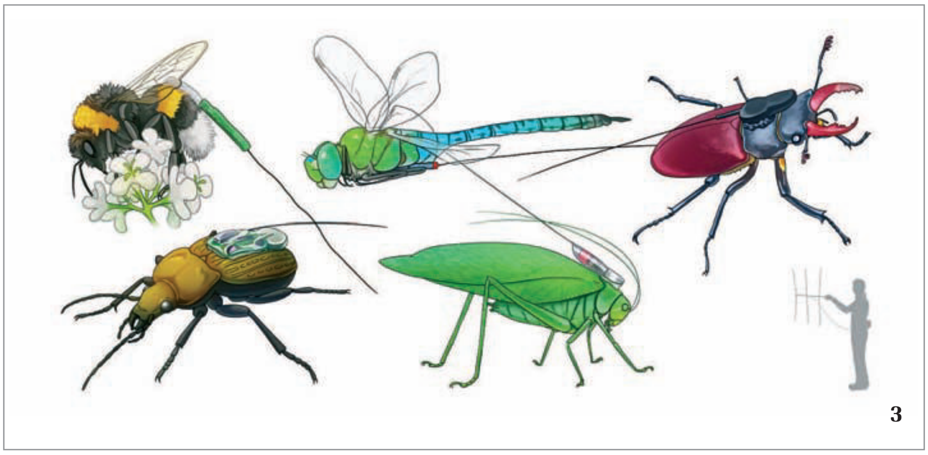
S nároky na velikost a hmotnost vysílačky souvisí vzdálenost, na jakou zachytíme její signál. Větší a těžší (v hmyzím měřítku) mají silnější signál, maximální vzdálenost detekce se udává až 500 m na rovném terénu. Většinou ale tato vzdálenost bývá mnohem kratší (300–100 m i méně). Svou roli ve výsledné kvalitě signálu hraje topografie terénu, hustota porostu a počasí. Např. po dešti se signál od mokré vegetace odráží a určit správný směr není tak jednoduché jako za sucha.

1 Přijímač a anténa – důležité vybavení při radiotelemetrickém sledování jedince označeného vysílačkou. Foto M. Hykel

2 Louka se sadem a skupinami stromů. Biotop, kde se střevlíci Ullrichovi (*Carabus ullrichii*) běžně vyskytují a kde jsme sledovali jejich pohybovou aktivitu. Foto J. Růžičková


1


2



3 Ukázky připevnění vysílačky u různých skupin hmyzu. Zleva nahoře: čmelák zemní (*Bombus terrestris*), americké šídlo *Anax junius*, roháč obecný (*Lucanus cervus*), střevlík Ullrichův a neotropická kobylka *Philophyllia ingens*. Překresleno podle původních studií. Orig. J. Růžičková
4 Střevlík Ullrichův s vysílačkou o hmotnosti 0,3 g. Foto M. Veselý

Přesto byla radiotelemetrie již úspěšně použita v několika entomologických studiích na větších druzích vážek, rovnokřídlých, blanokřídlých, střechatek, motýlů a brouků, zejména v oblasti migrace, pohybové aktivity, stanovištních (habitatových) preferencí, velikosti domovského okrsku nebo vybraných aspektů chování zkoumaných druhů. Kvantitativní měření průměrné a maximální vzdálenosti, kterou sledovaný druh urazí v přirozeném prostředí za určitý časový interval, patří mezi nejčastější cíle radiotelemetrických prací. Nelétavé druhy urazí za den desítky, výjimečně stovky metrů, u létajících se tento údaj může pohybovat až v řádu kilometrů. Např. roháč obecný (*Lucanus cervus*) je schopen na jeden zátah uletět až 1 720 m a americké šídlo *Anax junius* během migrace zvládne v průměru 11,9 km za den.

Z nelétajících brouků se díky své velikosti a zajímavému způsobu života hodí pro radiotelemetrii zejména velké druhy střevlíků rodu *Carabus*. Jsou relativně těžcí, naše největší druhy váží i více než 1,5 g, a až na výjimky zcela bezkřídlí (apterní). Proto nehrozí, že by dokázali odletět z dosahu přijímače. Je až s podivem, že do současné doby byly pomocí radiotelemetrie studovány pouze dva druhy velkých střevlíků. Výsledky výzkumů přinesly zajímavé novinky pro jejich biologii (Riecken a Rath 1996, Negro a kol. 2008). Např. jaký biotop vyhledává endemit italských Alp střevlík *C. olympiae* – znalost habitatových preferencí je důležitá pro efektivní ochranu tohoto ohroženého druhu, vedeného v červeném seznamu jako zranitelný. Nebo že střevlík kožitý (*C. coriaceus*) nepatří mezi druhy s typicky noční aktivitou, jak se dříve běžně předpokládalo. Případně, jakou vzdálenost dokáže jedinec urazit za 12 hodin (u střevlíků kožitých je rekord 51 m), resp. za celou dobu sledování (389 m za 17,5 dne). Něco takového by se dříve dalo zjistit jedině pomocí padacích zemních pastí a označením velkého množství jedinců. Radiotelemetrií lze dohledat zkoumaného živočicha v jakoukoli denní dobu s přesností na několik centimetrů. Avšak je třeba si dávat pozor, abychom hledaného jedince nezašlápli.

V r. 2015 jsme poprvé využili radiotelemetrii při výzkumu pohyblivosti velkých střevlíků i my (Růžičková a Veselý 2016). Jako modelový druh jsme vybrali střevlíka Ullrichova (*C. ullrichii*, obr. 4), měděně zbarveného 22–33 mm velkého brouka, který je relativně běžným druhem střední a východní Evropy. Svým výskytem zasahuje od jihozápadního Německa po západní Ukrajinu, Rumunsko a Bulharsko. U nás je zaměnitelný s dalšími dvěma podobně zbarvenými druhy. Známější a zhruba stejně velký střevlík měděný (*C. cancelatus*) se liší tím, že má červená stehna a první články tykadel. Střevlík zrnitý (*C. granulatus*) je štíhlejší a menší. Střevlík Ullrichův patří k původním druhům listnatých lesů, můžeme ho ale nalézt i v čistě nelesních biotopech – v zahradách, sadech, na loukách a polích, od nížin do podhůří. Na podzim vylíhlí jedinci přezimují a v květnu a červnu se rozmnožují. Během léta v červenci a srpnu se setkáme s larválními stadii nebo se starými jedinci, v závěru sezony potom i s čerstvými dospělci.

V naší pilotní studii jsme se zaměřili zejména na použitelnost radiotelemetrie při výzkumu střevlíka Ullrichova. Dalším, neméně důležitým cílem bylo zjistit, jak se brouci pohybují v konkrétním biotopu a jakou vzdálenost v něm dovedou překonat. Výzkumnou plochou byl pozemek o velikosti 0,7 ha v obci Jarcová na levém břehu Vsetínské Bečvy na Valašsku. Šlo o zahradu s loukou, sadem a skupinami stromů, kde se tito střevlíci běžně vyskytují (obr. 2). Na čtyři jedince (samce a tři samice) jsme pomocí vteřinového lepidla připevnili vysílačky o hmotnosti 0,3 g s 2,5 cm dlouhou anténou (obr. 4). Transmitter představoval zhruba 20–30 % hmotnosti brouka. Signál bylo možno zachytit až ze vzdálenosti 50 m, polohu jedinců jsme zaznamenávali každé tři hodiny ve dne i v noci po dobu 10 dnů.

Brouci se během výzkumu pohybovali na louce a pod stromy v sadu. Jejich průměrná rychlost kolísala od 1,7 do 13,4 m za den. Přesto byli schopni urazit za tři hodiny až 14,1 m. Neměli problém se zahrabat do země nebo nalézt potravu. Běžně jsme v prostoru, z něhož vycházel signál, nacházeli natrávené žížaly, které tvoří obvyklou potravu střevlíků (podobně jako potápníci nebo pavouci mají mimotělní trávení). Další výsledky naznačují, že pohybová aktivita tohoto druhu nezávisí na denní době. Podobně jako zmíněný střevlík kožitý ani námi sledovaný střevlík Ullrichův nepředstavuje typicky noční druh. Jeho aktivitu ovlivňují jiné faktory, velmi pravděpodobně teplota. Během sledování jsme zaznamenali vrchol aktivity mezi 15–17,4 °C. Nicméně závěry založené na pouhých čtyřech jedincích nechceme považovat za konečné, a proto plánujeme v dalším výzkumu ověřit naše výsledky na větším počtu brouků, ve více biotopech a s dalšími faktory prostředí. Jen pro úplnost – na konci sledování jsme všechny jedince vyhledali, vysílačky sundali a brouky pustili zpět do přírody.

Technický pokrok jde mílovými kroky kupředu a dává naději na další miniaturizaci a zvyšování životnosti vysílaček. Nadcházející roky tak nejspíše přinesou nové entomologické studie využívající i tuto progresivní metodu.

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