# 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℃. 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

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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  $(13 \times 5 \times 3 \text{ mm})$ ; 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-

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)
		$1.21\,$	23.1	79.8	$7.98 \pm 5.5$	16.5	10.4
2	m	0.92	30.4	$16.6\,$	$1.69 \pm 3.7$	11.6	6.0
3		1.34	20.9	120.9	$13.43 \pm 6.0$	22.3	14.1
$\overline{4}$		1.08	25.9	111.6	$11.16 \pm 10.9$	29.3	13.0

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

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  $\pm$  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  $0-6$   $(0.2 \pm 0.9)$  m for the least active specimen and 0–14.1 (1.7  $\pm$  2.8) m for the most active specimen. Per day the range varied between 0–11.6 (1.7  $\pm$  3.7) m and  $4.7-22.3$   $(13.4 \pm 6.0)$  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<sup>-1</sup> 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<sup>-1</sup> for C. coriaceus in meadow (Riecken & Raths 1996); 9.3–15.0 m day<sup>-1</sup> 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<sup>-1</sup> for *C. nemoralis* Müller, 1764 in set-aside areas and 2 m h<sup>-1</sup> in seminatural 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◦ C. 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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#### References

Andorkó R. 2014. Studies on carabid assemblages and lifehistory characteristics of two Carabus (Coleoptera, Carabidae) species. Ph.D. thesis. Faculty of Sciences, Eötvös Loránd University, Budapest, 97 pp.

- Baars M.A. 1979. Patterns of movement of radioactive carabid beetles. Oecologia 44 (1): 125–140. DOI: 10.1007/BF00346 411
- Bates D., Maechler M., Bolker B. & Walker S. 2014. lme4: Linear mixed-effects models using S4 classes. R package version 1.1- 7. http://CRAN.R-project.org/package=lme4
- Bérces S. & Elek Z. 2013. Overlapping generations can balance the fluctuations in the activity patterns of an endangered ground beetle species: long-term monitoring of Carabus hungaricus in Hungary. Insect Conserv. Divers. 6: 290–299. DOI: 10.1111/j.1752-4598.2012.00218.x
- Bretz F., Hothorn T. & Westfall P. 2010. Multiple Comparisons Using R. Boca Raton, CRC Press, 205 pp. ISBN: 978-1-58488- 574-0
- Brouwers N.C. & Newton A.C. 2009. Movement rates of woodland invertebrates: a systematic review of empirical evidence. Insect Conserv. Divers. 2 (1): 10–22. DOI: 10.1111/j.1752- 4598.2008.00041.x
- Chiari S., Carpaneto G.M., Zauli A., Zirpoli G.M., Audisio P. & Ranius T. 2013. Dispersal patterns of a saproxylic beetle, Osmoderma eremita, in Mediterranean woodlands. Insect Conserv. Divers. **6 (3):** 309-318. DOI: 10.1111/j.1752-4598.2012.00215.x
- Firle S., Bommarco R., Ekbom B. & Natiello M. 1998. The influence of movement and resting behaviour on the range of three carabid beetles. Ecology 79 (6): 2113–2122. DOI: 10.2307/176714
- Hagen M., Wikelski M. & Kissling W.D. 2011. Space use of bumblebees (Bombus spp.) revealed by radio-tracking. PLoS One 6 (5): e19997. DOI: 10.1371/journal.pone.0019997
- Hedin J., Ranius T., Nilsson S.G. & Smith H.G. 2008. Restricted dispersal in a flying beetle assessed by telemetry. Biodivers. Conserv. 17 (3): 675–684. DOI: 10.1007/s10531-007-9299-7
- Holland J.M. & Luff M.L. 2000. The effects of agricultural practices on Carabidae in temperate agroecosystems. Integrated Pest Manage. Rev. 5 (2): 109–129. DOI: 10.1023/A:10096193 09424
- Hothorn T., Bretz F. & Westfall P. 2008. Simultaneous Inference in General Parametric. Biom J. 50 (3): 346–363. DOI: 10.1002/bimj.200810425
- Hůrka K. 1996. Carabidae of the Czech and Slovak Republics. Kabourek, Zlín, 566 pp. ISBN: 80-901466-2-7
- Hůrka K. 2005. Beetles of the Czech and Slovak Republics. Kabourek, Zlín, 394 pp. ISBN: 8086447111
- Kareiva P. 1990. Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B 330 (1257): 175–190. DOI: 10.1098/rstb.1990.0191
- Kawaga Y. & Maeto K. 2009. Spatial population structure of the predatory ground beetle Carabus yaconinus (Coleoptera: Carabidae) in the mixed farmland-woodland satoyama landscape of Japan. Eur. J. Entomol. 106 (3): 385–391. DOI: 10.14411/eje.2009.049
- Kennedy P.J. 1994. The distribution and movement of ground beetles in relation to set-aside arable land, pp. 439–444. DOI: 10.1007/978-94-017-0968-2\_66. In: Desender K., Dufręne M., Loreau M., Luff M.L. & Maelfait, J.P. (eds), Carabid Beetles Ecology and Evolution, Series Entomologica Vol. 51, Kluwer Academic Publisher, Dordrecht, Boston, London, 476 pp. ISBN: 978-90-481-4320-7, DOI: 10.1007/978-94-017-0968-2
- Kenward R.E. 2000. A Manual for Wildlife Radio Tagging. Academic Press 2<sup>nd</sup> ed., San Diego, 311 pp. ISBN-10: 0124042422, ISBN-13: 978-0124042421
- Kissling D.W., Pattemore D.E. & Hagen M. 2014. Challenges and prospects in the telemetry of insects. Biol. Rev. 89: 511–530. DOI: 10.1111/brv.12065
- Kotze D.J., Brandmayr P., Casale A., Dauffy-Richard E., Dekoninck W., Koivula M.J., Lövei G.L., Mossakowski D., Noordijk J., Paarmann W., Pizzolotto R., Saska P., Schwerk A., Serrano J., Szyszko J., Taboada A., Turin H., Venn S., Vermeulen R. & Zetto T. 2011. Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation, pp. 55–148. DOI: 10.3897/zookeys.100.1523. In: Kotze D.J., Assmann T., Noordijk J., Turin H. & Vermeulen R. (eds), Carabid Beetles as Bioindicators: Biogeographical, Ecological

and Environmental Studies, ZooKeys 100 (Special Issue), 573 pp. ISBN: 9789546425904

- Kromp B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agr. Ecosyst. Environ. 74 (1-3): 187–228. DOI: 10.1016/S0167-8809(99)00037-7
- Levett S. & Walls S. 2011. Tracking the elusive life of the Emperor Dragonfly Anax imperator Leach. J. Br. Dragonfly Soc. 27  $(1): 59-68.$
- Lorch P.D., Sword G.A., Gwynne D.T. & Anderson G.L. 2005. Radiotelemetry reveals differences in individual movement patterns between outbreak and non-outbreak Mormon cricket populations. Ecol. Entomol. 30 (5): 548–555. DOI: 10.1111/j.0307-6946.2005.00725.x
- Lövei G.L., Stringer I., Devine C. & Cartellieri M. 1997. Harmonic radar – a method using inexpensive tags to study invertebrate movement on land. N. Z. J. Ecol. 21 (2): 187–193.
- Lövei G.L. & Sunderland K.D. 1996. Ecology and behaviour of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. 41: 231–256. DOI: 10.1146/annurev.en.41.010196.001 311
- Luff M.L. 1978. Diel activity pattern of some field Carabidae. Ecol. Entomol. 3 (1): 53–62. DOI: 10.1111/j.1365- 2311.1978.tb00902.x
- Lys J.A. & Nentwig W. 1991. Surface activity of carabid beetles inhabiting cereal fields. Seasonal phenology and the influence of farming operations on five abundant species. Pedobiologia 35 (3): 129–138.
- Niehues F.J., Hockmann P. & Weber F. 1996. Genetics and dynamics of a Carabus auronitens metapopulation in the Westphalian lowlands (Coleoptera, Carabidae). Ann. Zool. Fenn. 33 (1): 85–96.
- Negro M., Casale A., Migliore L., Palestrini C. & Rolando A. 2008. Habitat use and movement patterns in the endangered ground beetle species, Carabus olympiae (Coleoptera: Carabidae). Eur. J. Entomol. 105 (1): 105–112. DOI: 10.14411/eje.2008.015
- Pasquet R.M.S., Peltier A., Hufford M.B., Oudin E., Saulnier J., Paul L., Knudsen J.T., Herren H.R. & Gepts P. 2008. Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. Proc. Natl. Acad. Sci. USA 105 (36): 13456–13461. DOI: 10.1073/pnas.0806040105
- QGIS Development Team 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org
- R Development Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org
- Ranius T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Popul. Ecol. 48 (3): 177–188. DOI: 10.1007/s10144-006-0262-3
- Ranjha H. & Irmler U. 2014. Movement of carabids from grassy strips to crop land in organic agriculture. J. Insect. Conserv. 18 (3): 457–467. DOI: 10.1007/s10841-014-9657-1
- Riecken U. & Raths U. 1996. Use of radio telemetry for studying dispersal and habitat use of Carabus coriaceus L. Ann. Zool. Fenn. 33 (1): 109–116.
- Riecken U. & Ries U. 1992. Untersuchung zur raumnutzung von laufkäfern (Col.: Carabidae) mittels radio-telemetrie. Methodenentwicklung und erste Freilandversuche. Z. Okol. Nat. ¨ Schutz. 1: 147–149.
- Rink M. & Sinsch U. 2007. Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. J. Zool. 272 (3): 235–243. DOI: 10.1111/j.1469-7998.2006.00282.x
- Svensson G.P., Sahlin U., Brage B. & Larsson M.C. 2011. Should I stay or should I go? Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio telemetry a case study on the threatened hermit beetle Osmoderma eremita. Biodivers. Conserv. 20 (13): 2883–2902. DOI: 10.1007/s10531-011-0150-9
- Szyszko J., Gryuntal S. & Schwerk A. 2004. Differences in locomotory activity between male and female Carabus hortensis (Coleoptera: Carabidae) in a pine forest and a beech forest in relation to feeding state. Environ. Entomol. 33: 1442–1446. DOI: doi:10.1603/0046-225X-33.5.1442
- Szyszko J., Gryuntal S. & Schwerk A. 2005. Nocturnal activity of Carabus hortensis L. (Coleoptera, Carabidae) in two forest sites studied with harmonic radar method. Pol. J. Ecol. 53 (1): 117-222.
- Thiele H.U. 1977. Carabid Beetles in their Environments. Zoophysiology and Ecology Volume 10, Springer Verlag, Berlin, 369 pp. ISBN: 978-3-642-81156-2
- Tuf I.H., Dedek P. & Veselý M. 2012. Does the diunal activity pattern of carabid beetles depend on season, ground temperature and habitat? Arch. Biol. Sci. 64 (2): 721-732. DOI: 10.2298/ABS1202721T
- Turin H., Penev L. & Casale A. (eds). 2003. The Genus Carabus L. in Europe. A Synthesis. Fauna Europaea Evertebrata No. 2, Pensoft Publisher, Sofia-Moscow-Leiden, 540 pp. ISBN: 954-642-120-0
- Wallin H. & Ekbom B.S. 1988. Movements of carabid beetles (Coleoptera, Carabidae) inhabiting cereal fields – a field tracking study. Oecologia 77 (1): 39–43. DOI: 10.1007/ BF00380922
- Watts C. & Thornburrow D. 2011. Habitat use, behavior and movement patterns of a threatened New Zealand giant weta, Deinacrida heteracantha (Anostostomatidae: Orthoptera). J. Orthoptera Res. 20 (1): 127–135. DOI: doi:10.1665/034.020.0112
- White G.C. & Garrott R.A. 1990. Analysis of Wildlife Radiotracking Data. Academic Press, San Diego, 383 pp. ISBN: 978-0-12-746725-2
- Wikelski M., Moskowitz D., Adelman J.S., Cochran J., Wilcove D.S. & May M.L. 2006. Simple rules guide dragonfly migration. Biol. Lett. 2 (3): 325–329. DOI: 10.1098/rsbl.2006.0487
- Zlatník A. 1976. Přehled skupin typů geobiocénů původně lesních a křovinných ČSSR. Zprávy Geografického ústavu ČSAV, Brno 13 (3/4): 55–64.

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