

**MINI REVIEW**

# Beetles on the move: Not-just-a-technical review of beetles' radio-tracking

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**Abstract**

Radio telemetry with very high-frequency transmitters is a powerful tool for studying the movement patterns of animals. Although this tracking technology is widely utilized for various vertebrates, its application is limited to only a fraction of large-bodied insect species. Among them, beetles are the most popular insect group used for radio-tracking due to their relatively large body size, solid exoskeleton, and to some extent the well-known ecological background of some species. Here, we review the available literature about radio telemetry applied to beetles, focusing on current methodological advantages and constraints to record their movement, as well as how this method can assist in understanding various ecological aspects of beetle life history. Regardless of the huge potential of radio-tracking, the number of tracked beetle species is still very low, covering so far only 13 species belonging to five families that were studied almost exclusively in the Western Palearctic region. Most studies were descriptive, measuring simple trajectory parameters and examining movement behavior as a single strategy that is not triggered by any particular internal or external cues. Ecological aspects have been accessed to a lesser extent, especially in relation to the effects of abiotic factors and habitat use. There are still conceptual knowledge gaps: promising statistical approaches for movement analyses can connect movement patterns with specific habitat utilization but they are not yet used by entomologists. Moreover, knowing the movement patterns of many individuals and species can assist us to understand the composition and dynamics at the community level.

**KEYWORDS**

Coleoptera, ecological application, habitat utilization, high-frequency transmitters, model group, movement, movement patterns, radio telemetry, radio-tracking, statistical approaches, tagging, VHF telemetry

**INTRODUCTION**

Animal movement is a fundamental driver of the structure and dynamics of populations, communities, and ecosystems and, in addition, provides essential insights into the life of individuals (Holyoak et al., 2008; Nathan et al., 2008; Kays et al., 2015). Understanding complex movement patterns on how, where, and when individuals move within and between habitats is therefore one of the most important tasks in ecology, especially in the light of current global changes (Bowler & Benton, 2005; Ewers & Didham, 2006; Nathan et al., 2008). As a consequence,

movement ecology is a rapidly developing research area with a growing amount of literature (Holyoak et al., 2008). Despite the increasing number of publications, only 11% of those focus on insects (Holyoak et al., 2008), even though these represent the vast majority of animal biodiversity and significantly contribute to ecosystem services (Mora et al., 2011; Prather et al., 2013). The movement patterns of many insect species, especially at the individual and fine-scale levels, remain unknown due to methodological constraints and the complexity of data collection (Holyoak et al., 2008; Kissling, 2015; Kral-O'Brien & Harmon, 2021).

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Over the last decades, various bio-logging techniques have emerged to record animal movement at different spatial scales, from local fine-scale movements to long-distance migration across the globe (Holyoak et al., 2008; Wilmers et al., 2015; Knight et al., 2019). However, the implementation of animal-borne bio-loggers on insects and other small invertebrates is limited due to the weight and size constraints of the devices used (Kissling et al., 2014). Moreover, entomologists especially focus on insect movement on very fine spatial scales, i.e., within and between small habitat patches, to describe species-specific habitat or even microhabitat utilization and quantify dispersal ability (Kissling et al., 2014; Kays et al., 2015). To record these fine-scale movement patterns, radio telemetry seems to be an optimal solution as technological developments in the last 3 decades have produced small and light-weight transmitters (tags) suitable for tracking large insects under natural conditions (Kissling et al., 2014; the first utilization on insects was in 1988 on dobsonfly larva, see Hayashi & Nakane, 1988). Radio telemetry involves three primary components: active transmitters, an antenna system, and a receiver device (White & Garrott, 1990; Kenward, 2000). The transmitter is attached to the animal and consists of a transmitting unit, a power source (usually a battery), and an antenna. The tag emits a radio signal at a specific, very high frequency (VHF), which is unique for each tag. The signal is detected by an antenna system and processed by a receiver unit. The receiver with an antenna system, such as multiple parallel elements compiled in a line (Yagi) or a short dipole antenna, is hand-held to determine the location of the tag based on the signal strength. Although the field tracking of insects is still dominated by manually operated devices (Kissling, 2015), the recently developed automated radio telemetry systems have the potential to remotely track large insects equipped with VHF transmitters (Fisher et al., 2020a; see also Lee et al., 2021 for a new tracking system based on sun-powered tags for long-distance migration of butterflies).

The comparison of active (i.e., battery-powered) radio telemetry with passive telemetric approaches that can be used in entomology, such as harmonic radar and radio frequency identification technology (RFID), was reviewed in Kissling et al. (2014). However, a comparative interspecific review for one insect group does not exist so far due to the small number of radio-tracking studies available for a particular taxon. There is only one article on true bugs (Hamer et al., 2018) and there are a few on butterflies (Liégeois et al., 2016; Knight et al., 2019; Wang et al., 2019; Fisher et al., 2020b). Hitherto, beetles are the most popular insect taxon in radio telemetry, comprising a relatively high amount of the existing literature. Their large body size together with their solid exoskeleton makes some beetle species ideal candidates for carrying transmitters. In addition, the solid ecological background of some taxa of Coleoptera allows a better ecological interpretation of movement studies, which can improve the credibility of these initiatives.

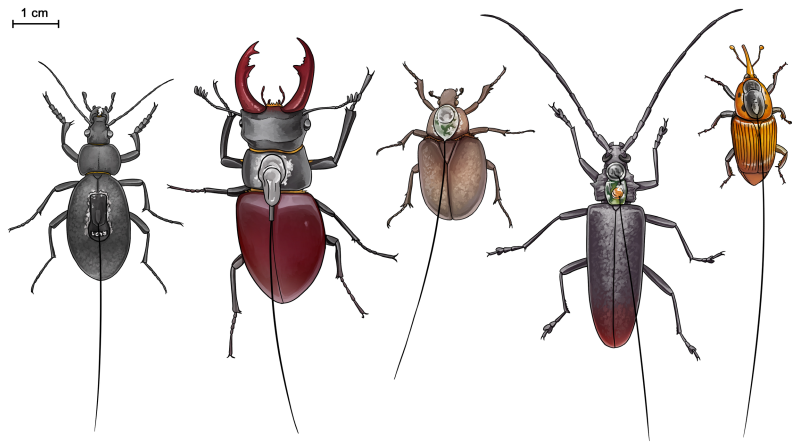
Attaching sophisticated and expensive equipment to an individual does not automatically guarantee that valuable biological information will be obtained. Therefore, our aim in this review is to first identify the major technical advances and constraints in tracking beetles with VHF transmitters. We highlight the methodological shortcomings and point out how to avoid them in future radio-tracking projects. Second, we focus on the ecological motivations of radio-tracking studies and describe the main topics of interest that include dispersal, abiotic factors affecting movement activity, and habitat use. Finally, we explore and assess the current knowledge gaps and suggest future research directions in the radio telemetry of beetles. Thus, our review may act as a 'cookbook' on how to track various beetle species in the field.

## LITERATURE DATABASE COMPILATION

This historic review is based on a reproducible literature search in the 'Web of Science Core collection' database (conducted on 15 September 2021). We used the keywords *radio telemetry* and *radio-track\** with a combination of *insect\** and *beetle\** keywords with no time limit for the date of publication. This search gave us 296 articles; their titles and abstracts were scanned for relevance. We selected those papers where radio telemetry with active VHF transmitters was implemented to study beetles. In the relevant articles found, we manually checked the reference list for additional publications. Other telemetry methods, such as RFID and harmonic radar, and other insect groups were excluded because Kissling et al. (2014) provided a recent review of these techniques. From the selected papers, we extracted information about the species, the number of tracked individuals, tag parameters (weight, battery life, and antenna length), individual body mass, duration of tracking, type of movement (ground-dwelling or flying), daily movement (mean distance covered per day), and the major motivation of the study.

## SELECTION OF BEETLE SPECIES

In total, 31 case studies involving radio-tracking conducted on 13 beetle species in five families (Figure 1, summarized in Table 1) were identified: six species of ground beetles (Carabidae), four of dung beetles (Scarabaeidae), one stag beetle [*Lucanus cervus* (L.), Lucanidae], one longhorn beetle (*Cerambyx cerdo* L., Cerambycidae), and a weevil [*Rhynchophorus ferrugineus* (Olivier), Curculionidae]. The most commonly radio-tracked species were *L. cervus* (seven publications) and *Osmoderma eremita* Motschulsky (six publications). Overall, the species selection was represented by large-bodied, flagship species with a solid conservation potential (e.g., Natura 2000, species protected by local authorities) or pests. In the case of carabids, some common and relatively



**FIGURE 1** Examples of radio-tracked beetles from different families, from left to right *Carabus coriaceus* (Elek et al., 2021), *Lucanus cervus* (Tini et al., 2017a), *Osmoderma eremita* (Hedin & Ranius, 2002), *Cerambix cerdo* (Drag & Čížek, 2018), and *Rhynchophorus ferrugineus* (Hamidi et al., 2017)

abundant species (e.g., *Carabus nemoralis* OF Müller or *Carabus ullrichii* Germar) were tracked. With a few exceptions (Beaudoin-Ollivier et al., 2003; Moore et al., 2017; Al Ansi et al., 2020), study sites were restricted to the Western Palearctic region. The number of tracked individuals varied between four (Růžičková & Veselý, 2016) and 74 (Hedin & Ranius, 2002) with a mean ( $\pm$  SD) of 27.5 ( $\pm$  20.6) individuals per study. If the type of movement is considered, the mean number of tracked individuals was 15.1 ( $\pm$  10.2) in ground-dwelling species and 36.0 ( $\pm$  20.7) in flying beetles.

## RADIO TELEMETRY AS A TOOL FOR STUDYING BEETLE MOVEMENT

### Impact of transmitter mass and shape on beetles

The transmitter's weight has decreased in the last 25 years (Figure 2). In 1996, a study on the ground beetle *Carabus coriaceus* L. used transmitters weighing between 0.6 and 0.7 g (Riecken & Raths, 1996), whereas today the frequently used tags weigh about 0.3 g or even less (McCullough, 2013; Hamidi et al., 2017). The most important limiting factor for further tag miniaturization is the energy source, i.e., a battery, which is the heaviest part of any transmitter. Smaller batteries mean lighter tags but this also shortens battery life (to a couple of days). Currently (i.e., accessed 12 January 2022), the lightest commercially produced transmitter weighs 0.13 g (model NanoPin, 11 × 3 × 3 mm; Lotek Wireless, Newmarket, ON, Canada), 0.15 g (T15, 11 × 3.4 mm; Advanced Telemetry Systems, Isanti, MN, USA), or 0.27 g (LB-2X, 8 × 4 × 2.8 mm; Holohil Systems, Carp, ON, Canada). The ATS model has a prolonged battery life span (11–22 days) but it has not yet been used for research purposes. Taking into account all these structural features, size and weight constraints still limit the feasibility of radio telemetry in entomological studies, as only few beetle species are large enough to carry the transmitters.

Tags are directly glued on the cuticle of the beetles. For attachment, cyanoacrylate glue in gel or liquid (e.g., Rink &

Sinsch, 2007; Negro et al., 2008; Tini et al., 2017b), silicone (Riecken & Raths, 1996), or hot-melt adhesives (McCullough, 2013; Moore et al., 2017) were used. In ground-dwelling apterous beetles (some carabids), transmitters were mounted on the top of elytra. In the case of macropterous species, the pronotum was used for tag fixation in order not to restrict flying (Figure 1). Before attachment, beetles' body temperature could be reduced in a refrigerator (Rink & Sinsch, 2007) or CO<sub>2</sub> was used as an anesthetic agent (Riecken & Raths, 1996).

The transmitter's weight may impact beetle behavior. In contrast to vertebrates (Kenward, 2000), there is no radio-tracking '5% rule' in insects, i.e., the tag mass should not exceed 5% of the body mass of the tracked individual. Observed load ranged from 2% (McCullough, 2013) to 30% (Chiari et al., 2013) in flying species, and from 14% (Elek et al., 2021) to 70% (Deichsel, 2007a) in ground-dwelling species. The lower load in flying species is in accordance with findings by Boiteau & Colpitts (2001), that a load exceeding 33% restricted the flying ability. Although the need to quantify the effects of transmitters on beetles is clear, relevant experiments are rare (Batsleer et al., 2020). In the available literature, the assessment of the tag impact is often not provided or just minimally justified; usually based on simple subjective evaluation of tracked individuals. For instance, some authors reported that radio-tracking likely did not substantially disturb the behavior because some of the tracked individuals were observed walking, flying (Hedin & Ranius, 2002; Drag & Čížek, 2018), mating with untagged partners (Negro et al., 2008), or feeding on earthworms (Růžičková & Veselý, 2016). In the reviewed studies, the load (tag/body mass ratio) does not seem to be the limiting factor for dispersal ability either by walking or flight (Figure 3). However, tag presence may significantly change the proportion of behavioral patterns of tagged individuals – see a case study in Batsleer et al. (2020); although the experiment was conducted on a digger wasp species, a similar impact of tags may occur in beetles, or see Kaláb et al. (2021) for a study on crickets. The origin of beetles also should be considered as a potential bias because laboratory-reared individuals can be more sedentary than wild-type ones (Al Ansi et al., 2020). Hamidi et al. (2017) reported that only 11%

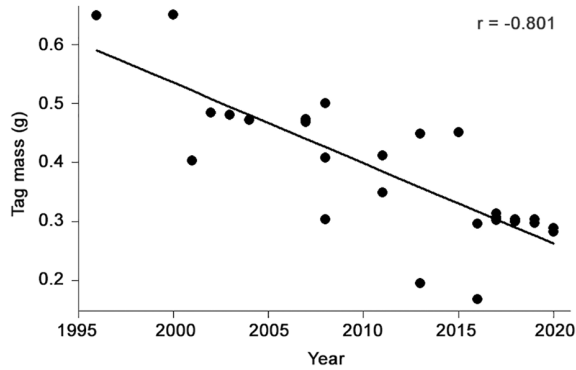
**TABLE 1** Summary of case studies (n = 31) using radio telemetry in beetles. Species are first grouped based on their dispersal power, then in alphabetical order. The load is a tag/body mass ratio. Study focus implies the categories 'dispersal' representing simple measurements of covered distances, 'habitat use' including various external factors (e.g., time of day, temperature, habitat type, treatment) affecting individual movement in studied habitat(s), and 'methodology' focusing on methodological aspects of radio telemetry, such as the feasibility of this approach for a particular species, exploring the effects of transmitters on movement behavior or recording fine-scale movement

Dispersal type	Species	Tag mass (g)	Load (%)	No. tracked individuals <sup>a</sup>	Study focus	Reference	
Ground-dwelling	<i>Carabus coriaceus</i>	0.29	14.0	6 (3 M, 3 F)	Habitat use	Elek et al., 2021	
					Habitat use/ methodology	Růžicková et al., 2021	
					Methodology	Růžicková & Elek, 2021	
			0.65	NA	22 (14 M, 8 F)	Dispersal/habitat use	Riecken & Raths, 2000
				35.0–50.0	18 (12 M, 6 F)	Dispersal/habitat use	Riecken & Raths, 1996
		<i>Carabus hungaricus</i>	0.3	34.5–49.2	10 (5 M, 5 F)	Dispersal/habitat use	Bérces & Růžicková, 2019
		<i>Carabus monilis</i>	0.45	NA	6 (4 M, 2 F)	Dispersal/habitat use	Riecken & Raths, 2000
		<i>Carabus nemoralis</i>	0.47	70.0	11 F	Dispersal	Deichsel, 2007a
					24 F	Methodology	Deichsel, 2007b
		<i>Carabus olympiae</i>	0.3	40.0	41 (23 M, 18 F)	Habitat use	Negro et al., 2017
					21 (13 M, 8 F)	Habitat use	Negro et al., 2008
		<i>Carabus ullrichii</i>	0.3	27.0–33.0	21 (10 M, 11 F)	Dispersal/habitat use	Růžicková & Veselý, 2018
				20.9–30.4	4 (1 M, 3 F)	Methodology/ dispersal	Růžicková & Veselý, 2016
	Flying	<i>Cerambix cerdo</i>	0.3	8.0–14.0	26 (15 M, 11 F)	Dispersal	Drag & Čížek, 2018
<i>Lucanus cervus</i>		0.3	8.0–23.0	12 F	Dispersal/habitat use	Thomaes et al., 2018	
		0.31	16.0–22.0	55 (34 M, 21 F)	Dispersal/habitat use	Tini et al., 2017a	
			NA	55 (34 M, 21 F)	Habitat use	Tini et al., 2017b	
			7.6–17.2	12 F	Habitat use	Tini et al., 2017c	
		0.35	7.1–20.8	56 (18 M, 38 F)	Dispersal/habitat use	Rink & Sinsch, 2011	
					Dispersal	Rink & Sinsch, 2007	
		0.4	12.1–21.0	8 (4 M, 4 F)	Dispersal/habitat use	Sprecher-Uebersax & Durrer, 2001	
<i>Oryctes rhinoceros</i>		0.3	8.5–17.8	33	Habitat use	Moore et al., 2017	
<i>Osmoderma eremita</i>		0.45	22.5	41 (20 M, 21 F)	Habitat use	Le Gouar et al., 2015	
				20.3–29.6	39 (15 M, 23 F)	Dispersal	Chiari et al., 2013
		0.41	14.0–29.0	50 F	Dispersal	Svensson et al., 2011	
		0.5	20.0–25.0	65 (39 M, 26 F)	Dispersal	Hedin et al., 2008	
		0.41	15.0–25.0	5 (3 M, 2 F)	Dispersal	Dubois & Vignon, 2008	
		0.48	20.0–25.0	74 (40 M, 34 F)	Methodology/ dispersal	Hedin & Ranius, 2002	
<i>Rhynchophorus ferrugineus</i>		0.17	20.2	42 (20 M, 22 F)	Methodology	Hamidi et al., 2017	
		0.28	18.9–19.2	24 (12 M, 12 F)	Methodology/ dispersal	Al Ansi et al., 2020	
<i>Scapanes australis</i>	0.48	5.0–7.0	11 (3 M, 8 F)	Dispersal/habitat use	Beaudoin-Ollivier et al., 2003		
<i>Trypoxylus dichotomus</i>	0.2	2.0–4.0	20 (15 M, 5 F)	Dispersal	McCullough, 2013		

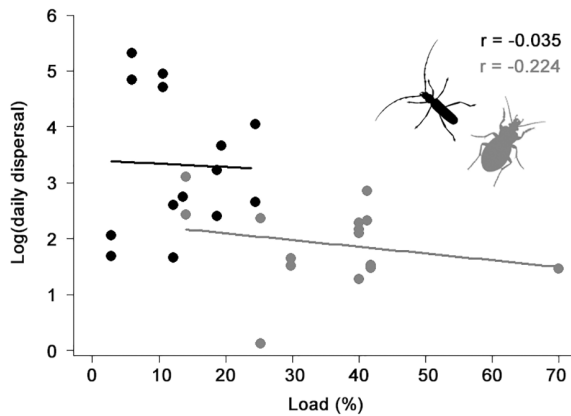
<sup>a</sup>M, male; F, female.

of tagged individuals flew normally under laboratory conditions and in the experiment of Al Ansi et al. (2020), the laboratory-reared specimens with attached tags did not fly

at all. Similarly, walking speed might be affected and individual responses can be either positive (i.e., hyperactivity) or negative and species-specific (Boiteau et al., 2010).



**FIGURE 2** Pearson correlation between the mass (g) of transmitters used and the year of publication



**FIGURE 3** Relationship between daily dispersal (m) on a log scale and load (tag/body mass ratio, %) in flying (black) and ground-dwelling beetles (gray). The dispersal and load data were collected from studies listed in Table 1. 'r' indicates Pearson correlation coefficients

In addition, some authors mentioned that only the largest and heaviest specimens were equipped with radio transmitters due to load reasons and sometimes only (the bigger) females were tracked (Deichsel, 2007a, b; Svensson et al., 2011; Tini et al., 2017c; Thomaes et al., 2018). Due to the dorsal position of the tag, transmitters not only change the individual body mass but also slightly alter the body shape and the center of gravity. We only found one study (Deichsel, 2007b) that examined how this altered body shape changed movement over various obstacles. The author found that tagged beetles had less tortuous trajectories than untagged ones and rested more. There is a rich literature on how tags influence energy balance (e.g., Barron et al., 2010; Wilson et al., 2021) or mortality (e.g., Rasiulis et al., 2014) in vertebrates; similar studies are urgently needed for beetles and other invertebrates.

### Localization and sampling intervals

In the field, tagged individuals have always been followed by researchers – but see the potential for automation in Fisher et al. (2020a) and Lee et al. (2021) – that may be

time-consuming because a tracking session can take several hours (Riecken & Raths, 1996; Hedin & Ranius, 2002; Tini et al., 2017c). Usually, so-called homing is implemented for localization (White & Garrott, 1990). It is based on tracking whereby the searching starts at the point (fix) where a tagged individual was found during a previous tracking session. The signal intensity guides the researcher to get as close as possible to the tagged individual and its location is recorded (with or without seeing it). Getting too close may be disruptive and, in ground-dwelling beetles, there is a trampling risk that may harm the targeted individual. Depending on the objectives of the study, the number of tracking sessions per day can vary from one (Negro et al., 2017; Drag & Čížek, 2018; Thomaes et al., 2018) to eight (Růžičková & Veselý, 2016, 2018), or the tracking can be conducted every hour in different time shifts to cover all parts of the day (Chiari et al., 2013; Tini et al., 2017a,b,c). For long-distance movement, tracking once per day seems to be enough to get sufficient data for dispersal estimations, but for the assessment of circadian activity or the effect of abiotic factors (temperature, humidity) on movement patterns, it is important to track beetles as frequently as possible. Moreover, maintaining a regular time schedule between tracking sessions is important for detailed trajectory analyses (Elek et al., 2021).

### Signal loss

A robust source of the signal and a good spreading medium are the two major parameters for good signal quality and detection. In the first case, the battery life and the antenna length are key for having a strong signal. In the studies found, the tag antenna (of different lengths) was always directed backward. A longer antenna means a stronger signal and a larger detection range. A tag with a 25-mm-long antenna could be detected up to 60 m (Růžičková & Veselý, 2016), whereas a 100-mm-long antenna had a detection range of approximately 300 m (Rink & Sinsch, 2007). However, the long and soft antenna wire cannot only hamper the movement of the tracked individual but can also be damaged. Burrowing behavior, especially, can cause the antenna to break at multiple points resulting in reduced signal quality (Hamidi et al., 2017; Thomaes et al., 2018). For instance, if the 150-mm-long antenna is reduced to half, the signal range is reduced by more than 75% (Hamidi et al., 2017).

The signal detection may be interfered with by bad weather conditions, especially heavy rains, when the signal is reflected several times from wet surfaces (vegetation) and localization may become almost impossible (Riecken & Raths, 1996). Contact with the individual may be lost completely. In addition, the transmitter may be lost due to digging activity of beetles (Thomaes et al., 2018) or high water/high moisture levels may reduce the quality of the used adhesive material. The signal may also be weakened due to battery problems. For instance, Hedin & Ranius (2002)

reported that they lost 71% of females and 20% of males of *O. eremita* before reaching the end of the nominal lifetime of batteries due to technical issues or water damage. Deichsel (2007a) was unable to recover five out of 11 individuals of *C. nemoralis*, presumably due to tag malfunction or predation. Al Ansi et al. (2020) lost >66% of tagged individuals due to predation. Dispersal could also create difficulties: Moore et al. (2017) lost 42% of *Oryctes rhinoceros* (L.) individuals immediately after release because they flew beyond the detection range.

## Movement data for analyses

The trajectory made by the tracked individual is usually recorded as a sequence of discrete movement steps that are characterized by two parameters: step length (distance) and turning angle (bearing; Turchin et al., 1991). The exact coordinates of each movement step are mostly recorded manually by various global positioning system (GPS) devices after the localization of the tracked beetle. Although this is a very convenient method, the positional imprecision of GPS devices adds a measurement error to the obtained geocoordinates. The magnitude of this error is affected by several factors including atmospheric interference, topography, canopy cover, or the device itself (Frair et al., 2010; Ranacher et al., 2016). Today's commercially available GPS loggers are extremely accurate at a landscape scale with a precision of approximately 3 m under normal weather conditions (Ranacher et al., 2016). In large-bodied vertebrates, the problems associated with GPS inaccuracy are less important because they move on spatial scales from hundreds to thousands of meters and on a temporal scale, from weeks to years (Frair et al., 2010). However, at smaller spatio-temporal scales (ground-dwelling carabids may move only 50 cm; Riecken & Raths, 1996; Růžičková & Veselý, 2018) and limited battery life of VHF transmitters, even a small degree of GPS imprecision may create a serious bias distorting trajectory shapes (Růžičková & Elek, 2021) and potentially completely mask the biological signal in movement data through erroneous model parameterization (Jerde & Visscher, 2005; Bradshaw et al., 2007). For instance, the measurement error of GPS in fine-scale movements of ground-dwelling beetles was 1.878 m for distance and 31.330° for bearings in the open area under sunny weather (Růžičková & Elek, 2021). Moreover, bearings were significantly more sensitive to measurement errors at short distances. Under dense canopy and rainy weather, the measurement error increased. The alternative recording approach of distance-bearing (also called coordinate geometry) seems to be more appropriate for recording fine-scale beetle movements (Růžičková & Elek, 2021). In the distance-bearing, the coordinates of the target location are obtained from the previously known position using directly measured distance and compass azimuth (Turchin et al., 1991).

## The cost of radio-tracking

Radio telemetry is not the cheapest method for tracking, due to the cost of the equipment. This issue rules out researchers with small budgets, including those from low-income countries (Hebblewhite & Haydon, 2010; Weaver et al., 2021). In some cases, researchers can compromise by using a few tracking devices with a risk of reduced data quantity and subsequent problems with publishing. This obstacle can be partially overcome by using relatively low-budget methods, such as direct observation (Drees et al., 2008; Cerda et al., 2015), capture-mark-recapture (Kagawa & Maeto, 2009; Svensson et al., 2011), or fluorescent powder applied on the ground (Perry et al., 2021). Unfortunately, these approaches have considerable limitations for obtaining detailed movement data suitable for trajectory analyses.

## ECOLOGICAL ASPECTS OF RADIO-TRACKING STUDIES ON BEETLES

The movement path is a result of dynamic interaction between components related to a focal individual as well as the surrounding environment (Holyoak et al., 2008; Nathan et al., 2008; Costa-Pereira et al., 2022). These components include the internal state of the individual (e.g., reproductive status, survival), its navigation ability, motion capacity, and external factors affecting movements, such as landscape, weather, resource distribution, and presence of competitors or predators. Although they can profoundly influence movement patterns, they are usually not considered in radio telemetric studies. This is an overall concern in insect radio-tracking research (Holyoak et al., 2008). Case studies conducted on various species often suffer from being purely descriptive, measuring simple movement parameters and examining movement behavior as a single strategy that is not triggered by any certain internal or external cues, thus opposing the principle of the movement framework described above (Holyoak et al., 2008). As we show below, this issue can also occur in beetle movement research.

## Trajectories, distances, and dispersal

The movement (dispersal) capacity of a radio-tracked individual is directly measured by covered distances per time unit. The covered distance is the simplest descriptor reported, also showing differences between sexes (e.g., Chiari et al., 2013; Růžičková & Veselý, 2018) or age classes (Tini et al., 2017a). Especially for saproxylic beetles associated with the occurrence of dead wood, it is important to correctly estimate such distances, because this will indicate the probability of successful dispersal between suitable habitat patches in fragmented landscapes. This, in turn, can guide management, and define the recommended

position of 'stepping stones' for conservation purposes (e.g., Hedin & Ranius, 2002; Hedin et al., 2008; Rink & Sinsch, 2011). Comparison of the dispersal ability between populations of the same species across its distribution range can be feasible for protected species such as the stag beetle *L. cervus* (e.g., Rink & Sinsch, 2007; Tini et al., 2017a; Thomaes et al., 2018). A sufficient number of recorded locations (ideally, >10 per individual; Turchin et al., 1991) can provide home range estimates based on minimum convex polygon or kernel density estimations (Tini et al., 2017a). Another option is to map the trajectory, visually evaluate its shape and measure the covered total distance and net displacement, i.e., the direct distance between the first and last recorded positions. The latter characteristic can also be considered as an effective distance as it clearly shows how far a radio-tracked individual can disperse from the point of release. Nevertheless, trajectories can be evaluated in a more sophisticated way by connecting movement parameters with habitat utilization at the individual level. There has been a progressive development in the analysis of animal movement in the last decade (Joo et al., 2020), e.g., in state-switching modeling (McClintock et al., 2020), although not yet used by entomologists (but see Elek et al., 2021). Hidden Markov models (HMM) have recently gained prominence in ecology, especially in interpreting animal movement patterns (McClintock et al., 2020). As movement is driven by underlying behavioral decisions, HMMs can sufficiently capture correlation structure in regular movement data and decompose it into distinct movement states to identify behavioral patterns during foraging or dispersal (Michelot et al., 2016). As a working example of the utilization of these tools, we applied hidden Markov models to segment the movement trajectories of a ground-dwelling beetle into two distinct activity stages: random walk and directed movement (Box 1).

## Abiotic factors and habitat use

The effect of various abiotic characteristics on beetle movement is not particularly surprising as beetles are ectotherms. Detailed descriptions of species-specific responses to particular factors are, however, still limited to a few species. Time of day (Negro et al., 2008; McCullough, 2013) and air and ground temperature (Tini et al., 2017b; Růžičková & Veselý, 2018) are the most common factors considered. They are followed by air humidity (Tini et al., 2017b; Bérces & Růžičková, 2019), which can be negatively correlated with the temperature (Elek et al., 2021). The assessment of habitat use is one of the most important aims of radio telemetry studies due to its importance for conservation and management (Kissling et al., 2014). Shapes of trajectories including its length and tortuosity can well describe habitat utilization. The spatial and temporal scales of movement can differ from short steps with frequent turns of ground-dwelling beetles within a habitat (Bérces & Růžičková, 2019) to long-distance dispersal between habitats exceeding a

few kilometers (Drag & Čížek, 2018). Some papers focused on movement in different habitats (i.e., meadow vs. forest) to describe preferred sites (Riecken & Raths, 1996; Negro et al., 2008) or even microsites (microhabitats) within a habitat mosaic (Negro et al., 2017; Bérces & Růžičková, 2019). Radio-tracking can be useful in identifying oviposition sites (Hedin et al., 2008; Tini et al., 2017c) or localization of scattered resources, such as hollow logs for breeding or sap runs for feeding (Chiari et al., 2013; Thomaes et al., 2018). Most of the studies were conducted in undisturbed natural or semi-natural habitats. Only one study considered roads as possible barriers for dispersal (Deichsel, 2007a), and two others studied forestry treatments and their direct impact on individual movement patterns of ground-dwelling species (Negro et al., 2017; Elek et al., 2021). Radio-tracking also clarified movement patterns of the red palm weevil between palm trees to identify their cryptic breeding and aggregation sites (Beaudoin-Ollivier et al., 2003; Moore et al., 2017; Al Ansi et al., 2020).

## Animal movement may predict dynamics in community structure

Movement data can be useful for the estimation of survival rates, population sizes, or dynamics (Kenward, 2000; Le Gouar et al., 2015). As radio telemetry is gradually becoming available for smaller species, changes in model assumptions might be necessary. Nathan et al. (2008) claimed that progressive technological development might be responsible for the shift from movement analyses based on population redistribution (so-called Eulerian approach) to individual path characteristics (Lagrangian approach; Duchesne et al., 2015). These current trends in movement ecology trigger improvements in analytical techniques (Nathan et al., 2008; Duchesne et al., 2015). Although numerous analytical techniques are available to evaluate internal and external factors shaping movement patterns, only a few of these have standardized and rigorous protocols (Duchesne et al., 2015; McClintock et al., 2020). Studies of the movement of beetles can be suitable for testing whether individual movement parameters of different species can help to understand interspecific and intraspecific interactions in structuring communities and their dynamics (Grüm, 1971a,b; Costa-Pereira et al., 2022). The species composition, richness, and abundance (often referred to as activity-density in ground-dwelling arthropods) are frequently used characteristics of insect/beetle communities. The activity-density is defined as the number of individuals that actively moved and were caught by a pitfall trap (Kotze et al., 2011). This definition gave a behavioral aspect to the interpretation as the activity of the individuals is positively correlated with the number of catches, suggesting a sort of habitat preference. Although this assumption seems logical at first sight, there are several cases when it may be limited due to the demographic structure of the local population, species-specific movement activity, or

### BOX 1 Assessing habitat use of a ground beetle by hidden Markov models (HMMs)

This is a working example of fitting HMMs on the movement dynamics of the ground-dwelling carabid *Carabus ullrichii* and the consequent assessment of its habitat use. Already Baars (1979) tracked carabid beetles marked by radioactive paint in the field and described their two typical movement patterns: *directed movement* is characterized by long steps and small turning angles and can be considered as dispersal or migration from adverse sites, and *random walk* is associated with short steps and more turns and it is a proxy for foraging. Although these distinct movement states were already known for carabids, they were considered by visual evaluation without any rigorous quantitative approach (Baars, 1979; Riecken & Raths, 1996).

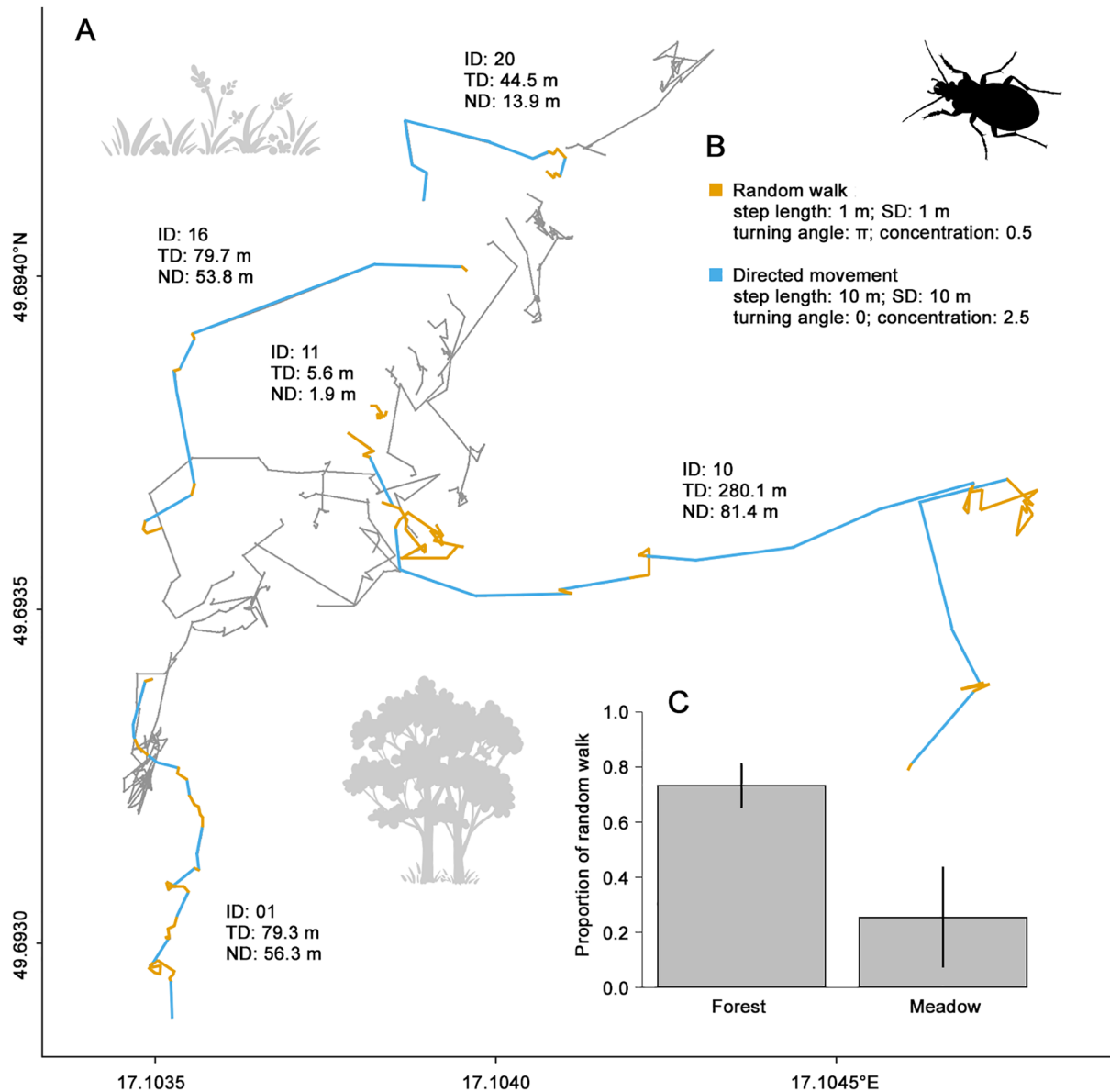
The model species, *C. ullrichii* is a relatively large and common ground beetle occurring in various habitats from deciduous forests to arable fields of Central Europe. The original study (Růžičková & Veselý, 2018) assessed the effect of abiotic variables, such as temperature, light conditions, or humidity on species' movement activity at the abrupt meadow-forest edge in a floodplain of the Morava River in the Czech Republic (49.6955°N, 17.1054°E). Originally, the beetles' trajectory profiles were, similar to the above studies, inspected only visually. For purposes of this working example, we used only trajectory data: longitude and latitude coordinates of all recorded fixes of 21 individuals (10 males, 11 females) equipped by PipoPip transmitters (0.3 g, 13 × 5 × 3 mm; Biotrack, Wareham, UK). Beetles were released at the forest-meadow transitions and radio-tracked over a period of 2 weeks or until the signal was lost. For each fix, the habitat type (forest or meadow) was also recorded.

Among HMM packages available in R, we used the *fitHMM* function from the 'moveHMM' package (Michelot et al., 2016). We used so-called complete pooling where all individuals share the same movement model in terms of parameterization. Although there was high individual heterogeneity in movement activity regardless of sex that likely emerged from the individual fitness (Figure B1 A; Pohle et al., 2017), the HMM still can provide optimal trajectory segmenting by the Viterbi algorithm (McClintock et al., 2020). The initial parameters for step length and turning angles are defined in Figure B1 B. Zero inflation was specified as 0.5 for both movement states. After fitting HMM, all segmented trajectories were plotted as a trajectory map, where each fix was colored according to a particular movement state to check optimal decoding. Then, the random walks and directed movements were counted for each trajectory and the effect of habitat type on the proportion of random walk was tested by a generalized linear mixed model with binomial distribution and logit link function (*glmer* function from the 'lme4' package; Bates et al., 2015). The results clearly showed that the proportion of random walk was higher in the forest than in the meadow ( $\chi^2 = 18.705$ , d.f. = 1,  $P < 0.001$ ; Figure B1 C), suggesting that meadows are less suitable habitats for *C. ullrichii* than forests, and that beetles used meadows only temporally. As this species occurs in a variety of habitats, from arable fields, meadows, orchards, to deciduous forests (Turin et al., 2003), these results may help to understand real habitat utilization of the species and its persistence in fragmented landscapes in terms of the selection of foraging and breeding sites.

It may occur that recorded trajectories resemble patterns of so-called Lévy walks that are characterized by clusters of multiple short steps and long travels between them (Bartumeus et al., 2005). Some authors consider Lévy walks as an efficient searching strategy when prey is randomly and sparsely distributed across the unknown space (see a review of Reynolds, 2018). Lévy walks are discrete and scale-invariant, creating fractal patterns with no characteristic scale (Bartumeus et al., 2005). In our case study, trajectories are discrete due to the sampling design; we do not know what happened between tracking sessions. In addition, locations were recorded only on one – rather small – spatial scale. Radio-tracked beetles also showed periods of inactivity that could last several tracking sessions. Therefore, these clues prompted us to conclude that the recorded trajectories cannot underline the presence of Lévy walks in ground beetles.

individual trajectory profiles (Grüm, 1971a,b; Matalin & Makarov, 2011; Růžičková et al., 2021). Grüm (1971a,b) suggested that the differences in movement activity between individuals are based on their physiological condition (chances of food intake) and population density. The rate of metabolism can be linked to population density, thus the movement probability will be higher in dense populations due to density-dependent movement behavior. This increased mobility will be manifested in the increased rate of metabolism. Grüm (1971b) revealed that the directional

movement between habitat patches may be compensation for the dissimilarities in energy balance between individuals in habitat mosaics. Moreover, an increased rate of mobility may lead to an increased rate of predation pressure (Grüm, 1971b; Elek et al., 2021), which reduces the population density and may affect individual behavior (Riecken & Raths, 1996). Thus, the observed predator avoidance behavior had an effect on the daily rhythm of the movement activity (Elek et al., 2021), as well as population density in habitat patches. All these clues suggest that the individual



**FIGURE B1** (A) Trajectory profiles of 21 radio-tracked specimens of *Carabus ullrichii* at meadow-forest transition. Beetles were released in a line, ca. 5 m apart on the abrupt meadow-forest transition and tracked every 3 h for 16 days or until signal loss (Růžičková & Veselý, 2018). Here, the meadow is on the left, the forest is on the right. (B) A two-state hidden Markov model (HMM) was fitted with the specified initial parameters for random walk and directed movement. For a better visibility, only five segmented trajectories are highlighted, the others are in grey. ID, individual number; TD, total distance (m); ND, net displacement (m), i.e., shortest distance between first and last recorded locations. (C) Mean (+ 95% confidence intervals) proportion of random walk in the two habitats

perspective may be a manifestation of physiological factors and the current state of the surrounding (micro)environment. Thus, these complex interactions of animals with their environment may manifest themselves in complex movement patterns, suggesting that the individual responses reflect a spectrum of decisions (Okuzaki, 2021).

## CONCLUSIONS

In this review, we showed that radio telemetry can be a powerful tool for studying various aspects of beetles' movement behavior and their interactions with the environment.

Although there are many relatively large species of beetles across the globe that can carry transmitters, the number of tracked species is very low and research has been restricted almost exclusively to the Western Palearctic region. The ongoing miniaturization of tags will open new opportunities to track smaller species. However, the costs of the equipment are currently one of the major obstacles to a wider application of this method in the field of insect ecology (Weaver et al., 2021).

New statistical approaches for trajectory segmenting can rigorously connect movement parameters with individual- and species-specific habitat use in a more sophisticated way than ever before. These tools can help to understand the link between movement paths and infer

behavioral responses to habitat, such as defining preferences or avoidance of particular habitat patches. In some cases, radio-tracking is potentially biased for technical reasons, such as tag weight, antenna length, and others. We recommend combining radio telemetry with other methods, traditional (e.g., capture-mark-recapture) as well as modern ones (e.g., remote sensing techniques; Rhodes et al., 2021) to open new insights into beetle behavior.

There is still a huge knowledge gap in long-term perspectives of beetles' movement behavior, especially in relation to population and (meta)community ecology. For most beetle communities, we do not know yet how movement responses at the individual level can assist in selection of the most parsimonious descriptors for community-level dynamics. The patterns of beetle movement can be a good proxy for any habitat alteration and can act as early warning signals preceding the changes in community structures. This issue should be visited in more detail in future research initiatives.

## AUTHOR CONTRIBUTIONS

**Jana Růžičková:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Zoltán Elek:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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## DATA AVAILABILITY STATEMENT

All data used are already published in the relevant publications provided in the reference list at the end of the manuscript.

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## REFERENCES

- Al Ansi A, Aldryhim Y & Al Janobi A (2020) First use of radio telemetry to assess behavior of red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Dryophthoridae) in the presence and absence of pheromone traps. *Computers and Electronics in Agriculture* 170: 105252.
- Baars MA (1979) Patterns of movement of radioactive carabid beetles. *Oecologia* 44: 125–140.
- Barron DG, Brawn JD & Weatherhead PJ (2010) Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1: 180–187.
- Bartumeus F, da Luz MGE, Viswanathan GM & Catalan J (2005) Animal search strategies: a quantitative random-walk analysis. *Ecology* 86: 3078–3087.
- Bates D, Mächler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Batsleer F, Bonte D, Dekeukeleire D, Goossens S, Poelmans W et al. (2020) The neglected impact of tracking devices on terrestrial arthropods. *Methods in Ecology and Evolution* 11: 350–361.
- Beaudoin-Ollivier L, Bonaccorso F, Aloysius M & Kasiki M (2003) Flight movement of *Scapanes australis australis* (Boisduval) (Coleoptera: Scarabaeidae: Dynastinae) in Papua New Guinea: a radiotelemetry study. *Australian Journal of Entomology* 42: 367–372.
- Bérces S & Růžičková J (2019) Habitat use of an endangered beetle *Carabus hungaricus* assessed via radio telemetry. *Acta Zoologica Academiae Scientiarum Hungaricae* 65: 335–348.
- Boiteau G & Colpitts B (2001) Electronic tags for the tracking of insects in flight: effect of weight on flight performance of adult Colorado potato beetles. *Entomologia Experimentalis et Applicata* 100: 187–193.
- Boiteau G, Vincent C, Meloche F & Leskey TC (2010) Harmonic radar: assessing the impact of tag weight on walking activity of Colorado potato beetle, plum curculio, and western corn rootworm. *Journal of Economic Entomology* 103: 63–69.
- Bowler DE & Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80: 205–225.
- Bradshaw CJ, Sims DW & Hays GC (2007) Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecological Applications* 17: 628–638.
- Cerda Y, Grez AA & Simonetti JA (2015) The role of the understory on the abundance, movement and survival of *Ceroglossus chilensis* in pine plantations: an experimental test. *Journal of Insect Conservation* 19: 119–127.
- Chiari S, Carpaneto GM, Zauli A, Zirpoli GM, Audisio P & Ranius T (2013) Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Insect Conservation and Diversity* 6: 309–318.
- Costa-Pereira R, Moll RJ, Jesmer BR & Jetz W (2022) Animal tracking moves community ecology: opportunities and challenges. *Journal of Animal Ecology* 91: 1334–1344.
- Deichsel R (2007a) Influence of habitat corridors on the movement behaviour of *Carabus nemoralis* (Coleoptera: Carabidae) in an urban environment. Habitatfragmentierung in der Urbanen Landschaft – Konsequenzen für die Biodiversität und Mobilität Epigäischer Käfer (Coleoptera: Carabidae und Staphylinidae) am Beispiel Berliner Waldfragmente. PhD Dissertation, Freie Universität Berlin, Berlin, Germany.
- Deichsel R (2007b) The influence of radio transmitters on the movement behaviour of large ground beetles. Habitatfragmentierung in der Urbanen Landschaft – Konsequenzen für die Biodiversität und Mobilität Epigäischer Käfer (Coleoptera: Carabidae und Staphylinidae) am Beispiel Berliner Waldfragmente. PhD Dissertation, Freie Universität Berlin, Berlin, Germany.
- Drag L & Čížek L (2018) Radio-tracking suggests high dispersal ability of the great capricorn beetle (*Cerambyx cerdo*). *Journal of Insect Behavior* 31: 138–143.
- Drees C, Matern A & Assmann T (2008) Behavioural patterns of nocturnal carabid beetles determined by direct observations under red-light conditions. *Back to the Roots and Back to the Future: towards a New Synthesis between Taxonomic, Ecological and Biogeographical Approaches in Carabidology* (ed. by L Penev, TL Erwin & T Assmann), pp. 20–24. Pensoft Publishers, Sofia, Bulgaria.
- Dubois G & Vignon V (2008) First results of radio-tracking of *Osmoderma eremita* (Coleoptera: Cetoniidae) in French chestnut orchards. *Revue d'Ecologie* 63: 131–138.
- Duchesne T, Fortin D & Rivest LP (2015) Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. *Plos One* 10: e0122947.
- Elek Z, Růžičková J & Ódor P (2021) Individual decisions drive the changes in movement patterns of ground beetles between forestry management types. *Biologia* 76: 3287–3296.

- Ewers RM & Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117–142.
- Fisher KE, Dixon PM, Han G, Adelman JS & Bradbury SP (2020a) Locating large insects using automated VHF radio telemetry with a multi-antennae array. *Methods in Ecology and Evolution* 12: 494–506.
- Fisher KE, Adelman JS & Bradbury SP (2020b) Employing very high frequency (VHF) radio telemetry to recreate monarch butterfly flight paths. *Environmental Entomology* 49: 312–323.
- Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ & Pedrotti L (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B* 365: 2187–2200.
- Grüm L (1971a) Remarks on the differentiation in Carabidae mobility. *Ekologia Polska* 19: 47–56.
- Grüm L (1971b) Spatial differentiation of the *Carabus* L. (Carabidae, Coleoptera) mobility. *Ekologia Polska* 19: 1–34.
- Hamer GL, Bejcek JR, Valdez EA, Curtis-Robles R & Hamer SA (2018) A pilot radio telemetry field study of triatomine vectors (Hemiptera: Reduviidae) of the Chagas disease parasite. *Journal of Medical Entomology* 55: 1380–1385.
- Hamidi R, Couzi P, Khfif K & Rochat D (2017) Impact of active and passive radio tags on the flying and burrowing behavior of the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae). *Applied Entomology and Zoology* 52: 165–173.
- Hayashi F & Nakane M (1988) A radio-tracking study on the foraging movements of the dobsonfly larva, *Protohermes grandis* (Megaloptera, Corydalidae). *Kontyû (Tokyo)* 56: 417–429.
- Hebblewhite M & Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B* 365: 2303–2312.
- Hedin J & Ranius T (2002) Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. *Computers and Electronics in Agriculture* 35: 171–180.
- Hedin J, Ranius T, Nilsson SG & Smith HG (2008) Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity and Conservation* 17: 675–684.
- Holyoak M, Casagrandi R, Nathan R, Revilla E & Spiegel O (2008) Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the USA* 105: 19060–19065.
- Jerde CL & Visscher DR (2005) GPS measurement error influences on movement model parameterization. *Ecological Applications* 15: 806–810.
- Joo R, Boone ME, Clay TA, Patrick SC, Clusella-Trullas S & Basille M (2020) Navigating through the R packages for movement. *Journal of Animal Ecology* 89: 248–267.
- Kagawa 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. *European Journal of Entomology* 106: 385–391.
- Kaláb O, Musiolek D, Rusnok P, Hurtik P, Tomis M & Kočárek P (2021) Estimating the effect of tracking tag weight on insect movement using video analysis: a case study with a flightless orthopteran. *Plos One* 16: e0255117.
- Kays R, Crofoot MC, Jetz W & Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348: aaa2478.
- Kenward RE (2000) *A Manual for Wildlife Radio Tagging*. Academic Press, London, UK.
- Kissling WD (2015) Animal telemetry: follow the insects. *Science* 349: 597.
- Kissling WD, Pattenmore DE & Hagen M (2014) Challenges and prospects in the telemetry of insects. *Biological Reviews* 89: 511–530.
- Knight SM, Pitman GM, Flockhart DT & Norris DR (2019) Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biology Letters* 15: 20190327.
- Kotze DJ, Brandmayr P, Casale A, Dauffy-Richard E, Dekoninck W et al. (2011) Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys* 100: 55–148.
- Kral-O'Brien KC & Harmon JP (2021) The expanding role of movement behavior in insect conservation ecology. *Current Opinion in Insect Science* 45: 69–74.
- Liégeois M, Tixier P & Beaudoin-Ollivier L (2016) Use of radio telemetry for studying flight movements of *Paysandisia archon* (Lepidoptera: Castniidae). *Journal of Insect Behavior* 29: 199–213.
- Le Gouar PJ, Dubois GF, Vignon V, Brustel H & Vernon P (2015) Demographic parameters of sexes in an elusive insect: implications for monitoring methods. *Population Ecology* 57: 227–236.
- Lee I, Hsiao R, Carichner G, Hsu CW, Yang M et al. (2021) mSAIL: milligram-scale multi-modal sensor platform for monarch butterfly migration tracking. *Proceedings of the 27th Annual International Conference on Mobile Computing and Networking*, pp. 517–530. Association for Computing Machinery, New York, NY, USA.
- Matalin AV & Makarov KV (2011) Using demographic data to better interpret pitfall trap catches. *ZooKeys* 100: 223–254.
- Michelot T, Langrock R & Patterson TA (2016) moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution* 7: 1308–1315.
- McCullough EL (2013) Using radio telemetry to assess movement patterns in a giant rhinoceros beetle: are there differences among majors, minors, and females? *Journal of Insect Behavior* 26: 51–56.
- McClintock BT, Langrock R, Gimenez O, Cam E, Borchers DL et al. (2020) Uncovering ecological state dynamics with hidden Markov models. *Ecology Letters* 23: 1878–1903.
- Moore A, Barahona DC, Lehman KA, Skabeikis DD, Iriarte IR et al. (2017) Judas beetles: discovering cryptic breeding sites by radio-tracking coconut rhinoceros beetles, *Oryctes rhinoceros* (Coleoptera: Scarabaeidae). *Environmental Entomology* 46: 92–99.
- Mora C, Tittensor DP, Adl S, Simpson AGB & Worm B (2011) How many species are there on Earth and in the ocean? *Plos Biology* 9: e1001127.
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R et al. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the USA* 105: 19052–19059.
- Negro M, Casale A, Migliore L, Palestini C & Rolando A (2008) Habitat use and movement patterns in the endangered ground beetle species, *Carabus olympiae* (Coleoptera: Carabidae). *European Journal of Entomology* 105: 105–112.
- Negro M, Caprio E, Leo K, Maritano U, Roggero A et al. (2017) The effect of forest management on endangered insects assessed by radio-tracking: the case of the ground beetle *Carabus olympiae* in European beech *Fagus sylvatica* stands. *Forest Ecology and Management* 406: 125–137.
- Okuzaki Y (2021) Effects of body size divergence on male mating tactics in the ground beetle *Carabus japonicus*. *Evolution* 75: 2269–2285.
- Perry KI, Sivakoff FS, Wallin KF, Wenzel JW & Herms DA (2021) Forest disturbance and arthropods: small-scale canopy and understory disturbances alter movement of mobile arthropods. *Ecosphere* 12: e03771.
- Pohle J, Langrock R, van Beest FM & Schmidt NM (2017) Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. *Journal of Agricultural, Biological and Environmental Statistics* 22: 270–293.
- Prather CM, Pelini SL, Laws A, Rivest E, Woltz M et al. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews* 88: 327–348.
- Ranacher P, Brunauer R, Trutschni W, van der Spek S & Reich S (2016) Why GPS makes distances bigger than they are. *International Journal of Geographical Information Science* 30: 316–333.
- Rasiulis AL, Festa-Bianchet M, Couturier S & Côté SD (2014) The effect of radio-collar weight on survival of migratory caribou. *Journal of Wildlife Management* 78: 953–956.
- Reynolds AM (2018) Current status and future directions of Lévy walk research. *Biology Open* 7: bio030106.
- Rhodes MW, Bennie JJ, Spalding A, Ffrench-Constant RH & Maclean IMD (2021) Recent advances in the remote sensing of insects. *Biological Reviews* 97: 343–360.

- Riecken U & Raths U (1996) Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. *Annales Zoologici Fennici* 33: 109–116.
- Riecken U & Raths U (2000) Radio telemetrische Untersuchungen zum Raum-Zeit-Verhalten von Laufkäfern am Beispiel von *Carabus coriaceus* (L., 1758) und *C. monilis* (Fabricius, 1792). *Angewandte Carabidologie* 2: 49–58.
- Rink M & Sinsch U (2007) Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. *Journal of Zoology* 272: 235–243.
- Rink M & Sinsch U (2011) Warm summers negatively affect duration of activity period and condition of adult stag beetles (*Lucanus cervus*). *Insect Conservation and Diversity* 4: 15–22.
- Růžičková J, Bérces S, Ackov S & Elek Z (2021) Individual movement of large carabids as a link for activity density patterns in various forestry treatments. *Acta Zoologica Academiae Scientiarum Hungaricae* 67: 77–86.
- Růžičková J & Elek Z (2021) Recording fine-scale movement of ground beetles by two methods: potentials and methodological pitfalls. *Ecology and Evolution* 11: 8562–8572.
- Růžičková J & Veselý M (2016) Using radio telemetry to track ground beetles: movement of *Carabus ullrichii*. *Biologia* 71: 924–930.
- 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.
- Sprecher-Uebersax E & Durrer H (2001) Verhaltensstudien beim Hirschkäfer mittels Telemetrie und Videoaufzeichnungen (Coleoptera, *Lucanus cervus* L.). *Mitteilungen Naturforschende Gesellschaften beider Basel* 5: 161–182.
- Svensson GP, Sahlén U, Brage B & Larsson MC (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*. *Biodiversity and Conservation* 20: 2883–2902.
- Thomaes A, Dhont P, Dekeukeleire D & Vandekerckhove K (2018) Dispersal behaviour of female stag beetles (*Lucanus cervus*) in a mosaic landscape: when should I stay and where should I go. *Insect Conservation and Diversity* 11: 523–533.
- Tini M, Bardiani M, Chiari S, Campanaro A, Maurizi E et al. (2017a) Use of space and dispersal ability of a flagship saproxylic insect: a telemetric study of the stag beetle (*Lucanus cervus*) in a relict low-land forest. *Insect Conservation and Diversity* 11: 116–129.
- Tini M, Bardiani M, Campanaro A, Chiari S, Mason F et al. (2017b) A stag beetle's life: sex-related differences in daily activity and behaviour of *Lucanus cervus* (Coleoptera: Lucanidae). *Journal of Insect Conservation* 21: 897–906.
- Tini M, Bardiani M, Campanaro A, Mason F, Audisio P & Carpaneto GM (2017c) Detection of stag beetle oviposition sites by combining telemetry and emergence traps. *Nature Conservation* 19: 81–96.
- Turchin P, Odendaal FJ & Rausher MD (1991) Quantifying insect movement in the field. *Environmental Entomology* 20: 955–963.
- Turin H, Penev L & Casale A (2003) *The Genus Carabus in Europe: a Synthesis*. Pensoft Publisher, Sofia, Bulgaria.
- Wang Z, Huang Y & Pierce NE (2019) Radio telemetry helps record the dispersal patterns of birdwing butterflies in mountainous habitats: golden birdwing (*Troides aeacus*) as an example. *Journal of Insect Conservation* 23: 729–738.
- Weaver SJ, Westphal MF & Taylor EN (2021) Technology wish lists and the significance of temperature-sensing wildlife telemetry. *Animal Biotelemetry* 9: 29.
- White G & Garrott R (1990) *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego, CA, USA.
- Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE & Yovovich V (2015) The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96: 1741–1753.
- Wilson RP, Rose KA, Gunner R, Holton MD, Marks NJ et al. (2021) Animal lifestyle affects acceptable mass limits for attached tags. *Proceedings of the Royal Society B* 288: 20212005.

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