

INDIVIDUAL MOVEMENT OF LARGE CARABIDS AS A LINK FOR ACTIVITY DENSITY PATTERNS IN VARIOUS FORESTRY TREATMENTS

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Activity density is one of the most common measures in ground-dwelling arthropods, including carabids. It is based on individuals' activity and population density, yet there is no available evidence whether the individual movement can be a good proxy for activity density. Therefore, in our study, we aimed to explore this link in two large ground beetle species, *Carabus scheidleri* Panzer, 1799 and *C. coriaceus* Linnaeus, 1758, in an oak-hornbeam forest in Hungary. We used pitfall traps for activity density and capture-mark-recapture and radio telemetry to record individual movement patterns in different forestry treatments, preparation cuttings and clear-cuttings, and their control plots. We found a link between activity density and movement of individuals via treatment types. Although activity density, mean walking speed and the proportion of active time were significantly higher in both treatments than in control plots, the individual movement revealed only temporal use of these habitats. Beetles left treatments within a few days. We concluded that the high turnover of individuals in treatments might indirectly suggest that these habitats probably act as temporary foraging sites for both species.

Keywords: *Carabus* spp., forest management, capture-mark-recapture, pitfall traps, radio telemetry.

INTRODUCTION

Ecological studies on assemblages of ground-dwelling arthropods often involve the use of pitfall traps (GREENSLADE 1964, LÖVEI & SUNDERLAND 1996). It is one of the oldest, most efficient, and convenient, but also heavily criticized sampling techniques because the numbers caught do not reflect the absolute abundance of a particular species (TOPPING & SUNDERLAND 1992, WOODCOCK 2005, KOTZE *et al.* 2011). The capture rate is proportional to the interaction between individuals' movement activity and population density in the sampled habitat (LÖVEI & SUNDERLAND 1996, BROWN & MATTHEWS 2016). Therefore, the pitfall trap catches should be rather treated as 'activity density' than abundance (THOMAS *et al.* 1998, LANG 2000). Moreover, the trapping efficiency is not

the same for all species due to species-specific behavioural responses (HALSALL & WRATTEN 1988) which may lead to underestimation of relatively sessile but very abundant species in the trap catches compared to rare but more active species (TOPPING & SUNDERLAND 1992, LANG 2000, WOODCOCK 2005). Regardless of these limitations, activity density is still one of the most common measures for ground-dwelling arthropods in community ecology studies. Carabids (Coleoptera: Carabidae) are one of the most frequently caught groups in the pitfall traps; thus, they are among the best indicators taxa within arthropods with an excellent background about their ecology and behaviour, especially for movement characteristics (THIELE 1977, LÖVEI & SUNDERLAND 1996).

Carabids' movement is modified by several factors, including biotic and abiotic ones. For instance, sex (THOMAS *et al.* 1998, KAGAWA & MAETO 2009), breeding season (KÁDÁR *et al.* 2017), and hunger level (WALLIN & EKBOM 1994, SZYSZKO *et al.* 2004) are considered as the most influential biotic factors affecting carabids. From environmental variables, especially (micro)habitat (BAARS 1979, RIECKEN & RATHS 1996, BÉRCES & RŮŽIČKOVÁ 2019), temperature (HONĚK 1997, SASKA *et al.* 2013, RŮŽIČKOVÁ & VESELÝ 2016) and light intensity (HALSALL & WRATTEN 1988, SZYSZKO *et al.* 2005) have been reported to influence carabid activity and distribution significantly. Moreover, these factors are confounded by behavioural peculiarities of each species at both the inter- and intra-individual level (BAILEY *et al.* 2020). Although the research interest in the individual movement of carabids is growing, especially with the technical development in radio-tracking and remote sensing, the selection of species is still biased and mostly focused on large or very common carabids. Without information on the species-specific movement activity, it is almost impossible to correlate the catches from pitfall traps to the factual abundance/population density estimations (TOPPING & SUNDERLAND 1992, WOODCOCK 2005, BROWN & MATTHEWS 2016). This concept is crucial for reliable interpretation of pitfall trap data; nevertheless, the link between movement parameters and activity density is still poorly understood. Decades ago, only GRÜM (1971*a, b*) reported that beetles walked faster in unsuitable habitats resulting in higher trap catches than expected, suggesting that higher activity density likely does not automatically mean a particular species or an assemblage prefers that sampled habitat.

In this study, we aimed to explore in detail whether the individual movement can be a good proxy for activity density of carabids in an oak-hornbeam Hungarian forest managed by different forestry treatments. A previous study (ELEK *et al.* 2018) showed significant effects of forest management on species composition of carabids. These findings were based on trap catches and report only assemblage-level responses. However, individuals' movement plasticity may bias species-specific responses to silvicultural treatments that can not be revealed by pitfall trapping. Therefore, we selected two common large flightless carabid species in the experimental area: *Carabus* (*Morphocarabus*)

scheidleri Panzer, 1799 and *C. (Procrustes) coriaceus* Linnaeus, 1758. First (1), we estimated the potential habitat utilization by capture-mark-recapture and radio telemetry between two forestry treatments (preparation cuttings and clear-cutting) and their controls. Then (2), we sought to link activity density data and movement patterns of individuals revealing true habitat utilization. We focused especially on individual movements within and between habitats, trajectory profiles, mean speed and the proportion of the active time.

MATERIAL AND METHODS

Study site – Our study was implemented as a part of the Pilis Forestry System Experiment (<https://www.piliskiserlet.okologia.mta.hu/en>), located in the vicinity of Pilisszántó village in the Pilis Mountains, northern Hungary (47.6741°N, 18.9105°E). The experimental area (40 ha) was a structurally homogenous, 80 years old, managed two-layered sessile oak-hornbeam forest. The upper canopy layer was dominated by *Quercus petraea* (Matt.) Liebl., 1784, *Q. cerris* Linnaeus, 1753, *Fagus sylvatica* Linnaeus, 1753 and *Prunus avium* Linnaeus, 1755, while *Carpinus betulus* Linnaeus, 1753 and *Fraxinus ornus* Linnaeus, 1753 made the lower layer. In 2014, four different forestry treatments in two different silvicultural systems were established to test the effect of these treatments on forest biodiversity and regeneration (see ELEK *et al.* 2018 for further details). For this study, we used two of the four implemented treatments representing characteristic stages of the rotation forestry system: (1) Clear-cutting (CC) was a circular clear-cutting area of 80 m diameter surrounded by the closed-canopy stand. (2) Preparation cutting (P) was created when 30% of the total basal area of the dominant tree layer and the whole secondary tree layer were removed in a spatially uniform way in a circle of 80 m diameter. Treatments were replicated in six blocks that also included control unmanaged forest stands (C), leading into 18 sampling plots in total.

Target species – We selected two large ground beetles, *Carabus scheidleri* and *C. coriaceus*. The first species, variable in colour morphs and 27–30 mm long *C. scheidleri*, was used for capture-mark-recapture. It is a generalist predator, predominantly occurring in forests, but it is also known from arable fields, meadows, and vineyards (TURIN *et al.* 2003). The species overwinters both as larvae and as adults with overlapping generations and several reproductive periods (ANDORKÓ & KÁDÁR 2009). The second species, *C. coriaceus*, is one of the most common species in the area. It is associated with various types of temperate forests, orchards and vineyards (TURIN *et al.* 2003). With a size of 33–40 mm, it is the largest carabid species in Hungary and suitable to mount radio transmitters (ELEK *et al.* 2019). It is a typical autumn breeder with an activity peak in autumn when copulation and oviposition occur and a second smaller peak in spring (TURIN *et al.* 2003).

Activity density – pitfall trapping – The activity density of *C. scheidleri* and *C. coriaceus* was recorded by pitfall traps made of 85 mm diameter plastic cups and filled with 50% solution of propylene glycol and water. A dark green roof was installed above every trap. We installed four pitfall traps in CC and P treatments as well as in control forest (C), all in six replicates. Thus in total, 72 traps were used per one sampling occasion. Between 2014 and 2018, one-month sampling sessions were conducted per season, one in spring, one in autumn. This regime corresponds with the highest activity peaks of ground beetles (ELEK *et al.* 2018). The pitfall trap catches were pooled on the plot level, and only activity densities of *C. coriaceus* and *C. scheidleri* were considered in this study.

Individual movement – capture-mark-recapture and radio telemetry – Two different approaches were used for recording individual movement. The capture-mark-recapture (CMR) was applied to *C. scheidleri*, while *C. coriaceus* was radio-tracked. The CMR of *C. scheidleri* was conducted in two blocks during spring 2017. We installed 10 (2 × 5) empty pitfall traps in 4 m grid in CC and P treatments and adjoining control forests. The distance between trap groups in the treatment and corresponding control plot was approximately 40 m. Traps were checked every five or six days, and collected beetles were individually marked by engraved numbers on their elytra and released nearby. We recorded movements within and between habitats.

The individual movement patterns of *C. coriaceus* were studied by radio telemetry in autumn 2018. Six living individuals (three males and three females) were collected in the experimental area by empty pitfall traps. Small VHF transmitters with unique frequencies (the PicoPip model, weight of 0.29 g, Biotrack Ltd, Wareham, England) were mounted on the top of elytra by superglue. Tagged beetles were released in the treatment core (P or CC), on its edge, and in the adjoining control forest. They were tracked every four hours for five consecutive days (for details see ELEK *et al.* 2019) and their locations were recorded by GPS device (Garmin Dakota 20, in WGS84 coordinate reference system). Based on the positional data, we calculated mean walking speed (m/h), the proportion of active time (i.e. time when beetles moved), and obtained trajectory profile.

Statistical analyses – We used generalized linear mixed models with the Poisson distribution to test the effects of forestry treatments (both species), mean walking speed and the proportion of active time (only *C. coriaceus*) on the activity density. In the case of *C. coriaceus*, we created single-argument models on each response variable (the *glmer* function in ‘lme4’ package, BATES *et al.* 2015) where year and block were used as random effects. Afterwards, all models were tested to select the best one based on the Akaike Information Criterion (AICc) corrected for small sample sizes (BURNHAM & ANDERSON 2002) using the *model.sel* function in ‘MuMIn’ package (BARTOŇ 2019). When AICc was lower than 2, the model was selected as the most parsimonious explanation for the fitted data. If any significant differences for the explanatory factor-type variable “forestry treatments” were detected, we used post-hoc test with Tukey contrasts for multiple comparisons of means (BRETZ *et al.* 2010) by the *glht* function in ‘multcomp’ package (HOTHORN *et al.* 2008). All analyses were conducted in R 3.6.1 (R Core Team 2019).

RESULTS

Carabus scheidleri – Between 2014 and 2018, we collected 1955 individuals of *C. scheidleri*. Its activity density significantly differed between treatments ($\chi^2 = 46.067$, $df = 2$, $p < 0.001$), it was higher in both treatments (CC, P) than in C (Fig. 1a). For CMR, we captured and marked 102 individuals of *C. scheidleri* in total; 56 males and 46 females, respectively. We captured 19 beetles in control forest, 60 in CC, and 23 in P. We recorded 10 movements (recaptures), most of them within the particular treatment. In three cases, beetles left the treatment (CC or P) and walked to control forest stands. No movement was recorded in the opposite direction, i.e. from control stands to the treatments (Fig. 2a).

Carabus coriaceus – In total, we collected 723 individuals of *C. coriaceus*. The model selection based on the calculated AICc revealed that the ‘treatment’ model was the most parsimonious explanation of the activity density

Table 1. Summary of the model selection for the activity density of *C. coriaceus*, using estimations based on the calculated AICc value of the models, serving as the weight of evidence in favor of the different models. Most parsimonious model (delta < 2) is emphasized in bold.

Models	df	logLik	AICc	Delta	Weight
Treatment	5	-338.654	687.8	0.00	0.769
Mean speed	4	-341.240	690.8	2.99	0.173
Active time	4	-342.601	693.6	5.71	0.044
null	3	-344.845	695.9	8.05	0.014

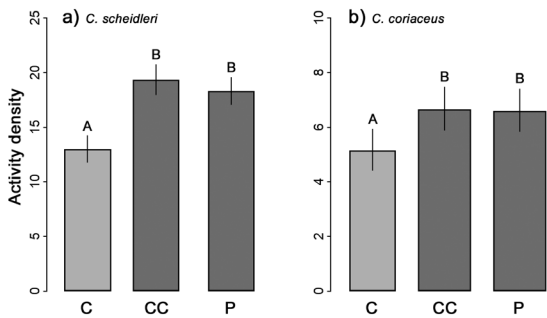


Fig. 1. Mean activity density of *Carabus scheidleri* (a) and *C. coriaceus* (b) per sampling plot in different forestry treatments (C = control, CC = clear-cutting, P = preparation cutting) between 2014 and 2018. Vertical lines represent a 95% confidence interval and capital letters above bars indicate significant differences based on Tukey's multiple comparisons of means

data (Table 1). Similarly to *C. scheidleri*, the activity density of *C. coriaceus* was significantly higher in both treatments than in the control forest ($\chi^2 = 11.897$, $df = 2$, $p = 0.002$; Fig. 1b). In contrast, the individual trajectories showed that beetles used both treatments only temporarily. They were faster and more active in P and CC than control forest (mean speed: 0.56 m/h in P, 0.33 m/h in CC, and 0.26 m/h in C; active time: 38% in P, 21% in CC and 18% in C). They also left preparation cutting and clear-cutting within few days (Fig. 2b).

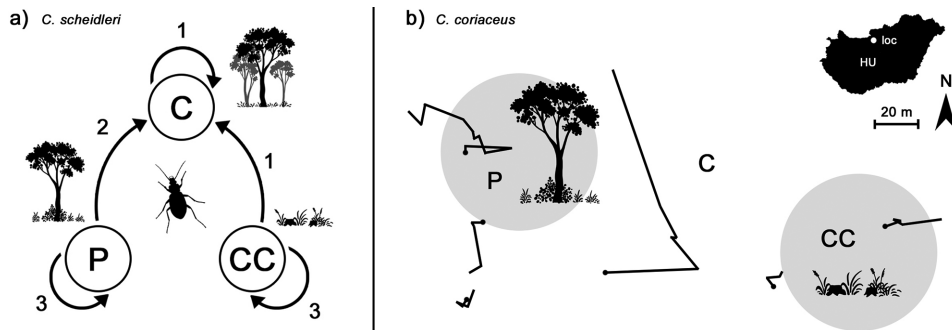


Fig. 2. Movements of *Carabus scheidleri* (a) within and between forestry treatments (C = control, CC = clear-cutting, P = preparation cutting) based on CMR. The number next to the arrow corresponds with the number of recorded movements. Individual trajectories of radio-tracked *C. coriaceus* (b) in the experimental area, black dots represent the first release point for each trajectory

DISCUSSION

Among ecologists, activity density is a widely used and important characteristic for community measures in ground-dwelling arthropods (LÖVEI & SUNDERLAND 1996, THOMAS *et al.* 1998). What activity density can tell about a particular species or assemblage is predominantly based on the movement of individuals as well as their population densities. Movement-related behavioural aspects, such as walking speed, the proportion of active time, or tortuosity of trajectory, usually change in response to different (micro)habitat utilization and/or particular part of the season (e.g. BAARS 1979, NIEHUES *et al.* 1996, BÉRCES & RŮŽIČKOVÁ 2019). As we showed here, pitfall traps catch can not be equivalent to positive habitat preference following a well-known rule: higher activity density, higher preference of the sampling site. We found an indirect link between activity density and individual movement of both *Carabus* species through treatment types. The activity density was significantly higher in both treatments than in control plots which may, at first glance, indicate that *C. scheidleri*, as well as *C. coriaceus*, tended to prefer managed habitats over undisturbed oak-hornbeam forest. Nevertheless, looking closely at individual movements, beetles used preparation cutting and clear-cutting plots only temporally: they were more active there, moved faster, and left the original release site within a few days.

GRÜM (1971a, b) found that the pitfall catches could be higher in unsuitable habitats since individuals are more active there because they want to avoid adverse environmental conditions. Indeed, the activity density of endemic species of Italian Alps, *C. olympiae*, was higher in rose shrubbery than in surrounding beech forest stands, but individual trajectories were less tortuous in shrubs (NEGRO *et al.* 2008). Although individuals did not leave the original habitat of release (a size of an experimental area was higher with an order of magnitude than ours), the authors assumed that beetles were induced to move more in rose shrubbery than in adjoining forest likely due to higher extremes in temperatures or to avoid predators.

What is the ecological relevance of the fact that the beetles were more active in unsuitable habitats? In undisturbed forests, various *Carabus* species may compete to limited food resources due to high spatial homogeneity in forest structure while clear-cuttings and preparation cuttings might ameliorate this competition (LENSKI 1982); such phenomenon can be described as an ecological trap (EWERS & DIDHAM 2005). This is especially true for *C. scheidleri*, which is associated with newly disturbed, human-modified habitats suggesting its relatively low competitiveness in homogeneous forests (ANDORKÓ & KÁDÁR 2006). Moreover for strictly forest species, the artificial edges, as a result of treatment implementation, can act as filters limiting their move-

ment out of forest stands and leaving treatments unoccupied (MAGURA *et al.* 2017, 2019, MAGURA & LÖVEI 2020). The majority of normal activity is connected with foraging, and starving beetles are more active than satisfied ones to increase their likelihood of encountering food (GRÜM 1971a, LENSKI 1984). Besides, we can presume that the spatio-temporal distribution of predatory ground beetles may follow potential prey changes due to the alterations in environmental conditions after forest management (KOVÁCS *et al.* 2018, 2020, TINYA *et al.* 2019). Thus, the high variation in abundance in both treatments might suggest that these habitats act as temporary foraging sites. These findings can be supported by no recorded movement of *C. schiedleri* from control forest stands to any of the treatments.

Moreover, its relatively low recapture rate (approximately 10%) can be indicative for emigration from the treatments after feeding, especially from clear-cuttings. Similarly, radio-tracked *C. coriaceus* individuals left both treatments quickly, and trajectories showed a typical carabid movement behaviour when random non-directional walk in short distances alternated with directed movement, i.e. long covered distances in a constant direction. While the random walk is considered as foraging behaviour, directed movement is an efficient strategy for dispersal through the filtering of unsuitable sites, possibly supported by orientation towards a dark forest silhouette (THIELE 1977, BAARS 1979, NIEHUES *et al.* 1996, RIECKEN & RATHS 1996).

However, the species identity, the inner motivation (hunger level), and prey density can also be determining factors for the dominance of one or the other movement state (WALLIN & EKBOM 1994). For instance, in high aphid density, *Poecilus cupreus* (Linnaeus, 1758) displayed directed movements regardless of hunger level, whereas the movement of *Pterostichus melanarius* (Illiger, 1798) was described mostly as a random walk (WALLIN & EKBOM 1994). Thus, individuals' behavioural peculiarities can notably affect movement activity and, consequently, the numbers of pitfall trap catches.

In conclusion, statements concerning a species composition of carabid assemblages and habitat preferences derived from pitfall traps seem to be heavily biased by the individual plasticity in movement behaviour. Activity density should be carefully considered as a relative measure for ground-dwelling arthropods and, in an ideal case, should be supported by additional methods recording individual movement, such as capture-mark-recapture or radio telemetry. Only then, pitfall catches and activity density can reveal reliable patterns in habitat utilization. Nevertheless, it has to be noted that our results are based on a relatively small-scale study; we, therefore, encourage other researches to explore more in detail the link between activity density and individual movement regarding other carabid species and different habitats.

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