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Life history adaptations of *Carabus* populations in a suburban park: A capture-recapture case study

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ABSTRACT

A two seasons capture-recapture study was preformed between 2016 and 2017, focusing on the *Carabus* species living in a suburban park in Budapest, Hungary. Eighty-four live-capture non-baited pitfall traps were placed in a grid covering an area of 567 m^2. Five *Carabus* species were captured in the park from the nine species in the potential species pool. The most numerous were *C. scheidleri*, *C. ulrichii* and *C. coriaceus*. *C. convexus* and *C. intricatus* were captured only a few times. All *Carabus* species were individually marked and released. We experienced high fluctuation in the estimated population size of *C. scheidleri* and *C. ulrichii,* the two most abundant species. The marking technique made possible to detect that the two dominant species overwinter both as larvae and as adults, and thus share remarkably similar life histories. Similar habitat preference, life cycle and low dispersal power sets stage for potential competition between the two species. Due to population sizes below viability limit and the potential for competitive interactions, we presume that a larger network of metapopulation structure makes it possible that these populations persist in a suburban park. The results indicate that urban parks, if they are sufficiently connected to other suitable habitat patches, can have a significant importance in preserving large bodied predatory *Carabus* species.

1. Introduction

Urban green areas can increase local and regional biodiversity especially when connected to rural landscape fragments with green corridors. The importance of green patches nowadays can be best shown in the context of ecosystem services. Ecosystem services in urban green areas provision benefits to the society such as positive effects on human health, recreation, the mitigation of the effect of urban heat islands, retain water and prevent flush floods, among other positive effects (Yu et al., 2017). Urbanization seriously affects a wide range of natural ecosystems in different ways which are not always easily distinguished, such as loss of quality, loss of quantity, loss of connectivity and loss of continuity over time (Hanski, 2005). These are related to concrete processes, for instance fragmentation, habitat loss and isolation, local climatic change, altered hydrological regimes, pollution, invasion and human disturbance (Parris,

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2016). All of these factors can lead to decreasing species numbers. To minimize biodiversity loss we need a better understanding of the biology of urban animal populations.

The response of many animal groups to urbanization, especially at a community level, shows inconsistent patterns. Such patterns may originate from variable species level sensitivities and responses to environmental changes (Magura and Lövei, 2020). Not all species groups are affected the same way by urbanization. Abundance and diversity of arthropod communities, particularly Coleoptera and Lepidoptera, are reported to be among the most negatively affected groups (Fenoglio et al., 2020). Within Coleoptera, large bodied predatory forest specialist ground beetles are especially sensitive to urbanization, and they are most likely to experience local extinction in cities (Martinson and Raupp, 2013). In a large city like Budapest the ground dwelling urban and suburban *Carabus* assemblage, compared to rural assemblages, is likely to be less diverse. We hypothesize that habitat specialists or species that are more sensitive to more extreme abiotic conditions can be found in rural sites only.

Budapest, like other metropolises, is expanding. Built-in areas grow at the expense of greenery and as a result the land cover of forests and parks shrank by 1846 ha between 1986 and 2011 (Csapó and Lenner, 2016). However, green areas serve as refuge for wildlife in general, even though more than often they are only remnants of the natural habitat with few of its original species retained. More than half of the remaining green area of Budapest is nature conservation area, which also efficiently restricts further expansion of the city.

The ecological characters of *Carabus* species occurring in the temperate-zone are well studied (Koch and Freude, 1989). Stenotopic species in or around Budapest usually live in rural or suburban areas in dry (*C. hungaricus*, *C. scabriusculus*) or wet habitats (*C. clathratus*, *C. granulatus*) (Merkl, 1996; Hegyessy and Szél, 2002). According to environmental conditions, the distribution of species can be biogeographically restricted. The east side ('Pest') of the capital is built on a floodplain originally belonging to the forest-steppe zone, while the west side ('Buda') lies in the low mountain range of Buda Hills, originally covered by closed broad-leaf forests. The distribution of many *Carabus* spp. follow this division of the original habitats. For instance, *C. montivagus* and *C. violaceus* do not live in Transdanubia, they only occur on the Pest side of the town (Szél et al., 2007). The natural *Carabus* species pool of the city parks and rural forests on the Buda side consist of eurytopic, mesophilic sylvicole species of broad-leaved oak (*Quercus*) and beech (*Fagus*) forests. Those *Carabus* species are common in Hungary, and are also widespread throughout Europe, inhabiting less dense forests or sometimes open habitats, such as *C. cancellatus*, *C. convexus*, *C. coriaceus*, *C. germarii*, *C. hortensis*, *C. intricatus*, *C. nemoralis*, *C. scheidleri*, *C. ulrichii* (Merkl, 1996; Hegyessy and Szél, 2002; Ködöböcz, 2009; Merkl and Szél, 2012; Duna-Ipoly National Park, 2021).

Species composition of suburban or urban habitats is largely determined by environmental filtering, but nestedness also affects

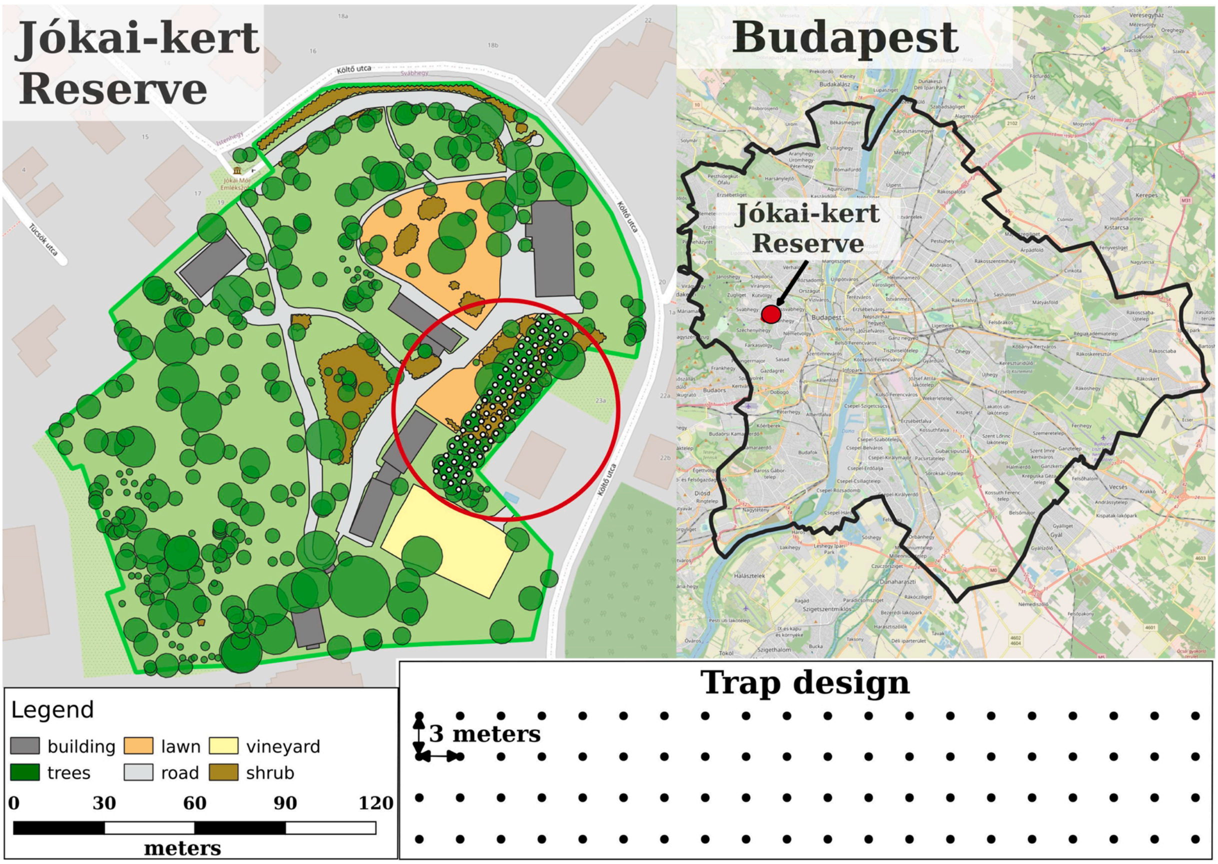

Fig. 1. Sampling site and the trap design in Jókai-kert Reserve, Budapest.

community assembly. For example, in scattered habitat patches smaller fragments hosted fewer habitat specialist species in a Hungarian study (Magura et al., 2008). A fragmented habitat, with small habitat patches is more exposed to stochastic changes in population size which may result in local extinctions. In practical conservation Franklin's rule can be widely used, which states that for short term survival of a population the effective population size must be over 50 individuals, while for long term survival this measure must be over 500. Although it has been questioned (Frankham, 2005; Jamieson and Allendorf, 2012), the rule is still considered being valid (Franklin et al., 2014) and could be used as a guideline for conservation. Habitat quality also interacts with population activity and density. For instance, when beetles disperse from a preferred habitat to a less suitable habitat, their walking behavior changes (Rijnsdorp, 1980; Bérces and Růžičková, 2019).

In this paper we present the results of a two seasons' study on *Carabus* species in a suburban park in Budapest, Hungary. In particular, we studied the large bodied forest specialist *Carabus* species with mark-release-recapture method, focusing on the two most abundant species *C. scheidleri*, *C. ulrichii* and partly on *C. coriaceus*. We asked the following questions: i) How substantial and diverse is the investigated suburban park's *Carabus* fauna compared to other European cities; how similar are the species compositions? ii) What are the population parameters, life cycles, activity and density patterns of the most abundant *Carabus* species in absolute terms and in comparison to similar studies? iii) We also assessed whether calculated population densities and parameters permit that the dominant and subdominant *Carabus* species maintain viable populations in the study area.

2. Material and methods

2.1. Study area

Almost half (48%, 5400 ha) of the total green area in Budapest, in the capital city of Hungary, are forests, mostly laying on the west side of the city in the Buda Hills region. The most forested (40.7%) is District XII. (Csapó and Lenner, 2016) where our sampling site was located. The study area was suited in a 3 ha suburban nature reserve named Jókai-kert Reserve (47°29'51.3"N; 18°59'33.3"E). In the 19th century this property was the summer residence of the famous Hungarian writer Mór Jókai, where he also had an extensive vineyard with a cellar, the park is protected since 1975. The property nowadays functions a park with five buildings, paved roads, regularly maintained lawn and a partly managed forest with variable canopy cover. Our *Carabus* study took place on a fraction of the whole territory. This particular area, where the traps were placed, was a narrow 15 m wide 80 m long unmanaged forest, approximately 1200 m^2 large. The patch was moderately isolated from the rest of the park by a vineyard, lawn, paved surfaces (garden road and a smallish parking lot) (Fig. 1.).

Total canopy layer in the trapping area covers about 70%, while shrubs cover 90% of the area. The tallest tree canopy layer consists mainly (80%) of 40 year old common ash (*Fraxinus excelsior*) trees, the rest is 20–40 year old Norway maple (*Acer platanoides*), with single sessile oak (*Quercus petraea*), pear (*Pyrus communis*) and horse chestnut (*Aesculus hippocastanum*) trees.

The whole park is attached through gardens covered by trees to the rural forests of the Buda Hills Landscape Protection area, the distance in a straight line is about 1.5 kilometers The tree cover is not continuous between the study site and the rural forest, it is a suburb divided by houses and roads.

2.2. Comparing urban Carabus faunas of cities

To compare the *Carabus* fauna of European cities a table was compiled mostly based on the paper by Martinson and Raupp (2013). Their data was extended using Internet search that targeted the keywords "urbanization" and "*Carabus*". Further papers of interest were found in the cited literature of the articles found, for example, faunistic works dealing with the list of *Carabus* in a certain area, or papers reporting red lists of particular cities. All together 33 publications were used to complete the *Carabus* data of European cities (see Supplementary data Appendix Table 1).

2.3. Target species of the capture-recapture analysis

Carabus scheidleri, *C. ulrichii* and *C. coriaceus* are brachypterous, large bodied, eurytopic predatory species living in the closed Querco-Fagetum forest belt of Central Europe. As most *Carabus*, the target species are also incapable of flight and have poor dispersal ability, therefore they are regarded to be highly sensitive to forest fragmentation (Matern et al., 2011). *Carabus scheidleri* has a restricted South-East European distribution, where it lives in deciduous forests (Turin et al., 2003; Szél et al., 2007). It has a flexible reproduction system, overwintering either as adults or as larvae. The eurytopic forest generalist *C. scheidleri* has no special preference for soil type or humidity; however, females were found to positively respond locally to higher daily maximum temperature values (Fülöp et al., 2021). There is every indication that ecologically *C. scheidleri* behaves similarly to its sister-species *C. monilis* which is also a eurytopic forest species with wide thermic, hygric and light preference ranges (Thiele, 1977). The species was shown to be associated with large young stands of beech forests (Warnaffe and Dufrêne, 2004). The ecology of *C. ulrichii* is also well studied. It is a typical, locally common species of the Central and Eastern European oak and beech forests (Hurka, 1996; Turin et al., 2003). *Carabus ulrichii* is a spring breeder with one reproductive period and non-overlapping generations (Andorkó, 2014). *Carabus coriaceus* is an autumn breeder with winter larvae, a forest and forest edge specialist (Riecken and Raths, 1996), probably an eurytopic and mesophilous species of hills and mountains, while it also has a restricted distribution in the Hungarian lowlands (Turin et al., 2003; Szél et al., 2007).

Table 1
Summary of catch data on the five *Carabus* species sampled in 2016 and 2017 in Jókai-kert Reserve, Budapest; the results of the mark-recapture study are also summarized. (Abbreviations: f: female, m: male, NA: not applicable.).

								Recapture occasion					
Species	Year	Sex	Frequency	Marked	Recapture (%)	Gross population size (N-hat)	Model	1 ×	2 ×	3 ×	4 ×	5 ×	6 ×
Carabus scheidleri	2016	m	328	181	39.22	338.4 (± 12.4)	Phi(t*g) p(t)pent(t)N(.)	39	20	5	9	1	2
	2016	f	332	187	42.25	345.6 (± 13.6)	Phi(t*g) p(t)pent(t)N(.)	37	17	16	4	2	0
	2017	m	117	59	59.68	92.5 (± 3.9)	Phi(t) p(t) pent(t) N(.)	22	12	3	0	0	0
	2017	f	112	64	41.18	99.7 (± 4.1)	Phi(t) p(t) pent(t) N(.)	16	9	2	1	0	0
Carabus ulrichii	2016	m	25	14	42.86	24 (± 4.9)	Phi(g) p(.) pent(t) N(g)	4	0	1	1		
	2016	f	15	7	57.14	10.3 (± 2.9)	Phi(g) p(.) pent(t) N(g)	1	2	1			
	2017	m	11	5	80	7.2 (± 1.6)	Phi(.)p(.)pent(t)N(g)	3		1			
	2017	f	15	6	66.67	9.9 (± 1.9)	Phi(.)p(.)pent(t)N(g)	1	2	1			
Carabus coriaceus	2016	m	2	1	100	NA	NA	1					
	2016	f	6	3	100	NA	NA	3					
	2017	m	9	7	28.57	NA	NA	2					
	2017	f	16	14	14.28	NA	NA	2					
Carabus convexus	2016	f	1			NA	NA						
	2017	m	1			NA	NA						
Carabus intricatus	2016	m	1			NA	NA						
	2017	f	1			NA	NA						

2.4. Sampling design

Eighty-four live-capture non-baited pitfall traps have been placed in a grid of 4 rows and 21 columns with 3 m trap distance, covering an area of 567 m^2 (Fig. 1.). Each trap consisted of two cups, a larger one (9 cm diameter, with a volume of 0.5 l) was dug flush into the ground. A smaller cup (with a diameter of 9 cm and volume of 0.3 l) was inserted into the larger one without a gap. This installation facilitates the lift out of the inner cup and the removal of the animals. Both cups have been perforated at the bottom and had a plastic roof at c. 2–4 cm above the ground level to prevent the collection of rain. Traps were functioning between April and August in 2016, and between May and July in 2017.

2.5. Marking the individuals

Captured *Carabus* specimens were identified to the species level in the field, individually marked by numbers, engraved on their elytra with a small drill. Tenerals were marked on their pronotum, which always had a harder surface, and these individuals have been repeatedly marked. Beetles have been released after handling c. 1 m South direction from the trap. On release, beetles usually hid in the litter on the spot. Handling and marking caused neither mortality nor any obvious harm to the beetles. Gender and visible injuries or anomalies of each individual was recorded in a database.

2.6. Data analysis – estimating the demographic parameters

Each investigated species was analyzed separately following the same procedure. Software Mark 9.0 (White and Burnham, 1999) was used to analyze capture-mark-release data, under the assumptions of the open population Jolly-Seber model with particularly robust parametrization (Schwarz and Arnason, 1996) to estimate gross population size (N), apparent survival probability (φ), recapture probability (p), and a combined parameter expressing the probability of entering the population (pent). We built models with parameters φ, p, pent and N being time (t) and gender (g) dependent or constant (.). The goodness of fit has been tested with the Release GOF TEST 2 + TEST 3.

Demographic parameters of the population have been estimated using constrained linear modeling, which applies the framework of generalized linear modeling (Lebreton et al., 1992). This approach provides high flexibility in the estimation of parameters and the opportunity to compare the models based on Akaike Information Criterion.

The data were plotted in R version 4.1.1 (R Core Team, 2021) using ggplot2 (Wickham, 2016). The final versions were created by Inkscape version 0.92 (Inkscape Project, 2021).

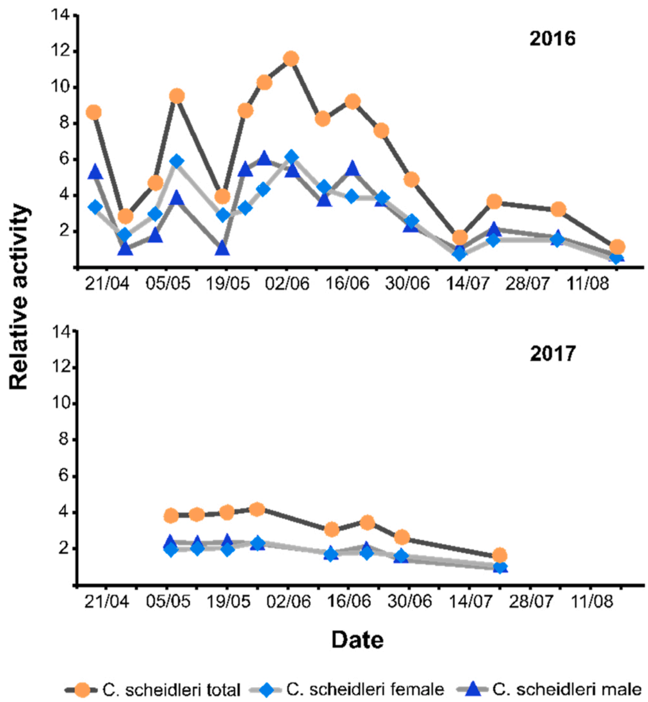

Fig. 2. Relative activity of *C. scheidleri* in 2016 and 2017 in Jókai-kert Reserve, Budapest.

3. Results

3.1. Captured species and individuals

Five *Carabus* species were captured during 2016 and 2017, data and main results are summarized in Table 1.

The most numerous were *C. scheidleri* and *C. ulrichii* with a total of 498 and 32 individually marked specimens, respectively. Capture-recapture data was evaluated for these two species.

The third most abundant species was *C. coriaceus.* We caught 25 individuals, out of which there were 8 male and 17 female specimens with 8 recaptures. Only two specimens of *C. convexus* and *C. intricatus* were captured for each species. Due to the small captured number of these three species the estimations of population parameters were not applicable.

3.2. Major activity and the estimated population parameters of C. scheidleri

Male and female specimens were caught almost in the same numbers each year, with the sex ratio being slightly female biased. From the total of 498 marked individuals 43.6% (217) were recaptured. More than half of the recaptured individuals (52.5%) were recaptured only once (114), the highest recapture rate for an individual was 6 times in one year. The number of marked individuals was 368 and 123 in 2016 and 2017, respectively, showing high between year variation (Table 1). We recaptured 3 males and 4 females after overwintering.

Plotting the relative activity of beetles, a high activity period can be observed in the first half of the year. Relative activity represents the number of individuals captured on a date divided by the number of days before the last capture occasions (Fig. 2.). Teneral beetles were observed in spring between the 14th April and 6th May (2016: 36 males, 49 females; 2017: 8 males, 3 females), with a single exception of a soft bodied specimen which have been captured on the 21st of July (Table 2).

Population parameters were obtained from the best supported models, which were different for the two study years. In the most supported model for 2016 apparent survival probability was time and gender-specific while recapture probability and the combined probability parameter of entering the population were only time dependent. The estimated population size was constant. Fitting the model to the data from 2017, gave support to an even simpler model. There was no effect of sex neither on the apparent survival or recapture probabilities nor on the probability of entering the population.

Estimated apparent survival rates were high throughout the whole period in both years, rates for males were usually higher than those of females. The estimated number of entrants was extremely low in both years. (Table 1, Fig. 3). Estimated gross population size varied between years significantly. In 2016 the estimated gross population size was 338.4 (± 12.4) males and 345.6 (± 13.6) females and in 2017 92.5 (± 3.9) males and 99.7 (± 4.1) females (Table 1).

The estimated number of entrants was low, recapture rate was high. For the density estimation the investigated population was assumed to be closed. This assumption does not mean that this population is closed from a biological point of view, since there are births and deaths in the population. The advantage of this presumption is that we may give a relatively good estimation of the population density of *C. scheidleri*. If we consider that not all the beetles were present throughout the year, we may calculate the maximum density of beetles present at the peak of activity in the investigated habitat patch. The maximum estimated number of *C. scheidleri* occurred in 2016 on the 3rd June, being 247 ± 36.8 individuals (113 ± 19.9 males, 134 ± 16.9 females). In 2017 the peak activity was on the 26th May, with 136 ± 15.7 estimated number of beetles (65 ± 7.6 males, 70 ± 8.1 females). Dividing the estimated maximal population size by the catchment area of 1000 m^2 gives the density figures of 0.25 individual/m^2 in 2016 and 0.14 individual/m^2 in 2017.

The longest daily distances covered by individuals were 10.9 m/day and 11.4 m/day for male and female individuals respectively. Out of 392 measured distances 31 recaptures were in the same trap as they were released (7.9% same trap recapture). The upper quartile of distances was lower than 1.4 m/day while the lower quartile was higher than 0.3 m/day (Fig. 3.a).

3.3. Major activity and the estimated population parameters of C. ulrichii

The second most common species was *C. ulrichii*, although only 32 specimens were marked in the two years (19 males and 13 females), the total number of captures was 66 specimens (35 males and 31 females). Relative activity was different, a higher density of beetles was observed in 2016 (Fig. 4), two overwintering females, and one male was captured.

The most supported model was one of the simplest where apparent survival was gender specific for 2016 and constant for 2017. For both years recapture probability was constant and the combined probability parameter of entering the population was only time

Table 2
Summarizing tenerals of *C. scheidleri* and *C. ulrichii* in 2016 and 2017 in Jókai-kert Reserve, Budapest.

		2016						2017		
		18. 04.	25. 04.	02. 05.	07. 05.	18. 05.	17. 06.	06. 05.	28. 06.	21. 07.
Carabus scheidleri	Male	20	7	11		3	2	7	1	
	Female	13	12	19	7	2		3		1
Carabus ulrichii	Male	1		1						
	Female			1						

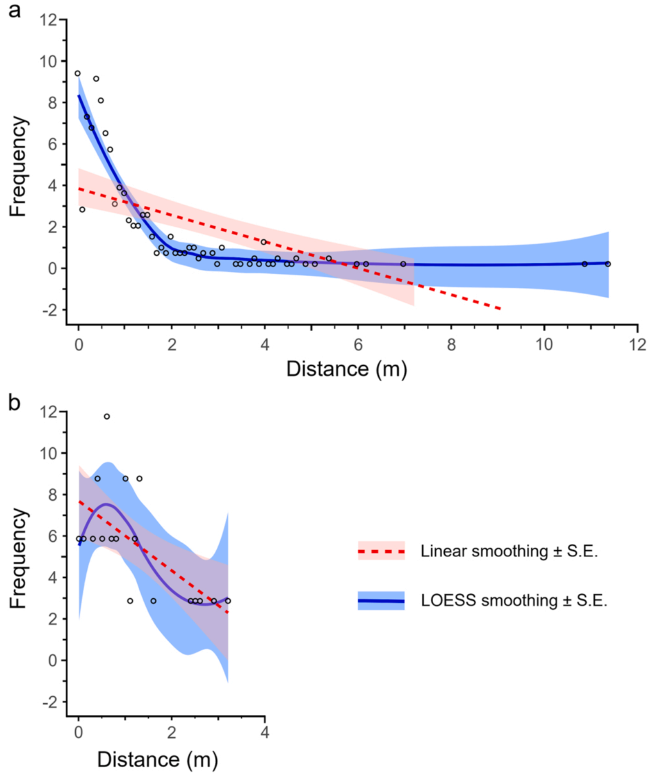

Fig. 3. Relative frequency of daily distances covered by *C. scheidleri* (a) and *C. ulrichii* (b) individuals in 2016 and 2017 in Jókai-kert Reserve, Budapest. (Line: LOESS smoothing with standard error; dashed line: Linear smoothing with standard error).

dependent. The model includes the estimated population size which was gender dependent for both years.

Estimated apparent survival rates were high in both years (2016: male 0.73, female 0.77; 2017: 0.71). The estimated number of entrants varied between years, the parameter had low values in 2016, high values in 2017. The estimated recapture probabilities were constant 0.4, 0.6 in 2016 and 2017 respectively. Gross population size varied between years significantly in 2016 it was estimated 24 (± 4.9) males and 10.3 (± 2.9) females, while in 2017 7.2 (± 1.6) males and 9.9 (± 1.9) females have been estimated (Table 1).

The population density calculated from the maximum of estimated number of specimens was very low: 0.015, 0.014 individual/m^2 in 2016, 2017 respectively. The calculation was based on the maximum number of estimated beetles (on 05.07.2016: 10.6 ± 4 males and 4.8 ± 1.9 females; on 12.05.2017 5.7 ± 1.2 males and 7.8 ± 1.4 females).

The longest daily distances covered by individuals were 3.2 m/day and 2.5 m/day for male and female individuals, respectively. Out of 32 measured distances one recapture was in the same trap as it was released (3.1% same trap recapture). The upper quartile of distance was lower than 1.3 m/day while the lower quartile was higher than 0.4 m/day (Fig. 3.b).

3.4. Comparing Carabus species richness of European cities

Literature search proved that in 22 European cities in total 27 *Carabus* species are present. *C. nemoralis* and *C. violaceus* species are widespread, they seem to be the least sensitive to urbanization as they were recorded in 17 cities, while *C. coriaceus*, *C. granulatus* and *C. hortensis* in 12, *C. convexus* in 10 cities. *C. cancellatus* and *C. ulrichii* were recorded from 8 and 7 cities, respectively (Appendix Table 1). In a European comparison, including the habitat specialist stenotopic species living in rural environments, the total *Carabus* species number in Budapest (15) is the highest followed by Lviv (14), Vienna (13) and Prague (10) (for detailed data see Appendix Table 1).

4. Discussion

In this paper we studied populations of *Carabus* species in a Budapest suburban forested park. We found five out of the nine forest dwelling *Carabus* species that occur in the surrounding rural forests of the Buda Hills region and can be regarded as the species pool of the park. The importance of the investigated suburban park in preserving biodiversity is without any doubt. In Budapest a total number of 15 *Carabus* species have been recorded, which figure is the highest among European cities, due to the variety of habitat types is the best explanation for the high number of *Carabus* species in Budapest. In the city, besides the most common deciduous forests, dry dolomitic, sand and loess grasslands, wet meadows and even swamps are present. Species tolerance to urbanization plays also an

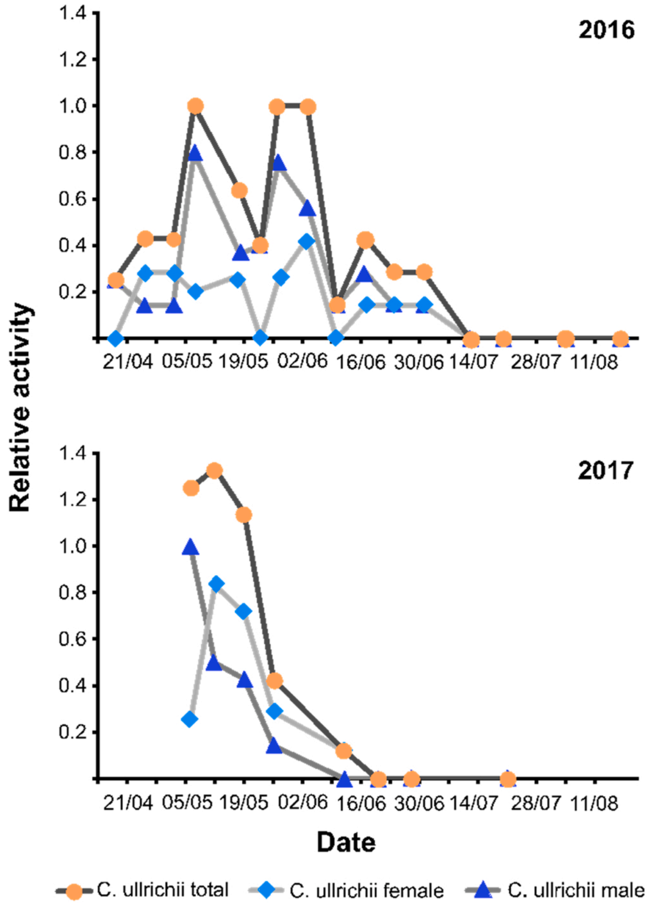

Fig. 4. Relative activity of *C. ulrichii* in 2016 and 2017 in Jókai-kert Reserve, Budapest.

important role when interpreting species occurrences. The urban character of the species can vary between cities. For example in Sofia *C. hortensis, C. intricatus* and *C. ulrichii* were strictly rural (Penev et al., 2008). In Budapest both species live in the rural and suburban area as well. Urban populations of *C. hortensis* live in Bratislava, Lviv and Hamburg, but so far this species seems to live only in the rural parts of Budapest. *C. convexus, C. nemoralis*, *C. scheidleri* and *C. violaceus* occur both in rural and urban sites; they were involved in urbanization studies as target species (Magura et al., 2008; Mizser et al., 2016). Interestingly, the two most frequent *Carabus* species of Budapest, *C. nemoralis* and *C. violaceus* were not recovered in the present study. Their lack in the studied forest patch could be a case of random extinction from small habitat patches (Magura and Lövei, 2020).

Abundance distribution of the five *Carabus* species was much skewed, with *C. scheidleri* captured 889 times, almost nine times more frequently than all other species combined. Marking was performed on the dominant *C. scheidleri*, the subdominant *C. ulrichii* and *C. coriaceus*, but due to low captures only the population parameters of *C. scheidleri* and *C. ulrichii* were calculated with mark-recapture models. Apparent survival rates were rather constant for both *C. scheidleri* and *C. ulrichii*, in both study years. Unlike survival, estimated population sizes showed more variation. For instance, the estimated population size of male *C. scheidleri* dropped to one third from one year to another. Such an extent of population change does not seem to be extreme compared to other *Carabus* species. A *C. violaceus* population doubled in two successive years in a black locust forest habitat (Szél and Kutasi, 2011), while a *C. granulatus* population in an open wetland habitat quadruplicated its size in successive years (Sághy et al., 2005). The sudden drop of the population size experienced in our study could be the result of increased mortality. Stochastic events such as changes in environmental conditions (temperature, humidity) and weather extremes could be potential explanations. *Carabus* species are overwintering burrowed in the soil under plant debris, rotting vegetation and under tree bark. Little is known about the freezing tolerance of different species (but see Kivimägi et al., 2008; Ploomi et al., 2012) but carabids usually prefer microhabitats with relatively high winter minimum temperatures (Lövei and Sunderland, 1996). Although humidity requirements of carabids and *Carabus* species are well studied, its role in overwintering is not well documented (Thiele, 1977; Assmann, 2003). The winter of 2016/2017 in Hungary, unlike previous years, had unusually cold weather, especially in January 2017. Average monthly mid temperature is usually above 0 °C but was under − 4 °C in 2017. In terms of precipitation conditions, it was significantly drier than years before, with almost only two-thirds of the precipitation usual in for the season falling (OMSZ, 2022).

The number of overwintering marked beetles was low, suggesting a considerable, perhaps sex specific winter mortality in adults, which would be a simple explanation for the experienced decrease in population size. We could not test the year-to-year variation in winter survival. However, long-lived individuals can also stabilize the population if they account for a substantial part of the individuals.

The persistence of a population can also be the outcome of a meta-population structure (den Boer, 1970). The surrounding populations might be a source of immigrants and may compensate for local extinction. The fact that we estimated practically no immigration may indicate the lack of suitable source populations and could be considered as a factor that contributes to the temporal variability of the population. In our two years' study we could only detect the collapse of the *C. scheidleri* population without rapid recovery, underlying the isolation related volatility of the observed population. To some extent *C. scheidleri* is a pioneer species, for which large population fluctuations should not be uncommon. The suburban forest this species was collected in is also a pioneer forest, with few fast-growing tree species (*Fraxinus*, *Acer*) and many shrubs. *C. scheidleri* tends to disappear with vegetational succession and is less common in climax forest communities (Kádár et al., 2017). Such sudden inter annual population collapses were also experienced in other *Morphocarabus* species. A population collapse and recovery of *C. excellens* was reported in the Lysa Hora park Kyiv, Ukraine. It was dominant in the late '90 s almost totally disappeared to 2017, and recently this species is dominant again (Putchkov et al., 2019).

Population changes, habitat isolation and dispersal behavior interact with each other. Movement behavior around habitat borders play a key role in influencing metapopulation processes. In a Czech study radio tagged *C. ullricii* when released on a habitat border, usually moved towards the interior of the preferred habitat (forest), where their movement could be described as random walk. Individuals that entered the less preferred habitat patch (grassland) moved there faster and in a more directional way (Růžičková and Veselý, 2018). An Italian study with *C. olympiae* also found more "convoluted" trajectories in the preferred forest habitat and more directional movement in open habitats (Negro et al., 2008). In another cursorial predatory arthropod, the wolf spider *Pardosa agrestis*, the directionality of movement was suggested to decrease with scale, meaning that individuals were likely to bounce back when reaching a boundary to an unfavorable habitat (Samu et al., 2003). A meta-analysis on Carabidae case studies (Magura et al., 2017) indicated that different edge types have different effects. Edges maintained by natural processes were more penetrable for forest specialist species, allowing population exchange, while these species could penetrate anthropogenic edges with a lower probability. Conversely, natural forest edges proved to be a strong barrier for open habitat species that could more easily enter a forest habitat through edges maintained by human interventions. Based on these literature data, we may speculate that an edge effect is likely to play a role in the movement of the studied *Carabus* species, with an overall effect that the population is less likely to spread out from the habitat patch compared to a hypothetical case with a random walking pattern of the individuals crossing natural edges.

The displacement pattern of *Carabus* species found in our study can be compared to movement patterns of similar species studied by radiotelemetry. Such studies indicated that *C. monilis*, the western European vicariant of *C. scheidleri*, moved 5.4 times faster in a forest habitat than in open area (Riecken and Raths, 2000). Similarly, decreased activity of *C. scheidleri* in more open thinned or clear-cut forests, and high movement fidelity in mature forest (control) habitats was observed (Elek et al., 2018). In our investigations *C. scheidleri* individuals moved with as high a speed as *C. monilis* exemplars in open habitats, albeit the majority of beetles displaced short distances. In our study *C. ulrichii* also moved short distances. Relative to radiotelemetry results reported in a Czechian study (Růžičková and Veselý, 2018), individuals in our study moved 6–12 times shorter average distances. However, it must be taken into account, that in the radio telemetry study distances covered were measured by establishing positions at every 3 h, whereas in a mark recapture study we measure net displacement over variable periods (whenever the next capture occurs). These studies have a different resolution. Regarding the present study, releasing beetles at 1 m from the trap where they were captured originally could hardly cause a bias, since recaptures in the same trap amounted for only 8% in the case of *C. scheidleri* and 3% in the case of *C. ulrichii.* Still, these comparisons suggest that in both species displacements were more restricted in the studied urban park compared to rural environments, leaving the question unanswered whether such a phenomenon is related to habitat quality or to habitat size.

The estimated population biological parameters especially the life history characteristics of *C. scheidleri* has been studied extensively (Andorkó and Kádár, 2009). This species is among the large bodied *Carabus* species with a flexible within year reproductive rhythm, two activity peaks and overwintering individuals reproducing in successive years (Andorkó and Kádár, 2009). The results presented in our study can refine the knowledge about *C. scheidleri*'s ecology. It seems in a suburban park they have a similar life history to what we have learned from rural environment studies. The flexible reproduction rhythm, unique among central European *Carabus* spp., was observed in our study as well.

The high early spring activity of the beetles consisted of both overwintering and freshly hatched individuals. A single teneral female was found as late as July, underlying the flexible reproduction present in this beetle's biology. The peak activity in June indicates the main mating period. A secondary mating period could not be observed until August, although it can be possible later in the autumn, from which period our investigation lacks data. In a pioneering rearing experiment, under outdoor ambient conditions a single female *C. scheidleri ssp. helleri* laid seven eggs over two days at the end of August (Arndt, 1982). Larval development from egg to L3 larva took about 45–60 days; L3 phase lasted also about 15–20 days unless the beetles went overwintering. Pupae phase lasted also 15–20 days, so the net development time without overwintering would take 75–100 days (Arndt, 1982). This means that beetles from the eggs laid at the end of May, beginning of June can reproduce from August to September. *Carabus scheidleri* can have two reproductive periods, one in early summer and another in late summer – early autumn. They overwinter as adults and larvae and may lay high number of eggs. Overall, with this strategy they can easily outnumber other competitors or colonize new habitat patches. This life cycle is remarkably similar to the cohort splitting life history strategy described in the wolf spider *Pardosa agrestis*. Similarly to *C. scheidleri*, *P. agrestis* is also a dominant wolf spider in ephemeral and anthropogenic habitats, outnumbering there congeneric spiders with less flexible developmental strategies (Kiss and Samu, 2005; Rádai et al., 2020).

In Hungary *C. ulrichii* represents a eurytopic forest species, with a preference for oak forests with closed canopy cover and moderate light (Kádár et al., 2017; Fülöp et al., 2021). In Western-Europe this species is also present in the fields and is less strictly a forest specialist (Hurka, 1996). *C. ulrichii* was a subdominant species in our study, which is also well known regarding its life history characteristics. This species is among the large bodied spring breeders with one reproductive period, low fecundity, two activity peaks. According to Verhoeff (Verhoeff, 1921), who was able to raise the species in laboratory conditions, larval development took from eggs laid to pupae 86 days. According to these observations the larvae develop from April to the end of July. The activity of the newly hatched individuals causes the second autumn activity peak. *C. ulrichii* specimens, after a foraging period in autumn, overwinter as adults (Kádár et al., 2017). We found evidence that generations overlap; not only young individuals can overwinter, unlike suggested before (Andorkó, 2014), albeit the number of overwintering individuals was low, only 3 marked specimens (2 males, 1 female) were recaptured in successive years.

According to our observations, both species may overwinter both as larvae and as adults. Overwintering in two different life stages may stabilize the population and prevent sudden extinction attributable to any stochastic effect that only one life stage is sensitive to den Boer (1970). We think that this phenomenon is probably not connected to the suburban environmental conditions, but is a general, previously overlooked biological feature, at least in the moderate climate of Europe. Based on our results and published data (Andorkó and Kádár, 2009; Kádár et al., 2017; Fülöp et al., 2021) the two species seems to have slightly different habitat preferences. *Carabus scheidleri* is usually more abundant in moderately shaded habitats while *C. ulrichii* prefers more closed canopy forests. The possible explanations behind this pattern could be competition or differences in microhabitat use. According to a comparative study of mature, old growth and beech-forests in Croatia, aged 60, 80 and 150 years, respectively, *C. scheidleri* occurred in the last two age classes, and was far most dominant in the ancient forest. *Carabus ulrichii* occurred in all forest types, with the highest abundance in the old growth forest (Jelaska et al., 2011). The assumption of interspecific competition is controversial among carabid assemblages (see Niemelä, 1993) and we did not undertake any direct investigation of it, although it is still possible that in different environments *C. ulrichii* and *C. scheidleri* outcompete each other. Regarding the microhabitat preference and diet of the two species our knowledge is very limited especially with respect to the larval stages. Overall, an unambiguous explanation of the observed pattern could not be made without further investigations.

The density estimates for *C. scheidleri* and *C. ulrichii* have not been reported prior to our study, therefore any evaluation of the received density figures is only possible in comparison to other *Carabus* species studied in rural environments. The density of *C. scheidleri* is comparable to the density of *C. auronitens*, a common eurytop, silvicol species, having the highest published density (Weber and Heimbach, 2001). While *C. ulrichii*'s density was as low as the lowest published value, observed for *C. nemoralis* a common eurytop, silvicol species (Weber and Heimbach, 2001). *Carabus scheidleri* can be considered a common and *C. ulrichii* a rare species in the studied suburban park. The question is whether *C. scheidleri* and *C. ulrichii* can stabilize their populations, or whether the population is large enough to maintain a viable population. Based on Franklin's rule a viable population with evolutionary potential must count 50 individuals to stay alive for a short period, and 500 to stay alive for longer time (Franklin, 1980). The population size of all the species found in our experiment were lower than the long-term survival limit.

5. Conclusions

We experienced high fluctuation in the population size of *C. scheidleri* and *C. ulrichii*, low dispersal power, varying densities and the potential of competition between the two species. Therefore, we must presume that these species are able to hold viable populations in a suburban park fragment only in a larger network of metapopulation structure. Habitat islands, green areas are refuge places for living organisms in cities. Biologists in search for biodiversity patterns describe and analyze the complexity of these patterns and are searching for the key drivers in urban biodiversity (Lepczyk et al., 2017). To the question, what's the worth of biodiversity, there is an economic answer: in a highly urbanized area like Budapest, property prices are the highest in the suburbs with connection to urban forests. This is one of the few cases when economists and biologists agree, biodiversity is important, and highly valuable. The results of this study showed that an urban park has a significant importance in preserving large bodied predatory *Carabus* species.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02086.

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