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METHODS

Using temporary emigration to inform movement behaviour of cave-dwelling invertebrates: a case study of a cave harvestman species

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Abstract. 1. Understanding of animal movement behaviour is critical for developing appropriate conservation strategies because of its profound implications for predicting species' responses to perturbations. To date there is a substantial knowledge gap of the movement behaviour of subterranean invertebrates.

2. In this study temporary emigration (TE), the probability that an individual is absent from the cave on a given sampling occasion, was used as a method to inform on the movement and behaviour of cave-dwelling invertebrates. Because these animals are difficult to study with traditional tracking techniques, the capture–recapture (CR) modelling framework was used to assess TE and to account for imperfect detectability and unobservable states.

3. Specifically, the influence of season, sex, and surface weather variables on the TE of the facultative cave-dwelling harvestman species, *Paranemastoma sillii sillii* (Herman, 1871), was investigated. Multistate CR models were used while accounting for individual heterogeneity on 999 individually marked adults of two populations inhabiting two caves, located in southwestern Romania.

4. Harvestmen demonstrated clear heterogeneity and seasonality in TE. Findings showed that the TE of harvestmen exhibited variation between caves and there was little support for surface weather variables influencing TE and for sex-specific TE patterns.

5. These results show that the study of TE patterns is useful to gain valuable insights into movement and intrinsic behavioural processes of cave-dwelling harvestmen. The method could potentially be used for other invertebrate groups with similar movement characteristics and when traditional tracking techniques are difficult.

Key words. Facultative cave-dwelling species, harvestman, movement behaviour, multi-event models.

Introduction

Understanding animal movement behaviour is critical for developing appropriate conservation strategies because of its profound implications for predicting species' response to perturbations given the unprecedented environmental changes (Jacoby *et al.*, 2012). Animal movements are inextricably bound to behavioural processes, e.g. animals move to feed, find mates and avoid predators or unfavourable environmental conditions (Miriam *et al.*, 2013), and understanding why and how animals move is not complete without an understanding of the animal behaviour.

To date, there is a substantial knowledge gap in the movement behaviour of invertebrates. The literature exploring movement behaviour primarily focuses on large animals, whose movements can be easily followed in their living environments, e.g.

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for birds, mammals, rodents (Edwards *et al.*, 2007; Gurarie *et al.*, 2009). Recently, advances of technology increased the number of smaller species chosen as study objects, whereby terrestrial epigean species, such as dragonflies, butterflies, collembolans and ants, have been investigated (Amorim *et al.*, 2008; Ovaskainen *et al.*, 2008; Robinson *et al.*, 2008; Dolný *et al.*, 2014). However, compared with epigean habitats for subterranean invertebrates and their populations, such studies do not yet exist, although the endogean fauna is clearly dominated by invertebrates (Gibert & Deharveng, 2002).

Cave-dwelling invertebrates are difficult to study (Elliott, 2006). The most commonly used techniques (e.g. radio transmitters or satellite technology) to track animal movement patterns and behavioural processes (Rubenstein & Hobson, 2004) are of no use in caves. Other techniques such as individual recognition tags have been used for many large animals (Gibbons & Andrews, 2004) but few studies have successfully used tags for smaller species (Harper & Batzli, 1996; Buhlmann & Tuberville, 1998). Advances in the design and application of stable isotope markers can allow them to be used for insect studies (Hobson, 2005), but their expense can limit their usage. Paint or ink marking is inexpensive and nondestructive but it is tedious and time-consuming (Hagler & Jackson, 2001) especially for small species. At the same time, this procedure might be impractical for non-obligate cave-dwellers, i.e. sub- and troglophiles, species that are associated with cave environments but might require epigean habitats to complete biological functions such as feeding or reproduction, or trogloxenes, species that cannot live exclusively in caves (Sket, 2008). For these species, measurements of movement behaviour require following individuals both in caves and in the above-surface habitats and under-surface layers, i.e. litter, soils, substrata voids and rocks. Compared with caves, tracking invertebrates in those habitats is notoriously difficult.

Capture–recapture (CR) data collected under the Pollock's robust design, e.g. sampling replication (secondary occasions) within each season (primary occasions), is the basis for estimating unbiased demographic parameters in the presence of temporal emigration (TE) and for estimating TE (Kendall *et al.*, 1997). However, very often secondary capture occasions are lacking, and therefore to estimate TE, multistate CR methods have been developed (Pradel, 2005). Temporal emigration is widely recognised in animals and plants and attributed to a physiological condition, reproductive status, behavioural state or location (Schaub *et al.*, 2004). Temporal emigration is defined as the transition from an 'observable' state to an 'unobservable' state, and back to an 'observable' state (Chapple *et al.*, 2016). Individuals can move between the states, such that the transition from an 'observable' to an 'unobservable' state is emigration, the probability that an individual has moved out (emigrated) from the study area between capture occasion i and $i + 1$, while the transition back to an 'observable' state is immigration, the probability that an individual has returned (immigrated) to the study area between capture occasions. Therefore, a multistate CR model including TE gives additional information about migratory (back and forth) movements of non-obligate cave-dwelling species. The approach requires capture–mark–recapture of individuals only in one study area, e.g. cave. This is important since the CR of individuals in the subsurface substrata and surface habitats is nearly impossible due to individual movements upwards and downwards between the above-cave substrata or out of and into the cave.

Mutistate CR methods have also been developed to model individual heterogeneity in capture and demographic rates (Pledger *et al.*, 2003; Pradel, 2009; Gimenez & Choquet, 2010; Gimenez *et al.*, 2018). There is increasing evidence that unmodelled individual heterogeneity causes negative bias in capture and survival (Pledger & Efford, 1998; Fletcher *et al.*, 2012; Gimenez *et al.*, 2018). For accurate estimates of demographic parameters, individual heterogeneity should be considered and accounted for in CR studies.

In this study, we tested the TE approach of multistate CR models to overcome the technical challenges described earlier and to enable the study of migratory movement behaviour of non-obligate cave invertebrates using a harvestman species, *Paranemastoma silli silli* (Herman, 1871). We applied a multistate CR model while accounting for individual heterogeneity on 999 individually marked adults of two *P. s. silli* populations inhabiting two caves, located in southwestern Romania. Specifically we investigated the influence of season, sex, and surface weather variables on TE. We predicted that season would affect TE since harvestmen are expected to emigrate out of caves in spring, summer and fall to feed and immigrate into caves in winter when surface environmental conditions are harsh. We hypothesised that TE would differ among caves due to their microclimates (Decu *et al.*, 1967). As weather is known to affect the demography of certain organisms, we expected the surface weather variables to have an effect on TE. We expected to find sex-specific patterns in TE because males and females vary in their mating strategies. As males actively search for females for mating opportunities, we expected higher TE in males than in females.

Materials and methods

Species, study area and capture details

Paranemastoma sillii sillii is an endemic harvestman species in the Carpathian Mountains (Decu *et al.*, 1967; Avram & Dumitrescu, 1969) that inhabits both caves and outside habitats, especially beech forests. The species feeds omnivorously upon small invertebrates, fungi, and plant material. The female lays eggs from which nymphal instars hatch depending on environmental conditions in up to half a year. The development time from egg to adult is ~3 months. The adult life span is up to 28 months (R. Plăiaşu & R. Băncilă, pers. obs.).

We conducted a CR study of *P. s. sillii* in two caves, Closani and Lazului. The caves are located in the Mehedinti Mountains, in southwestern Romania, at 433 and 370 m a.s.l., respectively. The caves are *c.* 3 km apart. The caves differ in their hydrological regime, surface vegetation and food resources. Closani Cave is a hydrologically inactive cave and the habitat above it consists of scree and subcontinental peri-Pannonic shrubs, such as *Prunus* sp., *Cornus* sp., *Crataegus* sp., *Cotinus* sp., and *Syringa* sp. The cave has a total length of 1458 m and has a small entrance. The two main horizontal passages of the cave are covered mostly with clay. Lazului Cave is a hydrologically active cave and is located in a beech forest. It is 2200 m long, has a wide entrance and consists of a mixed network of fossil, subfossil and active galleries. The cave passages are covered mostly with stones, except for some parts of the lower-level passages, which are covered by sand and gravel, and of the upper level passages, which are covered with clay. Closani Cave has old guano deposits, whereas in Lazului Cave small amounts of fresh guano are present. In both caves the guano-producing bats are insectivorous.

In both caves, several passages were flooded during some of the scheduled capture occasions and therefore not accessible, whereas chimneys were difficult to sample on a regular basis because special rope-climbing techniques are required. Thus, based on cave passages' accessibility and previous observations of the spatial distribution and preferred microhabitats by harvestmen in the two caves (see Plăiaşu *et al.*, 2017) we selected three sampling transects: (i) a transect of 300 m in Closani Cave that started from the entrance of the cave and covered the entire width of the main gallery, which is *c.* 7 m; (ii) a transect of 200 m in the lower level of the Lazului Cave main gallery; the transect stretched from the entrance and was 3 m wide; and (iii) a transect of 20 m in the upper level of Lazului Cave hall covering a width of 15 m. While we cannot exclude the possibility that harvestmen migrated to inaccessible places, i.e. chimneys and flooded passages, for the following reasons we predicted migratory movements of harvestmen from and to caves, rather than to other places in caves: (i) the harvestman is a trogophilic species and therefore, individuals are expected to migrate both to surface habitats to feed or to avoid subterranean extreme events, such as flooding and to caves to avoid harsh surface environmental conditions, such as extreme hot temperatures and severe droughts; (ii) although not studied in this species, harvestmen prefer humid but not damp habitats and therefore it is unlikely that harvestmen will remain in the flooded passages of the cave; (iii) before starting the mark–recapture study we documented the spatial distribution of harvestmen in both caves and we included in the study the cave zones with the highest probability of harvestmen occurrence (Plăiaşu *et al.*, 2017). Harvestmen were never observed in the chimneys. They were mostly distributed on the cave floor and exhibited a clumped distribution around food resources or due to their gregarious behaviour.

To capture *P. s. sillii*, visual encounter surveys were conducted by the same two experienced researchers (RP and RB). The researchers searched the floor and walls and under rocks and logs. For each capture occasion the researchers spent 4–5 h in each cave. As the main aim of the study was to investigate seasonal variation of movement, the capture occasions were conducted monthly for a year, between December 2008 and November 2009, to cover the four seasons characteristic of a temperate continental climate. Capture sessions were done on the same date of the month to assure an equal capture interval, and at the same hour during the day to avoid overlooking harvestman due to their emigration from the cave to feed or as part of their activity rhythm. All captured adult harvestmen were sexed and individually marked using non-toxic acrylic ink following the procedures described in Mestre and Pinto-da-Rocha (2004). The adult harvestmen were sexed based on the body shape and the cheliceral morphology (Avram, 1973b). The individuals with nymphal characteristics were not marked because they moult six times in ~2.5 months (Avram, 1973a). To individually mark each harvestman, we used a combination of different colour marks: for units 1–8, we drew one horizontal line on the femur of the corresponding leg, where legs were counted clockwise; for unit 9 we drew two horizontal lines on the femur of the first leg; for units 10–90s we drew different symbols (i.e. .., ..., … ., >, <, ∨, ∧, Δ and ∇) on the scutum magnum; and for units 100–900, we used different colours and the + symbol drawn on the scutum magnum. To draw the marks we used a very fine brush that allowed application of a very thin yet recognisable layer of dye. All marks were recognisable until the end of the study. The time needed to mark one individual was less than 10s. The marked individuals were released at the place of capture.

The 24-h temperature and rainfall values were recorded at 6-h intervals at Closani village (Romania), with an iROX PRO-X portable weather station. Temperature and rainfall were included in the study as mean air surface temperature and mean precipitation during the day of the capture occasion and during the week prior to the capture occasion (henceforth abbreviated tempm, precipm, tempw and precipw, respectively). Before the analysis, all environmental covariates were standardised to have mean zero and unit variance.

Data analysis

We analysed the CR data of harvestmen over a period of 11 months using multistate CR models (Lebreton *et al.*, 2009) expressed as multi-event models (Pradel, 2005). We recorded the 'events' as 'seen' and 'not seen' and considered the states 'alive and observable' (OU), 'alive and unobservable' (UO), and 'dead' (D). Individuals that are in the state 'unobservable' and 'dead', during a sampling occasion are unavailable for recapture, and therefore the corresponding recapture probability is fixed to 0. Individuals are allowed to move between the states, such that the transition from an 'observable' to an 'unobservable' state is the act of emigration, the probability that an individual has moved out (emigrated) from cave between capture occasion i and $i + 1$, while the transition back to an 'observable' state is the act of immigration, the probability that an individual has returned (immigrated) to the cave during the capture occasion.

To include individual heterogeneity in TE, we built two discrete classes of individuals, g_1 and g_2, which refer to two possible paths at the first observation. The classes are states of the multi-event model: 'alive and observable in g_1', 'alive and unobservable in g_1', 'alive and observable in g_2', and 'alive and unobservable in g_2'. The classes are associated with distinct values of initial states.

For model formulation, we considered: (i) $P\Pi$, the vector of probabilities of presence in the various initial states (π), (ii) $P\Phi$, the matrix of survival probabilities (S); (iii) $P\psi$, the matrix of transition probabilities (ψ) corresponding to TE; and (iv) PB, the matrix of detection probabilities (p). The full description of the vectors and matrices can be found in the Supplementary Material Online Resource 1.

Because the transition probabilities depend only on the states in which an individual was before a transition, we modelled

TE as a Markovian or state-dependent transition (Schaub *et al.*, 2004).

Model selection

We were interested in TE, but different model structures can be used to model the sampling process and the survival upon which the TE is conditional (Pradel, 2005). For example, one may hypothesise that the recapture (the probability that an animal is alive and remains in the study area, i.e. in the cave, and hence is available for capture and is encountered at occasion *i*) differs among observers due to different levels of experience. Both capture and survival probabilities may vary with time, (e.g. occasion, season) or time-specific covariate (e.g. weather), or harvestmen can exhibit cave and sex-specific capture and survival probabilities. Consequently, we considered models representing different combinations of observer, time, cave, sex, season, tempm, and precipm on capture probability, and cave, sex, season, tempw, and precipw on survival probability. To assess the hypotheses of TE, we built models representing combinations of the same covariates as the survival probability. We distinguished between models with and without individual heterogeneity by considering no classes or two classes, respectively, in the matrix of transition probabilities associated with distinct values of the initial states (for details see Online Resource 1).

In total, we designed 119 models. We used E-SURGE 1.9.0 (Choquet *et al.,* 2009a) to perform model selection based on Akaike's information criterion corrected for small sample size (QAICc) (Burnham & Anderson, 2002) and to obtain maximum likelihood estimates of the parameters. In the results, for brevity, we chose to present only the models with ΔAICc < 20.

Goodness-of-fit

Goodness-of-fit tests were performed on CR histories. We used the Test3.SR method from the U-CARE software to test for transience [i.e. lower chance of recapture of first encountered individuals than individuals already encountered (Pradel *et al.*, 1997, Choquet *et al.*, 2009b]. We used Test2.CT to test for trap-dependence and in particular for trap-happiness (i.e. higher capture probability at time $t + 1$ for living individuals that were captured at time t than living individuals not captured at time t) (Choquet *et al.*, 2009b). We computed the overall and separate cave and sex GOF-statistics for transience and trap-dependence, from Test3.SR and Test2.CT, respectively.

Results

A total of 1524 captures of 999 individual harvestmen were made, as follows: (i) in the Lazului Cave, 344 captures of 323 males and 407 captures of 262 females; and (ii) in the Closani Cave, 350 captures of 228 males and 423 of 186 females. The number of unmarked, marked and the total number of males and females caught at each capture occasion (i.e. monthly) for each cave are provided elsewhere (see Plăiaşu *et al.*, 2017).

The directional tests for transience and trap-happiness were statistically non-significant, and thus there was no need to correct for transience or trap-happiness or to account for overdispersion (Table 1).

From the set of candidate models, the data best supported the model with individual heterogeneity and an effect of season on TE; along with cave and sex effects on survival, and cave, sex and tempm effects on recapture (Table 2). The model without heterogeneity, but with season and cave effects on TE, along with cave and sex effects on survival, and a time effect on recapture, received some support and was ranked second with 3.860 ΔAICc (Table 2).

Based on the best model, recapture decreased with higher temperature during the day of capture occasion in both caves and sexes, being higher in males than in females (Fig. 1a,b). In both caves, females and males exhibited high survival probabilities (Fig. 2). Emigration probability was high in autumn, spring and summer for g_1 individuals and low for g_2 in all seasons except winter (Fig. 3). The immigration was high in winter for g_1 individuals and in autumn for g_2 individuals (Fig. 4).

Discussion

Application of a multistate CR model allowed the estimation of relevant demographic parameters to inform movement patterns and behavioural processes of a non-obligate cave-dwelling harvestman species. Our approach revealed evidence for individual heterogeneity and seasonality in TE.

Table 1. Goodness-of-fit tests showing no transience, trap-happiness or overdispersion; d.f. degree of freedom; *P* level of significance.

		Closani Cave					Lazului Cave				
		3.SR	3.SM	2.CT	2.CL	Global	3.SR	3.SM	2.CT	2.CL	Global
Male	χ^2	2.93	26.51	10.13	11.17	50.74	7.74	2.4	9.73	8.67	28.54
	d.f.	10	11	9	10	40	9	5	8	8	30
	P	0.98	0.001	0.34	0.32	0.12	0.56	0.79	0.31	0.37	0.54
Female	χ^2	3.59	3.7	4.93	16.06	28.28	5.55	4.54	6.2	5.86	22.15
	d.f.	9	11	9	12	41	7	5	7	6	25
	P	0.94	0.98	0.84	0.19	0.93	0.59	0.47	0.52	0.44	0.63
Pooled	χ^2					79.02					50.69
	d.f.					81					55
	P					0.54					0.64

Table 2. Model selection with deviance (DEV), Akaike's information criterion corrected for small sample size (AICc), differences in AICc (ΔAICc) and number of estimable parameters (K) for the candidate models with $\Delta AICc < 20$ (for brevity, models with $\Delta AICc > 20$ are not shown). The candidate models vary in the presence (h+) and absence (h−) of heterogeneity in temporary emigration (TE) and effect of cave (a group variable with two categories: Closani Cave and Lazului Cave), sex (a group variable with two categories: female and male), season (a group variables with four categories: autumn, spring, summer, winter), time (capture occasion time effect), tempm (mean air surface temperature during the day of capture), tempw (mean air surface temperature during the week prior to the capture occasion), precipw (mean precipitation amount during the week prior to the capture occasion); +, additive effect; :, interaction effect.

Model		Survival	TE	Recapture	*K*	DEV	AICc	ΔAICc
1	h+	Cave + sex + cave : sex	Season	Cave + sex + tempm	30	5931.324	5991.946	0.000
2	h−	Cave + sex	Cave + season	Time	23	5949.438	5995.806	3.860
3	h+	Cave + sex	Cave + season	Cave + sex + season	28	5942.382	5998.924	6.979
4	h+	Cave + sex	Cave + season	Sex + season	28	5943.232	5999.774	7.828
5	h+	Cave + sex	Cave + sex + tempw	Cave + sex + tempm	46	5907.283	6000.735	8.789
6	h+	Cave + sex	Season	Cave + season	26	5947.876	6000.344	8.398
7	h+	Cave + sex	Sex + season	Cave + sex + tempm	38	5924.895	6001.888	9.942
8	h−	Cave + sex + season	Cave + sex	Cave + sex + tempw + precipw	28	5945.477	6002.020	10.074
9	h−	Cave + sex + season	Cave + sex	Cave + season	20	5966.626	6006.905	14.959
10	h−	Cave + sex + season	Cave + sex	Cave + sex + season	24	5959.481	6007.881	15.935

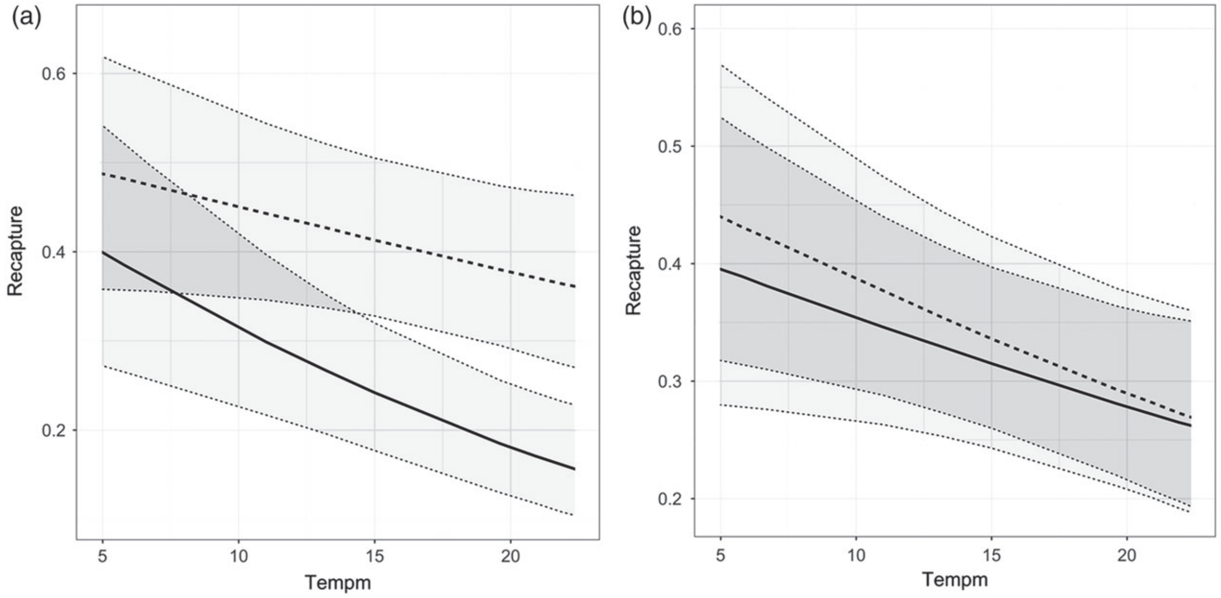

Fig. 1. Effect of mean air surface temperature during the day of capture (tempm) on monthly recapture probabilities of female (solid line) and male (dashed line) harvestmen in Closani (a) and Lazului (b) caves. Estimates are based on the most parsimonious capture–recapture model (model 1 in Table 2). The shaded areas represent the 95% confidence intervals.

Several studies have documented individual variation (individuality) in movement patterns (Vardanis *et al.*, 2011; Brodersen *et al.*, 2012). The recognition of individuality can provide novel insights into the causes and consequences of individual differences in movement. Using assumptions of two heterogeneity classes in the model construction, we showed significantly different patterns of emigration/immigration among seasons between the two classes. Individual heterogeneity has been linked to genetic differences or different experienced conditions during development (Fox *et al.*, 2006), variation in individual quality and strategies (Hamel *et al.*, 2008), sex-specific dispersal rates, or different behaviour (Whitehead & Wimmer, 2005; Crespin *et al.*, 2008).

We cannot disentangle the mechanisms causing individuality in our study. To understand and predict the individuality in the movement patterns of facultative cave-dwellers, future research is needed. Behavioural studies under both natural and experimental conditions (in which the availability of food resources can be manipulated) should investigate how non-obligate cave-dwelling species decide to leave the cave. Individual-level mechanisms, such as individual foraging behaviour and information use, which are the main drivers governing departure decisions and central to optimal foraging theory (Giraldeau & Caraco, 2000), would be worth investigating. Moreover, for animals that are able to choose feeding patches, as is the case with troglophiles, the profitability of

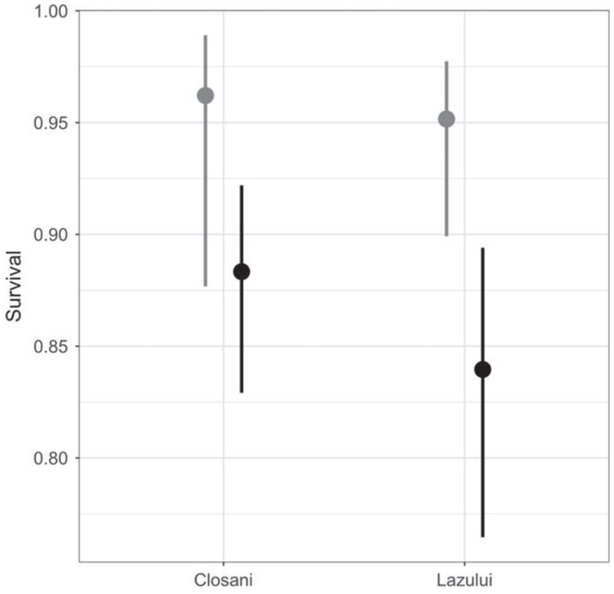

Fig. 2. Estimated monthly survival probabilities of female (grey) and male (black) harvestmen in Closani and Lazului caves. Estimates are based on the most parsimonious capture–recapture model (model 1 in Table 2). The vertical bars represent the 95% confidence intervals.

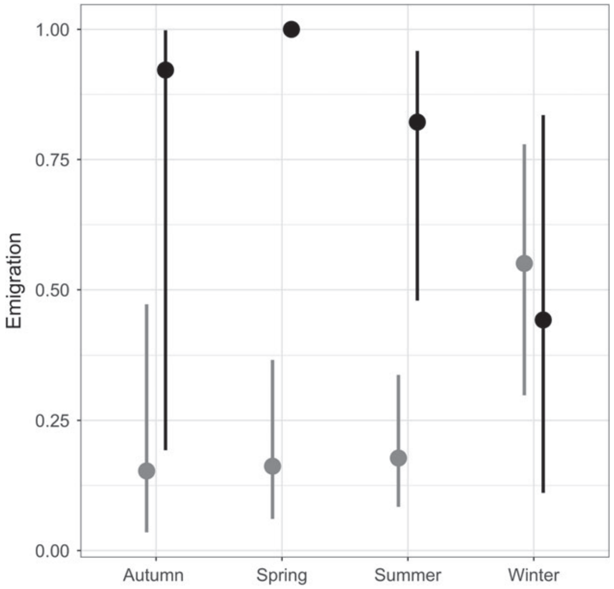

Fig. 3. Estimated seasonal emigration rates of harvestmen from the two heterogeneity classes, g_1 (black) and g_2 (grey). Estimates are based on the most parsimonious capture–recapture model (model 1 in Table 2). The vertical bars represent the 95% confidence intervals.

a feeding patch depends not only on the food abundance but also on the presence and quality of competitors (Fretwell & Lucas, 1970). In cave systems, food resources are scarce, potentially causing cave-dwellers to experience strong inter- and intraspecific competition (Manenti *et al.*, 2015). Theory predicts that individuals showing good competitive abilities are allowed to choose the feeding patch with the most abundant food, whereas individuals with less competitive abilities have to feed away from individuals with good competitive abilities (Van Duren & Glass, 1992). Therefore, future experimental studies are required to test whether good competitors are more likely to leave the cave to feed in the surface habitats than their less successful competitors.

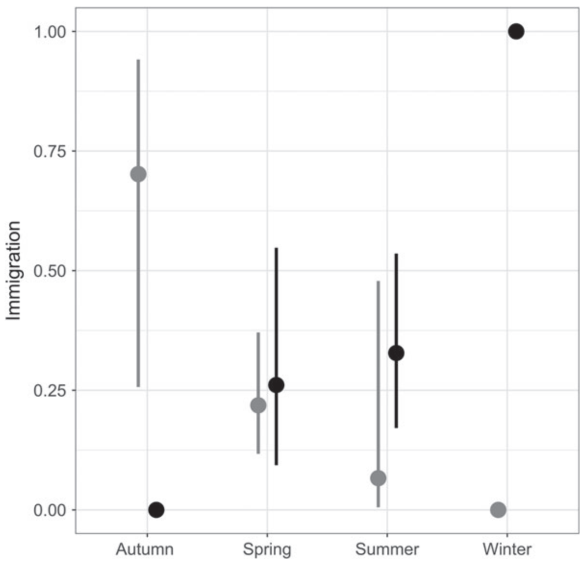

Fig. 4. Estimated seasonal immigration rates of harvestmen from the two heterogeneity classes, g_1 (black) and g_2 (grey). Estimates are based on the most parsimonious capture–recapture model (model 1 in Table 2). The vertical bars represent the 95% confidence intervals.

Seasonal variation in TE is probably linked to foraging or reproductive behaviour of *P. s. sillii*. The harvestman is a troglophilic species (Avram & Dumitrescu, 1969) and consequently could rely on surface habitat to complete vital functions such as feeding. It is therefore expected that *P. s. sillii* illustrates strong emigration/immigration seasonality with high emigration and low immigration in spring, summer and autumn, and low emigration and high immigration in winter. Our TE models confirmed the expected variation of emigration/immigration movements among seasons. Our results are also in agreement with studies on activity rhythm of other facultative cave-dwelling harvestman species. Several studies showed that harvestmen use caves as shelters, but will periodically leave the cave to forage or for reproduction (Hoenen & Gnaspini, 1999; Gnaspini *et al.*, 2003; Machado *et al.*, 2003; Chelini *et al.*, 2011). In addition, our finding is in line with previous reported foraging movements of facultative cave-dwellers (Kunz, 1982; Fagan *et al.*, 2007). Due to the limited food resources in caves, it has been reported that many non-obligate cave-dwelling species (*sensu* Sket, 2008) of bats (Kunz, 1982) and crickets (Fagan *et al.*, 2007) leave the cave and forage primarily externally, rather than within the cave.

The results further indicate that if the individual heterogeneity is not accounted for, season and cave drive the observed emigration/immigration rates. The two studied caves have different microclimates (Decu *et al.*, 1967). They are characterised by different hydrological regimes, air flow, temperature, humidity, trophic resources, and outside surface habitat. This indicates that TE may be promoted by variability in cave microclimate. Although not studied in this species, harvestmen strongly respond to habitat heterogeneity (Mestre & Pinto-da-Rocha, 2004). Moreover, troglophilic species have shown habitat preferences, and their occurrence in caves is associated with specific cave environmental features (Lunghi *et al.*, 2014). This suggests that *P. s. sillii* might actively select caves and that the analysis of movement attributes in the light of the cave environmental conditions may be an attractive approach for designing future studies to identify habitats of facultative cave-dwelling animals.

We found little support for surface weather variables in controlling TE. Weather is known to affect the demography of organisms both directly and indirectly (Moreno & Møller, 2011). The lack of an effect of surface weather variables on TE suggests that caves are capable of buffering the fluctuations of external weather factors. Our current results therefore reinforce the hypothesis that for facultative cave-dwelling species, caves can function as refuges from unfavourable surface environmental conditions (e.g. too dry or too hot) (Manenti *et al.*, 2009; Manenti *et al.*, 2011; Ficetola *et al.*, 2012; Manenti *et al.*, 2013).

Results showed no significant support for sex differences in TE. We hypothesised sex-specific patterns in the TE of harvestmen because males and females vary in their mating strategies. As males actively search for females for mating opportunities, we predicted higher TE in males than in females. Sexual disparity in TE has been linked to disparate demography or behaviour (e.g. social and mating strategies) between sexes (Chapple *et al.*, 2016). However, movement is the result of interactions between morphology, physiological performances (movement capacity), and behavioural decisions (movement decision) (Ducatez *et al.*, 2012). Thus to understand the TE sex-dependency, additional studies are necessary to test the relationship between the TE and various movement traits.

Until recently, TE was known to generate complications in CR studies, and several approaches have been developed for dealing with these issues (Fujiwara & Caswell, 2002; Kendall & Nichols, 2002; Schaub *et al.*, 2004). In this study, we presented TE as the parameter of biological interest and we provided a pertinent framework within which to consider TE as transition between an 'observable' and 'unobservable' state. The TE approach of a multistate CR model can be applied to other studies to gain information on movement patterns and behavioural processes of animals that are difficult to track with the currently available intrinsic and extrinsic tracking techniques. Moreover, it can be used when a robust design (Pollock, 1982) cannot be implemented. However, an important assumption of the proposed modelling approach is that TE should be Markovian, i.e. the probability of being an emigrant is dependent on the state (migrant or non-migrant) in the previous occasion. When TE is random, it is necessary to sample all potential locations of marked individuals. We suggest using a multistate CR approach where unobservable states are inevitable, but in general we recommend setting up a study under Pollock's (1982) robust design.

Conservation implications

Cave systems are characterised by perpetual darkness, relatively constant humidity and temperature, and without many of the temporal environmental cues of surface environments. Due to these particularities, caves are unique habitats and many of them are biodiversity hotspots for invertebrates (Culver & Pipan, 2009; Souza Silva & Ferreira, 2016). While there is growing evidence that cave-dwelling invertebrates face an increased disturbance due to global environmental changes, reliable estimates of demographic parameters for cave arthropods are often lacking, thereby precluding the design of appropriate conservation and management practices of cave-dwelling invertebrates. In the current study we successfully developed an approach for studying the movement patterns of a facultative cave-dwelling harvestman species. Harvestmen play an important role in the food chain of cave communities (Reddell, 2012) and are common inhabitants of caves. Therefore demographic studies on harvestmen populations are useful to establish reliable conservation and management plans. Furthermore, the approach identified in this study could be used for other invertebrate groups with similar movement characteristics and when tracking and marking techniques other than ink or paint marking are impractical, difficult or too expensive to use. In terms of general conservation purposes, our study broadens the understanding of where and how cave-dwelling animals utilise cave systems. This is particularly important because it allows us to gain valuable insights into ecological effects and consequences of general processes such as subsurface dispersal or migration (Culver & Pipan, 2009) related to foraging and breeding movements (Woiwod *et al.*, 2001) that are fundamental to inform conservation actions.

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