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Raluca I Băncilă, Roger Pradel, Rémi Choquet, Rodica Plăiașu, Olivier Gimenez. Using temporary emigration to inform movement behaviour of cave-dwelling invertebrates: a case study of a cave harvestman species. *Ecological Entomology*, 2018, 43 (5), pp.551 - 559. 10.1111/een.12645 . hal-03499394

HAL Id: hal-03499394

<https://hal.science/hal-03499394>

Submitted on 4 Jan 2022

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

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27
28 **Abstract**

29 Cave systems are less transparent than surface habitats and significantly less is known about
30 movement patterns and intrinsic behavioural processes of cave-dwelling animals. Here, we introduce
31 temporary emigration (TE), the probability that an individual is absent from a cave at a given sampling
32 occasion, to inform about movement and behavior of cave-dwelling animals. Because these animals are
33 difficult to study with traditional tracking techniques, we resort to the capture-recapture (CR) modeling
34 framework to assess TE to account for detectability less than one and unobservable states. We
35 investigated the influence of cave, surface weather variables, season, individual heterogeneity and sex on
36 the TE of the subtroglophile harvestman species, *Paranemastoma silli*. We used multistate CR models on
37 999 individually marked adults of two *P. silli* populations inhabiting two caves, Closani and Lazului
38 Caves, located in the Mehedinti Mountains in southwestern Romania. Adult harvestmen demonstrated
39 clear seasonality and heterogeneity in TE. We found that TE of harvestmen exhibited between caves
40 variation and there was little support for surface weather variables in controlling TE and for sex specific
41 TE patterns. Our results highlight that the study of TE patterns is useful to gain valuable insights into
42 movement and intrinsic behavioural processes of cave-dwelling species.

43
44 **Key words:** animal movement and behavior, cave-dwelling species, individual heterogeneity,
45 season, temporal emigration
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Introduction

Understanding animal movements is important in animal ecology because of the profound implications for population dynamics (Piper 2011). Animal movements are inextricably bound to behavioural processes (Miriam et al. 2013), e.g. animals move to feed, find mates and avoid predators or unfavorable environmental conditions. Hence understanding why and how animals move is not complete without an understanding of the animal behaviour. Furthermore, several studies have documented individual variation (individuality) in movement patterns (Vardanis et al. 2011; Brodersen et al. 2012). The recognition of individuality can provide fresh insights in the causes and consequences of individual differences in movement that behavioural ecology has already taken.

The literature exploring animal movement and behaviour is primarily focused on terrestrial and oceanic systems. Cave systems are much less transparent and significantly less is known about movement of cave-dwelling animals. Understanding where and how cave species travel through space is particularly important. This will allow us to gain valuable insights into broader ecological effects and consequences of general processes such as subsurface dispersal or migration (Culver and Pipan 2009) or behavioural processes such as foraging and breeding movements (Woiwod et al. 2000).

However, cave-dwellers, especially invertebrates, are difficult to study. The most commonly used techniques (e.g. radio transmitters or satellite technology) to track animal movement patterns and behavioural processes (Rubenstein and Hobson 2004) are of no use in caves. Individual tags provided good data for larger animals but not for many smaller ones. Advances in the use of stable isotope markers offer new promise for insects (Hobson 2005) but the cost are still prohibitive.

Multistate capture-recapture (CR) methods allow estimation of temporary emigration (TE) (Pradel 2005). TE is the transition from an “observable” state to an “unobservable” state, and back to an “observable” state (Chapple et al. 2016). TE is widely recognized in animals and plants and was attributed to a physiological condition, reproductive status, behavioural state or location (Schaub et al. 2004). Here,

we argue that an important application of TE, especially for cave-dwellers, is to inform about animal movements over space, e.g. emigration from and immigration to cave. Frequently sampling is conducted only in cave. Considering a multistate CR model with states “observable” and “unobservable” between which individuals are allowed to move, the transition from an “observable” to an “unobservable” state is the 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 immigration, the probability that an individual has returned (immigrated) to cave during capture occasion. Multistate CR methods have been also developed to model individual heterogeneity in capture and demographic rates (Pledger et al. 2003; Pradel 2009; Gimenez and Choquet 2010) and there is increased evidence that unmodeled individual heterogeneity causes bias in capture and survival estimates (Pledger and Efford 1998; Fletcher et al. 2012). While individual heterogeneity is expected in movement patterns, no CR study investigated the effect of individual heterogeneity on TE.

Subtroglaphiles are a category of non-obligate cave-dwellers defined as species intimately associated to cave environments, but requiring the epigean habitats during some period, or to complete some biological function such as reproduction or feeding (Lunghi et al. 2013). Those species likely have strong seasonality in the emigration/immigration rates. One can hypothesize high emigration and low immigration in spring, summer and fall and low emigration and high immigration in winter. Due to reliance on surface habitat of the subtroglaphiles the emigration/immigration rates may depend also on cave microclimate or surface environmental factors, e.g. surface weather variables. Moreover, it is commonly assumed that intra-specific competition avoidance plays an important role in promoting emigration (Dieckmann et al. 1999). In caves the food resources are very scarce and cave-dwellers might experience strong inter- and intra-specific competition. The variation in competitive abilities may generate individual heterogeneity in emigration/immigration rates. Individuals that decide to remain inside cave are expected to be more competitive and fight for these scarce resources while individuals that decide to leave and feed outside cave are expected to be less competitive.

In this study we investigated the influence of cave, surface weather variables, season, individual heterogeneity and sex on the TE of the subtroglophile harvestman species, *Paranemastoma silli*. We used a multistate CR model on 999 individually marked adults of two *P. silli* populations inhabiting two caves, Closani and Lazului Caves, located in the Mehedinti Mountains in southwestern Romania. To quantify individual heterogeneity, we used two discrete classes of individuals that refer to two possible paths: competitive individuals and uncompetitive individuals. We predict that season and individual heterogeneity have significant effect on TE. We expect that less competitive individuals to show high seasonal TE while more competitive individuals will experience lower TE regardless of season. We predict that TE is different between the two caves because the caves are characterized by different microclimates. We expect that surface weather variables have an effect on TE because weather is known to affect the demography of organisms. We predict sex-specific patterns in TE because of possible disparate demography or behaviour between the sexes.

Material and methods

Study area and capture details

Paranemastoma silli (Hermann 1871; Dyspnoi: Nemastomatidae) is an subtroglophilic endemic harvestman species in the Carpathian Mountains (Avram & Dumitrescu 1969) that inhabits caves but also habitats outside caves, especially beech forests.

We conducted a CR study of *P. silli* in two caves: Closani and Lazului. The caves are located in Mehedinti Mountains, southwestern Romania, at 433 and 370 m a.s.l., respectively. The caves are ca. 3 km apart.

The caves differ in the hydrological regime, surface vegetation and food resources. Closani Cave is a hydrologically inactive cave and the outside habitat consists mainly of dry scrubs. Lazului Cave is a hydrologically active cave and is located in a beech forest. Closani Cave has an old guano deposits whereas in Lazului Cave little amounts of fresh guano are present.

We conducted visual encounter surveys to search for harvestmen in teams of two researchers once a month between December 2008 and November 2009, separately in each cave. We individually

marked all caught adult harvestmen using non-toxic acrylic ink (Mestre and Pinto-da-Rocha 2004). A combination of different colour marks that were still recognizable after several recaptures was used to individually mark each harvestman. The marked individuals were released at the place where they were collected. The immature stages were not marked because they moult six times in ~2.5 months (Avram 1973). The adult harvestmen were sexed based on the cheliceral morphology.

The daily temperature and rainfall values were recorded at Closani village, with an iROX PRO-X portable weather station. Temperature and rainfall were included in the study as mean air surface temperature and mean precipitation amount during the day of capture occasion and during the week prior to the capture occasion (tempm, precipm, tempw and precipw, respectively). All environmental covariates were standardized for the analysis.

Data analysis

We analysed the CR data of 999 adult harvestmen for a period of 11 months using multistate CR models (Lebreton et al. 2009) expressed as multievent models (Pradel 2005). We recorded the ‘events’ as “seen” and “not seen” and considered the states “alive and observable” (OU) and “alive and unobservable” (UO) and “dead” (D). Individuals that are in the state “unobservable” and dead during a sampling occasion are unavailable for recapture, therefore the corresponding recapture probability is fixed to 0.

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 first observation. The classes are states of the multievent model: “alive and observable in g_1 ”, “alive and unobservable in g_1 ”, “alive and observable in g_2 ”, “alive and unobservable in g_2 ”. The classes are associated with distinct values of the initial states.

For model formulation we considered: i) Π , 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 matrixes can be found in the Appendix S1.

Because the transition probabilities depend only on the states in which an individual was before a transition we modeled 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 on which the TE is conditional. For, example one may hypothesize that the recapture 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 same covariates as for survival probability but we distinguished between models with and without individual heterogeneity by considering no classes or two classes, respectively, in matrix of transition probabilities, associated with distinct values of the initial states (for details see Appendix S1).

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 and Anderson 1998) and to obtain maximum likelihood estimates of the parameters. In the results, for brevity we choose to present only the models with $\Delta AICc < 20$.

Goodness-of-fit

Goodness-of-fit tests were performed on CR histories. We used Test3.SR for transience (lower chance of recapture of first encountered individuals than individuals already encountered (Pradel et al. 1997) and Test2.CT for trap-dependence and for trap-happiness (higher probability to encounter at time $t+1$ the individuals encountered at time t than to individuals not encountered at time t but known to be alive because of previous and future recaptures). We computed the overall and separately on cave and sex GOF-statistics for transience and trap-dependence, from Test3 and Test2 respectively. The GOF tests were performed using U-CARE (Choquet et al. 2009b).

Results

The directional tests for transience and trap-happiness were statistically not significant, thus there was no need to correct for transience or trap-happiness or to account for overdispersion (Table 1).

From the set of the candidate models, the model with heterogeneity and season effect on TE, along with cave and sex on survival and cave, sex and tempm on recapture was best supported by the data (Table 2). The model with no heterogeneity, season and cave effect on TE, along with cave and sex on survival and time on recapture received some support and was the second-ranked at 3.860 Δ AICc after the best model (Table 2).

We estimated parameters from the best model (Fig 1-3). Recapture decreased with the increase of the temperature during the day of capture occasion in both caves and sexes (Fig.1). Recapture was the higher in males from Closani than from Lazului cave and lower in females from Closani than from Lazului cave (Fig.1). The emigration probability was high in autumn, spring and summer for g_1 individuals and low for g_2 in all seasons except winter (Fig. 2). The immigration was high in autumn for g_1 individuals and high in spring and summer for g_2 individuals (Fig. 3).

Discussion

In this study the application of a multistate CR model was able to estimate relevant demographic parameters to inform movement patterns and behavioural processes, when data cannot be collected for other established frameworks, e.g. animal tracking techniques. Our approach revealed clear seasonality and captured individual heterogeneity in the TE of a subtroglophile harvestman species.

Seasonal variation in TE is likely due to foraging behavior. Foraging movements from cave were reported for many bat (Kunz 1982) and several cricket species (Fagan et al. 2007). Strong seasonality is also in agreement with studies on activity rhythm of non-obligate cave harvestmen species. Several studies showed that harvestmen use caves as shelters and reproductive sites but leave the cave periodically to forage (Hoenen and Gnaspini 1999; Machado et al. 2003).

Using assumptions of two heterogeneity classes during model construction, we showed significant different patterns of emigration/immigration among seasons between the two classes.

Although we can only speculate on this the heterogeneity in TE is likely linked to differences in the competitive abilities for food. The scarcity of the food resources in caves is common and it has been shown that non-obligate cave-dwellers forage primarily external rather than within cave (Kunz 1982; Fagan et al. 2007). However, some individuals reside inside the cave and rely upon the resources available in cave, maybe due to their better competitive abilities. This question requires experimental studies to test whether individuals showing good competitive abilities are more likely to reside in cave and if these inter-individual differences are consistent across time.

The results further indicated that once the heterogeneity is not accounted for, season and cave drive the observed emigration/immigration rates. The two studied caves have different microclimate (Decu et al. 1967). They are characterized by different hydrological regime, airflow, temperature, humidity, guano deposit and outside surface habitat. This indicates that TE may be promoted by variability in cave microclimate.

We found little support for surface weather variables in controlling TE. Weather is known to affect directly and indirectly the demography of organisms (Moreno and Møller 2011). The lack of an effect of surface weather variables on TE suggests that caves buffer well the fluctuations of weather factors in the habitats above and reinforce the hypothesis of caves as refuges from unfavorable surface environmental conditions (e.g., too dry or too hot) (Manenti et al. 2009, 2011, 2013; Ficetola et al. 2012).

Results also showed no strong support for sex differences in TE. Sexual disparity in TE was linked to disparate demography or behaviour between sexes (Chapple et al. 2016). Movement is the result of interactions between morphology, physiological performances (movement capacity), and behavioural decisions (movement decision) (Ducatez et al., 2013). Additional studies are necessary to test TE sex-dependency in correlation with various movement traits.

TE was until recently viewed as causing problems in CR studies and several approaches have been developed for dealing with it (Fujiwara and Caswell 2002; Kendall and Nichols 2002). In this study we presented TE (Schaub et al. 2004) 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 movements pattern and behavioural processes of animals difficult to track with the available intrinsic and extrinsic tracking techniques. Moreover, it can be used when a robust design (Pollock 1982), e.g. sampling replication (secondary occasions) within each season (primary occasion) cannot be implemented. However, it is still preferable to sample all potential locations of marked individuals and we recommend multi-state CR approach where unobservable states are inevitable but in general we recommend setting up a study under Pollock's (1982) robust design.

Acknowledgements

This work was supported by a short-term postdoctoral research fellowship offered by French Embassy and French Institute of Romania and a grant of Romanian National Authority for Scientific Research, CNCS – UEFISCDI, projects number: PN-II-RU-TE-2014-4-1536 to RB.

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Table 1. Goodness-of-fit tests showing no transience, trap-happiness or overdispersion.

		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 ($\Delta AICc$) 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), time (capture occasion time effect), tempm (mean air surface temperature during the day of capture occasion), tempw (mean air surface temperature during the week prior to the capture occasion).

Model		Survival	TE	Recapture	K	DEV	QAICc	$\Delta AICc$
1	h+	cave+sex+cave:sex	season	cave+sex+tempm	30	5.931.324	5.991.946	0.000
2	h-	cave+sex	cave+season	time	23	5.949.438	5.995.806	3.860
3	h+	cave+sex	cave+season	cave+sex+season	28	5.942.382	5.998.924	6.979
4	h+	cave+sex	cave+season	sex+season	28	5.943.232	5.999.774	7.828
5	h+	cave+sex	cave+sex+tempw	cave+sex+tempm	46	5.907.283	6.000.735	8.789
6	h+	cave+sex	season	cave+season	26	5.947.876	6.000.344	8.398
7	h+	cave+sex	sex+season	cave+sex+tempm	38	5.924.895	6.001.888	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

Figure captions

Figure 1. Effect of mean air surface temperature during the day of capture occasion (tempm) on monthly recapture probabilities (SE) of female and male harvestmen in Closani and Lazului Caves. Estimates are based on the most parsimonious CR model (Model 1 in Table 2).

Figure 2. Estimated seasonal emigration rates (SE) of harvestmen form the two heterogeneity classes, g_1 (grey) and g_2 (black). Estimates are based on the most parsimonious CR model (Model 1 in Table 2).

Figure 3. Estimated seasonal immigration rates (SE) of harvestmen form the two heterogeneity classes, g_1 (grey) and g_2 (black). Estimates are based on the most parsimonious CR model (Model 1 in Table 2).

— Closani Female ··· Closani Male - - Lazului Female - · Lazului Male