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

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Abstract

Cave systems are less transparent than surface habitats and significantly less is known about movement patterns and intrinsic behavioural processes of cave-dwelling animals. Here, we introduce temporary emigration (TE), the probability that an individual is absent from a cave at a given sampling occasion, to inform about movement and behavior of cave-dwelling animals. Because these animals are difficult to study with traditional tracking techniques, we resort to the capture-recapture (CR) modeling framework to assess TE to account for detectability less than one and unobservable states. 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 multistate CR models 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. Adult harvestmen demonstrated clear seasonality and heterogeneity in TE. We found that TE of harvestmen exhibited between caves variation and there was little support for surface weather variables in controlling TE and for sex specific TE patterns. Our results highlight that the study of TE patterns is useful to gain valuable insights into movement and intrinsic behavioural processes of cave-dwelling species.

Key words: animal movement and behavior, cave-dwelling species, individual heterogeneity, season, temporal emigration

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55 **Introduction**

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

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

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

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

79 we argue that an important application of TE, especially for cave-dwellers, is to inform about animal
80 movements over space, e.g. emigration from and immigration to cave. Frequently sampling is conducted
81 only in cave. Considering a multistate CR model with states “observable” and “unobservable” between
82 which individuals are allowed to move, the transition from an “observable” to an “unobservable” state is
83 the emigration, the probability that an individual has moved out (emigrated) from cave between capture
84 occasion i and $i+1$ while the transition back to an “observable” state is the immigration, the probability
85 that an individual has returned (immigrated) to cave during capture occasion. Multistate CR methods have
86 been also developed to model individual heterogeneity in capture and demographic rates (Pledger et al.
87 2003; Pradel 2009; Gimenez and Choquet 2010) and there is increased evidence that unmodeled
88 individual heterogeneity causes bias in capture and survival estimates (Pledger and Efford 1998; Fletcher
89 et al. 2012). While individual heterogeneity is expected in movement patterns, no CR study investigated
90 the effect of individual heterogeneity on TE.

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

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

116 **Material and methods**

117 *Study area and capture details*

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

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

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

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

130 marked all caught adult harvestmen using non-toxic acrylic ink (Mestre and Pinto-da-Rocha 2004). A
131 combination of different colour marks that were still recognizable after several recaptures was used to
132 individually mark each harvestman. The marked individuals were released at the place where they were
133 collected. The immature stages were not marked because they moult six times in ~2.5 months (Avram
134 1973). The adult harvestmen were sexed based on the cheliceral morphology.

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

140 **Data analysis**

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

147 To include individual heterogeneity in TE, we built two discrete classes of individuals, g_1 and g_2 ,
148 which refer to two possible paths at first observation. The classes are states of the multievent model:
149 “alive and observable in g_1 ”, “alive and unobservable in g_1 ”, “alive and observable in g_2 ”, “alive and
150 unobservable in g_2 ”. The classes are associated with distinct values of the initial states.

151 For model formulation we considered: i) \mathbf{PI} , the vector of probabilities of presence in the various
152 initial states (π), ii) $\mathbf{P\Phi}$, the matrix of survival probabilities (S); iii) $\mathbf{P\psi}$, the matrix of transition
153 probabilities (ψ), corresponding to TE ; and iv) \mathbf{PB} , the matrix of detection probabilities (p). The full
154 description of the vectors and matrixes can be found in the Appendix S1.

155 Because the transition probabilities depend only on the states in which an individual was before a
156 transition we modeled TE as a Markovian or state-dependent transition (Schaub et al. 2004).

157 *Model selection*

158 We were interested in TE, but different model structures can be used to model the sampling
159 process and the survival on which the TE is conditional. For, example one may hypothesize that the
160 recapture differs among observers due to different levels of experience. Both capture and survival
161 probabilities may vary with time, (e.g. occasion, season) or time specific covariate (e.g., weather) or
162 harvestmen can exhibit cave and sex-specific capture and survival probabilities. Consequently, we
163 considered models representing different combinations of observer, time, cave, sex, season, tempm and
164 precipm on capture probability and cave, sex, season, tempw and precipw on survival probability. To
165 assess the hypotheses of TE we built models representing combinations of same covariates as for survival
166 probability but we distinguished between models with and without individual heterogeneity by
167 considering no classes or two classes, respectively, in matrix of transition probabilities, associated with
168 distinct values of the initial states (for details see Appendix S1).

169 In total we designed 119 models. We used E-SURGE 1.9.0 (Choquet et al. 2009a) to perform
170 model selection based on Akaike's Information Criterion corrected for small sample size (QAICc)
171 (Burnham and Anderson 1998) and to obtain maximum likelihood estimates of the parameters. In the
172 results, for brevity we choose to present only the models with $\Delta\text{AICc} < 20$.

173 *Goodness-of-fit*

174 Goodness-of-fit tests were performed on CR histories. We used Test3.SR for transience (lower
175 chance of recapture of first encountered individuals than individuals already encountered (Pradel et al.
176 1997) and Test2.CT for trap-dependence and for trap-happiness (higher probability to encounter at time
177 $t+1$ the individuals encountered at time t than to individuals not encountered at time t but known to be
178 alive because of previous and future recaptures). We computed the overall and separately on cave and sex
179 GOF-statistics for transience and trap-dependence, from Test3 and Test2 respectively. The GOF tests
180 were performed using U-CARE (Choquet et al. 2009b).

181 **Results**

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

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

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

195 **Discussion**

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

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

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

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

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

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

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

229 TE was until recently viewed as causing problems in CR studies and several approaches have
230 been developed for dealing with it (Fujiwara and Caswell 2002; Kendall and Nichols 2002). In this study
231 we presented TE (Schaub et al. 2004) as the parameter of biological interest and we provided a pertinent
232 framework within which to consider TE as transition between an observable and unobservable state. The

233 TE approach of a multistate CR model can be applied to other studies to gain information on movements
234 pattern and behavioural processes of animals difficult to track with the available intrinsic and extrinsic
235 tracking techniques. Moreover, it can be used when a robust design (Pollock 1982), e.g. sampling
236 replication (secondary occasions) within each season (primary occasion) cannot be implemented.
237 However, it is still preferable to sample all potential locations of marked individuals and we recommend
238 multi-state CR approach where unobservable states are inevitable but in general we recommend setting up
239 a study under Pollock's (1982) robust design.

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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).

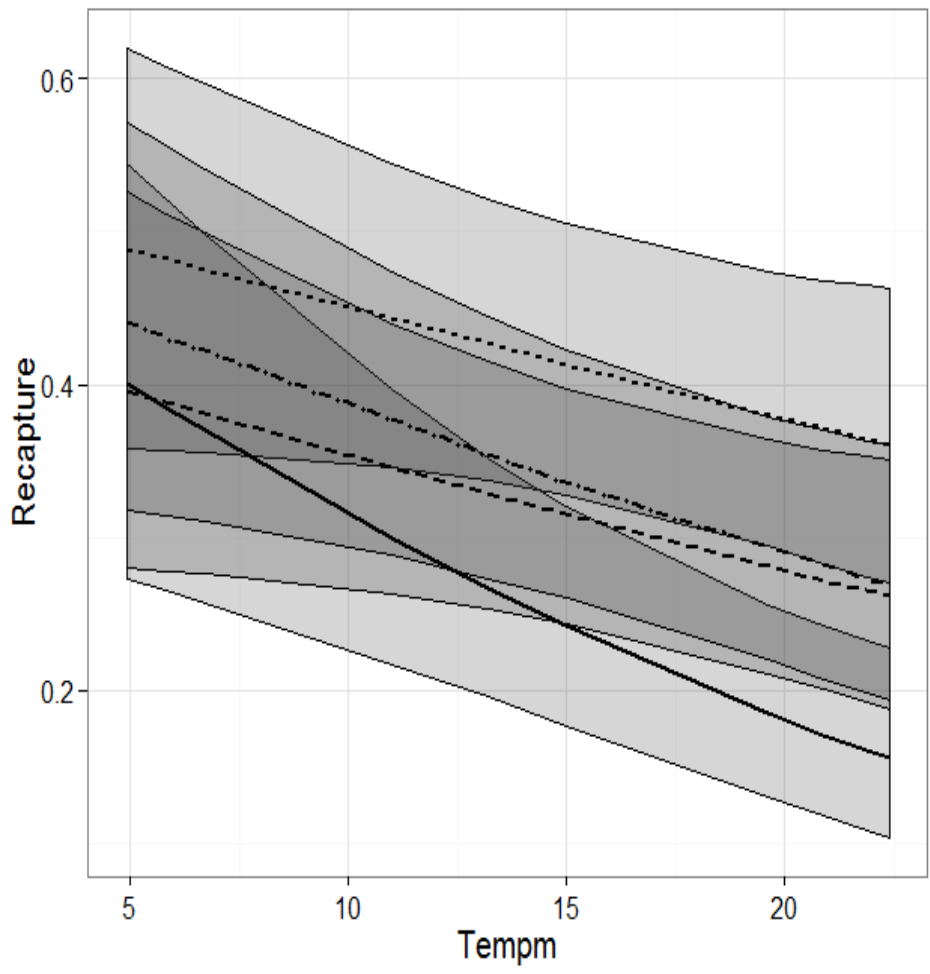
Model	Survival	TE	Recapture	K	DEV	QAICc	$\Delta AICc$	
1	h+	cave+sex+cave:sex	season	cave+sex+tempm	30	5.931.324	5.991.946	0.000
2	h-	cave+sex	cave+season	time	23	5.949.438	5.995.806	3.860
3	h+	cave+sex	cave+season	cave+sex+season	28	5.942.382	5.998.924	6.979
4	h+	cave+sex	cave+season	sex+season	28	5.943.232	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 ($temp_m$) 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 from 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 from 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

