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# Out of the ground: Coexisting fossorial species differ in their emergence and movement patterns

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## Abstract

Understanding the way species with similar niches can coexist is a challenge in ecology. The niche partitioning hypothesis has received much support, positing that species can exploit available resources in different ways. In the case of secretive species, behavioural mechanisms of partitioning are still poorly understood. This is especially true for fossorial frogs because individuals hide underground by day and are active only during the night. We investigated the nocturnal activity and tested the niche partitioning hypothesis in two syntopic fossorial spadefoot toads (*Pelobates fuscus* and *P. syriacus*) by examining interspecific variation in emergence from the soil. We employed a night vision recording system combined with video-tracking analyses in a replicated laboratory setting to quantify individual movement patterns, a procedure that has not been used until now to observe terrestrial amphibians. Most individuals appeared on the surface every night and returned to their original burrow (about 60% of the times), or dug a new one around morning. There was a large temporal overlap between the two species. However, *P. syriacus* was significantly more active than *P. fuscus* in terms of total distance covered and time spent moving, while *P. fuscus* individuals left their underground burrow more frequently than *P. syriacus*. Consequently, *P. fuscus* adopted more of a sit-and-wait behaviour compared to *P. syriacus*, and this could facilitate their coexistence. The use of night video-tracking technologies offered the advantage of individually tracking these secretive organisms during their nocturnal activity period and getting fine-grain data to understand their movement patterns.

**Keywords:** amphibians, foraging strategy, resource partitioning, species coexistence, night video-tracking

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## 1. Introduction

Understanding the structure and dynamics of ecological communities is a major challenge in ecology, and the factors governing species richness have been the focus of many studies in the last decades (Dayan and Simberloff, 2005; Schellekens et al., 2010; Albouy et al., 2011; Comte et al., 2016). Stable coexistence requires potential competitors to differ in their niches, and phylogenetically related species living in syntopy should limit their ecological similarity in order to reduce competition (Schoener, 1974; Pfennig and Pfennig, 2010). Niche partitioning theory stipulates that if each species is superior to its competitors in a niche segment, then competition is decreased, facilitating long term coexistence (Futuyma and Moreno, 1988; Uiblein et al., 1992; Loreau and Ebenhoh, 1994).

In species that use similar food and habitat resources, an important aspect of niche dimension along which they can partition is related to the foraging effort. Pianka (1966) described foraging strategies along two extremes: active foragers and sit-and-wait (ambush) predators. Increased mobility contributes to foraging success (Azevedo-Ramos et al., 1992; Werner and Anholt, 1993) and offers access to very localized prey. However, it is energetically expensive (Taigen and Pough, 1985), and generates higher mortality risks caused by predators (Anholt and Werner, 1995) as well as higher exposure to unfavourable abiotic factors like desiccation (Case and Taper, 2000; Escoriza and Hassine, 2015). On the opposite side of the spectrum, sit-and-wait predators have smaller home ranges, can capture highly mobile prey, and have reduced energetic necessities and predation risks (Toft, 1980; Butler, 2005). Between the two extremes, observed foraging behaviour is almost always variable, even in stationary environments (Nishimura, 1999). The pattern of foraging will depend on individual physiological state and mobility; resource size, profitability and availability; presence of competitors and predators; and environmental conditions (Nomura and Rossa-Feres, 2011). Since a rise in foraging activity increases both food acquisition and mortality risks, the two components of activity - foraging speed and time spent foraging - typically hold an inverse relationship (Werner and Anholt, 1993).

Another means to reduce competition is temporal segregation, which can decrease direct confrontation and lessen the effect that one forager has on prey availability for another (Kronfeld-Schor and Dayan, 2003). Diel activity patterns are the evolutionary result of interactions between physiological constraints and ecological selective forces (Rubal et al., 1992; Fraser et al., 1993; Winandy et al., 2016). Temporal partitioning was shown to exist between syntopic species (Cotton, 1998; Wasserberg et al., 2006; Gerber et al., 2012), or even between members of the same species: juveniles vs. adults (Gries et al., 1997), males vs. females (Woolbright, 1985), or subordinate vs. dominant individuals (Craig and Douglas, 1984; Alanärä et al., 2001).

Studies of coexistence in syntopic species of amphibians have usually focused on differences in morphology (Pfennig and Murphy, 2003), feeding habits (Toft, 1980; Joly and Giacoma, 1992; Salvidio et al., 2012), reproductive strategies (Crump, 2015) and habitat use (Menin et al., 2005). Niche partitioning through behavioural mechanisms has been the centre of intense research in larval stages (e.g. Pfennig et al., 2007; Manenti et al. 2013), but little information is available on the patterns of movement in adults (Strussmann et al., 1984; Woolbright, 1985; Seebacher and Alford, 1999; Indermaur et al., 2009), apart from studies of their distribution collected from radio-tracking in the field (Jehle, 2000; Jehle and Arntzen, 2000).

The fossorial life in many organisms such as toads is usually interpreted as an adaptation to dry environments. For species that lack physiological adaptations for limiting water loss, reliant on behavioural strategies in order to survive, the fossorial life provides a solution to their challenging environment (Wells, 2010). Spadefoot toads avoid unfavourable conditions on the surface by remaining buried in the soil for long periods without feeding. Because the act of digging is energy-consuming, these toads are better equipped to sustain longer periods of moderate activity, compared to jumping frogs, which are only capable of short bursts of strenuous activity (Seymour, 1973; Taigen et al., 1982). The way burrowing toads exploit the resources in their terrestrial environment is poorly known. Particularly, important behavioural patterns such as their emergence rate out of the ground and the complete distance they travel have not been explored experimentally.

We aimed to determine and compare the behavioural strategies of two spadefoot toad species (genus *Pelobates*) that share a narrow overlap in distribution range (Iosif et al., 2014; Sillero et al., 2014). The two species are similar in many life-history attributes: both are obligate burrowers, nocturnal, active and reproducing during the same period of the year, use similar aquatic habitats for reproduction and forage in the same terrestrial habitats (Cogălniceanu et al., 2014). All these traits suggest a large overlap of resource use and a high probability of competition. We hypothesized that the two species would differ in activity patterns in terms of frequency of their emergence out of the ground, time spent outside the burrows, and movement on land.

## 2. Materials and Methods

### *2.1. Study species and maintenance*

We collected 24 spadefoot toads (6 males and 6 females from each species) from the southern part of the Danube Delta Biosphere Reserve, Romania (44º27.37'N, 28º44.48'E, -1 m a.s.l.), where the two species occur in syntopy. Experiments took place outside the breeding season, so they would reflect activity patterns not directly connected with reproduction. Toads were kept in 60x40x30 cm terrariums in the university laboratory for acclimatization for at least one month before the start of the experiments, with four similarly sized conspecifics housed in each. Terrariums were lined with a 10cm-deep layer of sandy soil, originating from the same area as the animals. The room temperature had a mean ± SE of 22 ± 1°C and the photoperiod was fixed at 14L:10D (night starting at 9 PM). The humidity was maintained relatively constant by daily spraying the sand with water. The toads were fed *ad libitum* with crickets and cockroaches. All the animals were released at the capture site at the end of the experiment.

At the beginning of the experiment, the snout-vent length (SVL) of each individual was measured using 0.1mm-precision dial callipers. The two species, but not sexes, significantly differed in size, *P. syriacus* being larger than *P. fuscus* (SVL = 66.5 ± 7.36 mm and 45.3 ± 5.17 mm, respectively) (GLM, $n = 24$: estimate ± SE for species = 0.171 ± 0.020, $t = 5.937$, $P < 0.001$; estimate ± SE for sex = 0.014 ± 0.029, $t = 0.501$, $P = 0.62$).

### *2.2. Experimental design*

For the experiment, the toads were placed in individual experimental enclosures, identical with the regular housing ones, three days before the first observations. They were kept there for the duration of the experiment - 30 days (Fig. 1). We performed two sets of observations, and each set followed the activity of 6 *P. fuscus* and 6 *P. syriacus*, with each individual being monitored during one night every 6 days, for a minimum of five nights for each (86 nights of observations for each species). Toads continued to receive *ad libitum* crickets over the course of the experiment except during the nights when their activity was monitored, so that the movement of insects would not affect their behaviour. The sand was sprayed with water every evening before dark, and a bowl (10x15x4 cm) filled with water was provided.

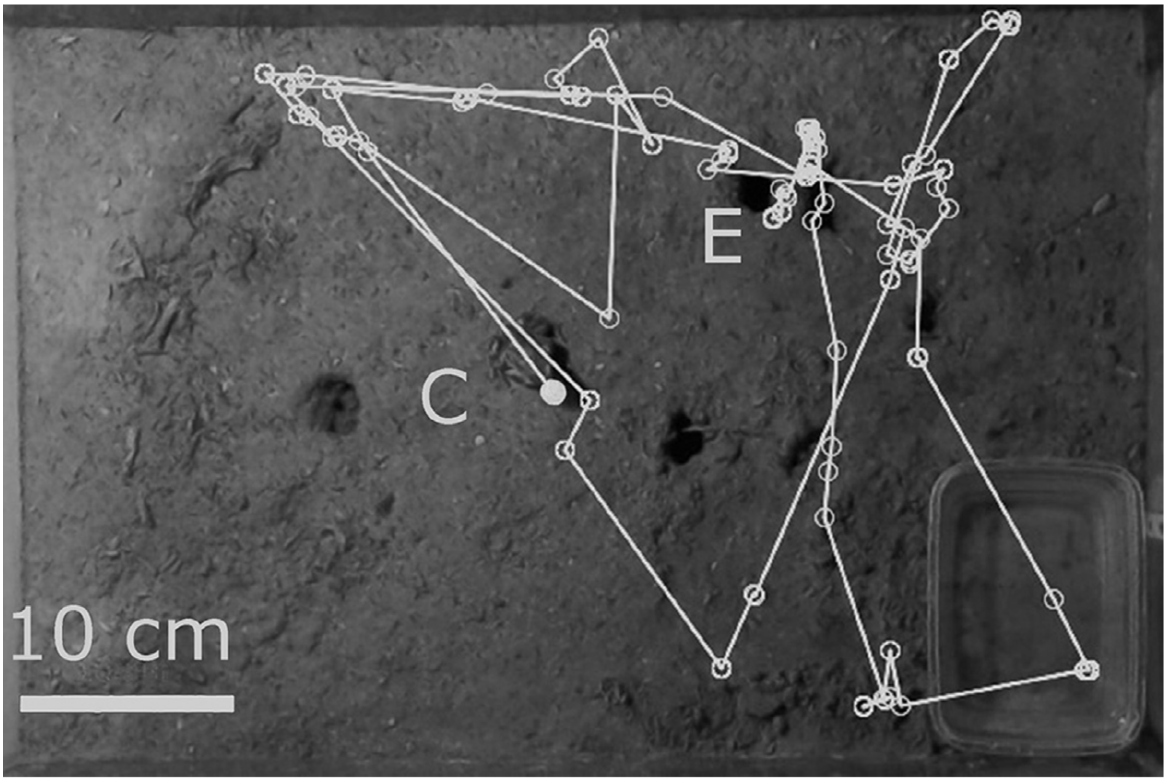

**Fig. 1.** Experimental tank showing a spadefoot toad and its track. E: emergence burrow and start of track, C: current toad position.

The enclosures were monitored using Logitech HD Pro C920 webcams positioned 150 cm above the soil level of the enclosures and connected to laptops. During the observation period, lighting for image recording was provided by ExoTerra Infrared light bulbs (50W, 800 nm) that did not interfere with the normal nocturnal activity of the animals (Buchanan, 1993). We used Chronolapse 1.0.7 software (Green C 2008, available at http://keeyai.com) to take time-lapse photos every 30 sec.

### *2.3. Data analysis*

The video sequences were analyzed using ImageJ 1.46r software (U.S. National Institute of Health) along with the MTrackJ 1.5.0 plugin (Meijering et al., 2012). This software produces individual tracks of movements of the studied organisms (see Manenti et al. 2013), taking into account the position of the animal within the enclosure every 30 sec. A total of 143 tracks summing 721 hours of toads out of their burrows were analyzed (i.e., 86728 individual positions).

For each observation night, we determined the following parameters: toad emergence out of the ground (yes/no), use of identical or different burrows within a single night (yes/no), total distance travelled (i.e., total length of an individual track, in cm), total time spent outside of burrows (i.e., total time while the animal was outside the soil, in min), and total active time (i.e., total time during which the animal moved). We use the term activity to refer to movement, as opposed to emergence to refer to the presence of toads above ground, indifferent of mobility state.

### *2.4. Statistical analyses*

We used a general linear model (GLM) with Gaussian distribution (link = identity) to test the effect of species, sex, and their interaction on emergence score (i.e., the proportion of nights when toads came out of the burrows). The response variable was quantified as the number of nights out of the burrow over the number of observation nights. We used an arcsin square root transformation to fit a normal distribution (observation of Q-Q plot). After removing the data of individuals that did not exit their burrows (i.e., 29 out of 172 observations), we computed a linear mixed model (LMM) with Gaussian distribution (link = identity) to test for the effect of species, sex, and their interactions on the distance travelled and time spent active on the ground (i.e., outside the burrows). We used a square root transformation to fit a normal distribution (observation of Q-Q plot). To avoid a too large number of descriptors with respect to sample size, we did not include additional fixed effects. We also added body length (log 10 transformed) as covariate in our analyses to control for variation in body size between individuals (see Denoël et al. 2010). Because this variable had no significant effect on the studied behavioural patterns and because it is recommended to avoid a large number of descriptors with respect to our sample size, the final linear models presented here do not include the covariate. For all analyses, we added individual identity and time as random factors. This procedure allows controlling for repeated use of individuals in the models and the potential habituation to the habitat. Significance of the fixed effects was assessed with Wald tests (Type II). For LMM analyses, degrees of freedom were approximated with the Kenward-Roger degrees of freedom and are consequently not integer values. We chose an error risk of 0.05 and used the R environment with the packages MASS, car and lme4 for computing the models.

The temporal niche partitioning of presence outside of the burrow (i.e., above ground) was determined by using the Czekanowski index of overlap (Feinsinger et al., 1981):

$$\alpha_{j,k} = 1 - 0.5\left(\sum_{i=1}^{n}\left|p_{ij} - p_{ik}\right|\right)$$

where $p_{ij}$ and $p_{ik}$ are the proportional use of time *i* by species *j* and *k*, respectively. The index was calculated to compare the two *Pelobates* species. The time spent outside the burrow was split into 12 1-h intervals (from 21:00 to 9:00 AM). The index ranges from 0 (no time interval in common, i.e. full partitioning) to 1 (all intervals in common, i.e. full overlap).

## 3. Results

There was a significant effect of species and sex, but not their interaction, on the emergence score of toads (GLM; Table 1, Fig. 2). There were 95% of exits in *P. fuscus* (82 out of 86 observation nights) versus 71% in *P. syriacus* (61 out of 86). All individuals, except one *P. syriacus* female individual (i.e. 96%, *n* = 24), exited their burrow during night-time. Males were more active in both species. *Pelobates fuscus* males got out of soil in all surveyed nights, while *P. syriacus* males emerged in 82% of observation nights. For females, emergence rates were 91% and 59% of observation nights, respectively. In 91% of cases, the toads emerged only once during the night, but there were also cases (12 out of 86 nights in *P. fuscus*, 7 out of 86 nights in *P. syriacus*) in which individuals emerged a second time, after spending on average 184, and 110 min, respectively, in their underground burrows. All the toads that exited during night time returned underground during the night or early morning (08:43 at the latest, but in 86% of all cases before daylight - 07:00). In 62% of cases for *P. fuscus* and 61% for *P. syriacus*, toads returned to the same burrow from which they emerged at the beginning of the night. The Czekanowski index of temporal overlap between the two species was 0.898 (Fig. 3).

**Table 1.** Results of a General Linear Model testing the effect of species, sex and their interaction on the rate of emergence out of burrows in spadefoot toads (*n* = 24).

| Parameters | Estimates ± SE | *F* | df | *P* |
|---|---|---|---|---|
| Species | -0.311 ± 0.136 | 9.956 | 1, 20 | 0.005 |
| Sex | -0219 ± 0.185 | 5.923 | 1, 20 | 0.02 |
| Species*sex | -0.245 ± 0.274 | 0.802 | 1, 20 | 0.40 |

*Pelobates fuscus* and males are coded 0; *P. syriacus* and females are coded 1. The rate of emergence is obtained from repeated observations of the 24 toads (143 observation nights).

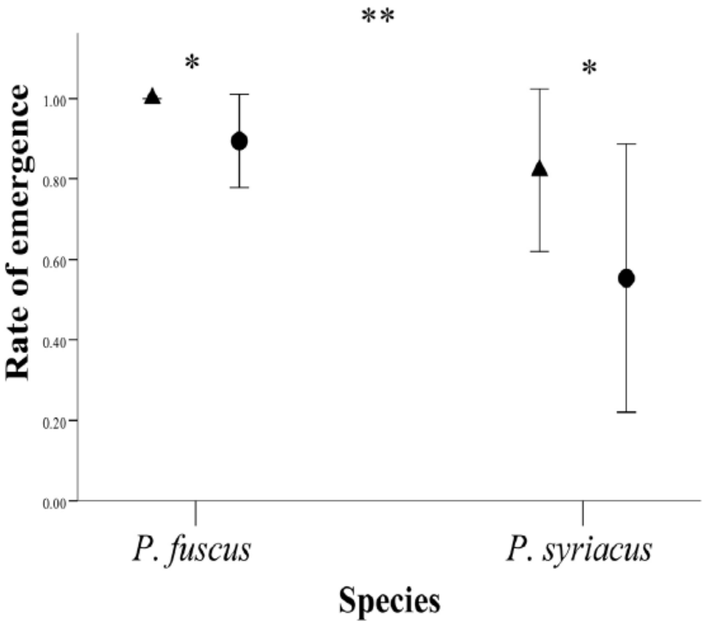

**Fig. 2.** Rate of emergence of spadefoot toads (*Pelobates syriacus*, $n = 12$ and *P. fuscus*, $n = 12$ adults) from their burrows (i.e., the proportion of nights when individuals came out of the burrows). Triangles represent males, circles, females. * $P < 0.05$, ** $P < 0.01$ (see Table 1 for statistical results).

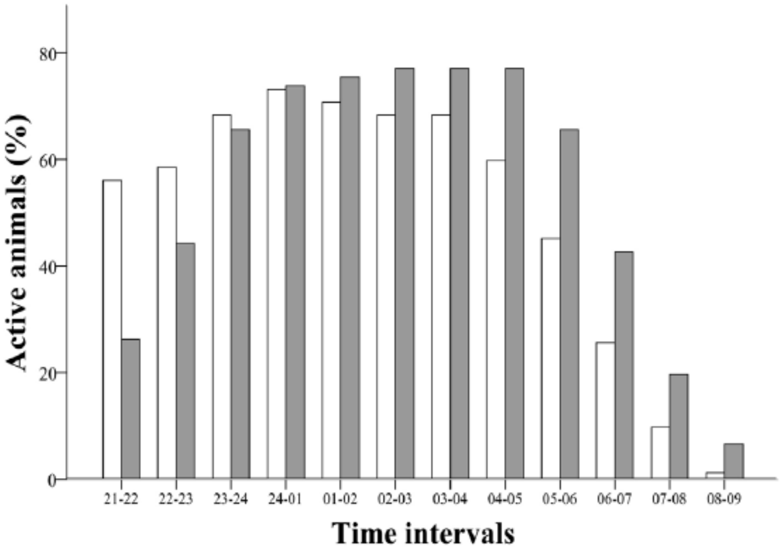

**Fig. 3.** Proportion of active spadefoot toads (*Pelobates syriacus*, $n = 11$ and *P. fuscus*, $n = 12$ adults) across time (12 1-h interval; night starting at 21:00). Open bars represent *P. fuscus*, full bars represent *P. syriacus*. The data are based on 143 tracks (i.e., observation nights when the toads came out of the ground).

There was a significant effect of species, but not of sex or the interaction between these two parameters, on the distance travelled and the time spent active out of the burrow (LMM; Table 2, Fig. 4). While out of burrows, *P. syriacus* individuals were active for longer periods of time than *P. fuscus* (108.1 ± 37.6 min, $n = 11$, compared to 74.3 ± 30.2 min, $n = 12$). They also travelled over greater distances (1070.4 ± 217.2 cm, $n = 11$, compared to 509.8 ± 268.1 cm, $n = 12$).

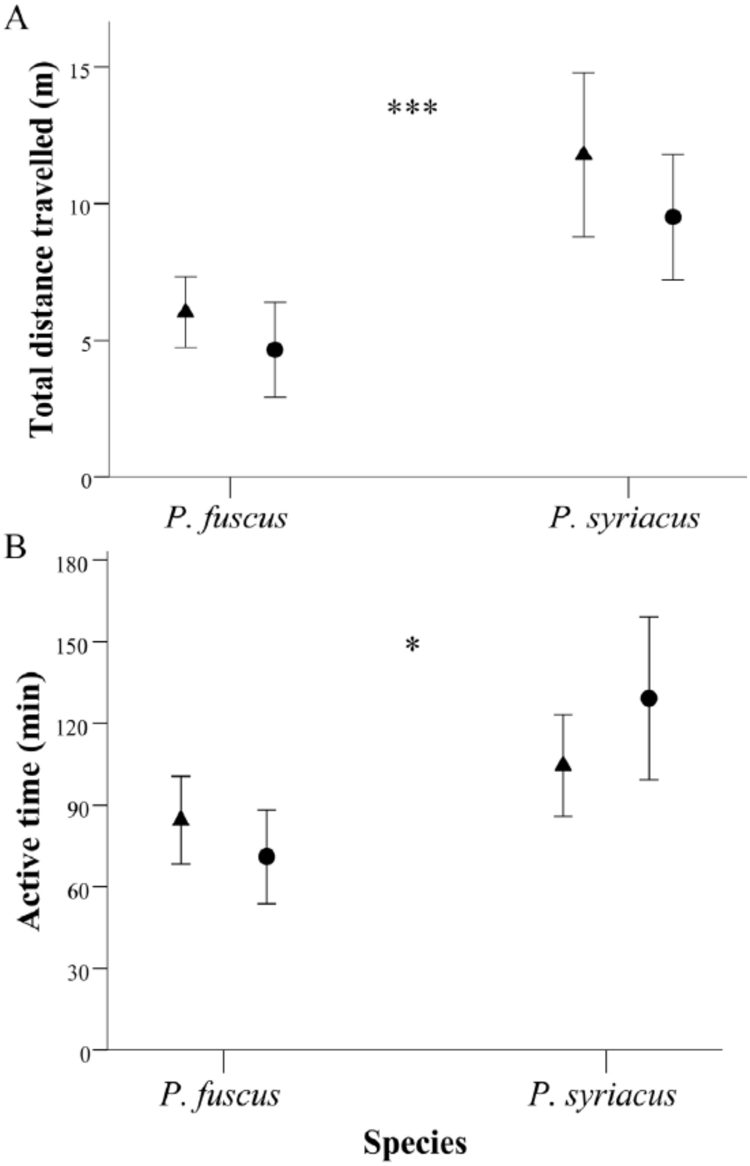

**Fig. 4.** Behavioural patterns of spadefoot toads (*Pelobates syriacus*, $n = 11$ and *P. fuscus*, $n = 12$ adults): A. Total distance travelled and B. Active time (i.e., time spent active by individuals outside their burrows). Triangles represent males, circles, females. The data are based on 143 tracks (i.e., observation nights when the toads came out of the ground). * $P < 0.05$, *** $P < 0.001$ (see Table 1 for statistical results).

**Table 2.** Results of Linear Mixed Models testing the effect of species, sex and their interaction on the behavioural patterns exhibited by spadefoot toads ($n = 23$) out of their burrow.

| Behaviour | Parameters | Estimates ± SE | *F* | df | *P* |
|---|---|---|---|---|---|
| Distance | Species | 9.007 ± 2.821 | 20.349 | 1, 16.5 | 0.0003 |
| | Sex | -4.304 ± 2.768 | 3.156 | 1, 16.3 | 0.09 |
| | Species*sex | 1.261 ± 4.205 | 0.088 | 1, 17 | 0.77 |
| Activity | Species | 8.636 ± 7.851 | 6.524 | 1, 18.3 | 0.02 |
| | Sex | -6.815 ± 7.752 | 0.02 | 1, 18.2 | 0.88 |
| | Species*sex | 13.114 ± 11.511 | 1.288 | 1, 18.4 | 0.27 |

Distance: distance travelled; Activity: duration of time when the individual is active. *Pelobates fuscus* and males are coded 0; *P. syriacus* and females are coded 1; df: Kenward-Roger degrees of freedom (thus not integer). The data are based on 143 observation nights (individual identity and time included as random factors in the models).

## 4. Discussion

### *4.1. Alternative strategies: Mobility versus emergence*

Our experiment shows that the two spadefoot toad species differ in their activity patterns. *Pelobates syriacus* was more locomotory active, moving over greater distance (almost twice) and for longer periods of time, but coming out of the soil less often than *P. fuscus*. Therefore, these species exhibit alternative behavioural strategies that can highlight different trade-offs with environmental risk as they do not maximise both patterns simultaneously. The differences in movement patterns might generate variations in food niches and space use and thus facilitate coexistence (Schoener, 1974; Tokeshi, 1999).

The diet of anurans shows contrasting patterns according to their foraging mode: widely foraging species eat more prey items, and they can benefit from access to sedentary prey species that are clumped or unpredictable, although usually abundant (Toft, 1980; Taigen and Pough, 1983). However, such movements are expected to be costly in terms of energetic expenses (Taigen et al., 1982; Pough and Taigen, 1990; Halsey and White, 2010). On the other hand, sit-and-wait foragers capture active, mobile prey, of larger size but fewer in numbers (Toft, 1980). Direct links between movements and predatory behaviours remain to be determined.

Since foraging activity is a result of the interaction between biotic and abiotic factors (Jaeger and Hailman, 1981; Navas, 1996; Alanärä et al., 2001), the observed divergence in activity levels between the two species may also be caused by physiological constraints. Because of the long distance travelled by *P. syriacus*, we suggest that this species might be better adapted to actively search for prey than *P. fuscus*. Studies performed on sympatric species of lizards showed that, although the foraging efficiency of active predators was higher, energetic costs associated with movement were much bigger (Anderson and Karasov, 1981); also in amphibians metabolic rate greatly increases when the animal is moving compared to resting metabolic rate (Halsey and White, 2010). By coming out of the ground on more nights, individuals can increase their food intake, which would explain the observed higher rate of emergence in *P. fuscus* in comparison to *P. syriacus*, compensating for the associated lower activity and exploration during the night.

Time is also an essential component of the ecological niche along which species can segregate (Schoener, 1974; Pimentel Lima and Magnusson, 1998; Kronfeld-Schor and Dayan, 2003; Winandy et al., 2016). In the case of the two *Pelobates* species, the niche overlap index showed a weak temporal resource partitioning. Temporal partitioning as a mechanism to allow coexistence is based on the assumption that resources vary predictably in time (e.g. Kotler et al., 1993), which might not be the case in the study area. Since both spadefoot species are reported to eat a large variety of invertebrates (Cogălniceanu et al., 1998; Tarkhnishvili and Gokhelashvili, 1999; Alekseev and Korzikov, 2013), the availability of prey may be low or show unpredictable variations over the course of the night, maintaining a high temporal overlap between the two consumer species.

### *4.2. Emergence frequency and burrow fidelity*

The fact that spadefoot toads do not come out of the ground every night was previously described from tracking individuals in natural conditions, such as in *Scaphiopus holbrookii* (Pearson, 1955; Timm et al., 2014; Ryan et al., 2015), *S. couchii,* and *S. multiplicatus* (Dimmitt and Ruibal, 1980) and *P. fuscus* (Eggert, 2002). The reported percentage of nights when individuals were active on the surface out of the monitored nights ranged from 8 to 65.5 %, rainfall being generally correlated with higher probability of emergence. For *P. fuscus,* periods of up to 5 consecutive nights of inactivity were frequent (Eggert, 2002). Another aspect of emergence reported by Pearson (1955) for *S. holbrookii* is the trend for two distinct activity peaks: one just after sunset, and one just prior to sunrise. In the case of the two *Pelobates* species, although some individuals emerged twice during the same night, the low number of cases and the fact that the exits are not following a temporal pattern indicates that such events are not common (Fig. 3).

Individuals tend to bury themselves in the same place from where they came out at the beginning of the night. This hold true even though the burrows have no permanent structure, and the soft sand crumbled onto the entrance of the burrow, covering it in most cases. The fossorial toads' fidelity to their burrows was observed also in natural habitat. Eggert (2002) observed one *P. fuscus* individual that returned to a hole it had previously used 11 days before, and another that burrowed in the same place for 37 consecutive nights. In *S. holbrookii*, 5 out of 17 radio-tracked individuals used the same burrowing location for over 100 days (Timm et al., 2014). The use of the same burrow could offer several advantages, among which are decreased energetic costs associated with digging, increased familiarity with surrounding microhabitat, and returning to a suitable microclimate.

### *4.3. Video-tracking versus radio-tracking*

Information about anuran movement is usually focused on home range size (Pröhl, 2005; Ringler et al., 2009), and includes migrations to and from reproductive ponds (Tozetti and Toledo, 2005; Pellet et al., 2006) and postmetamorphic dispersal (Leskovar and Sinsch, 2005; Pittman and Semlitsch, 2013). Radio-tracking individuals provides essential information on space use within and across patches (Indermaur et al., 2009) and reveals how organisms use their environment. It also gives information about the distances travelled by animals, but the time scale is of days (Bulger et al., 2003; Rowley and Alford, 2007) or weeks (Lemckert and Brassil, 2003) between readings. Consequently, it has rarely been used for depicting the exact track of individuals, and it did not provide detailed, diel activity data. For fossorial species of toads, tracking is made especially difficult by the fact that these animals burrow in the soil during the day. This explains why very few studies examined the individual patterns of movement in such species. However, in a study done in France, Eggert (2002) was able to track a few individuals of *P. fuscus*, using a combination of implantable transmitters and fluorescent pigments, whereas (Leeb et al., 2013) managed to determine the use of an hibernation burrow in fire salamanders and other species using a camera-trapping system. Because the size of the enclosures used in the experiment is below the individual home range, our results referring to distance travelled by individuals are probably not directly transferrable to natural situations. Nonetheless, we feel confident that our findings offer relevant information concerning differences in the patterns of emergence and of movement between the two species of spadefoot toads valid for natural environment as well.

Although video-tracking techniques have been widely used on a variety of organisms (Delcourt et al., 2013), they have not yet been applied to study the terrestrial movements of amphibians. Using such techniques during night-time has been even more rarely done (Delcourt et al., 2011; Manenti et al., 2013). By combining continuous video-tracking and infra-red lighting, our study offers fine-scale information concerning individual movement activity in controlled laboratory conditions over the entire nocturnal activity period of two closely related fossorial toad species.

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