

Local predation risk and matrix permeability interact to shape movement strategy

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Abstract

In fragmented landscapes, the reduced connectivity among patches drives the evolution of movement strategies through an increase of transience costs. Reduced movements may further alter heterogeneity in biotic and abiotic conditions experienced by individuals. The joint action of local conditions and matrix permeability may shape emigration decisions. Here, we tested the interactive effects of predation risk and matrix permeability on movement propensity, movement costs and movers' phenotype in the common toad *Bufo bufo*. In a full-crossed experimental design, we assessed the movement propensity of juveniles in three connectivity treatments (from poorly to highly permeable matrix), with or without predation risk in their living patch. We also assessed the relationships between movement propensity and morphological traits (i.e. body and leg length) and how it affected the movement cost (i.e. mass loss). Movement propensity increased in presence of predation risk, while matrix permeability had no effect. However, matrix permeability interacted with predation risk to influence movers' phenotype and the physiological cost they endured while moving. In particular, a well-known movement syndrome in toads (i.e. movement propensity positively related to longer legs) depended on the interaction between matrix permeability and predation risk and resulted in differences in mass loss among matrix types. Movers lost more mass on average than residents except when they also displayed longer legs or when they crossed the most permeable matrix in the presence of predation risk. Our results show that matrix permeability shapes the physiological cost of dispersal by changing the identity of individuals moving away from local conditions. As the movers' phenotype can importantly alter (meta)population dynamics, context-dependency of dispersal syndromes should be considered in studies predicting the functioning of human-altered natural systems.

Keywords: animal movement, fragmented landscapes, movement costs, inter-patch permeability, phenotypic syndrome.

Introduction

Movement is a major aspect of animal ecology, and how individuals move through the landscape can have strong consequences for metapopulation dynamics, gene flow and population persistence (Clobert et al. 2012, Bonte and Doherty 2017). In the current context of global environmental change, human activities fragment large continuous habitats into small and isolated patches, which greatly affect organisms' movements (Baguette et al. 2012). Habitat fragmentation erodes biodiversity by reducing species habitat availability and increasing risk of population extinction (Fahrig 2003). Both the increase of inter-patch distance and the hostility of the matrix to be crossed (i.e. temperature, food availability, predation risk) influence the re-colonization of extinct patches and the reinforcement of occupied patches (Fahrig 2007, Eycott et al. 2012). Given the accelerating habitat conversion from natural ecosystem to agriculture, habitat fragmentation can be an important selective force acting on the evolution of movement strategies. Unraveling the underlying mechanisms of its impact is therefore crucial to understand (meta)population dynamics and subsistence in a changing world (Cheptou et al. 2017, Cote et al. 2017).

Theoretical models and empirical studies provide considerable evidence that animal movement is a highly variable and complex process shaped by the costs and benefits of moving across habitats (Clobert et al. 2009, Bonte et al. 2012). Moreover, the degree of landscape connectivity depends greatly on individual specific traits such as the ability to cross borders and gaps, or the existence of phenotypic attributes facilitating movements through unfavorable matrix (Bowler and Benton 2005, Knowlton and Graham 2010). Therefore, in a same landscape, movements (i.e. foraging, migration, dispersal) as well as the cost and benefits associated with them, can differ considerably between individuals.

Movement propensity depends on both individual phenotypic traits and environmental conditions. Individuals with high and low movement propensity tend to differ in their life histories, physiology, morphology and behavior (e.g. Ronce and Clobert 2012 for dispersal syndrome). For instance, dispersing individuals can display enhanced locomotor skills such as longer wings in flying species or longer legs in terrestrial species (Legrand et al. 2015, Trochet et al. 2016). A larger body size also enhances locomotion efficiency and has been associated with dispersal propensity because it reduces energetic costs of movements (Stevens et al. 2004, 2014). Yet, environmental conditions, such as competition, predation risk and habitat quality, also influence movement's basic features (e.g. probability, timing and distances), as well as more understated ones like movement phenotypic specialization (Bowler and Benton 2005, Clobert et al. 2009, Ousterhout and Semlitsch 2018). As fragmentation may likely change the variability of environmental conditions within and among patches (e.g. predator occurrence), movement strategies may be modified directly by landscape features or through the interplay with local conditions (Cote et al. 2017). Indeed, while local conditions can generate variation in movement strategies in habitat patches, the environmental conditions in the landscape (i.e. matrix suitability, inter-patch distance) may also shape movers' phenotype and decisions through changes in the physiological cost and the mortality risk encountered while moving between habitats (Bonte et al. 2012, Cote et al. 2017). For example, in species moving on the ground, crossing a corrugated ploughed field demands much more energy than crossing a meadow, and the mortality risk can increase because of higher visibility to predators (Joly et al. 2003). In such conditions, phenotypic adaptations improving movement efficiency in hostile environments, and therefore reducing its associated costs and risks, should emerge. Despite this theoretical framework, independent and interactive effects of environmental

conditions on movement features have been largely overlooked (but see Pennekamp et al. 2014, Bestion et al. 2015, Legrand et al. 2015, Ousterhout and Semlitsch 2018).

In the present study, we assessed the interactive effects of predation risk and matrix permeability on movement propensity, phenotypic traits, and the cost of moving in the common toad *Bufo bufo*. Using a full-crossed experimental design, we exposed half of the toads to odor of grass snake (*Natrix natrix*), while the other half were exposed to neutral odor. Afterwards, all individuals were distributed in three different conditions of matrix type (using different types of substrates) and testing for movement patterns. The common toad is a widespread species in Europe in which movement and habitat preferences have been well studied (Scribner et al. 2001, Janin et al. 2009, 2011). Amphibians are particularly susceptible to landscape fragmentation (Cushman 2006, Becker et al. 2007) because seasonal migrations between aquatic breeding habitats and growing terrestrial habitats could compel them to regularly cross inhospitable landscape matrix exposing them to a higher risk of desiccation, predation and road killing (Mazerolle and Desrochers 2005, Santos et al. 2007, Rittenhouse et al. 2009, Pittman et al. 2014). We focused our study on juvenile toads aged of a few months after metamorphosis (around 3-4 months old). This life stage is characterized by nomadism to select a proper terrestrial habitat after leaving the water, and also by a higher propensity to disperse since they are able to wander over large distances during several years before reaching sexual maturity (Reading 1991, Semlitsch 2008, Janin et al. 2012). We predicted that both local condition and matrix permeability (and their interaction) would influence toad's movement through physiological cost. Permeability can be quantified with respect to both the willingness to move and the costs inflicted by moving (Popescu and Hunter 2011). In our experimental design, low matrix permeability was characterized by the substrate unsuitability such as drier conditions and the absence of shelter. Habitat alteration should decrease the propensity to move

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and increase the cost of moving, here measured as body mass loss during movement due to, among others, evaporative water loss (Rittenhouse et al. 2008, Cosentino et al. 2011, Watling and Braga 2015). In addition, in *Bufo* species, the leg length is linked to movement ability: toads with long legs move faster and cover longer distances (Choi et al. 2003, Phillips et al. 2006). In amphibians, a large body size also favors longer movements due to better water retention (Van Bocxlaer et al. 2010), which decreases desiccation risk (Cosentino et al. 2011). Therefore, we also expected that toads with larger body size and longer legs would move more, and that this movement syndrome (i.e. the correlation between enhancing traits and movement propensity) would be strengthened in fragmented landscapes. Yet, predation risk may force individuals to move and cancel both the effect of matrix resistance on movement and the movement syndrome

Material and Methods

Study site, housing conditions and measurement of phenotypic traits

The study took place in the Station for Theoretical and Experimental Ecology (Moulis, France). We used 53 juvenile toads from a semi-natural population maintained in the Metatron (Legrand et al. 2012; authorizations #09-2014-02), a system of enclosures made of natural habitat providing resources fulfilling toad needs (i.e. dense vegetation, pools, hides and rocks). Fences around the Metatron prevented any predators from entering in enclosures, making sure that toads never encountered a predator. We captured toads in autumn 2015, few months after they completed their metamorphosis. Afterward, they were maintained in 4 terraria of 35 x 17.5 x 22.5 cm with 5 cm of soil litter covered with rocks and pieces of egg carton used as refuges. Terraria were sprayed daily with water to ensure high humidity level. Toads were fed *ad libitum* with bloodworms and small crickets.

Before the experimental test, toads were individually identified taking pictures of their ventral patterns with a Canon EOS 600D camera (Fig.1a). Individuals were then measured for their snout-vent length and posterior left leg length using a caliper by the same experimenter (to the nearest mm). Finally, they were weighted (to the nearest 0.01 g). After the experimental test, pictures of ventral patterns were taken again to identify each individual. Body mass was measured again to assess physiological costs (i.e. dehydration) of movements. At the end of the experiment, toads were released in the Metatron.

Predator treatments

As predator treatment, we used olfactory cues from the grass snake, *Natrix natrix*. This species feeds mostly on anurans, and particularly on common toads (Reading and Davies 1996). Previous studies showed that *Bufo* species detect and avoid scent of predatory snake (Flowers and Graves 1997, Gonzalo et al. 2008). Moreover, naïve tadpoles have an innate recognition of water snakes as predator using only cues (Kiesecker et al. 1996, Griffiths et al. 1998), which is not surprising when two species have coevolved on the long term (Ewert and Traud 1979). Common toads produce a toxic compound, the bufadienolides, which protects them from many predators (Daly 1995). The toxin quantity is lowest at the post-metamorphic stage explaining a higher propensity of behavioral defense than chemical ones (Jara and Perotti 2009, Üveges et al. 2017). Grass snake have further evolved resistance to the toxic effects of bufadienolides (Mohammadi et al. 2016) making this predator species particularly relevant to induce behavioral avoidance and escape reactions in common toad (Ewert and Traud 1979). While responses to predator scents was only tested and observed using other snake species, it is therefore very likely that common toads recognize and respond to grass snake cues as well.

We used young grass snakes from a breeding facility in Moulis (authorizations #2012-11). Snakes were maintained individually in plastic boxes (25 x 15 x 10 cm) with a basking area, a water bowl and absorbent papers on the floor to collect snake odor. After three days, we collected papers from two snakes with gloves and introduced them in the two terraria of toads from the predator cues treatment. Toads were exposed to predator cues during two weeks before the experimental test and new odors were added every three days. Toads in the no predator cues treatment received absorbent papers from snake-free terraria maintained in another room than the snake terraria and therefore were devoid of odor. These absorbent papers from the no odor treatment were also replaced every three days.

Experimental test of matrix permeability

We used 6 systems made of 4 cattle tanks (diameter: 1.70 m, Fig. 1b) containing soil litter and linearly connected by a plastic pipe (diameter: 20 cm and 25 cm long). The two tanks at the extremity contained 20 cm of soil litter, dense vegetation, water dishes, and rocks and logs serving as shelters (Fig. 1c). Toads were released in the first tank of the system, called the departure tank. To go from this departure tank to the last tank of the system, called the arrival tank, toads had to cross two other tanks defining the matrix treatments (3.5 meters). The substrate of these two intermediate tanks was similar and manipulated to create 3 different matrix types (spatially replicated 2 times each, Fig. 1c): 1) a *road* substrate filled with a fake tarmac (using bitumen rolls), 2) a *path* substrate covered with a thin and packed layer of soil (~ 5cm deep), and 3) a *natural* substrate covered with a deep layer of soil (20cm deep) and clumps of vegetation. These intermediate tanks were always devoid of shelters. Total systems are 7-meters long (4 meters of matrix), which allows mimicking different degrees of matrix permeability to movements commonly encountered in natural environments (from low resistance in fully natural environment to putatively high resistance encountered while crossing a

road). To prevent toads moving back to the arrival tanks, the last connecting pipe was raised of 10 cm from the bottom of the tank. However, toads could circulate freely between departure and intermediate tanks. By testing matrix effect experimentally, we can disentangle the effect of the substrate itself (e.g. the absence of shelter and the poor humidity condition), acting as a barrier to movement without the actual risk encountered in real conditions such as road traffic. Using these 6 systems, we could not carry out the experiment on all individual ($n = 53$) at the same time, so we performed two temporal replicates of the experiment resulting into 12 experimental groups (2 predation treatments x 3 connectivity treatments x 2 replicates) made of 4 to 5 individuals previously treated with predator cues or not (see above). Among combinations of matrix type and predation risk, the number of individuals was homogeneous ($\sim 8.2 \pm 0.31$, range: 7 to 9 individuals), and body and leg lengths, as well as body masses were not significantly different before the experimental test ($p > 0.29$ for simple effects and the interaction). Experimental groups of toads were released in the departure tank for a 48-hour acclimation period during which the connecting pipes were closed to prevent any movement from the departure tank. We then opened the pipes during a 24-hour period. We finally closed all connecting pipes and captured afterwards resident and movers (i.e. toads found in departure and arrival tanks, respectively). No toads were captured in the intermediate tanks (i.e. matrix tanks). We recaptured 49 toads of the 53 released, the four remaining were assumed to be dead and were therefore not included in the analyses.

Climatic condition inside the three matrix types of the experimental system were measured in autumn 2017, as we could not measure them during the experiment. We used data loggers (HOBO) that recorded temperature ($T^{\circ}\text{C}$) and luminosity (lux) every 10min, 24/24h for two months. Ten loggers were placed in the central area of the tanks. There were significant effects of matrix types on both the temperature and the

luminosity (statistics and mean \pm SE of the climatic variables in the three matrix types during the day and the night are resumed in Supplementary Table 1): Temperature was different between road, path and natural matrices: during daytime (8 am to 8 pm) roads were the warmest and natural matrix were the coolest, during the night (8 pm to 8 am) the differences of temperature in the 3 matrix types was much less contrasted. In addition, natural matrix presented the smallest variation of temperature between day and night. Luminosity was different day and night with natural matrix being the less lighted.

Statistical analyses

We first modeled the effects of matrix type (natural, path or road), predation risk (presence or absence) and their interactions on movement propensity (i.e. the probability to be a mover *versus* a resident), using a generalized mixed model with a binomial error distribution and a logit link. Fixed effects were matrix type, predation risk, body length (snout-vent-length) and leg-length and the two double and triple interactions between predation risk, matrix type and each phenotypic trait (i.e. body length and leg length). Since leg length is correlated with snout-vent length ($R^2=0.811$, $F_{1,47}=206.4$, $P < 0.001$), we used the residuals of the linear regression of leg length by snout-vent length to prevent collinearity and test for independent effects (i.e. relative leg length). The full model testing the effect of matrix type, predation risk, phenotypic traits (body and leg length) and their interactions did not converge properly, so following Zuur et al. (2009), we selected the best random structure by estimating the importance of random intercepts with likelihood ratio tests and variance explained. Random intercepts, experimental group (n=12) and the tank identity (n=6), were removed from the models as their variance \pm standard deviation were respectively 0.00 ± 0.00 , $LRT = -6.395e-14$, $P > 0.999$; and 0.00 ± 0.00 , $LRT = 1.208e-13$, $P > 0.999$. The temporal replicate (n=2) was not significant ($\chi^2=0.0413$, $P=0.840$) and therefore

also removed from the final model. Interactions between treatments and phenotypic traits would suggest a conditional “movers” syndrome, i.e. phenotypic differences between movers and residents varying with ecological context. To properly test for such a syndrome, we added a linear mixed model with phenotypic traits as response variables and matrix type, predation risk, individual movement status (i.e. resident *versus* mover) and their interactions as fixed effects.

Afterward we assessed movement cost using a linear mixed model testing the effect of matrix type (natural, path or road), predation risk (presence or absence), movement status (movers *versus* resident) and their interactions on body mass change. Body length and relative leg length were added as covariates in the model, as well as the body mass before the experimental test, to analyze relative changes in body mass. We did not analyze the proportion of body mass change on initial body mass because the analysis of proportion with linear general models raises statistical issues. Adding the denominator as a covariate is the recommended statistical approach (Darlington and Smulders 2001, García-Berthou 2001) and it led to the same results as analyzing such proportion.

Compliance with requirements of the fitted linear mixed-effect models were checked using Shapiro-Wilk normality test and Levene test for homogeneity of variance ($P > 0.1$ for both test on each model). In all models, we included the experimental group (n=12) and the tank identity (n=6) as random intercepts and the temporal replicate (n=2) as covariate. To estimate the significance of factors, we applied Wald χ^2 and likelihood ratio tests removing not significant interactions during model selection (with *a priori* level of significance of 0.05). Effect size of significant interactions were assessed using R Squared Difference Test, testing for a statistically significant difference (d) in

explained variance between two candidate models (i.e. with and without the significant interaction). In each matrix types, we computed the effect size of predation, movement propensity and their interaction on phenotypic traits (body length and relative leg length) and cost (body mass change) using beta standardized coefficients (Nakagawa and Cuthill 2007). Analyses were performed in R 3.4.2 using lme4, lmerTest, r2glmm and sjstats package.

Results

Movement propensity

The movement propensity was significantly higher in toads previously exposed to predator cues than in control toads (mean \pm SE: 0.577 ± 0.099 and 0.391 ± 0.104 respectively), while there was no main effect of matrix type on toad movement propensity (Table 1). However, phenotypic traits significantly affected movement propensity resulting in differences of phenotypic traits between movers and residents varying with environmental conditions (aka conditional movement syndromes, Table 1 and Supplementary Table 2). Movers were on average larger than residents (mean \pm SE: 2.992 ± 0.101 cm and 2.696 ± 0.087 cm respectively) and also tended to have longer legs (relative to body length) than residents (0.031 ± 0.034 and -0.03 ± 0.024 respectively). However, these differences between movers and residents in leg length depended on the interaction between predation risk and matrix type as shown by the significant triple interaction between predation risk, matrix type and movement status (Supplementary Table 2). The model with the triple interaction better explained the variance in response trait than the model without the triple interaction (R^2 model with interaction = 0.343, R^2 model without interaction = 0.243, $d = 0.099$, $P < 0.001$).

When splitting the dataset by matrix type, we found a significant interaction between movement propensity and predation on leg length in toads crossing the path matrix

(Supplementary Table 3, Fig. 2b): in absence of predation risk only, movers have significantly longer legs than residents ($\chi^2_1 = 6.608$, $P = 0.01$, Fig. 2b). There was no significant effect of movement status, predation or their interaction on leg length when toad crossed the natural or the road matrix (Supplementary Table 3, Fig.2a and Fig. 2c, respectively). There were no effect of movement propensity and predation on body size in any of the three matrices (Supplementary Table 3).

Movement cost

During the experimental test, toads exposed to predator cues lost less mass than toads unexposed to predator cues (mean \pm SE: -0.026 ± 0.0172 and -0.115 ± 0.0179 respectively, Table 2) and movers lost more mass than residents (mean \pm SE: -0.123 ± 0.0217 and -0.0156 ± 0.0115 respectively, Table 2). However, these effects varied with the matrix type as shown by the significant triple interaction between predation risk, matrix type and movement status (Table 2, Supplementary Table 3). The model with the triple interaction better explained the variance in response trait than the model without the triple interaction (R^2 model with interaction = 0.415, R^2 model without interaction = 0.302, $d = 0.113$, $P < 0.001$).

In natural matrix, when compared to residents, movers tended to lose mass in the absence of predation risk and gained mass in the presence of predation risk (Fig. 3a, $\chi^2_1 = 4.983$, $P = 0.026$ and $\chi^2_1 = 4.019$, $P = 0.045$ respectively). In the path matrix, we found an interaction between movement status and predation (Supplementary Table 3): in predation risk treatment residents did not lose mass while movers did ($\chi^2_1 = 11.129$, $P < 0.001$, Fig. 3b); in absence of predation risk, there was no significant difference in mass loss between residents and movers ($\chi^2_1 = 0.528$, $P = 0.468$, Fig. 3b). When crossing the road matrix, movers lost mass while residents did not in both predation risk

treatments (Supplementary Table 3, $\chi^2_1 = 3.477$, $P = 0.06$ and $\chi^2_1 = 12.804$, $P < 0.001$ in absence and in presence of predation risk respectively, Fig. 3c).

Discussion

This study provides insights into the impacts of landscape fragmentation on movement features in juvenile toads. We experimentally addressed how matrix type affects movement. Rather than focusing on movement propensity only, we considered movement as a multi-component process in which a suite of costs and benefits shape the variation in movement rate, as well as the variation in other movement characteristics such as the phenotype of movers relative to residents' phenotype (Clobert et al. 2009). In such an approach, we are able to detect the variation of movement with local conditions and individual phenotypes. Indeed, even when habitat fragmentation may have little effects on departure rate *per se*, it can shape interactive effects of internal and external factors on the costs of movement and the resulting decisions (Cote et al. 2017). Here, the recreated matrix type did not impact the positive relationship between body length and movement, but interacted with relative leg length and the local risk of predation to drive departure decisions. This component of the movement syndrome (i.e. movers having longer legs than residents) depended on both the type of matrix and the risk of predation, through changes in physiological costs and the benefits of movements. Movers lost more mass on average than residents except in the most permeable matrix in the presence of predation risk where movers gained mass compared to residents, which can be the consequence of both moisture condition and antipredator strategies.

The study of the ecology and evolution of movements in biphasic life cycle amphibians requires making a distinction between migration and dispersal processes. While migration is an intra-population process involving seasonal movements between

aquatic breeding sites and terrestrial habitats, dispersal is an inter-population process characterized by unidirectional movements from natal ponds to other breeding sites that are not part of the population of origin (Semlitsch 2008). Yet, estimating the distance moved in juvenile amphibians is quite difficult because movements occur over discrete intervals for several years. However, during their first year, it seems that newly metamorphosed amphibians usually do not move more than a few tens of meters from their natal pond (Semlitsch 2008). Therefore, in the case of postmetamorphic individuals, it is difficult to predict if the first emigration from the pond will lead to dispersal or not: some juveniles will stay in the neighborhood of their natal pond and reproduce in it after reaching sexual maturity while another portion of individuals will disperse during the juvenile stage and colonize non-natal ponds (Semlitsch 2008). In our study, it is likely that the movement observed in juvenile toads could act as a proxy of these two processes. The combined effect of landscape fragmentation and predation risk on movements could therefore have an implication at both population and metapopulation levels.

The experimental manipulation of matrix type has previously been shown to be an effective approach to assess the impact of fragmentation in small vertebrate movement (Stevens et al. 2004, Prevedello et al. 2010, Cline and Hunter Jr 2014, Trochet et al. 2019). In addition, similar experimental approach, i.e. creation of habitat variability in small-sized outdoor mesocosms, has proven powerful to study the local determinants of emigration decisions in other small animals (Trochet et al. 2013; Legrand et al. 2015; Reim et al. 2018). In this study, at first glance, the matrix type had no effect on toad's willingness to move. Indeed in comparison with a natural matrix, altered matrix characterized by road tarmac or packed soil did not decrease the individual propensity to move. A previous study showed that landscape alteration did

not appear as a drastic stressor in toad since it did not suppress the responsiveness of the hormonal system as some rough and chronic stressors can do (Janin et al. 2011). Moreover, it seems that road offers low resistance to toad movements (Stevens et al. 2004) and that the invasive cane toad can even actively select roads to disperse faster (Brown et al. 2006). In natural environment, movements across roads can however increase mortality risk due to traffic (Cayuela et al. 2017), a consequence that was obviously not assessed in our study. Yet, as we will discuss it later, independently of traffic risk, crossing such altered matrix can also have consequence on body hydration increasing the risk of desiccation (Cosentino et al. 2011). The propensity to move was on the contrary higher when there was a local risk of predation. Therefore the observed toads' movement may be a strategy to escape predation as shown in other species (in invertebrates: Baines et al. 2014; in vertebrates: Bestion et al. 2014). Juvenile toads are particularly at risk with predators due to their small size and their low toxicity (Jara and Perotti 2009, Üveges et al. 2017). Given their nomadic life style (Pittman et al. 2014), they might therefore react promptly to predation risk by dispersing away from their living habitats.

Interestingly, while matrix type did not change movement propensity, it influenced movement strategies through its dependencies on local conditions and individual phenotypes. In amphibian species, large body size and legs increase movement capacity by improving locomotion performance both in terms of endurance and speed (Goater et al. 1993, Stevens et al. 2004, Trochet et al. 2016, 2019). In this study, larger toads had a higher rate of movement whatever the local conditions or the type of matrix. A larger body size can improve mobility on a variety of habitat. In meadow and forest, larger toad are better to step over grass or leaves without being trapped under the substrate, while in field or road, a larger body size can confer a better

water retention enhancing movement and decreasing desiccation risk (Stevens et al. 2004, Van Bocxlaer et al. 2010, Cosentino et al. 2011). Alternatively, the larger toads can also be older than the smaller ones, which could also influence their movement propensity. However all toadlets were aged of few months post-metamorphose since the experiment took place in October (toads were around 3-4 months old) and thus the age variation should be low. While toads with longer legs tended to move more, we found that this leg length/movement covariation was context-dependent: it varied with both local conditions and matrix permeability. In absence of predation risk, moving toads had longer legs than resident ones as expected (Choi et al. 2003, Phillips et al. 2006), but it depended on the substrate they had to cross. In highly permeable matrix, movement propensity was not linked to leg length. Moving across highly permeable matrix might not strain individual locomotor skills as much as crossing coarse environments. In altered landscapes, toads crossing the path matrix had longer legs than residents, while this effect did not exist when individuals had to cross a road tarmac. These results suggest that bare soil might represent a more resistant substrate than a road tarmac in the common toad. Alternatively, the road tarmac provides warmer thermal conditions (Supplementary Table 1), which might attract toads regardless of their inclination to move. In this case, movements across the road matrix would partially be a side effect of basking behaviors (Puky 2005). Besides, movement inclination through a hostile matrix can also depend more on other factors such as boldness rather than on leg size. This movement syndrome observed in the path matrix was however cancelled when the departure was induced by predation risk. Movement syndromes have been shown to be cancelled or reinforced when movements were induced by predation risk (Gilliam and Fraser 2001, Cote et al. 2013, Bestion et al. 2014 but see Baines et al. 2015). On one hand, in presence of predators in a landscape, moving might be a risky behavior and a covariation between the propensity to move and locomotor

skills or antipredator defenses may reduce the risks. Accordingly, the presence of predators has been shown to strengthen the dependency of dispersal on body size in killifish *Rivulus hartii* (Gilliam and Fraser 2001) and on tail length in common lizards *Zootoca vivipara* (Bestion et al. 2014). On the other hand, the presence of stressors can force individuals to move even if they are not particularly inclined or skilled to move across a landscape (Legrand et al. 2015). When the predation risk is locally high, it might be better to move to a safer patch despite poor locomotor skills, the benefits of leaving a dangerous patch outweighing the energetic cost of movement (Bonte et al. 2012, Clobert et al. 2012). Such context-dependency of movement syndromes should thus be more frequent than previously thought.

Movement strategies result from the balancing effects of the costs and benefits of moving, which should vary with environmental conditions and individual phenotypes (Bonte et al. 2012). In our study, we observed that the type of matrix substrate did not affect the willingness to move, a major component of matrix permeability (Popescu and Hunter 2011). Yet, a second aspect of matrix permeability is the cost inflicting by moving and in this case the drier condition of the substrate did impose a physiological cost to the moving toads. In amphibians, movement cost is indeed mainly associated with desiccation risk, especially in altered landscape (Cosentino et al. 2011) and dehydration can be assessed by measuring mass loss after movement (Rittenhouse et al. 2008, Cosentino et al. 2011, Watling and Braga 2015). Therefore, in our study, the variation of mass is probably mainly due to water evaporation/absorption than to food differences between matrix types. The results showed that individuals moving across habitats lost mass with two exceptions. First, movers did not lose mass relatively to resident while crossing the path matrix in the absence of predation risk, a situation in which they also displayed longer legs. This suggests that longer legs may indeed

constitute locomotor skills reducing movement costs. However, toads that did not cross the path matrix lost mass too, which can also explain the absence of significant difference between movers and residents. Second, in presence of predation risk, movers gained mass when they crossed natural matrix. The positive effect of predation risk on hydration in permeable matrix can be explained by burrowing while moving, an antipredator behavior reducing visibility but also increasing water retention (Hoffman and Katz 1989, Toledo et al. 2011). Such behavior being undoable in road or path matrices, this could explain the mass loss found in these two treatments. This result is consistent with previous studies showing that toad body condition was worse when they had to cross a matrix characterized by low forest availability (Janin et al. 2011). Another non-exclusive explanation could be that moving away from a stressing environment might remove high energy costs of being stressed along with relaxing competition for food (Peacor 2002, Relyea 2007). Although we could not assess the cost of movement on individual fitness, dehydration can have important consequences such as a lower survival (Rothermel and Luhring 2005, Rittenhouse et al. 2008, 2009), a decrease of locomotor performance (Preest and Pough 1989) and a greater predation risk (Rohr and Madison 2003). It therefore suggests that the movement success could be lowered when individuals have to undertake costly movement in altered landscape.

This study shows that multiple external factors such as fragmentation and predation risk interplay to determine multiple facets of animal movements from the willingness to move to the phenotype of individuals moving. Consequently, such correlations between phenotypic traits and movement can be disrupted in response to specific environmental conditions (Legrand et al. 2016). The point that movement can vary a lot between individuals means that studies should focus at the individual level as much as possible. Once these individual traits and their associated costs are determined,

more accurate prediction can be made about how population will respond to specific landscape change due to fragmentation (Knowlton and Graham 2010). To a greater extent, determining whether fragmentation can modify patterns of traits covariations and potentially affects (meta)population dynamics and effective gene flow is a major question that requires the incorporation of the potential cost of movement in altered landscape (Cote et al. 2017).

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Figure Legends

Fig. 1 a Pictures of toad's ventral patterns allowing individual identification; **b** the 6 experimental systems (white surrounding) made of 4 cattle tanks linearly connected by a plastic pipe; **c** the top picture represents extremity tanks (i.e. departure and arrival tanks), the natural matrix type contained the same amount of vegetation but was devoid of shelters and water dishes; the center picture represents the path matrix type covered with a thin and packed layer of soil and the bottom picture represents the road matrix type filled with a fake tarmac.

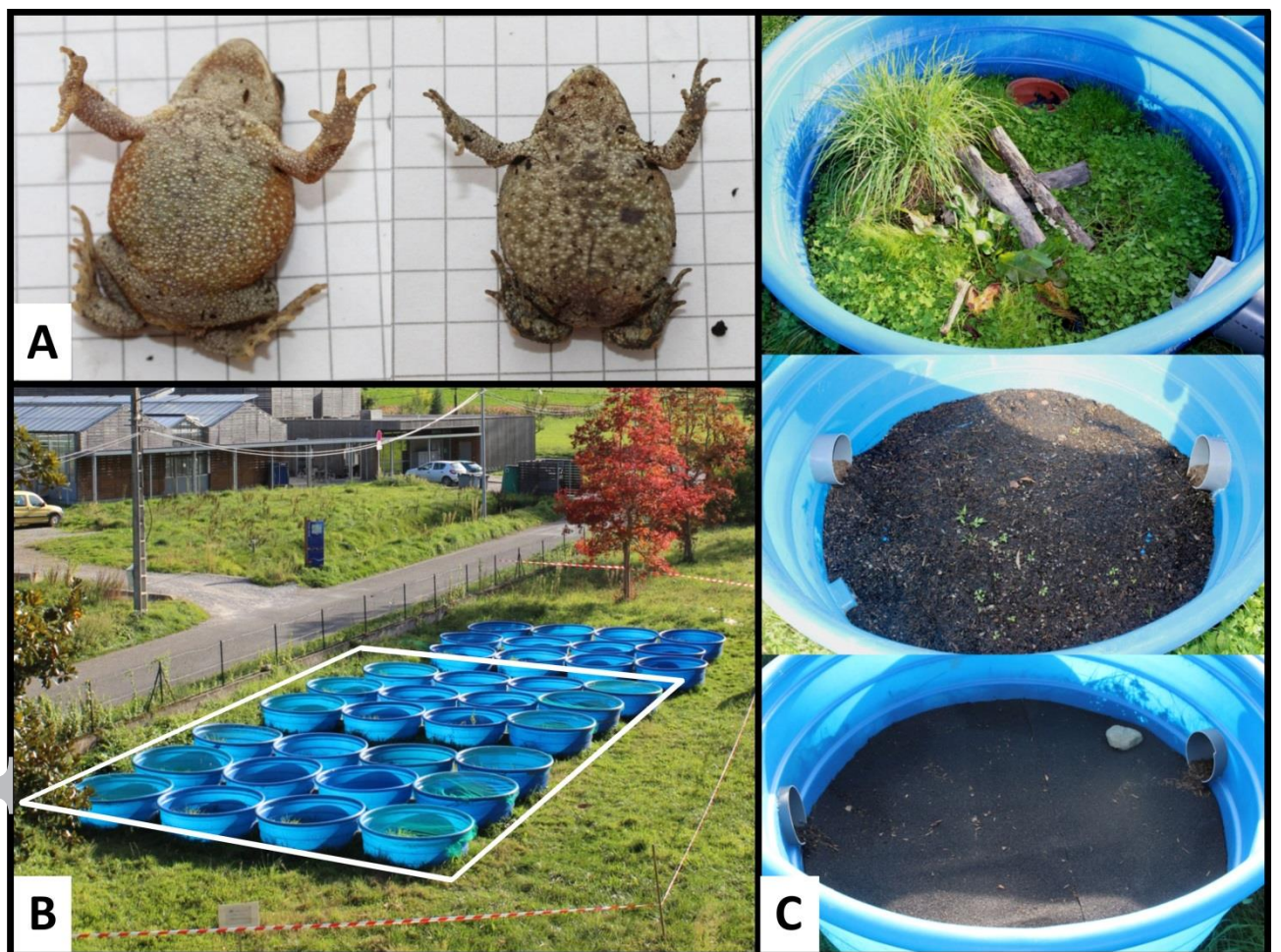


Fig. 2 Effect of predation treatment: P+ with predation cues and P- without predation cues and movement status: dark bars for movers and light bars for residents toad relative leg length (mean \pm SE, residuals from snout vent length) in each matrix type: **a** natural matrix, **b** path matrix and **c** road matrix. See Supplementary Table 2 and results for statistics.

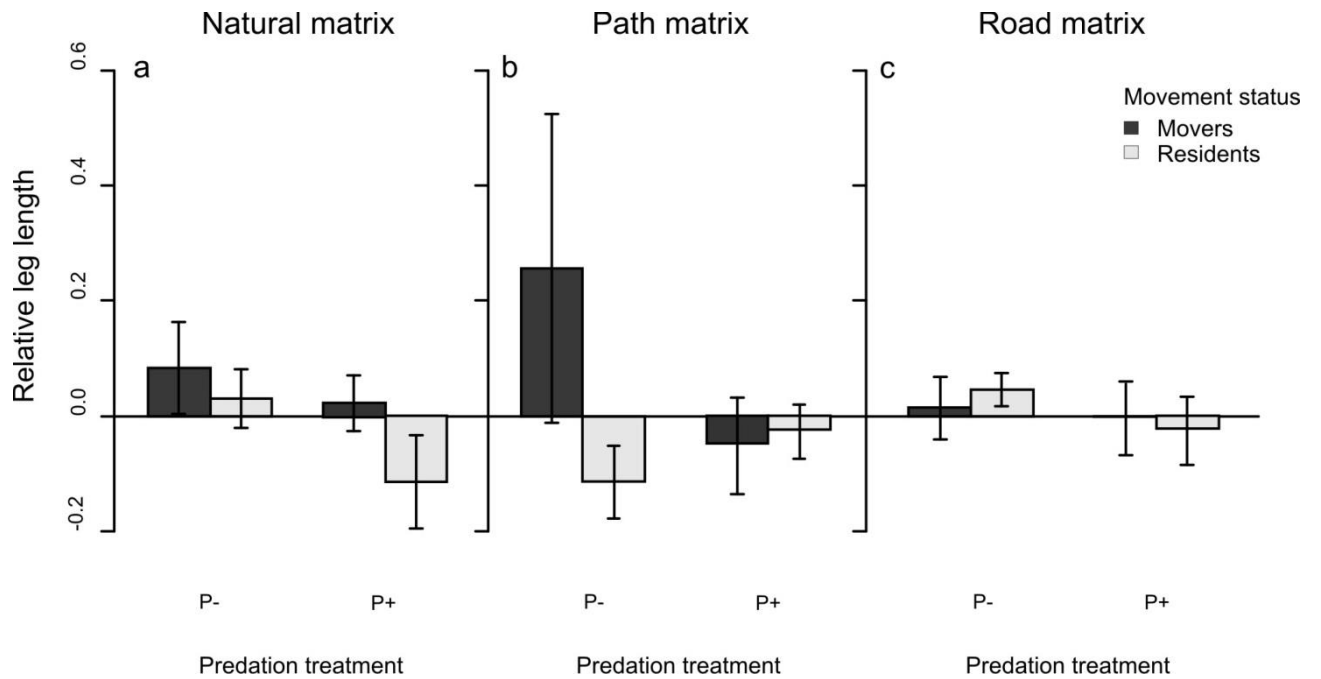


Fig. 3 Effect of predation treatment: P+ with predation cues and P- without predation cues and movement status: dark bars for movers and light bars for residents on the variation of toad body mass from before to after assay (mean \pm SE, residuals of body mass change from initial body mass) in each matrix type: **a** natural matrix, **b** path matrix and **c** road matrix. See Supplementary Table 2 and results for statistics.

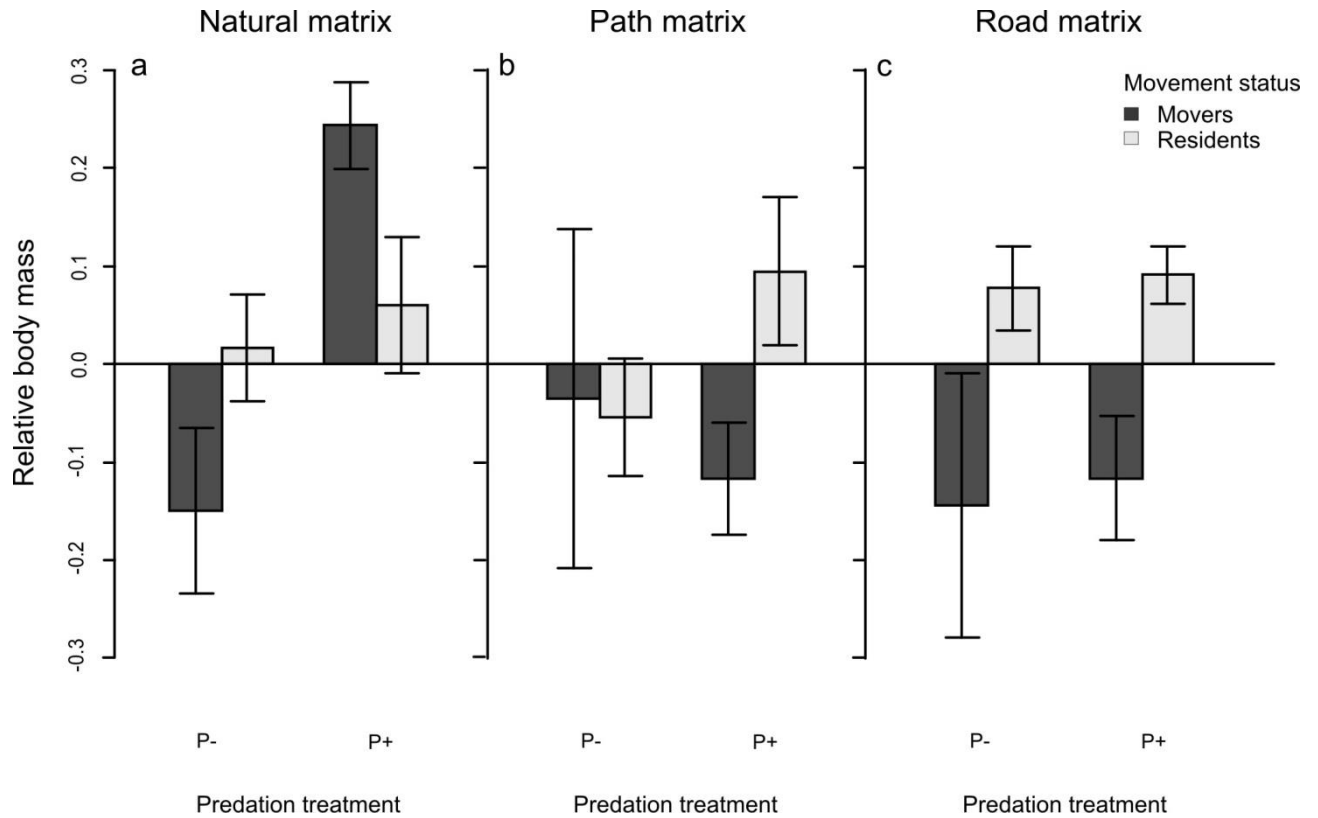


Table Legends

Table 1. Results of GLM testing the impact of predation risk, matrix type and toad phenotypic traits (body and relative leg length) on movement probability. Significant and marginal effects are respectively highlighted in bold and underlined.

Phenotypes	Factors	χ^2	d.f.	<i>P</i>
Movement probability	Predation	3.738	1	<u>0.053</u>
	Matrix type	0.162	2	0.922
	Body length	5.485	1	0.019
	Relative leg length	3.990	1	0.046
	Predation*Matrix type	1.215	2	0.545
	Predation* Body length	0.090	1	0.765
	Matrix type* Body length	0.165	2	0.921
	Predation* Relative leg length	0.088	1	0.767
	Matrix type* Relative leg length	0.278	2	0.870
	Predation*Matrix type* Body length	5.553	2	0.062
	Predation*Matrix type* Relative leg length	6.832	2	0.033

Table 2. Results of LMM testing the impact of predation risk, matrix type and movement status (movers *versus* residents) on toad movement cost (body mass change).

Significant effects are highlighted in bold.

Phenotypes	Factors	χ^2	d.f.	<i>P</i>
Movement cost: Body mass change	Predation	5.613	1	0.018
	Matrix type	5.502	2	0.064
	Movement status	6.179	1	0.013
	Initial body mass	3.518	1	0.061
	Body length	3.269	1	0.071
	Leg length	1.749	1	0.186
	Predation*Matrix type	3.72	2	0.156
	Predation* Movement status	0.121	1	0.728
	Matrix type* Movement status	8.479	2	0.014
	Predation*Matrix type* Movement status	7.973	2	0.019