Influence of substrate types and morphological traits on movement behavior in a toad and newt species

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Background. Inter-patches movements may lead to genetic mixing, decreasing both inbreeding and population extinction risks, and is hence a crucial step in amphibian meta-population dynamics. Traveling heterogeneous landscapes might be particularly risky for amphibian species that are sensitive to both terrestrial and aquatic environmental changes. Understanding how amphibians perceive their environment and how they actually move in heterogeneous habitats is an essential step in metapopulation functioning and can be important for conservation policy and management. **Methods**. Using an experimental approach, the present study focused on the movement behavior (crossing speed) on different substrates mimicking landscape components (human-made and natural substrates) on two contrasting amphibian species, the common toad (*Bufo bufo*), a hopping and burrowing toad, and the marbled newt (*Triturus marmoratus)*, a walking salamander. Considering those species allowed testing the hypothesis that species could react differently to substrate nature, depending on specific ecological requirements or locomotion modes because of morphological and behavioral differences. **Results**. In both species, substrate types influenced individual crossing speed, with individuals moving faster on soil than on cement. We also demonstrated that morphological traits were related to movement behavior (body index or leg length) but depending on sexes. **Discussion**. The simultaneous and comparative study of both amphibian species (anuran vs urodele) provides additional insights into the processes that drive population dynamics and persistence, providing valuable knowledge for biodiversity conservation and management.

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Abstract

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Results. In both species, substrate types influenced individual crossing speed, with individuals moving faster on soil than on cement. We also demonstrated that morphological traits were related to movement behavior (body index or leg length) but depending on sexes.

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Key words

Matrix permeability, inter-patches movements, roads, fragmented landscapes, common toads, marbled newts

Introduction

Inter-patches movements, and dispersal in particular, is a key process for maintaining gene flow among populations (Kareiva & Wennergren, 1995; Ronce, 2007) with strong consequences on metapopulation dynamics and population persistence (Clobert et al., 2001; Bowler & Benton, 2005; Clobert et al., 2012). Since many decades, the architecture of landscapes has severely changed with the development of human activities. The anthropogenic practices, such as agriculture, urbanization or the expansion of road network, have led to the emergence of discontinuities in the habitat matrix: the continuous patches of habitats became smaller and more isolated from each other, resulting in the well-known habitat fragmentation pattern, associated to habitat loss (Collinge, 2009; Wilson et al., 2016). To ensure a sufficient connectivity among populations in spite of these environmental changes, individuals could be force to adapt their movement behavior (Arendt, 1988; Andreassen & Ims, 1998; Kuefler et al., 2010) and to move further and/or longer across the habitat matrix. This change in movement behavior may increase the costs associated to dispersal by exposing individuals to higher mortality rate during the transience phase (when crossing roads for example; Carr, Pope & Fahrig, 2002) and increasing the population extinction risk. Elucidating how individuals react and adapt their movement pattern in the disturbed landscapes might improve our knowledge in evolutionary ecology.

Due to ecological requirements, amphibians are exposed to a variety of habitat types (i.e. both terrestrial and aquatic) throughout their life cycle, often in patchy and heterogeneous landscapes (Marsh & Trenham, 2001). During the terrestrial phase, individual movements are more risky, through predator and UV-B exposures, and desiccation risk (Joly, Morand & Cohas, 2003). Many studies have considered the multiple effects of habitat fragmentation -and their related landscape components- on amphibian populations, both at the individual and population levels. Particularly, agricultural landscapes, urban areas and human-made infrastructures negatively affect these species, with a reduction of species richness (Riley et al., 2005; Rubbo & Kiesecker, 2005; Youngquist & Boone, 2014) or gene flow events (Lenhardt et al., 2017). Roads have also been found to be an important barrier to amphibian dispersal, limiting dispersal events (Marsh et al., 2005) and increasing the mortality risk occurring during crossing (Mazerolle, 2004a). Nevertheless, some amphibian species can also benefit from certain landscape elements. For instance, drainage ditches may facilitate movement events in the green frog (Mazerolle, 2004b), and cane toads seemed to use roads as dispersal corridors in Australia (Brown et al., 2006). Habitat-species interactions are complex and highly specific, as already demonstrated in previous studies (Kolozsvary & Swihart, 1999; Trochet et al., 2016) suggesting that adaptation of movement behaviors to landscape conversion could strongly diverge between species.

The costs associated to inter-patches movement can be high (Van Dyck & Baguette, 2005) and could lead to high selective pressures on dispersal and associated phenotypic traits (Bonte et al., 2012). According to this expectation, many studies focus on the correlation between movement and phenotypic traits. At the intra-specific level, phenotypic differences related to dispersal ability between individuals have been reported. For instance, larger and/or longer individuals are generally expected to be dispersers, because they should benefit from high level of competition to disperse further (Léna et al., 1998). Evidence for this relationship between body size and movement has been described in many taxa (in insects: Anholt, 1990; Legrand et al., 2015; in mammals: Gundersen, Andreassen & Ims, 2002; Holekamp & Sherman, 1989; O'Riain, Jarvis & Faulkes, 1996; in reptiles: Léna et al., 1998; in birds: Barbraud, Johnson & Bertault, 2003; Delgado et al., 2010; in fishes: Radinger & Wolter, 2014). For walking and/or hopping animals, selection for efficient displacement might lead to leg elongation. As a result, morphological adaptations to movement are also expected to be deduced from estimates of leg length (Moya-Laraño et al., 2008). This correlation between movement and leg length (i.e. hind-limb length, hereafter HLL) was demonstrated in some species (in reptiles: Losos, 1990; in spiders: Moya-Laraño et al., 2008; in amphibians: Bennett, Garland & Else, 1989; Choi, Shim & Ricklefs, 2003; Phillips et al., 2006), but still remains unclear.

One third of the amphibian species are currently threatened worldwide, with 43% of species having declined in the last decades (Stuart et al., 2004). Habitat fragmentation has been identified as one of the most important factor affecting amphibians (Cushman, 2006). Understanding how amphibians perceive their environment and how they actually move in heterogeneous habitats is an essential step in metapopulation functioning and can be important for conservation policy and management. However, despite the crucial importance of inter-patch movements in altered landscapes, little is known about the direct inter-specific interaction between individual movements and the different substrates that individuals can encounter during transience in the habitat matrix (Ims & Yoccoz, 1997; Wiens, Schooley & Weeks, 1997; Wiens, 2001; Stevens et al., 2004). To that purpose, the present study focused on the movement behavior (crossing speed) on different substrates mimicking landscape components (human-made and natural substrates) on two contrasting amphibian species, the common toad (*Bufo bufo*), a hopping and burrowing toad, and the marbled newt (*Triturus marmoratus)*, a walking salamander. Common toads and marbled newts can live into the same habitat, such as grassland, woodland or agricultural areas, and could therefore face the same environmental pressures during terrestrial movements. Considering those species allowed testing the hypothesis that species could react differently to substrate nature, depending on specific ecological requirements or locomotion modes because of morphological and behavioral differences.

Materials & Methods

Studied species

The common toad (*B. bufo*) is the most widely distributed, and one of the most abundant anuran species in Europe (Gasc et al., 1997). This species occupies various habitats such as coniferous, mixed and deciduous forests, bushlands, but also urban areas such as gardens and parks. Common toads hibernate singly or in groups from September to February, on land and occasionally in streams and springs. Usually, reproduction occurs in February, and large numbers of toads disperse to breeding sites (i.e. ponds) where the males compete for mating. After an explosive breeding season, toads leave ponds and return to terrestrial habitats (Gittins, 1983).

The marbled newt (*T. marmoratus*) is a large-bodied urodele species from Western Europe, found in France, Spain and Portugal (Sillero et al., 2014). Reproduction takes place in a large range of aquatic habitats, including well-vegetated ponds, pools, ditches and streams, from the beginning of March until the middle of August. After breeding, adults leave water bodies by walking, and join deciduous or mixed woodland, where they found refuges under dead and rotting wood, and other hiding places (Jehle & Arntzen, 2000).

Sampling and morphological measurements

Our work complies with the international animal care guidelines of the Association for the Study of Animal Behaviour, and all required French permits relating to an authorization of capture, marking, transport, detention, use and release of protected amphibian species; and animal experimentation accreditation n°A09-1) have been obtained (permit nos. 09-2014-14 and 32-2014-07) from the DREAL Occitanie ("Direction Régionale de l'Environnement, de l'Aménagement et du Logement"). Ethical approval was included under the protected species handling permit from the DREAL Occitanie. The project was approved by the "Conseil National de la Protection de la Nature" the 14th of September 2014 and by the "Conseil Scientifique Régional du Patrimoine Naturel (CSRPN)" of the region Midi-Pyrénées the 14th of October 2014.

In total, 83 common toads (68 males and 15 females) and 46 marbled newts (23 males and 23 females) were captured in different ponds to avoid our potential impact on populations in south of France (geographical coordinates: 43.671781 ° N, 0.504308 ° E; 43.076347 ° N, 1.351639 ° E), then brought back to the lab for experimentation and released between June and July 2015. During experiments, animals were housed at the Station d'Ecologie Théorique et Expérimentale (Moulis, France) in same-species groups of 4 to 6 individuals in semi-aquatic terrarium of 60×30×30 cm at room temperature. They were fed *ad libitum* with live mealworms and tubifex worms. For unambiguous identification, all individuals were PIT-tagged (RFID Standards ISO 11784 & 11785 type FDX-B, 1.4×8 mm, 134.2 khz from BIOLOG-ID, France; animal experimentation accreditation n°A09-1) before the experiments following the protocol developed in Le Chevalier et al. (2017). We then measured snout-to-vent length (*SVL*) and hind limb length (*HLL*) to the nearest 1 mm and body weight (*mass*) to the nearest 0.01 g.

Movement tests

All tests were performed in June and July 2015, after the breeding season when all individuals were in the terrestrial phase. In order to test the crossing capacities of both species, we made them move along two tracks (200 cm long × 10 cm wide × 20 cm high), each filled with two different substrates: cement (human-made) or soil (natural). During the experiments all individuals were chased down the tracks and forced to move by gently poking their back after each stop. Only one individual was tested at a time and we recorded the number of stops (*stops*) and the *crossing speed* (in cm/sec) to the nearest 0.1s to travel 200 cm from departure to arrival line. In order to provide reliable estimates of crossing capacity using repeated-measure design while minimizing stress, every individual was tested three times on each substrate with only one trial per day. Each animal were therefore kept in captivity for six days in average (mean ± SD: 6.37 ± 11.62; min-max = 1-35 days; individuals were kept for another experiment not detailed here), during which animals were returned to the aquaria. Because locomotion in amphibians are influenced by temperature (Herrel & Bonneaud, 2012; James et al., 2012; Šamajová & Gvoždík, 2010), all tests were performed in a greenhouse under controlled-temperature conditions (mean ± SD: 25°C ± 1°C).

Some individuals (n = 32) did not complete the 200 cm run (stopping completely or turning back), these individuals and their replicates were removed from the analyses for statistical reasons. We therefore included 77 toads (77 toads × 3 replicates × 2 substrates = 462 tests) and 20 marbled newts (20 newts × 3 replicates × 2 substrates = 120 tests) in the analyses.

Statistical analyses

Mass and *HLL* were strongly related to *SVL* ($r_s = 0.866$, $P < 0.001$, and $r_s = 0.691$, $P < 0.001$ respectively). To avoid collinearity in our model, we used a body index (*BI*), estimated by the residuals of the regression of log(*mass*) on log(*SVL*) (Jakob, Marshall & Uetz, 1996; Denoël et al., 2002), and the relative size of the *HLL* (named after *leg*) estimated by the residuals of the linear regression between *HLL* and *SVL*. We built linear mixed-effect models (LMMs) for each species using the *crossing speed* (log-transformed) as response variable, individual as a random factor and *BI*, *leg*, *substrate, sex* and first order interactions as fixed effects. Because the *crossing speed* was strongly related to the number of stops in both species (*T. marmoratus*: $r_s = 0.543$, $P < 0.001$; *B. bufo*: $r_s = 0.767$, $P < 0.001$), we also added *stops* as covariate in our models. LMMs were performed using the lme4 R-package (Bates et al., 2017).

Model selection was performed using backward selection. Interactions were removed when they were not significant, and the less significant variable was then removed step by step. Between each step, successive models were compared using likelihood ratio tests (LRT) to determine the significance of the variable removed, as recommended by Burnham & Anderson (2002). If the effect of this variable was not significant, the new model was kept and the backward selection was continued. The procedure was stopped when all explanatory variables had a significant effect on the response variable. Models were run using R 2.14.2 (R Development Core Team 2011).

Results

After model selection, the best models explaining variation in *crossing speed* retained *substrates* (soil and cement), *sex* and interactions between morphological traits and *sex* in both species (*T. marmoratus*: $\chi^2 = 5.925$, d.f. = 1, P = 0.015; *B. bufo*: $\chi^2 = 4.769$, d.f. = 1 , P = 0.029). *Crossing speed* was significantly lower on soil than on cement (Table 1; Figure 1).

Crossing speed was also correlated to several morphological traits depending on species. In the marbled newt, *crossing speed* was related to *BI* with an influence of sexes. Female newts with a high *BI* moved slowly while in males, individuals with a high *BI* crossed faster (Table 1; Fig. 2A). No relationship between *crossing speed* and *leg* was found in the marbled newt. In the common toad, long-legged males moved faster while females with long legs had a weak crossing speed (Table 1; Fig. 2B). In the common toad the *crossing speed* was not related to *BI*.

Discussion

Inter-patches movements may lead to genetic mixing, decreasing both inbreeding and population extinction risks, and is hence a crucial step in amphibian meta-population dynamics. Traveling heterogeneous landscapes might be particularly risky for amphibian species that are sensitive to both terrestrial and aquatic environmental changes. Despite being generally considered as poor-dispersers -even if toads and frogs have a better potential to disperse than newts- many studies showed that amphibians are strongly affected by the landscape structure at a large spatial scale (Riley et al., 2005; Rubbo & Kiesecker, 2005; Youngquist & Boone, 2014; Lenhardt et al., 2017). By comparing movement behavior in both an anuran and an urodele species, we experimentally investigated the influence of substrates and morphological characteristics on movements in species with distinct modes of locomotion. Our results demonstrated that both species were affected by substrate types, moving significantly slower on a human-made (cement) than on a natural (soil) substrate. Movement behavior was also related to morphological traits, but depending on sexes in both species.

Influence of substrate type on crossing speed

Inter-patches movement is expected to depend on the nature of the substrate crossed. Some landscape features may be associated with high resistance to movement while others facilitate movement (low resistance). In a previous study, Stevens et al. (2006) experimentally demonstrated that the natterjack toad (*Bufo calamita*) significantly preferred substrates mimicking forest and bare than those mimicking agricultural lands. In our experiment, the cement substrate represented linear roads, both in its nature (mixture of bitumen and gravel) and length (2 meters wide road), that are often associated with a high mortality rate in amphibians (Fahrig et al., 1995). Moreover, roads constitute a very hostile environment for amphibians (dry and warm substrate that could induce a desiccation risk). According to our assumptions, our results showed that substrate type influenced the movement behavior of both species tested, with individuals moving faster (higher crossing speed, Fig. 1; Table 1) on soil than on cement. Consequently on roads, both marbled newts and common toads could be more exposed to traffic, and suffer more from both desiccation and mortality risks (Petronilho & Dias, 2005; Santos et al., 2007; Sillero, 2008; Elzanowski et al., 2009; Matos, Sillero & Argaña, 2012). In the context of a contrasted and fragmented landscape, our results corroborated such negative effect of roads on amphibians, a finding already demonstrated in studies on population movement at large spatial scale (Fahrig et al., 1995; Carr, Pope & Fahrig, 2002; Sotiropoulos et al., 2013). Here, we highlighted a direct influence of the substrate on the displacement of two amphibian species, with divergent ecological requirements and locomotion modes. Those results emphasized the importance of road-crossing structure and landscape management at a small spatial scale for amphibian conservation.

Movement-related traits in both species

According to our expectations, our results showed an influence of morphological traits on the *crossing speed* in both species. Various morphological variables enable organisms to be adapted for ecologically effective movement (Bennett, Garland & Else, 1989; Losos, 1990; Choi, Shim & Ricklefs, 2003; Phillips et al., 2006; Moya-Laraño et al., 2008). Anurans have a streamline body with elongated hind limbs, which could make them efficient jumpers. Based on this hypothesis, a meta-analysis among several anuran species actually demonstrated that jumping performances were strongly correlated to hind limbs after correcting by snout-to-vent length (Gomes et al., 2009). We also demonstrated that movement behavior was related to the limb length (*leg*) in the common toad, an association already found in few anuran species (Choi, Shim & Ricklefs, 2003; Phillips et al., 2006). Indeed, long-legged males moved faster than females with long legs (Table 1), which corroborates the idea that limb length may be tightly associated to movement behavior adaptations in anurans. In males, longer legs could facilitate more rapid or longer-distance displacement events for populations (Phillips et al., 2006), as well as generating other advantages such as improved predator evasion and simplifying the negotiation of barriers and obstacles. As a consequence, the mortality risk of longer-legged males could be lower than individuals with short legs. Differences between sexes may be driven by divergent breeding benefits, which could lead to a trade-off between movement and high energetic costs of reproduction in females. We did not find a similar relationship between leg length and movement behavior in the marbled newts. Indeed in salamander species, authors suggested a trade-off between speed and endurance, which seemed to be not adapted to efficient movement abilities (Bennett, Garland & Else, 1989). More studies on the movement behavior in salamanders are needed to tackle this issue. On the other hand in the marbled newt, we found that males with high body index moved faster than individuals with low body index, independently of substrate (Table 1). Evidence for such relationship has been described in many taxa (Léna et al., 1998; Radinger & Wolter, 2014; Legrand et al., 2015), because larger individuals should benefit from high level of competition to disperse further (Léna et al., 1998). As for the common toad, this difference depending on sexes could be explain by divergent breeding benefits.

Conclusions

Inter-patches movement is a multifactorial process, subject to internal and external factors. Our findings demonstrated effects of substrates and their associated estimated costs to cross them on the movement behavior in two contrasting amphibian species, having divergent modes of locomotion. In particular, individuals were slower in the cement, making them more vulnerable on roads. In both species, we also showed significant relationship between morphological traits and movement behavior. We underlined the importance of considering spatial scale when studying population dynamics, which is a crucial issue in ecological management. The simultaneous and comparative study of both amphibian species (anuran vs urodele) provides additional insights into the processes that drive population dynamics and persistence, providing valuable knowledge for biodiversity conservation and management.

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Data Availability

The raw data has been supplied as a Supplementary File.

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Figure caption

Figure 1. Crossing speed (in cm/sec) on cement and soil substrates in (a) the marbled newt and (b) the common toad. **: P < 0.01. Error bars represents standard error.

Figure 2. Relationships between (a) crossing speed (log-transformed) and body index (residuals of the regression of log(body mass) on log(snout-to-vent length) depending on sexes in marbled newts; (b) crossing speed (log-transformed) and leg (residuals between hind limb length and snout-to-vent length) depending on sexes in common toads. Males are in black points and females are in grey points.

Figure 1

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**: P < 0.01. Error bars represents standard error.

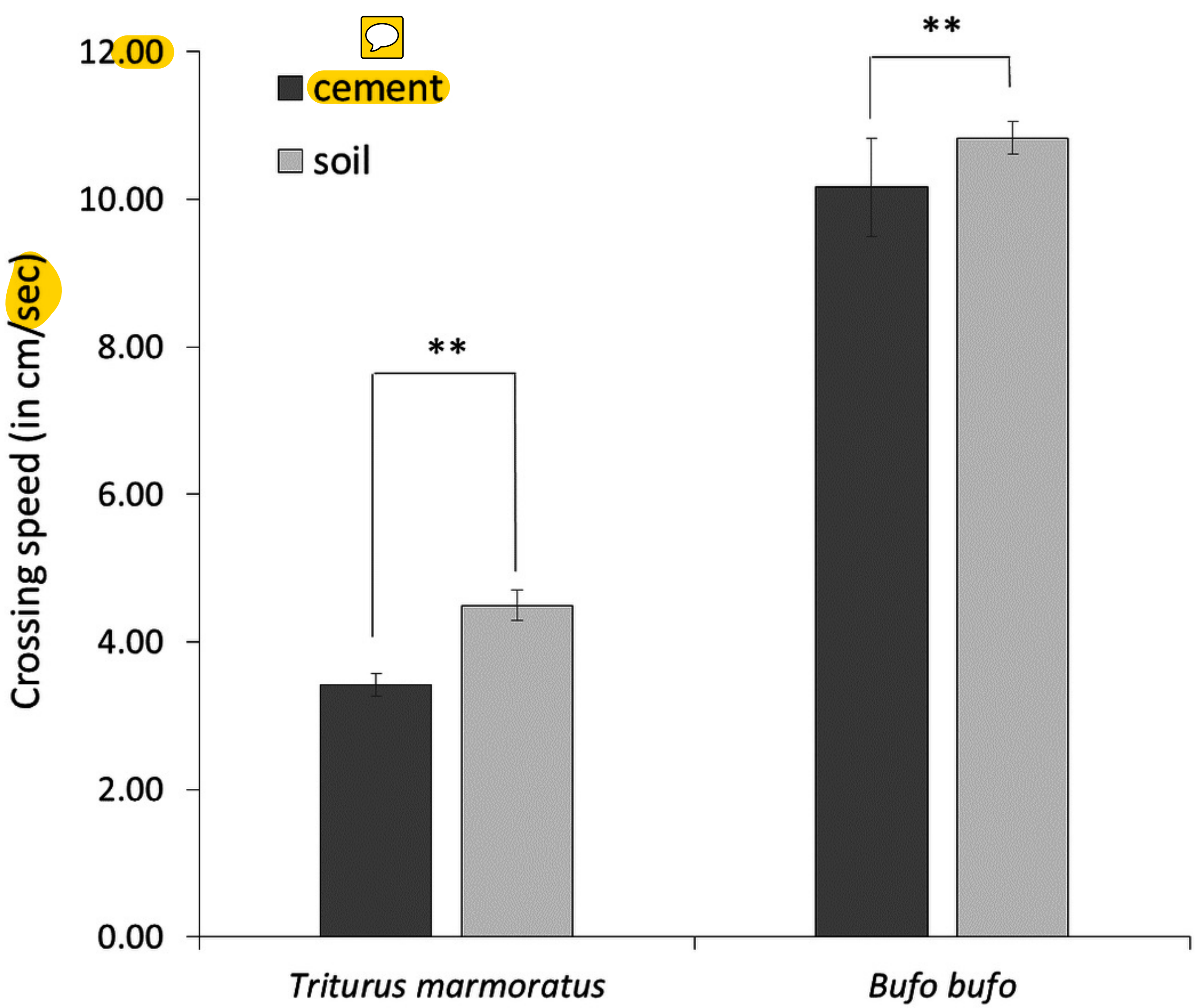

Figure 2

Figure 2. Relationships between (a) crossing speed (log-transformed) and body index (residuals of the regression of log(body mass) on log(snout-to-vent length) depending on sexes in marbled newts; (b) crossing speed (log-transformed) and leg (residuals be

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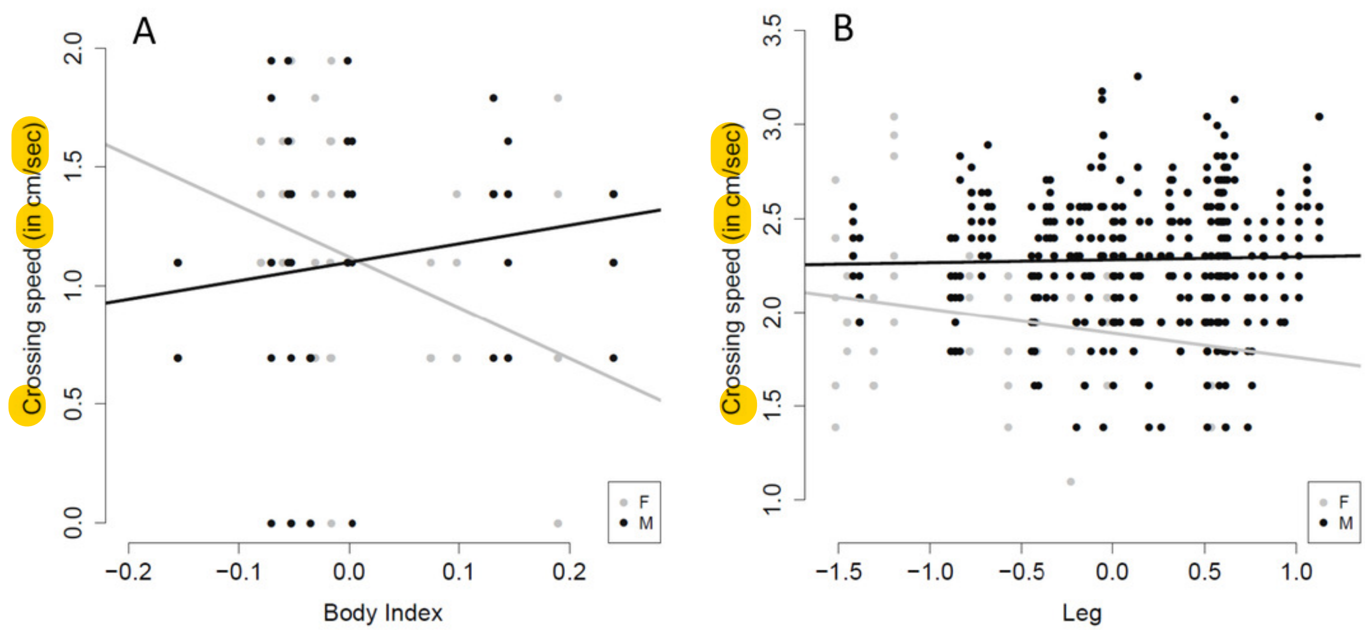

Table 1(on next page)

Table 1. Summary of the best models showing the influence of significant variables on the crossing speed for marbled newt (*Triturus marmoratus*) and common toad (*Bufo bufo*). BI: body index; leg: relative hind-limb length.

***: P < 0.001, ** : P < 0.01, * : P < 0.05.

Table 1. Summary of the best models showing the influence of significant variables on the crossing speed for marbled newt (*Triturus marmoratus*) and common toad (*Bufo bufo*). BI: body index; leg: relative hind-limb length. *** : P < 0.001, ** : P < 0.01, * : P < 0.05.

	Marbled newt *(Triturus marmoratus)*			Common toad *(Bufo bufo)*		
	Estimate	*P*		Estimate	*P*	
(Intercept)	1.415	< 0.001	***	2.843	< 0.001	***
Substrate (soil)	0.208	0.003	**	0.060	0.001	**
leg	-	-	-	-0.094	0.114	
BI	-1.790	0.007	**	-	-	-
sex (male)	-0.007	0.947		0.120	0.082	
BI * sex (male)	2.151	0.021	*	-	-	-
leg * sex (male)	-	-	-	0.144	0.032	*
stops	-0.066	< 0.001	***	0.080	< 0.001	***