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Short communication

Landscape influences the morphology of male common toads (*Bufo bufo*)

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A B S T R A C T

In Europe, the recent agricultural intensification has strongly homogenised the landscape. This loss in habitat diversity and the use of agrochemicals are considered as major causes of the global erosion of biodiversity. Landscape changes may also favour phenotypic variation with divergences between populations even at a small spatial scale. We investigated this notion in the common toad (*Bufo bufo*), a species that inhabits a wide variety of rural habitats. Specifically, we compared the morphology of male adult toads from three contrasting landscapes: forests, traditional farming landscape and intensive farmlands. Overall, individuals from open landscapes were larger and heavier, had longer hind legs and larger parotoid glands than their forest counterparts; suggesting that open landscapes positively influence body size in this species. However, toads from intensive farmland were less symmetrical, suggesting that these individuals may have experienced environmental stress during larval and/or post-metamorphic development. Overall, our results suggest that landscape-specific traits can influence the morphology of male toads in complex ways. Further studies are required to comprehensively assess the impacts of environmental and anthropogenic pressures on amphibians in agroecosystems.

1. Introduction

During the last century, strong changes in land-use priorities have provoked a shift from natural or ancestral rural landscapes to large scale agricultural and urban systems (Chapin et al., 2000; Foley et al., 2005). In Europe, the revolution in agricultural practices that occurred after World War II led to land consolidation, which has strongly homogenised the landscape, from a complex matrix of small fields and meadows bordered by hedges, to very large fields hosting monocultures (intensive farmland; Benton et al., 2003; Tscharntke et al., 2005). In addition, agricultural intensification is also characterised by considerable use of agrochemical substances (Geiger et al., 2010). Overall, these changes in land-use and landscape structure are considered as driving forces in the global biological diversity loss that affects most taxonomic groups at a global scale (Vitousek et al., 1997; Fischer and Lindenmayer, 2007).

Although biodiversity and population trends (declines or outbreaks) seem to be influenced by landscape heterogeneity (Van Burskirk and Arioli, 2004), changes in landscape structure might also bear other consequences on organisms. For instance, the locomotor capacities required to live in a forest may strongly diverge from those required to successfully forage in an extended monoculture. Similarly, the strategy adopted by an individual to evade predation should vary depending on landscape structure (Murdoch et al., 1996; Krivan, 1998). Finally, in agricultural environment, species must face the presence of many agrochemical substances (Berger et al., 2012), which have been suggested to induce trait changes in nontarget species (Lawrence and Isioma, 2010; Relyea, 2012). Taken together, these elements suggest that landscape changes should be responsible for new pressures that could lead to phenotypic divergence between populations from different habitats (Van Burskirk and Arioli, 2004; Phillips et al., 2006; Janin et al., 2011).

We investigated this notion using the common toad (*Bufo bufo*) for several reasons. First this widespread species can live in a variety of habitats and persist even in highly modified agricultural areas, thereby allowing comparisons between landscapes. Second, as most amphibians, it displays a high level of phenotypic plasticity, thereby allowing to investigate the impact of landscapes on phenotype (Newman, 1992; Brady and Grifiths, 2000). Third, it is an explosive breeder which allows sampling individuals in large

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numbers (Janin et al., 2011). Importantly, the terrestrial part of the life cycle occurs within 2 km from the breeding sites, which allow straightforward classification of the surrounding landscapes (Janin et al., 2011).

We compared the morphology of adult male toads from forest, traditional farming landscape and intensive farmland. We predicted that 1) Body condition should be lower in altered intensive agricultural landscapes where trophic resources are expected to be poorer and scarcer, 2) locomotion-related traits (body size, relative limb size) should be more developed in intensive farmland, because toads should travel more to forage successfully or to evade predation, 3) defensive attributes (parotoid glands which secrete an alkaloid substance to deter predators) should be larger in altered agricultural landscapes where the refuges needed to evade predation are scarcer, and 4) asymmetry should be greater in intensive farmlands, because of altered developmental conditions (i.e., suboptimal habitats).

2. Materials and methods

2.1. Study species

The common toad, *Bufo bufo*, is one of the most common anuran species in Europe. Toads emerge from hibernation in early spring (March) and massively migrate towards aquatic breeding sites (Reading and Clarke, 1983). Breeding toads usually come back to the sites at which they were spawned (Reading, 1991). Males remain at the breeding site for several weeks, while females leave shortly after mating and egg-laying (Reading and Clarke, 1983). The remaining part of the annual cycle occurs in various terrestrial environments usually within 2 km from the breeding site (Janin et al., 2011). Because males can be captured in larger numbers at breeding sites, we restricted our sampling to adult males.

2.2. Sampling sites and landscape classification

Sampling took place in March 2015 in an area centred on the Centre d'Etudes Biologiques de Chizé (46°09′N, 0°24′W) in France. Reproduction sites (e.g. ponds) were localized using Google Earth, and surveyed during the day to determine accessibility and toad presence. A total of 12 non-overlapping sites were sampled. Study sites were classified into three landscape categories following the main structures of our study area: forest, traditional farming landscape composed by a complex matrix of small fields and meadows bordered by hedges (hereafter hedgerow network, Forman and Baudry, 1984) and intensive farmland composed by extended arable fields (hereafter farmland).

To create landscape categories relevant at the spatial scale used by a toad, for each study site we applied three buffers that span the potential distance travelled by a toad to reach a breeding site (radii of 500 m, 1000 m and 2000 m; Janin et al., 2011). Classification was done using the "BD Ortho" and "BD Topo" vector databases provided by the Institut Géographique National (IGN, available at http://professionnels.ign.fr/bdortho and http://professionnels.ign.fr/bdtopo). Using QGIS (version 2.8.1), we assessed the quantity of hedges ($m\,ha^{-1}$) and the tree cover (%) for each radius. We classified each sampling site according to the dominant surrounding landscape: Sites around which the hedge linear exceeded $40\,m\,ha^{-1}$ were classified as "hedgerow network" (Baudry et al., 2000), sites around which the tree cover exceeded 30% were classified as "forest", and the remaining sites were considered as "farmland" (Appendix A). In practice, no conflicts emerged using these threshold values (e.g., no site was characterized by more than

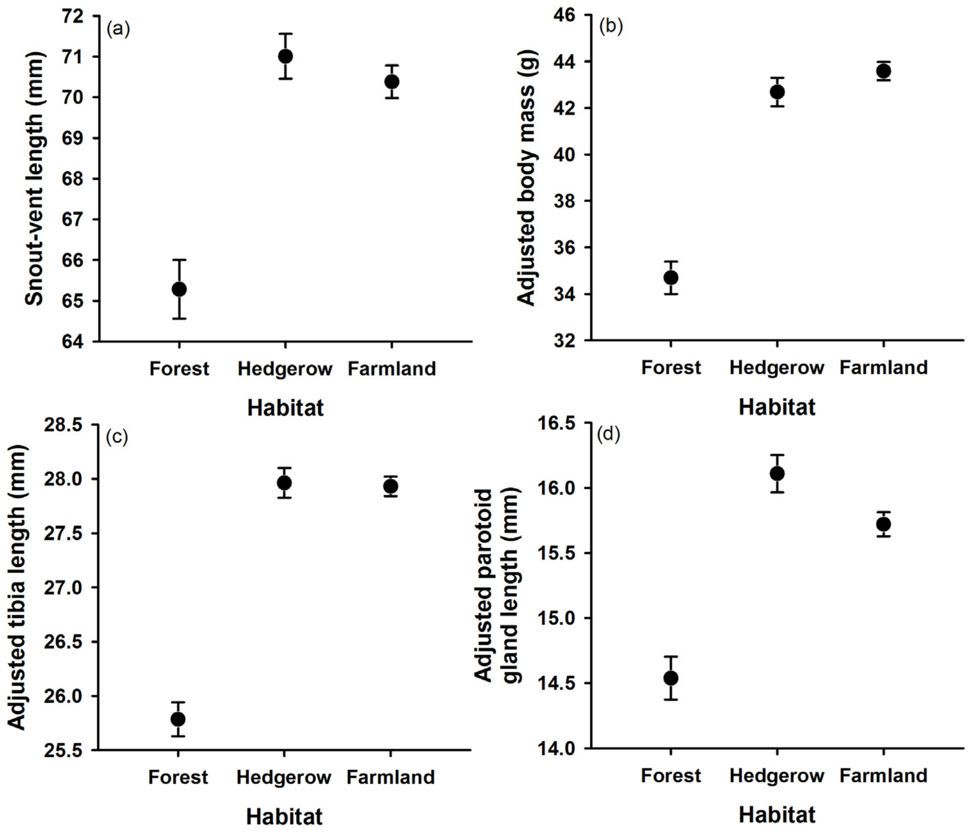

Fig. 1. Morphological traits of toads from three landscapes measured at a spatial scale of 500 m. (a) Snout-vent length, (b) Adjusted body mass, (c) Tibia length and (d) Parotoid gland length. "Hedgerow" stands for hedgerow network. Data are presented as their mean ± S.E.

40 m ha^{-1} of hedge and more than 30% tree cover, Appendix A). Classification of a given site varied very slightly according to the size of the buffer used (one site shifted from agricultural at 500 m to forest at 1000–2000 m and one site shifted from forest at 500 m to hedgerows at 1000–2000 m), but overall our classification method remained relatively stable across spatial scales. Classification was identical for buffers of 1000–2000 m and we kept only the 2000 m buffer in our final analysis.

2.3. Capture and measurements

Sampling was conducted at night by patrolling slowly along the breeding sites. Toads were captured with nets and stored in large buckets. Individuals were measured and released, usually within an hour since capture. This process prevented the capture and measurement of the same individuals multiple times. All individuals were weighed (±0.1 g), and their snout-vent length, forearms length (left and right), tibias length (left and right), length and width of parotoid glands (left and right) were measured with an electronic calliper (±0.01 mm). For paired characters, we used the mean of left and right values. We also produced a fluctuating asymmetry index (FA) following the formula of Palmer and Strobeck (1986) $FA = (ABS(C_l - C_d))/\text{mean}\ (C_l, C_d)$, where C_l and C_d are respectively the size of the left and right character and ABS is the absolute value of the expression. For consistency, measurements were performed by HG.

2.4. Statistical analyses

We tested the difference between each parameter according to their landscape type. The snout-vent length and all the FA indexes were analysed using analysis of variance (ANOVA). As they are correlated to the snout-vent length, all the other parameters were analysed using analysis of covariance (ANCOVA) using the snout-vent length as a covariate. These analyses were followed by Fisher's LSD post-hoc tests.

3. Results

Statistical analyses are summarized in Appendix B.

Within a radius of 500 m, forest toads were smaller (Fisher's LSD, $p < 0.001$), exhibited lower body condition (size-adjusted mass, $p < 0.001$), and had proportionately smaller hind legs ($p < 0.001$) compared to the other groups (Fig. 1). The length of the parotoid glands was significantly different between the three landscapes (all $p < 0.02$, Fig. 1). Forest toads had forelegs that were more symmetrical on average than toads from open landscapes ($p = 0.008$).

Within a radius of 2000 m, forest toads were smaller ($p < 0.001$), exhibited lower body condition ($p < 0.001$), and had smaller parotoid glands (all $p < 0.001$). Farmland toads had less symmetrical hind legs than forest toads ($p = 0.01$), and less symmetrical forelegs than toads from either hedgerow network or forest (all $p < 0.02$) (Fig. 2).

4. Discussion

Our results highlight a morphological similarity between toads from open landscapes as compared to individuals from forest (Fig. 1). Overall, individuals from both traditional hedgerow network and intensive farmland are larger and heavier, have longer hind legs and larger parotoid glands than their forest counterparts. Importantly, forested areas constitute the original habitat of toads (Janin et al., 2011). This suggests that some specificities of open agroecosystems enhanced body size and condition and modified body proportions in male toads. Alternatively, differences in body size may reflect differential mortality and different age structure. However, demographic variation can hardly be invoked to explain the differences in body condition and body proportion we found.

Hedgerows network and farmlands may induce a reduced intra- and/or interspecific competition for trophic resources, and therefore provide better food availability, that would allow individuals from agricultural habitats to reach larger body size and better body condition. It is plausible that agricultural landscapes harbour less dense populations of toads (Bishop et al., 1997; Janin et al., 2011) or decreased diversity and abundances of other, potentially competing, species. Future studies should investigate the consequences of landscape-dependent levels of intra- and/or interspecific competition and their consequences on toad morphology (Evans, 2004; Kauffman et al., 2007). Open landscapes may also impose significant locomotor constraints on male toads, favouring larger body size and relative leg size. For instance, because resources are scarcer and poorer in agricultural environment (Tews et al., 2004), individuals may need to move much more in these landscapes to forage successfully, thereby selecting for very mobile individuals (larger and with relatively longer hind legs, Choi et al., 2003; Phillips et al., 2006). Furthermore, forests are characterized by higher soil and air moisture than open areas (Chen et al., 1993). Because smaller toads have a larger surface-area to volume ratio, they may be more susceptible to desiccation in open environment (Rothermel and Semlitsch, 2002). Finally, open landscapes may be

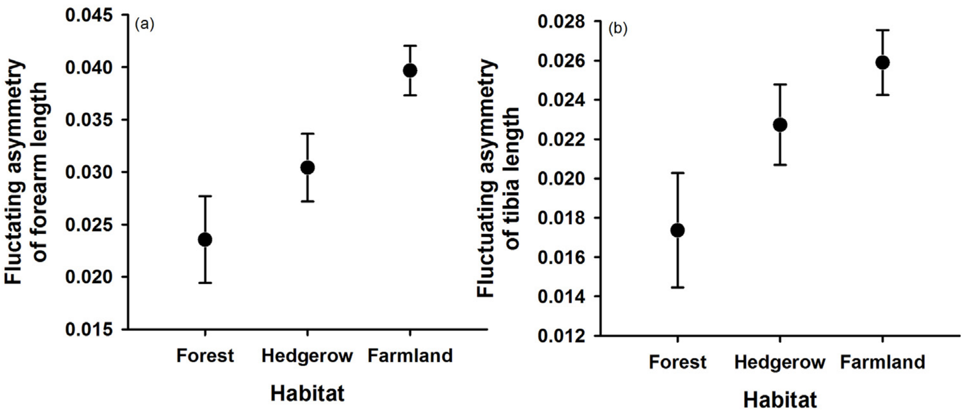

Fig. 2. Fluctuating asymmetry of foreleg (a) and hind leg (b) of male common toads from three landscapes measured at a spatial scale of 2000 m. "Hedgerow" stands for hedgerow network. Data are presented as their mean ± S.E.

characterized by higher predation pressure because of a lower availability of refuges (Murdoch et al., 1996; Krivan, 1998). This would favour locomotion-related traits (body size and hind leg length, see above) and defence-related traits (parotoid glands), both of which would expedite escape.

Our results show a strong influence of farmland on fluctuating asymmetry (Fig. 2), a proxy of developmental stress, and thus of individual quality (Tomkins and Kotiaho, 2001). We found that on average, farmland toads had the least symmetrical legs (either hind of forelegs), while forest toads were the more symmetrical (Fig. 2). These results suggest that male toads from agroecosystems, have experienced higher environmental stress during larval and/or post-metamorphic growth resulting in altered development (Söderman et al., 2007). Whether these results are due to direct effects of agricultural practices (Brunelli et al., 2009; Berger et al., 2012), or indirect consequences of morphological changes (Brown et al., 2007) remain to be assessed.

To conclude we found that toads from open landscapes differ from individuals from forested areas. Our study focused on males and future studies should investigate whether these results apply on females. In addition, common garden experiments should help disentangling the relative contributions of phenotypic plasticity *versus* local adaptation on the morphological divergences we found (Shine et al., 2011; Luquet et al., 2015). A comprehensive assessment of the influences of environmental and anthropogenic factors on common toads requires both empirical and experimental approaches.

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Appendix A.

Mean values (±S.D.) of the landscape metrics (quantity of hedges [m ha^{-1}] and the tree cover [%]) used to create landscape categories relevant at the spatial scale used by a toad (radii of 500 m, 1000 m and 2000 m). "Hedgerow" stands for hedgerow network.

	500 m		1000 m		2000 m	
	Tree cover (%)	Hedge quantity (m . ha^{-1})	Tree cover (%)	Hedge quantity (m . ha^{-1})	Tree cover (%)	Hedge quantity (m . ha^{-1})
Farmland	6.5 ± 5.1	19.8 ± 10.3	3.9 ± 1.7	24.0 ± 8.9	4.4 ± 1.3	26.4 ± 10.7
Hedgerow	6.3 ± 3.4	73.8 ± 25.1	6.3 ± 3.2	71.8 ± 13.4	4.1 ± 1.4	58.7 ± 5.8
Forest	52.6 ± 24.5	19.9 ± 12.6	49.0 ± 11.4	16.7 ± 13.1	52.1 ± 22.5	20.9 ± 17.4

Appendix B.

Mean values (±S.D.) of morphological traits measured on toads from forest (500 m radius: N = 65, 2000 m radius: N = 57), hedgerow network ("Hedgerow", 500 m radius: N = 84, 2000 m radius: N = 116) or intensive farmlands (500 m radius: N = 202, 2000 m radius: N = 178). "Hedgerow" stands for hedgerow network. Test indicates the results from statistical comparisons.

Variable	500 m				2000 m			
	Forest	Hedgerow	Farmland	Test	Forest	Hedgerow	Farmland	Test
Snout-vent length	**65.2 ± 5.8**	**71.0 ± 5.0**	**70.4 ± 5.8**	**$F_{2,348}$ = 24.43, p < 0.001**	**66.0 ± 6.3**	**70.2 ± 5.2**	**70.4 ± 6.0**	**$F_{2,348}$ = 13.04, p < 0.001**
Body mass[a]	**34.6 ± 9.6**	**42.6 ± 8.5**	**43.9 ± 11.5**	**$F_{2,347}$ = 3.99, P = 0.01**	36.3 ± 10.8	42.0 ± 8.6	43.7 ± 12.0	$_{F2,347}$ = 1.35, p = 0.26
Parotoid gland length[a]	**14.5 ± 1.6**	**16.1 ± 1.4**	**15.7 ± 1.5**	**$F_{2,347}$ = 5.69, P = 0.004**	14.7 ± 1.7	15.8 ± 1.5	15.7 ± 1.5	$F_{2,347}$ = 2.11, p = 0.12
Parotoid gland width[a]	5.7 ± 0.6	6.0 ± 0.6	5.9 ± 0.7	$F_{2,326}$ = 1.21, p = 0.29	5.7 ± 0.5	5.9 ± 0.6	5.9 ± 0.7	$F_{2,326}$ = 0.42, p = 0.65
Forearm length[a]	20.8 ± 1.7	22.2 ± 1.7	22.0 ± 1.8	$F_{2,326}$ = 0.30, p = 0.74	21.0 ± 1.8	21.9 ± 1.6	22.0 ± 1.8	$F_{2,326}$ = 0.19, p = 0.83
Tibia length[a]	**25.7 ± 2.1**	**27.9 ± 1.9**	**27.9 ± 2.0**	**$F_{2,347}$ = 7.02, P = 0.001**	26.6 ± 2.4	27.5 ± 2.1	27.9 ± 2.0	$F_{2,347}$ = 2.67, p = 0.07
FA Parotoid gland length	0.07 ± 0.05	0.09 ± 0.06	0.09 ± 0.07	$F_{2,347}$ = 2.01, p = 0.13	0.07 ± 0.06	0.09 ± 0.06	0.08 ± 0.07	$F_{2,347}$ = 1.22, p = 0.29
FA Parotoid gland width	0.11 ± 0.11	0.10 ± 0.09	0.10 ± 0.07	$F_{2,326}$ = 0.44, p = 0.64	0.12 ± 0.09	0.11 ± 0.10	0.10 ± 0.07	$F_{2,326}$ = 1.39, p = 0.25
FA forearm length	**0.02 ± 0.02**	**0.03 ± 0.02**	**0.03 ± 0.03**	**$F_{2,325}$ = 3.73, P = 0.02**	**0.02 ± 0.02**	**0.03 ± 0.02**	**0.04 ± 0.03**	**$F_{2,325}$ = 6.69, P = 0.001**
FA tibia length	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.02	$F_{2,348}$ = 1.37, p = 0.25	**0.01 ± 0.01**	**0.02 ± 0.02**	**0.02 ± 0.02**	**$F_{2,348}$ = 3.35, P = 0.03**

[a] indicates traits which were compared using an ANCOVA with the snout-vent length as the covariate. FA stands for fluctuating asymmetry. Bold face highlights significant differences.

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