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The importance of phenotypic diversity in conservation: Resilience of palmate newt morphotypes after fish removal in Larzac ponds (France)

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ABSTRACT

Resilience of organisms after threat removal is an essential feature to justify conservation efforts. Amphibians are particularly threatened with a worldwide decline, showing a low resistance to invaders such as fish. Previous research has shown that they could recover after fish extirpation due to metamorphosed colonisers. However, not all amphibian phenotypes are able to persist fish introduction and disperse. In many species of newts and salamanders, paedomorphs retain gills in the adult stage, which makes them fully aquatic. A proposed way to conserve this phenotype would be to remove introduced fish from their habitats. However, because paedomorphosis is usually not expressed in the presence of fish, it is unknown whether fish removal could allow the resilience of paedomorphs. This would be possible only if progenies of metamorphosed individuals could become paedomorphic in restored habitats. Through a quantitative survey in three types of ponds, including control ponds without fish, ponds in which fish were extirpated, and fish ponds, we determined abundances of paedomorphic and metamorphic palmate newts (*Lissotriton helveticus*). The results show that paedomorphosis resilience is possible and even highly frequent, as paedomorphs were found in 80% of ponds where fish disappeared. Abundances were similar between these ponds and control ponds whereas fish ponds had almost no newts, indicating a very low resistance to invaders. This shows that conserving common phenotypes can help to preserve endangered phenotypes, as paedomorphs were produced through the reproduction of metamorphs. There is thus hope of maintaining intraspecific biodiversity though conservation action involving threat removal.

1. Introduction

The populations of many organisms exhibit variations such as local specialisations, the persistence of ancestral traits, and genetically and environmentally induced polymorphisms (West-Eberhard, 2003; Baker et al., 2010). These phenotypes are often seen as evolutionary significant units that are an inherent component of biodiversity (Fraser and Bernatchez, 2001; Moritz, 2002). Although some phenotypes can be abundant, common and widespread over large geographic ranges, others can be rare and localised, and thus, are more likely to suffer global decline. Moreover, some phenotypes are particularly adapted to specific environmental conditions and when these conditions deteriorate, such as following anthropogenic pressures, they could be more at risk than more tolerant phenotypes (Hendry et al., 2006; Denoël, 2007; Lescak and von Hippel, 2011). For instance, in sticklebacks, specialised phenotypes show a pelvic reduction that is considered to be the result of their evolution in a predator-free environment. In contrast to the less endangered armoured phenotypes, these phenotypes are now exposed to a high risk of predation from large introduced fish species that contribute to their decline (Von Hippel, 2008; Baker et al., 2010; Lescak and von Hippel, 2011).

Paedomorphosis in newts and salamanders provide a particularly interesting example of phenotypic diversity with conservation relevance. Most pond-breeding species exhibit facultative paedomorphosis in some of their populations. This means that two phenotypes can coexist: metamorphs that can live on land but need water to breed and paedomorphs that retain larval traits, such as gills at the adult stage, and stay aquatic. This is an adaptive process that is driven by heterochrony, i.e., changes in the time or rate of development between phenotypes (Gould, 1977; Denoël et al., 2005b). The rarest paedomorphic phenotype can exploit specific resources and mature at an early age by avoiding the costs of metamorphosis, but is highly endangered by disturbance of its aquatic habitat, such as alien fish introductions (Denoël et al., 2005a; Denoël, 2007). Similar to sticklebacks, which cannot leave water, paedomorphs are thus constrained to share the same habitats as introduced fish (Denoël et al., 2005a). As a consequence, the populations of salamandrid paedomorphs have declined, with extinctions being recorded in almost 50% of populations at the continental scale in Europe (Denoël et al., 2005a). Similar reports were

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also made for other families, such as facultatively paedomorphic ambystomatids in Northern America (Whiteman and Howard, 1998). The most famous example is without any doubt the axolotl (*Ambystoma mexicanum*), a nearly obligate paedomorphic species, which is now at the edge of extinction in the wild because of fish introductions and the destruction of its aquatic habitat (Contreras et al., 2009; Zambrano et al., 2010).

Similar to the two above-mentioned examples, the introduction of alien species is one of the main causes of biodiversity loss (McGeoch et al., 2010). Among the large variety of alien taxa involved, fish occupy a primary role due to the global scale of their introduction (Cambray, 2003). Fish introductions particularly affect native species, such as many species of amphibians, which usually live in habitats that are naturally devoid of fish (Cox and Lima, 2006; Salo et al., 2007). As a consequence, amphibians often become extinct or show reduced abundances in the presence of fish (Kats and Ferrer, 2003). Together with other local and global causes, such as habitat alteration and destruction, pollution and emerging diseases, these fish introductions cause amphibian populations to decline at such an unprecedented rate that they are involved in the sixth world mass extinction (Stuart et al., 2004; Wake and Vredenburg, 2008).

Despite their low resistance to environmental disturbance such as fish introductions, amphibians can also show a high degree of resilience, i.e., the ability to return to their previous configuration once the perturbation is removed (Knapp et al., 2001). For instance, the removal of fish from lakes allowed the restoration of frog and salamander populations (Vredenburg, 2004; Knapp et al., 2007; Pope, 2008). This resilience was enhanced in many species of bi-phasic amphibians that are able to disperse on land, and can thus colonise managed aquatic habitats from nearby wetlands. However, whether rare phenotypes such as paedomorphs would be expressed again once aquatic conditions returned to an undisturbed fishless situation following the extirpation of alternative rare native phenotypes, is a question that remains unanswered. This leads to a second major question concerning the evolutionary conservation of polyphenisms such as facultative paedomorphosis: whether the protection of common phenotypes is a solution to maintain rare phenotypes.

Because alternative phenotypes can be environmentally driven, it is to be expected that a single genotype can lead to the whole range of phenotypes when conditions are suitable (West-Eberhard, 2003). However, years of selection for or against metamorphosis could prevent the resilience of paedomorphosis, i.e. its re-expression after disappearance in the population. Indeed, artificial selection experiments with a facultatively paedomorphic species of ambystomatid salamander showed that breeding metamorphic individuals together, produces progeny that are more likely to undergo metamorphosis than to reproduce as paedomorphs (Semlitsch and Wilbur, 1989). A quantitative trait locus for metamorphosis timing that explains the additive effect of selection for either metamorphosis or paedomorphosis has been subsequently identified (Voss et al., 2012). In salamandrids, the potential of paedomorphs to metamorphose shows that this is a polyphenism. On another hand, the restricted geographic localisation of paedomorphs suggests the presence of a genetic cause that favours the expression of paedomorphosis versus metamorphosis. Two isolated cases in the Alpine newt (*Ichthyosaura alpestris*) showed the absence of resilience of paedomorphs but not of metamorphs after fish removal (Denoël et al., 2005a). Therefore, fish introductions might have caused populations to lose their potential for paedomorphosis (e.g., alleles for delayed metamorphosis: Voss et al., 2012). As shown in frogs (Vredenburg, 2004; Knapp et al., 2007; Pope, 2008), natural populations are thus likely to be recolonised by metamorphic dispersers, but whether the progeny of newts or salamanders could again exhibit the rare paedomorphosis developmental pathway has not been yet demonstrated in the wild. This is a crucial pattern to determine the value of conservation efforts for maintaining such uncommon or endangered phenotypes. Moreover, studying the potential for the re-expression of the paedomorphs after their extinction would then also allow a better understanding of the evolution of facultative paedomorphosis across environmental pressures (see also Bonett et al., 2014).

Many species (e.g., of Ambystomatids and Salamandrids in Europe and North America) can exhibit both paedomorphosis and metamorphosis within the same population (i.e., facultative paedomorphosis). However, there are not much geographic areas where there are a sufficient number of ponds that allows a statistical comparison of ponds with or without fish, and also those where fish have become extinct (Petranka, 1998; Denoël et al., 2005a). These conditions are fulfilled on the Larzac plateau in southern France, which contains a large number of ponds that are inhabited by paedomorphic and metamorphic palmate newts (*Lissotriton helveticus*) and that are known to be affected by fish introductions (Denoël et al., 2005a; Denoël and Ficetola, 2014, 2015). On the basis of quantitative censuses on such populations, our main aim was to test the hypothesis that paedomorphosis can show resilience, i.e., that it can be re-expressed following fish extirpation, because of the persistence of metamorphosed individuals in the environment (Denoël et al., 2005a, 2016). At a broader scale, we wanted to demonstrate the value of conservation actions such as fish removal on the re-expression of endangered phenotypes. By doing this, we also wanted to highlight the importance of maintaining both common and rare phenotypes, to conserve phenotypic diversity.

2. Material & methods

2.1. Study sites

We surveyed thirty ponds in Southern Larzac plateau (Herault and Gard Department, France; between 43°45′N and 43°57′N and 3°16′E and 3°33′E) during the peak of the breeding season (April–June 2014), i.e. when the highest abundances of the newt phenotypes can be found (Denoël and Ficetola, 2014). Larzac is a traditional agricultural area, part of the Mediterranean Basin hotspot (Durand-Tullou, 1959). All ponds were located within the distribution range of both paedomorphic and metamorphic palmate newts (Gabrion et al., 1977; Denoël and Ficetola, 2015) (see Fig. 1a for an example of a typical pond in Larzac and Fig. 2 for a map of the area). They were classed in three categories (hereafter pond type): ten ponds (hereafter control ponds) have never been reported to have contained fish (Gabrion et al., 1977; Denoël and Ficetola, 2014); ten ponds (hereafter extirpation ponds) had fish that were extirpated by conservation management (i.e., removal, $n = 4$) or natural disappearance ($n = 6$) between 2000 and 2006; and ten ponds (hereafter fish ponds) had fish present during the 2014 survey (Supplementary Table 1). Previous visits to the fish ponds showed that they also contained fish in the period 2001–2013 (Denoël and Ficetola, 2014). The presence of fish in extirpation ponds was also determined by our own previous field observations for eight ponds and by local reports for two ponds (Rondeau et al., 2000) (Supplementary Table 1). All of the studied ponds were selected to have adequate features (except fish presence in fish ponds) to sustain newt populations and paedomorphs, following our previous results on the ecology of palmate newts in Larzac (Denoël and Lehmann, 2006; Denoël and Ficetola, 2014). This means that temporary and recently built ponds were not included in this study.

2.2. Newt sampling

An index of abundance of the two phenotypes was determined once for each pond by using blind dip-netting sweeps over the entire surface of each pond for exactly 2 h with two persons involved at the same time. During censuses, newts were placed in tanks filled with pond water, and then counted and identified according to phenotype. Paedomorphs differ from metamorphs by multiple traits, such as the presence of gills and gill slits (Fig. 1b). Their adulthood was established by the presence of a developed cloaca. Newts were released into their capture pond on the same day. The aim was not