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Habitat selection and reproduction of newts in networks of fish and fishless aquatic patches

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The spatial distribution of organisms in patchy environments can be determined by the relationship between habitat quality and animal behaviour. In species with complex life cycles, such as pond-breeding amphibians, the selection of a suitable wetland is crucial. While the traditional view of amphibian ecology suggests strong site fidelity and low vagility, more recent research highlights mechanisms involving active site choice through avoidance behaviour and bet-hedging strategies in heterogeneous environments. The introduction of fish to the aquatic environment is one of the factors that may alter site selection and lead to local dispersal. In this context, we investigated the habitat choice of Alpine newts, *Ichthyosaura alpestris*, in networks of fish (*Carassius auratus*) and fishless aquatic patches. Using a laboratory design consisting of aquaria divided into two water tanks connected by a terrestrial platform, we assessed newt distribution and movement between patches. During the breeding period, we compared the reproductive success of individuals in two types of networks. We found that newts escaped fish by rapidly changing aquatic patches and then aggregating in safe aquatic patches that were free of fish. In the fish network, newts maintained reproduction, but the high local abundance resulted in decreased sexual activity and egg production and increased use of the terrestrial habitat. However, in the fishless network, newts moved between aquatic patches several times, exhibited more courtship behaviour and laid more eggs than they did in the fish networks. Our results showed both adaptive habitat switching due to environmental risks in the fish network and habitat supplementation (i.e. use of alternative resources) in the fishless network. Such studies on movement behaviour and habitat selection have conservation implications in showing that the persistence of native species in invaded networks depends on the rescue effect, with immigration to fish-free habitats potentially preventing local extinction.

Understanding patterns in the distribution and abundance of organisms is one of the main challenges in ecology. The existence of a relationship between habitat structure or quality and animal behaviour helps to determine the spatial distribution of organisms and improves our understanding of habitat selection (Boyce et al., 2016; McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010). Studying habitat choice is particularly relevant in species with complex life cycles requiring both terrestrial and aquatic habitats that provide nonsubstitutable resources (Denoël, Perez, Cornet, & Ficetola, 2013; Dunning, Danielson, & Pulliam, 1992). Indeed, such habitat complementation is present in many stream- or pond-breeding insects and amphibians that radically shift from major habitats (i.e. water to land) at metamorphosis. Adults often only use water for reproduction, whereas aestivating, wintering and dispersal usually occur in the terrestrial habitat (Wilbur, 1980). In insects and anurans, it is well known that another process, habitat supplementation, can be involved, where individuals supplement their resource levels by moving to patches that provide similar resources within an accessible part of the local landscape (Dunning et al., 1992). For instance, pond-breeding species can use several aquatic habitats and lay eggs in various sites (Khatchikian, Dennehy, Vitek, & Livdahl, 2010; Refsnider & Janzen, 2010). This can result from an active choice or from a bet-hedging strategy, if assessment of habitat quality is not possible (Kaplan & Cooper, 1984; Schulte et al., 2011). Indeed, the highly unpredictable variability of environmental conditions can make it almost impossible for parents to predict the future quality of a pond for their offspring development. Therefore, depositing eggs in several

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selected habitats could minimize the risk of total offspring loss in uncertain environments (Erich, Ringler, Hödl, & Ringler, 2015).

However, the traditional view of the community ecology of a variety of amphibian species, particularly newts and salamanders, is that they show strong breeding site fidelity and low vagility, which are characteristics of a metapopulation structure (Smith & Green, 2005). This pattern has been found at a regional scale where amphibian communities live in wetlands that are isolated by distances beyond the normal range of terrestrial movement (Gill, 1978; Joly & Miaud, 1989). In newts, the usual distance of migration is within a few hundred metres (Denoël et al., 2013). However, at a more local scale, when the interpond distances are short, some research suggests a 'patchy population' model of organization, showing more active habitat selection (Petranka & Holbrook, 2006; Sinsch, 2014). In particular, studies have shown that many amphibians have evolved behavioural avoidance mechanisms in response to unfavourable aquatic patches (Resetarits, 2005; Resetarits & Wilbur, 1989).

Movement between habitats and levels of aggregation can vary with numerous ecological factors, but resource distribution and predation risk are often two of the most important factors influencing habitat selection (Amburgey, Bailey, Murphy, Muths, & Funk, 2014; Heithaus et al., 2007; Indermaur, Schaub, Jokela, Tockner, & Schmidt, 2010). The best example is breeding site selection, where females may assess habitat quality for their future offspring and avoid giving birth or laying eggs in ponds containing predators or with high conspecific densities, which may increase competition for resources (Resetarits & Wilbur, 1989; Rieger, Binckley, & Resetarits, 2004). Therefore, within the limits of their movement capacities, field studies have shown that amphibians can colonize alternative ponds where they can breed (Kopecký, Vojar, & Denoël, 2010; Perret, Pradel, Miaud, Grolet, & Joly, 2003). It is yet unknown how species such as newts and salamanders use alternative breeding habitats during a single period of reproduction.

One of the factors that may affect population structure in wetlands, and lead to dispersion, is the introduction of alien species (Consentino, Schooley, & Phillips, 2011; Unglaub, Steinfartz, Drechsler, & Schmidt, 2015). Freshwater ecosystems are among the most invaded in the world and many levels of ecological organization can be affected simultaneously, including individuals, populations, communities and ecosystems (Ricciardi & MacIsaac, 2011). Among invasive species, fish are one of the main causes of amphibian decline (Bucciarelli, Blaustein, Garcia, & Kats, 2014), as amphibians did not usually coevolve with fish (Cox & Lima, 2006). Many longitudinal environmental studies have confirmed exclusion patterns between fish and amphibians by showing amphibian extirpation after the introduction of fish and resilience after their removal (Knapp, Boiano, & Vredenburg, 2007). Decreases in native amphibian populations can be caused by consumptive effects, i.e. the direct predation of eggs, larvae or adults (Leu, Lüscher, Zumbach, & Schmidt, 2009), and indirectly through resource competition (Joseph, Piovia-Scott, Lawler, & Pope, 2011). However, a nonconsumptive effect that is often overlooked, but can also have ecological consequences, is behavioural avoidance in response to fish (Binckley & Resetarits, 2003; Petranka & Holbrook, 2006). This could range from microhabitat shifts within a pond (Orizaola & Braña, 2003b; Teplitsky, Plenet, & Joly, 2003) to shifts between aquatic and terrestrial habitats (Winandy, Darnet, & Denoël, 2015). The consequences are usually a decrease in both foraging and mating opportunities (Winandy & Denoël, 2013b, 2015). Moreover, in response to the presence of fish, newts can leave the water and remain on land during the entire mating period, thereby forgoing reproduction (Winandy et al., 2015). Indeed, in a landscape structure in which ponds were isolated, even when high emigration of newts was observed, only a very small number of movements between distant fish and fishless ponds were observed (Unglaub et al., 2015). Therefore, a high connectivity between ponds could offer amphibians more choices in site selection (Joly, Miaud, Lehmann, & Grolet, 2001; Marsh, Fegraus, & Harrison, 1999). Wholesale shifts of breeding populations between ponds were observed after the introduction of fish into some ponds of a network (Petranka & Holbrook, 2006). It is of great importance to determine how organisms use such networks during the breeding period, i.e. whether they show habitat supplementation and habitat selection based on behavioural avoidance, and what the consequences are in terms of reproductive output.

In this study, we aimed to assess the habitat selection and movement patterns of an amphibian species, the Alpine newt, *Ichthyosaura alpestris*, at a local scale in two connected aquatic habitats with and without fish. We used goldfish, *Carassius auratus*, as a model species because this is the most introduced ornamental species in the world (Maceda-Veiga, Escribano-Alacid, de Sostoa, & García-Berthou, 2013) and it is causing declines in newts (Denoël & Ficetola, 2014; Denoël et al., 2013). Goldfish are not thought to predate on adult newts, but they can forage on the eggs and larvae of salamanders (Monello & Wright, 2001). We took an experimental approach, using a laboratory-replicated design throughout the period of newt reproduction. Using a PIT-tag marking method, we recorded individual movements and newt abundance in networks with or without fish. We also assessed the impact of habitat selection on sexual activity and egg production. We predicted that newts would be capable of active habitat choice for breeding. Therefore, in fish pond networks, newts should avoid fish patches and reach higher densities in fishless patches, resulting in reduced reproduction in comparison to fishless networks.

METHODS

Species

We caught 64 adult Alpine newts using dip netting (32 individuals of each sex) at the beginning of the reproductive period (March 2014) in a fishless pool (Romerée, Belgium, 50°08′N, 4°40′E). There were no fish present in the ponds within the usual dispersal distance of newts around the capture site, so the newts were completely naïve to fish. After capture, we kept the sexes separated in six 9-litre tanks, which were filled with water, stuffed with towels, and then placed in two large 230-litre refrigerated boxes. We then brought them directly to the laboratory. The Alpine newts had a mean ± SE snout–vent length of 5.27 ± 0.53 cm ($N = 64$).

We used four goldfish from the Aquarium of Liège and stored them in a large tank (180 × 80 cm and 60 cm water depth) in our laboratory. They had a typical orange colour and a mean ± SE standard length (i.e. from the tip of the snout to the posterior end of the last vertebra) of 14.2 ± 0.39 cm.

Laboratory Maintenance

We distributed the newts between eight identical and independent aquaria networks (116 × 60 cm and 40 cm water depth, 278 litres). Each network consisted of two identical tanks, separated by waterproof, opaque glass. A terrestrial platform (60 × 17.5 cm) allowed the newts to move between the two tanks. The platform was made of a slab of slate and devoid of shelter; therefore, it functioned only as a connection between aquatic patches. An access ramp (60 × 16 cm with angle of 40°) was placed in the tanks to facilitate the transition between aquatic and terrestrial habitats. Four individual newts (two of each sex) were