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Research

Dispersal and alternative breeding site fidelity strategies in an amphibian

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Dispersal (i.e. movement from a natal or breeding site to another breeding site) is a central process in ecology and evolution as it affects the eco-evolutionary dynamics of spatially structured populations. Dispersal evolution is regulated by the balance between costs and benefits, which is influenced by the individual phenotype (i.e. phenotype-dependent dispersal) and environmental factors (i.e. condition-dependent dispersal). Even though these processes have been extensively studied in species with simple life cycles, our knowledge about these mechanisms in organisms displaying complex life cycles remains fragmentary. In fact, little is specifically known about how the interplay between individual and environmental factors may lead to alternative dispersal strategies that, in turn, lead to the coexistence of contrasted site fidelity phenotypes. In this paper, we examined breeding dispersal in a pond-breeding amphibian, the great crested newt *Triturus cristatus*, within usual walking distances for a newt. We took advantage of recent developments in multi-event capture–recapture models and used capture–recapture data (946 newts marked) collected in a spatially structured population occupying a large pond network (73 ponds). We showed a high rate of breeding site infidelity (i.e. pond use) and the coexistence of two dispersal phenotypes, namely, a highly pond faithful phenotype and a dispersing phenotype. Individuals that were site faithful at time $t-1$ were therefore more likely to remain site faithful at time t. Our results also demonstrated that the probability that individuals belong to one or the other dispersal phenotypes depended on environmental and individual factors. In particular, we highlighted the existence of a dispersal syndrome implying a covariation pattern among dispersal behavior, body size, and survival. Our work opens new research prospects in the evolution of dispersal in organisms displaying complex life cycles and raises interesting questions about the evolutionary pathways that contribute to the diversification of movement strategies in the wild.

Keywords: dispersal polymorphism, dispersal syndrome, amphibian

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Introduction

Dispersal in its wide meaning includes all attempts to move from a natal or breeding site to another breeding site (Clobert et al. 2009) and therefore encompasses natal dispersal in the first case and breeding dispersal in the later one (Clobert et al. 2012, Matthysen 2012). By inducing gene flow and reducing the effect of genetic drift, dispersal is a central process in ecology and evolution as it affects the eco-evolutionary dynamics of spatially structured populations (Bowler and Benton 2005, Ronce 2007). It is a three-stage process which includes the departure phase (emigration), the transfer in the landscape matrix phase (transience), and the settlement phase (immigration) (Ronce 2007, Clobert et al. 2009). A recurrent finding of evolutionary models of dispersal is that the evolution of this behavior is regulated by the balance between costs and benefits at each of these three stages (Bonte et al. 2012). Environmental factors, including kin competition, mate choice, and habitat quality, have been found to deeply influence the cost-benefit balance of the evolution of dispersal. Such payoffs may result in condition-dependent dispersal, meaning that individuals adjust their dispersal choice according to environmental cues or social information (i.e. 'informed dispersal' sensu Clobert et al. 2009). Simultaneously, the individual's phenotype can also strongly affect the cost-benefit balance of dispersal, leading to phenotype-dependent dispersal (Clobert et al. 2009). Indeed, movement propensity and ability often correlate with a suite of phenotypic traits, which results in divergence between dispersers and residents in terms of physiological (Zera and Denno 1997), morphological (Roff 1986, Sinervo et al. 2006), behavioral (Cote et al. 2010), and life history traits (Guerra 2011, Stevens et al. 2013). In some cases, these phenotypic differences can involve reversible or irreversible associations of traits termed 'dispersal syndromes' (Clobert et al. 2009, Cote et al. 2017a). Despite these evidences, understanding how the complex interaction between environmental factors and phenotypic traits shape dispersal strategies within wild populations currently remains a critical challenge for ecologists.

Even though phenotypic-dependent and condition-dependent dispersal have been extensively studied in several species with relatively simple life cycles (e.g. birds: Duckworth and Badyaev 2007, lizards: Cote and Clobert 2012), our knowledge about these mechanisms in organisms displaying complex life cycles remains fragmentary. In these species, dispersal implies major habitat shifts (Laudet 2011), which often entail increased costs due to obligatory morphological and/or physiological changes (Pandian and Marian 1985, Shi 2000). If habitat complementation (i.e. the use of habitats that provide different resources) is often an obligatory process resulting in routine and migratory movements in such species, habitat supplementation (i.e. the use of habitats providing similar and substitutable resources) is usually facultative (Dunning et al. 1992). Both processes can be exhibited in organisms with simple and complex life cycles but at an expected stronger extent in the later ones due to the radical habitat shift and associated physiological changes (Hourdry and Beaumont 1985). In this context, individual decisions to leave a habitat patch or settle in a new one are expected to depend on the quantity and the quality of local resources, as well as the individual phenotype. Therefore, the habitat supplementation process – when it concerns breeding resources – should be greatly influenced by the interplay of phenotype-dependent and condition-dependent dispersal in organisms with complex life cycles (Bowler and Benton 2005, Benton and Bowler 2012). Such interactions could result in alternative patch fidelity strategies, leading to the coexistence of contrasted site fidelity phenotypes (e.g. dispersing and site faithful phenotypes) at the population level. Yet, this issue has been poorly investigated and our understanding of these mechanisms is mainly based on empirical studies in a few crustacean (daphnids: Altermatt and Ebert 2010) and insect species (butterflies: Schtickzelle and Baguette 2003, Ducatez et al. 2012; beetles: Bates et al. 2006). Moreover, by studying species with complex life cycles where the use of one of the habitats is associated with reproduction and when alternative reproductive patches are available, this allows to determine movement strategies in the framework of dispersal.

To close this gap, we aimed at examining whether distinct breeding site fidelity strategies may coexist at the intra-population level and how breeding resource characteristics and individual phenotype may affect these strategies in pond-breeding amphibians. These species are excellent biological models for studying such dispersal strategies of organisms with complex life cycles. First, they display a biphasic cycle, including an aquatic phase for reproduction and early development (egg and larval stages) and a terrestrial phase for feeding and overwintering after metamorphosis. These organisms display both obligatory habitat complementation, implying migratory movements between aquatic and terrestrial habitats (i.e. before/after the reproductive period from/to overwintering and estivating terrestrial sites), and facultative habitat supplementation, resulting in breeding dispersal among ponds during the reproductive period and not considered as migratory events (Semlitsch 2008, Pittman et al. 2014). Natal dispersal usually involves habitat complementation as gilled organisms leave water after metamorphosis (Mathiron et al. 2017) whereas breeding dispersal can include both habitat complementation and supplementation depending whether the terrestrial phase is only used for movement across breeding patches or used for other activities such as estivation or overwintering. To date, few studies have shown that breeding pond characteristics may affect dispersal decision among ponds and result in condition-dependent dispersal (see for instance Cayuela et al. 2016a). Other works also suggested that phenotypic traits, such as body mass, affect locomotor performance and movement ability (Goater et al. 1993, Beck and Congdon 2000), which should ultimately have an effect on dispersal decision and success. Moreover, studies revealed that dispersal ability and/or propensity may differ between sexes (Lampert et al. 2003, Trochet et al. 2016) and may covary with life history traits, such as survival, fecundity, and developmental rates (Phillips et al. 2010, Allen et al. 2017). All of these elements, therefore, indicate the existence of both condition-dependent and phenotype-dependent dispersal in amphibians.

In this paper, we examined whether distinct dispersal strategies (here defined as movements between breeding patches) may coexist within a population and how these strategies correlate with environmental variation (pond surface) and an individual's trait (body size, sex, and survival) in the great crested newt *Triturus cristatus* (Amphibia, Salamandridae). To examine this issue, we took advantage of recent developments in multi-event capture–recapture models (Lagrange et al. 2014). We used capture–recapture data (946 newts marked) collected during a 3-yr period in a spatially structured population of *T. cristatus* occupying a large pond network (73 ponds). First, we aimed at quantifying the proportion of site (i.e. pond) faithful and lowly faithful individuals at the intra-annual and inter-annual levels (i.e. at determining the absence or presence of breeding dispersal). Because intra-annual movements are facultative and inter-annual ones usually obligatory, we expected a higher rate of breeding site fidelity at the intra than at the inter-annual level. Second, our goal was to demonstrate that the dispersal behavior is relatively stable over time by showing that faithful individuals to their breeding site (i.e. pond) at $t-1$ exhibit a high probability of remaining faithful at time t at both the intra and inter-annual scales. Third, we aimed at testing whether two breeding site fidelity strategies may coexist in the population: newts can be either highly or lowly breeding site faithful (i.e. not dispersing and dispersing between ponds, respectively). Fourth, we aimed at analyzing how these strategies may correlate with environmental variation and individual traits. Concerning the environmental effects, because dispersers are expected to settle in ponds where the drought risks are lower for offspring survival, we hypothesized that individuals belonging to the dispersing phenotype occur in ponds that have, on average, a large surface. In other words, we expected that dispersing newts were more likely to settle in large ponds, and we predicted a positive relationship between the mean surface of ponds occupied by the individuals during the 3-yr study and the probability that they would display a dispersing strategy. On another hand, we expected the existence of a dispersal syndrome implicating morphological and life history traits. As body size usually positively affects movement capacity/propensity (Beck and Congdon 2000, Brodin et al. 2013) and survival at post-metamorphic stages (Schmidt et al. 2012, Cayuela et al. 2016b) in amphibians, we hypothesized that the individuals involved in the dispersing strategy have a relatively large body size and a high survival. Furthermore, because males are more sexually active than females in newts (Hedlund 1990), we expected them to have a higher probability of belonging to the dispersing phenotype.

Material and methods

Study species, sampling site, and data collection

Crested newts *T. cristatus* are widely distributed in Europe and are an endangered species (Denoël 2012) (Supplementary material Appendix 1). They are biphasic amphibians that remain in water during their gilled larval stage in the few months following their birth and during breeding after the cold winter season once they become mature. They are usually considered as more selective for their aquatic habitat than other newt species (Joly et al. 2001, Denoël et al. 2013). At the juvenile stage and after breeding, they usually remain terrestrially close to ponds (Jehle 2000, Jarvis 2016). Their adulthood arises at 2–3 yr in similar environments. Although a life expectancy of a maximum of 17 yr was recorded, the mode was at 2 and 3 yr (depending on study years/sites) with a fast drop of the number of older individuals (Miaud et al. 1993). Survival analyses also suggest that adult life expectancy can be short in such lowland populations, ranging from 1 to 2 yr in some cases (Cayuela et al. 2017a). We found a similar pattern in this study where adult life expectancy was estimated at 2 yr (see Results).

The study site consists in a network of ponds in a military base (Camp Albert 1er) in Marche-en-Famenne, Belgium (50.26°N, 5.37°E, 207 m a.s.l.) (Supplementary material Appendix 2). It is part of the protected Natura2mil network (i.e. the Natura2000 network within military areas of Wallonia), and access to it is forbidden without authorization because of lethal risk due to military operations. All studied ponds ($n=73$), located on flat and not urbanized area, originated from the ancient passage of tanks and did not have water connections. This means that newts caught in more than one pond had to have moved on land. These movements are considered breeding dispersal because they link two breeding patches (Clobert et al. 2009). This number of ponds was chosen to encompass all ponds where marked newts were found as we did not find marked newts outside the study site where ponds are also present. Because there are no physical barriers or differences of elevation in the study area, the matrix is considered permeable to newts. All the studied area is also surrounded by lands protected under the Natura2000 protected network. The minimum convex polygon linking these ponds covered an area of 9.16 ha, i.e. 423 × 293 m (Supplementary material Appendix 2). The mean ± SD distance and nearest distance separating each pond inhabited by the newts was 149.4 ± 75.2 m and 21.1 ± 13.3 m, respectively. Crested newt movements can be large (up to 299 m: Schabetsberger et al. 2004) and some newts were seen to use the different parts of the studied area, i.e. several hectares (Dalleur and Denoël unpubl.). The study therefore was done at the scale of the usual walking distances by newts. The mean ± SD of the average area of the ponds was 92.7 ± 89.9 m^2. Adult crested newts were the largest aquatic predators present in the ponds; no fish or crayfish were present.

Adult newts were caught by dip netting and trapping. Adulthood and sexes were primarily identified on the basis of a well-developed and sexually dimorphic cloaca. Immediately after capture, newts were placed in a 1-l anesthetic bath (phenoxyethanol, 0.7%) the time to get asleep, subsequently measured from the tip of the snout to the end of the cloaca to determine the snout-vent-length (SVL), and at their first capture tagged with glass-encapsulated passive integrated transponder (PIT) tags (1.4 × 9 mm) using a needle inserted under the skin at the margin of the belly. This marking system remains in the body and does not affect growth, survival, reproduction, or feeding in newts (Winandy and Denoël 2011). After marking and before release, the newts were placed in a tank filled with fresh water from their pond until they wake up.

The survey was divided into 16 sessions of capture, which covers the breeding aquatic phase of the life cycle of adult newts, i.e. from March to June (5 sessions in 2010, 9 in 2011, and 2 in 2012). These capture sessions allowed us to analyze data on 946 adult newts (451 females and 495 males), totalizing 5103 captures (Supplementary material Appendix 3). We marked newts as they were captured without trying to have a similar number of males and females, so these values represent the sex-ratio in the population. Data on the pond identity were recorded at each session whereas its water surface was done every two to three sessions. In addition to trapping which allowed to catch and measure newts, we optimized the number of individual detections of marked newts by using an underwater radio-frequency identification (RFID) telemetry technique (Cucherousset et al. 2005). To this end, we used at each session a portable transceiver system (2001-F, Destron Fearing, TX) equipped with a submersible antenna (BP model, Biomark, Boise, ID) to do transects over the entire surface area of each pond to locate marked newts without manipulating them.

Multi-event capture–recapture model

To analyze our dataset, we extended the multi-event capture–recapture (CR) model recently proposed by Lagrange et al. (2014), which allows modeling dispersal probabilities, when the number of sites is large and dispersal parameters are intractable, with the use of classical multisite CR models. In this model, 'states' gather movement information, namely, whether the individual occupies the same location as on the previous capture occasion (*S* for 'stayed') or not (*M* for 'moved'), as well as information about whether the individual was captured or not on both the previous and the current occasion (i.e. at time $t - 1$ and time t, respectively). This information regarding capture status is critically needed in state coding since it affects our ability to assess whether an individual moved or not. The states are denoted by prefixing to the breeding site fidelity status (*S* or *M*) and the previous capture status ('+' if detected or 'o' if not detected) and suffixing to its current capture status (same notations). The repeatability of the dispersal behavior was assessed by considering correlated successive movement ('a memory effect'): the movement status at $t - 1$ is retained in the model and the probability of remaining in the pond can be made dependent on the fact that the individual moved or was faithful to its breeding site (i.e. pond) at $t - 1$ (Lagrange et al. 2014, Cayuela et al. 2017b). To track the existence of different site fidelity strategies in the population, we added heterogeneity mixtures on survival and dispersal (Pradel 2009, Péron et al. 2010). Two discrete classes of individuals were developed to accommodate heterogeneity, each class being associated with a distinct value of the parameter(s); these classes were the actual states of the multi-event model leading to the consideration of two dispersal phenotypes: 'lowly site faithful' (LSF) and 'highly site faithful' (HSF) individuals. The states associated with one or the other of the dispersal phenotypes are either coded as 1 or 2 after the site fidelity status (*S* or *M*): for instance, S1o corresponds to an individual of the heterogeneity group 1 that remained faithful with a probability α to its site between $t - 1$ and t and was not captured at t; oM2+ corresponds to an individual of the heterogeneity group 2 that moved between $t - 1$ and t with a probability $1 - \alpha$, was not captured at $t - 1$, and was captured at t. This led to the consideration of models including 13 states (described in Table 1).

In order to examine whether internal or environmental factors influence the individual assignment to one site fidelity phenotype or another, we coded the initial states of the model in two steps (Fig. 1): the first step embeds the probability r that an individual is assigned to one or the other phenotype LSF vs HSF (Fig. 1 and 2). The second step includes the movement and capture state of a newly encountered individual (Fig. 1). When an individual is caught for the first

Table 1. Descriptions of the states in the multievent models.

State	State description
S1o	In the same site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and not captured at t
oS1+	Not captured at $t - 1$, in the same site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and captured at t
+S1+	Captured at $t - 1$, in the same site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and captured at t
M1o	In a different site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and not captured at t
oM1+	Not captured at $t - 1$, in a different site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and captured at t
+M1+	Captured at $t - 1$, in a different site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and captured at t
S2o	In the same site at t that the one occupied at $t - 1$, in the heterogeneity group 2, and not captured at t
oS2+	Not captured at $t - 1$, in the same site at t that the one occupied at $t - 1$, in the heterogeneity group 2, and captured at t
+S2+	Captured at $t - 1$, in the same site at t that the one occupied at $t - 1$, in the heterogeneity group 2, and captured at t
M2o	In a different site at t that the one occupied at $t - 1$, in the heterogeneity group 1, and not captured at t
oM2+	Not captured at $t - 1$, in a different site at t that the one occupied at $t - 1$, in the heterogeneity group 2, and captured at t
+M2+	Captured at $t - 1$, in a different at t that the one occupied at $t - 1$, in the heterogeneity group 2, and captured at t
D	Dead

Initial states 1

$$\begin{array}{cc} \text{oS1} & \text{oS2} \\ \left(r\right. & \left.1-r\right) \end{array}$$

Initial states 2

$$\begin{array}{c|cccccccccccc} & \text{S1o} & \text{oS1+} & \text{+S1+} & \text{M1o} & \text{oM1+} & \text{+M1+} & \text{S2o} & \text{oS2+} & \text{+S2+} & \text{Mo2} & \text{oM2+} & \text{+M2+} \\ \text{oS1} & 0 & i & 0 & 0 & 1-i & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{oS2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & i & 0 & 0 & 1-i & 0 \end{array}$$

Step 1: survival

$$\begin{array}{c|ccccccccccccc} & \text{S1o} & \text{oS1+} & \text{+S1+} & \text{M1o} & \text{oM1+} & \text{+M1+} & \text{S2o} & \text{oS2+} & \text{+S2+} & \text{M2o} & \text{oM2+} & \text{+M2+} & \textbf{D} \\ \text{S1o} & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oS1+} & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+S1+} & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{M1o} & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oM1+} & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+M1+} & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{S2o} & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 1-\phi \\ \text{oS2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 1-\phi \\ \text{+S2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 1-\phi \\ \text{M2o} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 1-\phi \\ \text{oM2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 1-\phi \\ \text{+M2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 1-\phi \\ \textbf{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Step 2: site fidelity

$$\begin{array}{c|ccccccccccccc} & \textbf{S1o} & \textbf{oS1+} & \textbf{+S1+} & \textbf{M1o} & \textbf{oM1+} & \textbf{+M1+} & \textbf{S2o} & \textbf{oS2+} & \textbf{+S2+} & \textbf{M2o} & \textbf{oM2+} & \textbf{+M2+} & \textbf{D} \\ \text{S1o} & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{oS1+} & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{+S1+} & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{M1o} & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{oM1+} & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{+M1+} & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{S2o} & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 \\ \text{oS2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 \\ \text{+S2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 \\ \text{M2o} & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 & 0 \\ \text{oM2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 & 0 \\ \text{+M2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 1-\alpha & 0 \\ \textbf{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Step 3: recapture

$$\begin{array}{c|ccccccccccccc} & \textbf{S1o} & \textbf{oS1+} & \textbf{+S1+} & \textbf{M1o} & \textbf{oM1+} & \textbf{+M1+} & \textbf{S2o} & \textbf{oS2+} & \textbf{+S2+} & \textbf{M2o} & \textbf{oM2+} & \textbf{+M2+} & \textbf{D} \\ \textbf{S1o} & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{oS1+} & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{+S1+} & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{M1o} & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{oM1+} & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{+M1+} & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \textbf{S2o} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 & 0 & 0 & 0 \\ \textbf{oS2+} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 \\ \textbf{+S2+} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 & 0 & 0 & 0 \\ \textbf{M2o} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & p & 0 & 0 \\ \textbf{oM2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 \\ \textbf{+M2+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & p & 0 \\ \textbf{D} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Events

$$\begin{array}{c|cccc} & 1 & 2 & 3 & 4 \\ \text{S1o} & 1 & 0 & 0 & 0 \\ \text{oS1+} & 0 & 0 & 0 & 1 \\ \text{+S1+} & 0 & 1 & 0 & 0 \\ \text{M1o} & 1 & 0 & 0 & 0 \\ \text{oM1+} & 0 & 0 & 0 & 1 \\ \text{+M1+} & 0 & 0 & 1 & 0 \\ \text{S2o} & 1 & 0 & 0 & 0 \\ \text{oS2+} & 0 & 0 & 0 & 1 \\ \text{+S2+} & 0 & 1 & 0 & 0 \\ \text{M2o} & 1 & 0 & 0 & 0 \\ \text{oM2+} & 0 & 0 & 0 & 1 \\ \text{+M2+} & 0 & 0 & 1 & 0 \\ \text{D} & 1 & 0 & 0 & 0 \end{array}$$

Figure 1. Matrices of initial states, state-state transitions (one for each of the three steps considered in the multi-event model) and events (see Table 1 for the description of states). *r* is the assignment probability to the heterogeneity group 1, *i* is the initial state probability, ϕ represents the survival probabilities, α is the fidelity probability and *p*, the recapture probability. The composite state embeds the following information: the heterogeneity groups corresponding to dispersal phenotypes (group 1 and 2), the site fidelity status ('stayed': S; 'moved': M) and the recapture status (recaptured, +; or not, letter o). Three events are considered, numbered 0, 1, 2 and 3. At each step, updated information appears in bold.

time, it is assigned with a probability *i* to one of the four following states: oH1, oE1+, oH2, or oE2+. From these initial states of departure, three steps of transition are considered between one capture session to the next. In the first step, the information related to survival is updated, and individuals may survive with a probability ϕ and die with a probability 1 – ϕ (Fig. 1). In the second step, the dispersal information is updated, and survivors remain at *t* in the same breeding site that the one occupied at *t* – 1 with a probability α, or may disperse to another one with a probability 1 – α (Fig. 1). This probability can depend on the site fidelity status of the individual at *t* – 1. In the third step, individuals can be captured at time *t* with a probability *p* or not with a probability 1 – *p* (Fig. 1). Finally, the last component of the multi-event CR model links events to states. The events corresponded to 'not captured' (coded 0), 'captured in the same site at *t* that the one occupied at *t* – 1' (coded 1), 'captured in a different site at *t* that the one occupied at *t* – 1' (coded 2), and 'not captured at *t* – 1' (coded 3), respectively. In our case, each state corresponds to only one possible event, but one event can correspond to several states and, thus, make the event probabilities trivial.

Building biological scenarios

This parameterization was implemented in the E-SURGE program (Choquet et al. 2009), which provides robust tools of advanced numerical convergence and refines parameter estimates by detecting redundant mathematical parameters. Competitive models were ranked through a model-selection procedure (Supplementary material Appendix 4 and 5) using Akaike information criteria (AIC) adjusted for small sample size (AICc) and relative AICc weights (Burnham and Anderson 2002). We considered that the model with lowest AICc was the best-supported by the data. Other models that were closed in terms of AICc (delta AICc < 2) were considered only if they had less parameters. In addition, we assumed that in all the models, since the time interval between capture

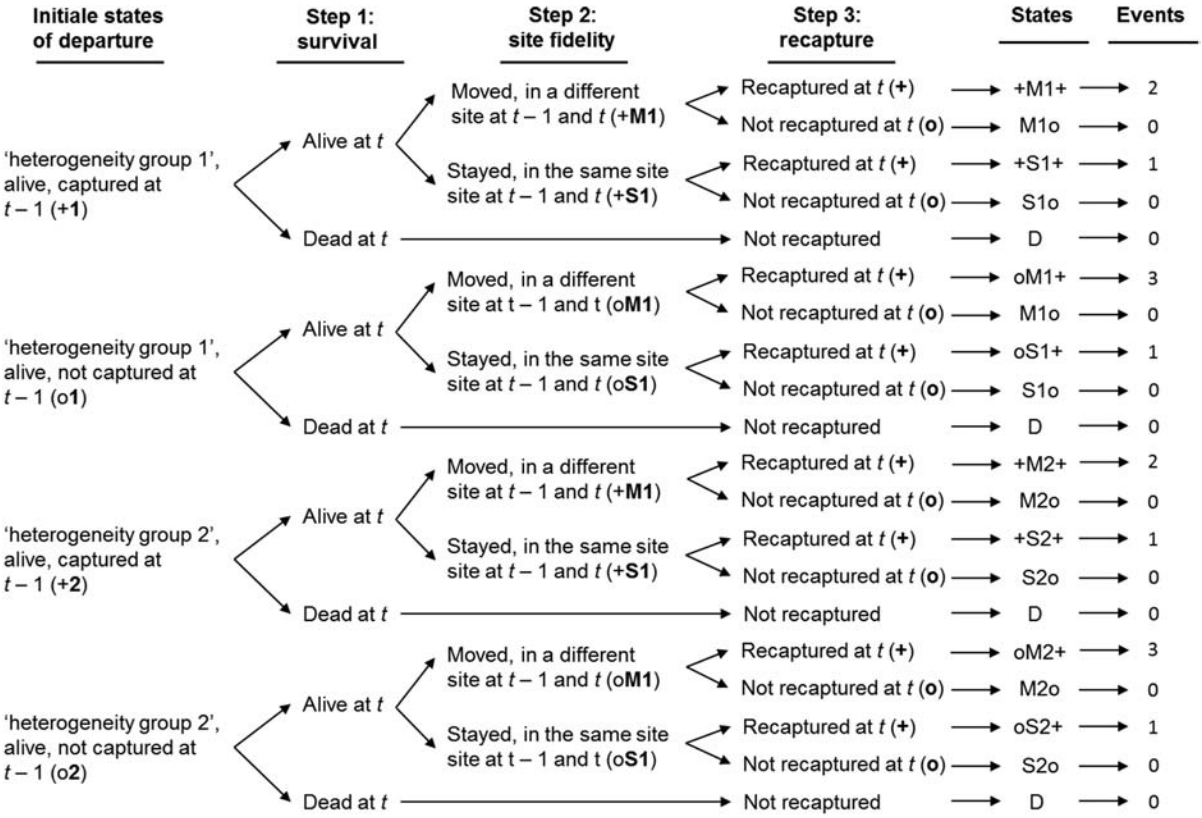

Figure 2. Transition steps of an individual from *t* – 1 to *t,* underlying states and field observations (i.e. events). The diagram shows the initial states of departure as well as the steps and associated transitions leading to events at *t* – 1 and *t*: heterogeneity groups corresponding to dispersal phenotypes (group 1 and 2), survival (alive or dead, D), dispersal ('stayed': S; 'moved': M) and recapture (recaptured, +; or not, letter o). At each step, updated information appears in bold. In the last step, we show the 13 states that can generate the four possible events (numbered 0, 1, 2, 3) we considered in the model. The 13 states are described in Table 1.

sessions varied over the study period, site fidelity was considered time-specific (T); meaning that one parameter was estimated for each time intervals allowing to deal with the heterogeneity of time interval length between field sessions. In addition, the intra-annual survival was forced at 1.

Modeling autocorrelated successive movements

First, we aimed at demonstrating that the dispersal behavior is relatively stable over time by showing that faithful individuals to their breeding site (i.e. pond) at *t* – 1 exhibit a high probability of remaining faithful at time *t*. We conducted a sequential model selection procedure. We first modeled recapture probability (p) and tested whether it varied between sexes (SEX), year (YEAR) or was constant (CST). We then kept the best effect on recapture probability based on AICc values (the model with the lowest AICc among the different models testing covariates on recapture probabilities), and we then tested whether the site fidelity probability (α) at time t depended on individual fidelity status at time $t-1$ by comparing the relative support of a model including a memory effect [r(CST), ϕ(CST), α(MEMORY+T), and p(SEX)] and a model without memory effect [r(CST), ϕ(CST), α(T), and p(SEX)]. To account for heterogeneous time intervals between capture sessions, we considered that site fidelity probability was time-specific (T) (as such site fidelity probabilities differ for all time intervals). Moreover, no heterogeneity classes were considered for survival (ϕ) and site fidelity behavior (α). To do so, we forced the different ϕ values of the survival matrix to be equal (Fig. 1). Similarly, all the α values of the site fidelity matrix were held to be equal. In the model including the memory effect, site fidelity behavior was made dependent on the individual's previous movement status (*S* vs *M*) by forcing the different α values for the rows 1, 2, 3, 7, 8, and 9 (site faithful at $t-1$) and for the rows 4, 5, 6, 10, 11, and 12 (site unfaithful at $t-1$) of the pond fidelity matrix (Fig. 1; see Table 1 for the correspondence between rows and states) to be equal. The probability to be site faithful at the breeding season scale was derived from the memory effect model. More specifically, it was calculated as the combination of the probabilities to stay in the pond for individuals that did not move at the previous time interval for all monitored intervals of the breeding season. These values were then averaged over the three studied years. The mean proportion of site faithful individuals between years was also estimated from the average values of the two inter-annual time-steps of the memory model. Confidence intervals were calculated using parametric bootstrapping. The complete model selection procedure is provided in the Supplementary material Appendix 4.

Inferring the existence of alternative dispersal strategies

We then examined the existence of two phenotypes, i.e. the highly site faithful (HSF) vs the lowly site faithful (LSF) individuals in the population using a new model selection procedure. As the number of models to test was extremely large given the number of combinations with all covariates, we conducted a sequential model selection procedure. We first modeled recapture probability (*p*) and tested whether it varied between sexes (SEX), year (YEAR) or was constant (CST). Then, we modeled individual heterogeneity in both survival (ϕ) and site fidelity behavior (α); for that purpose, we included heterogeneity mixture in the two parameters. Next, we tested whether the probability of being assigned to one of the two site faithful phenotypes (r) depended on three factors: 1) sex (SEX), 2) body size (SVL), and 3) the mean surface of the ponds occupied by the individual during the three years of study (SURF). The same hypotheses were then tested on survival. For both phenotype assignment and survival probabilities, we tested all possible combinations of the two variables that were included in an additive way. In addition, we considered interactions between SEX and SVL and between SEX and SURF. The complete model selection procedures are provided in the Supplementary material Appendix 5 and 6.

Results

Among the 946 tracked newts, 841 were recaptured at least once (average: 6 captures) (Supplementary material Appendix 3).

Modeling autocorrelated successive movements

The recapture probability was sex-specific and was slightly lower in females (0.51, 95% CI: 0.49–0.53) than in males (0.55, 95% CI: 0.54–0.57), but did not vary between years. The AICc difference (90.33 points) between the model including a memory effect [*r*(CST), ϕ(CST), α(MEMORY + T), and *p*(SEX)] and the model without a memory effect [*r*(CST), ϕ(CST), α(T), and *p*(SEX)] indicated that the probability of staying in the same site between each time step (i.e. *t* – 1 and *t*) depended on individual site fidelity status at *t* – 1 (Supplementary material Appendix 4). The probability of remaining in the same breeding site was higher in individuals that were already site faithful at *t* – 1 (Fig. 3A, B).

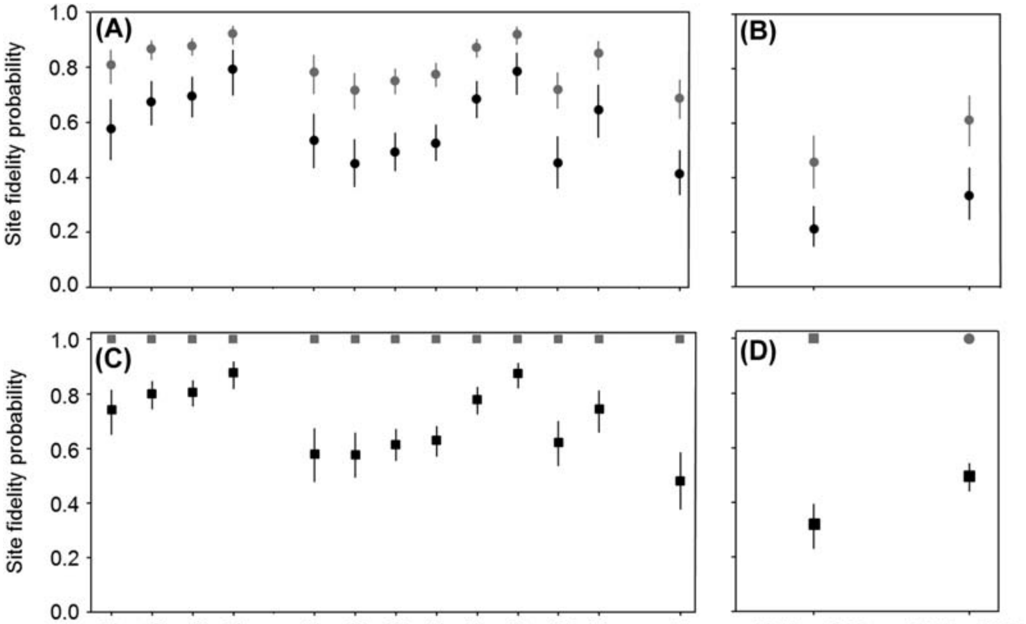

Figure 3. Breeding site fidelity probabilities of the highly site faithful (HSF) and lowly site faithful (LSF) phenotypes in crested newts during three years of survey (2010–2012). The estimates and the 95% CI are extracted from the best-supported model (Supplementary material Appendix 4). In (A) (intra-annual) and (B) (inter-annual), the site fidelity probability at time *t* depends on the fidelity status of the individual at *t* – 1; the probability of being site faithful at *t* given the individual was faithful at *t* – 1 (in grey) or not (black). In (C) (intra-annual) and (D) (inter-annual), site fidelity probability is shown for individuals of the highly site faithful (in grey) and lowly site faithful (black) phenotypes. The time *t* corresponds to the time interval between two capture sessions. Since the time intervals are irregular, we considered a time-specific effect on site fidelity probability in our models.

Inferring the existence of alternative dispersal strategies

The best-supported model [r(SEX + SVL + SURF), ϕ(HET + SURF + SVL), α(HET + T), and p(SEX)] (see Supplementary material Appendix 5 for the model selection procedure) supports the hypothesis that two distinct site fidelity strategies occurred in the population and that individuals belonging to each strategy differed in terms of survival. At both intra- and inter-annual scales, the site fidelity probability was always 1 in the 'highly site faithful' phenotype (HSF, corresponding to heterogeneity mixture 1), while this probability fluctuated greatly over time in the 'lowly site faithful' phenotype (LSF, corresponding to heterogeneity mixture 2) (Fig. 3C, D). The mean site fidelity probability between each time step was 0.70 (95% CI: 0.68–0.72) at the intra-annual level and 0.41 (0.34–0.49) at the inter-annual level (we derived this parameter from a memory effect model without time-specific variation, [r(CST), ϕ(CST), α(MEMORY), and p(SEX)]). Globally, the best model lead to an estimated proportion of site faithful individuals of 0.59 (0.56–0.62) over an entire breeding season and 0.53 (0.46–0.60) between breeding seasons. The probability of being assigned to the LSF phenotype was 0.70 (95% CI: 0.66–0.78) – extracted from the model [r(CST), ϕ(HET), α(HET + T), p(SEX)] where covariates were applied on assignment and survival probabilities. Our results also demonstrated that the probability of being assigned to the LSF phenotype depended on both intrinsic and extrinsic factors (i.e. sex, body size and pond surface). Males had a higher probability of belonging to the LSF phenotype than females (odds ratio: 2.62; 95% CI: 1.55–4.42), and, in both sexes, this probability increased with body size (Fig. 4A, B). Furthermore, the probability of being in the LSF phenotype slightly increased with the mean surface of the pond occupied by the individuals during the three-year study period (Fig. 4C, D).

Survival probability depended on both intrinsic and extrinsic factors (i.e. body size and pond surface); the mean survival probability, extracted from a model where survival was constant, was 0.64 (95% CI: 0.61–0.66). The HSF phenotype was characterized by a lower survival probability than the site LSF phenotype (odds ratio HSF/LSF: 0.63; 95% CI: 0.43–0.94, Fig. 5). In both HSF and LSF phenotypes, survival increased with body size (Fig. 5A, B) and the mean surface of the pond occupied by the individuals (Fig. 5C, D). However, we did not detect a sex effect on survival in one or the other phenotype (Supplementary material Appendix 5).

Discussion

Our study revealed the existence of a dispersal polymorphism at the population level in the crested newt. We highlighted the coexistence of two dispersal phenotypes, namely, a highly site (i.e. pond) faithful phenotype and a

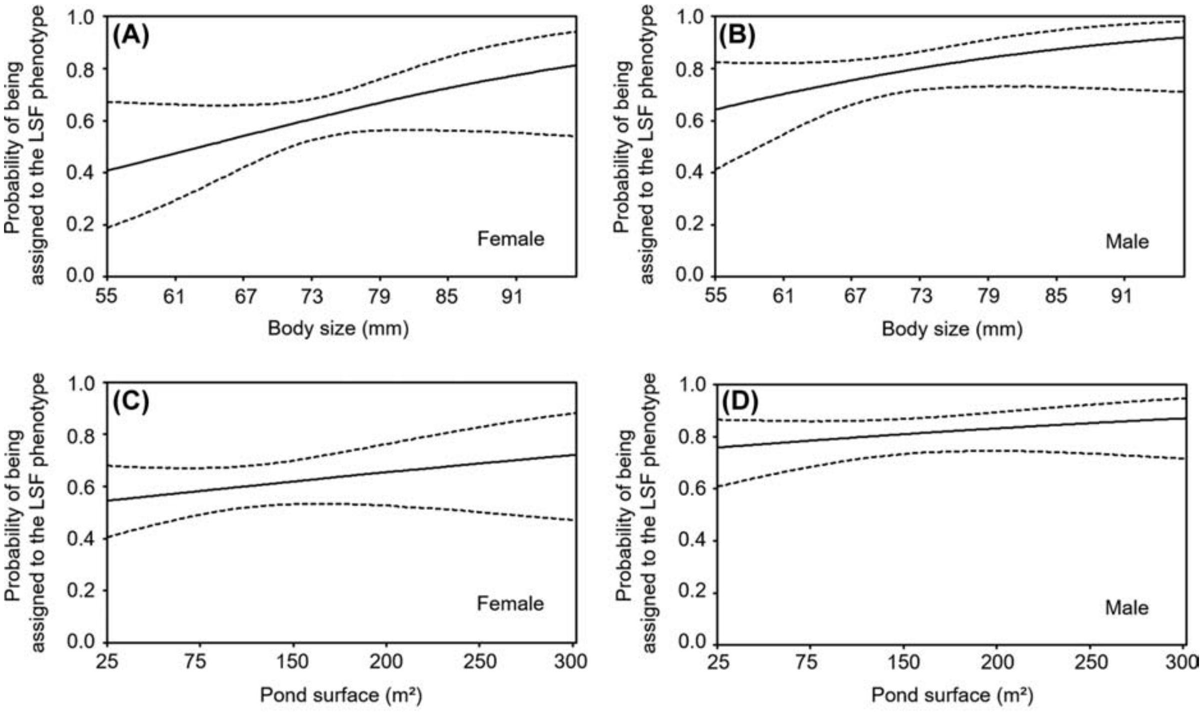

Figure 4. Breeding site infidelity (i.e. probability to be assigned to the LSF phenotype) in crested newts in function of individual (A–B) and environmental factors (C–D) in females (A–C) and males (B–D). The estimates and the 95% CI are extracted from the best-supported model (Supplementary material Appendix 5). Broken lines represent 95% confidence bands. LSF: 'lowly site faithful' phenotype.

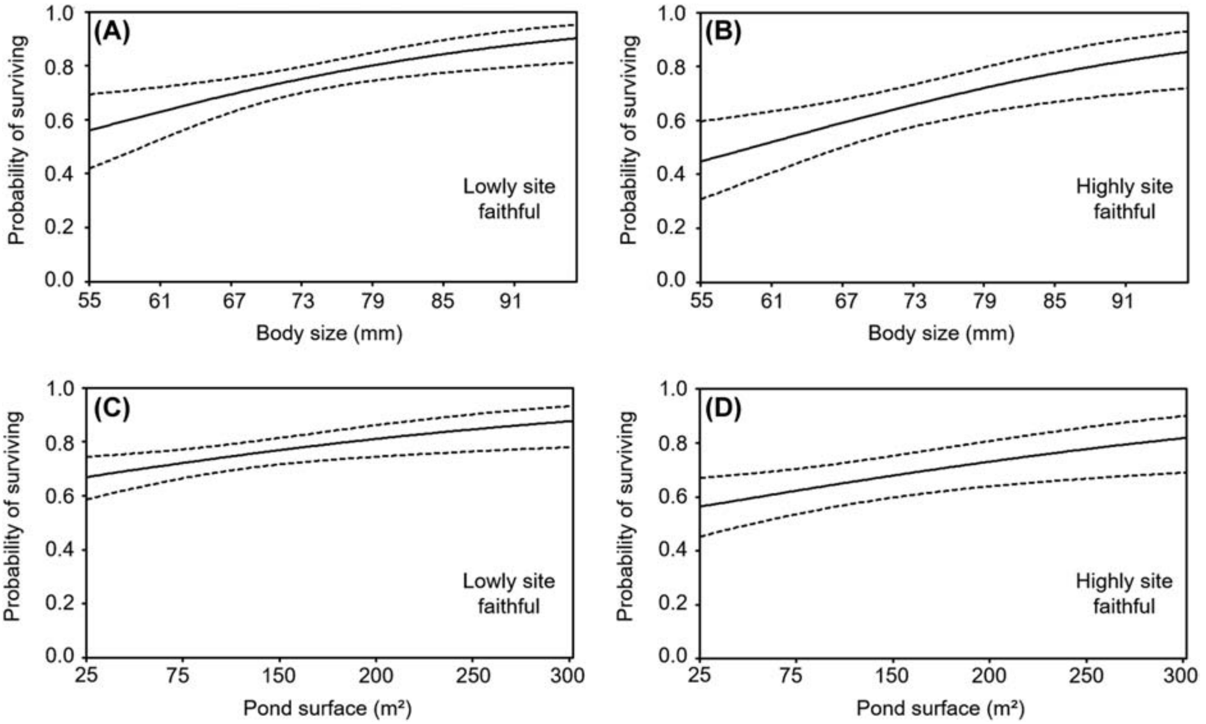

Figure 5. Survival probabilities in crested newts in function of individual ((A–B): body size) and environmental factors ((C–D): pond surface) in the two dispersal phenotypes ((A–C): LSF, 'lowly site faithful' phenotype; (B–D): HSF, 'highly site faithful' phenotype). The estimates and the 95% CI are extracted from the best-supported model (Supplementary material Appendix 5). Broken lines represent 95% confidence bands.

lowly site faithful phenotype (i.e. a dispersing phenotype) at both intra and inter-annual scales. Our results also showed that the probability that individuals belong to one or the other dispersal phenotypes depended on environmental and individual factors.

Divergent site fidelity phenotypes within the population

Newts and salamanders, including species such as crested newts, are typically described as philopatric to their water body (Gill 1978, Unglaub et al. 2015, Mori et al. 2017). However, there is also evidence that they can change ponds between years (Miaud et al. 1993, Trenham et al. 2001, Perret et al. 2003) and even within a single breeding season, i.e. involving habitat supplementation (Whiteman et al. 1994, Denoël et al. 2007, Kopecky et al. 2010). In our study, we showed an unexpectedly high infidelity rate, including during the breeding season, which contrasts with the currently held idea of breeding site fidelity of organisms with a complex life cycle such as newts in the field, but it fits well with experimental data (Winandy et al. 2017). This indicates that newts are not just biphasic twice in a year, but can exhibit multiple biphasic phases in the breeding season provided that such alternative aquatic habitats are available within usual walking distances (i.e. a few hundred meters) (Schabetsberger et al. 2004, Denoël and Dalleur unpubl.). This is particularly astonishing in such complex life cycle species because they have to cross the water-air interface to reach alternative breeding patches, what can involve different physiological adaptations and/or constraints (Hourdry and Beaumont 1985). On another hand, future studies should examine how the distance to reach an alternative breeding patch (i.e. pond isolation) influences the probability of dispersal both at the scale of small and large range movements, that means within a few hundred meters and at further distances, respectively (Smith and Green 2005, Semlitsch 2008). Therefore, it would be worth to test whether dispersal distances are inversely proportional to the probability to disperse (see also Scott et al. 2013). Moreover, identifying whether males and females differ in their likelihood to move over short versus long distances and if these movements are connected with habitat features remain an interesting perspective of the present work (Trochet et al. 2016, 2017).

Our analyses revealed that there is a temporal autocorrelation of the site fidelity behavior: individuals that have been site faithful at time $t-1$ have a higher probability to remain site faithful at time t than individuals that moved over the previous time interval. This indicates a temporal consistency of the individual dispersal behavior: individuals that have moved at a specific time-interval were more prone to move again at the next time-interval. Yet, the probability to be site faithful between two capture occasions given the individual was previously site faithful was higher at the intra-annual than at the inter-annual level (0.70 vs 0.40). These results are congruent with the hypothesis of Bell et al. (2009) that individuals are more consistent over short intervals compared to long intervals. Moreover, both dispersal and migration occur during inter-annual time intervals and errors could be made by individuals when they try to locate the pond they occupied during the previous breeding season. By contrast, only dispersal occurs during the breeding season and site fidelity thus strictly reflects the propensity of individuals to remain in their breeding sites or to disperse to another one. This could therefore result in a higher consistency of the site fidelity behavior at the intra-annual level than at the inter-annual level.

Our mixture model demonstrated the coexistence of two site fidelity phenotypes in the studied population, i.e. a strictly site faithful phenotype over the three studied years and a lowly site faithful phenotype (i.e. a dispersing phenotype). The model therefore supports the results of the first modeling approach by showing a high consistency of individual site fidelity behavior. This shows that a substantial proportion of the individuals are strictly faithful to their breeding site during their entire lifespan. Our results are congruent with previous works showing that alternative movement strategies can occur within or among amphibian populations. Concerning complementation movements, Grayson et al. (2011) demonstrated that movement between the aquatic and terrestrial habitats can be facultative in newts, resulting in partial migration and the coexistence of two migratory phenotypes (i.e. resident individuals which stayed in their ponds and migrating individuals, which escaped early their pond for land). As in our study, they showed that individuals that migrated the previous year were more likely to migrate the following year, suggesting that migratory behavior can also be stable over time (Grayson et al. 2011). Concerning supplementation movements (i.e. movements between ponds), recent studies (Cayuela et al. 2016b, c) demonstrated the existence of two dispersal phenotypes among the different populations of an anuran, *Bombina variegata*. In populations suffering high rates of breeding patch turn-over, individuals displayed a high dispersal propensity associated with accelerated life histories (high fecundity and low survival), while the reverse was found in populations experiencing low turn-over rates. In this study case, dispersal behavior also appeared to be stable over time among the populations. Taken together, these studies indicate the existence of stable alternative movement strategies in amphibians. Yet, the mechanisms underlying the evolution of complementation and supplementation movements are likely different (Dunning et al. 1992). It is probable that the evolutionary mechanisms promoting polymorphism in site fidelity behavior differ within and among populations. To our knowledge, our study provides the first empirical evidence of the existence of alternative breeding site fidelity strategies coexisting at the intra-population level.

Environmental correlates of breeding site fidelity strategies

Our results showed the existence of a condition-dependent dispersal: the probability that an individual being assigned to one or the other breeding site fidelity phenotype depended on the mean surface of the ponds that individuals occupied over the three years of study. Individuals displaying the lowly site faithful phenotype (i.e. the dispersal strategy) occupied, on average, larger ponds than individuals displaying the highly site faithful phenotype. This result is also in accordance with previous studies in amphibians, showing that both sexes avoid aquatic patches whose environmental conditions are detrimental to their own survival or the survival of their offspring (Winandy et al. 2015, Cayuela et al. 2017c). In fact, females usually display an active oviposition site choice and preferentially spawn their eggs in aquatic patches that reduce the risk of larval mortality prior to metamorphosis (Resetarits and Wilbur 1991, Spieler and Linsenmair 1997). As larger ponds are expected to be more permanent than smaller ones, reproducing in large aquatic patches is often thought of as a risk-avoidance strategy that reduces offspring mortality when ponds dry up (Murphy 2003, Goldberg et al. 2006). Overall, our results are, therefore, congruent with the idea that dispersers are more likely to settle in patches that optimize their own fitness (Clobert et al. 2009, Matthysen 2012). However, we cannot rule out that alternative processes associated with pond surface area are not involved. For instance, densities may vary across ponds as well as predators (Hovestadt and Nieminen 2009, Grayson et al. 2011). No aquatic predators of adult crested newts were found during the study but we could expect that newt densities may be higher in small ponds, a trait that can be advantageous for mate choice but induce a large competition. For instance, Winandy et al. (2017) showed that females laid less eggs at high newt densities and that both sexes used alternative breeding patches when available, what ultimately led to lower densities. Consequently, future analyses of newt movements between breeding patches should also consider biotic variables.

Phenotypic correlates of breeding site fidelity strategies

Our analyses also revealed the existence of a phenotype-dependent dispersal: the probability that an individual being assigned to one or the other site fidelity strategy varied according to individual characteristics, including sex, morphology, and life history traits. First, we found evidence of male-biased dispersal, which is congruent with the theoretical prediction of the local mate competition hypothesis stating that male-biased dispersal is expected when the distribution of males is determined by the distribution of females and not by any a priori resource partitioning (resource competition hypothesis, see Greenwood 1980). This theoretical prediction has been empirically validated in some amphibians (Lampert et al. 2003, Liebgold et al. 2011), although additional factors are also likely to affect sex-biased dispersal as females can also be the first to escape waters (Grayson et al. 2011, Winandy et al. 2017).

In addition, beyond this difference between sexes, we highlighted the existence of a dispersal syndrome (Clobert et al. 2009, Cote et al. 2010, Stevens et al. 2013) in which dispersal covaries with a morphological trait, i.e. body size, and with a life-history trait, i.e. survival. Individuals with a lowly site faithful phenotype had a larger body size and higher survival rate. They can also be expected older because size can, on average, increase with age across years in crested newts (Mori et al. 2017). In amphibians, body size usually has a positive influence on locomotor capacities and individual movement propensity (Denoël et al. 2010, Brodin et al. 2013, Maes et al. 2013). Accordingly, body size most likely has a substantial effect on the costs and benefits balance of dispersal by improving individual vagility and reducing the mortality risks caused by dehydration during a transfer within the terrestrial landscape matrix (i.e. during the transience stage of the three-step process). In addition, body size often positively influences survival in amphibians (Altwegg and Reyer 2003, Schmidt et al. 2012), which probably explains why dispersing individuals have a higher survival in our study system. Overall, our results suggest that the breeding site fidelity behavior is relatively stable over time and that the eventual shifts of strategy probably result from modifications in the cost and benefit balance of dispersal over newt lifetime. Thus, individuals with a large body size may be more likely to become dispersing individuals due to a reduction of dispersal costs, especially survival costs.

Conclusions

Taken together, this study and other recent works (Grayson et al. 2011, Gruber et al. 2017) call into question the ideas that amphibians are organisms with a reduced mobility and that their movement strategies are relatively fixed over space and time. Conversely, they emphasize the existence of a substantial heterogeneity in individual dispersal strategies at both intra-population and inter-population levels. They also show that the dynamics of amphibians' spatially structured populations are not always mainly driven by natal dispersal (Marsh and Trenham 2001, Pittman et al. 2014), but that breeding dispersal between ponds can also play a central role. More broadly, these works open new research prospects in the evolution of dispersal in organisms displaying complex life cycles. They raise interesting questions about the evolutionary pathways that contribute to the diversification of movement strategies in the wild (Cote et al. 2017b): is dispersal only a by-product of the evolution of migratory movement providing temporary escape from the environmental constraints of the aquatic habitat (e.g. predation and drying up: Winandy et al. 2015, Mathiron et al. 2017). And, alternatively, is there a coupling of the evolutionary forces shaping migration and dispersal, implying selective pressures that act jointly on morphological, physiological, and behavioral traits affecting the movement? Such important questions suggest that further studies should be undertaken to increase our knowledge of the evolutionary mechanisms underlying the evolution of movement strategies in complex life cycle organisms.

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Supplementary material (Appendix ECOG-03296 at <www.ecography.org/appendix/ecog-03296>). Appendix 1–5.