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Environmentally mediated reproductive success predicts breeding dispersal decisions in an early successional amphibian

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Dispersal is a central mechanism in ecology and evolution. Dispersal evolution is driven by a trade-off between costs and benefits, which is influenced by interindividual variability and local environmental conditions (context-dependent dispersal). Many studies have investigated how dispersal decisions may be influenced by environmental factors, including density, predation and interspecific competition. Yet few have attempted to examine how habitat disturbance may affect the dispersal process in spatially structured populations. In early successional species, one might expect individuals to adjust their dispersal decisions based on two main factors that potentially have an influence on reproductive success: patch size and the level of patch disturbance. In this study, we examined how these two factors affect breeding success and dispersal decisions in an early successional amphibian, the yellow-bellied toad, *Bombina variegata*. To this end, we used capture—recapture data collected on a spatially structured population occupying 28 breeding patches. We took advantage of recent developments in multievent capture—recapture models to detect signs of context-dependent dispersal. The results revealed that the probability of successful reproduction and the number of newly metamorphosed individuals increased with both the size and the proportion of disturbance of a patch. In addition, our results showed that the factors affecting breeding success also influenced breeding dispersal probability. Large patch size negatively influenced emigration probability; in contrast, it positively influenced immigration probability. Equally, higher disturbance had a strong negative influence on emigration probability and slightly positively affected immigration probability. These findings strongly suggest that individuals make context-dependent dispersal decisions, adjusted to maximize future fitness prospects in a patch, allowing them to better cope with rapid changes in environmental conditions resulting from the ecological succession process. This opens new areas of potential research into the role of dispersal in organism specialization along an ecological succession gradient.

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Dispersal, the movement of an individual from its site of birth to its reproduction site (i.e. natal dispersal), or between successive reproduction sites (i.e. breeding dispersal), is a central mechanism in ecology and evolution (Clobert, Galliard, Cote, Meylan, & Massot, 2009; Matthysen, 2012; Ronce, 2007). Dispersal has a broad influence on the dynamics of spatially structured populations, as it affects local population density, the risk of local extinction and the possibility of patch (re)colonization (Gilpin, 2012; Hanski & Gaggiotti, 2004). Moreover, it has a strong influence on evolutionary processes since it affects genetic variation and adaptation through gene flow (Legrand et al., 2017; Ronce, 2007). Dispersal is usually considered a three-stage process that includes emigration (or departure), transience (or transfer within the landscape matrix) and immigration (or arrival) (Ims & Yoccoz, 1997; Ronce, 2007). A major advance in dispersal studies was the recognition that dispersal evolution is driven by a balance between costs and benefits at each stage of the process (Bonte et al., 2012). This trade-off is influenced by factors related to the individual (phenotype-dependent dispersal) and to local environmental conditions (context-dependent dispersal) (Clobert et al., 2009; Matthysen, 2012).

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Contrary to the assumption made in many demographic models, dispersal is thus not a random process (Edelaar, Siepielski, & Clobert, 2008). Individuals adjust their dispersal decisions according to environmental and social cues that provide information about their future fitness prospects in a given patch (i.e. 'informed dispersal'; Clobert et al., 2009), resulting in asymmetric dispersal rates in spatially structured populations.

Many studies have investigated how dispersal decisions may be influenced by environmental factors such as density, predation, interspecific competition and landscape characteristics (reviewed in Bowler & Benton, 2005; Cote et al., 2017; Matthysen, 2012). Yet few have attempted to examine how the level of habitat disturbance may affect the dispersal process in spatially structured populations (Altermatt & Ebert, 2008, 2010; Bates, Sadler, & Fowles, 2006; Duckworth, 2012). A disturbance is a temporary change in physical environmental conditions (e.g. due to fire, flood or drought) and can be caused by natural or anthropogenic factors (Pickett & White, 1985). Disturbances play a central role in community and ecosystem dynamics by initiating ecological successions, that is, the sequential replacement of species following the loss of biomass due to a disturbance event (Prach & Walker, 2011; Turner, Baker, Peterson, & Peet, 1998). In addition, disturbances can create new habitat patches by reshaping the physical environment. In early successional species (i.e. those occurring at the early stages of succession), the disturbance regime has a strong influence on population dynamics, as it affects the distribution and the amount of suitable habitat across a landscape (Amarasekare & Possingham, 2001; Moloney & Levin, 1996). In this context, dispersal is expected to be a central mechanism in population dynamics, as it allows individuals to escape rapid detrimental changes in environmental conditions (e.g. declining quality of a patch through the succession process) and to colonize newly available habitat patches resulting from disturbance (Clobert et al., 2009; Reigada, Schreiber, Altermatt, & Holyoak, 2015).

In early successional species, one might expect individuals to adjust their emigration and immigration decisions based on two main factors that potentially have an influence on reproductive success. First, large patches often support abundant resources and/or increase the possibility of mate encounters, and therefore provide high fitness prospects. Emigration and immigration probabilities would thus be expected to be negatively correlated with patch size (Gascoigne, Berec, Gregory, & Courchamp, 2009; Schtickzelle & Baguette, 2003; Wahlberg, Klemetti, & Hanski, 2002). Second, an early successional habitat patch only persists for a limited amount of time before it becomes unsuitable for breeding through the succession process (Prach & Walker, 2011; Turner et al., 1998). The quality of the patch, and therefore the fitness prospects of early successional organisms, would be expected to decline over time (Duckworth, 2012). Hence, when a patch is regularly disturbed (partly stopping the succession process), one might expect a negative relationship between the emigration and immigration probabilities and the extent of the patch's surface area disturbed. Yet to our knowledge, few studies have investigated how patch-dependent fitness prospects may predict dispersal decisions in early successional organisms.

To study this issue, pond-breeding amphibians are suitable biological models, as many of these species reproduce in early successional aquatic habitats (Canessa, Oneto, Ottonello, Arillo, & Salvidio, 2013; Cromer, Lanham, & Hanlin, 2002; Morand & Joly, 1995; Warren & Büttner, 2008). In temperate forests of Europe and North America, amphibians reproduce in temporary waterbodies, which in the past mainly resulted from natural disturbances (e.g. flooding or trees uprooted by wind; DeMaynadier & Hunter, 1995; Joly & Morand, 1994). Over the last century, however, human activity and forest management practices have rapidly modified the characteristics of amphibians' aquatic breeding habitats, drastically affecting their population dynamics (see, for instance, Cayuela et al., 2016a, 2016b). The promotion of dense, monospecific forests with trees of uniform age has reduced the probability of windfall trees, decreasing the availability of naturally formed breeding waterbodies. In parallel, forest harvesting has led to the creation of seminatural waterbodies (i.e. puddles formed in ruts and residual tracks made by logging vehicles such as skidders), which are now used by amphibians as replacement breeding habitats (Cromer et al., 2002; DiMauro & Hunter, 2002; Kopecký, Vojar, & Denoël, 2010). Yet these breeding habitats only persist for a limited time before they become unsuitable for reproduction due to natural silting. Accordingly, the long-term persistence of a local population strongly depends on (1) the continuous creation of new breeding patches (i.e. groups of ruts) that can be colonized to compensate for deterministic local extinctions triggered by waterbody silting dynamics and/or (2) frequent anthropic disturbance (i.e. from the passage of vehicles) in existing patches to limit the natural silting process of waterbodies.

In this study, we examined how patch size and the level of patch disturbance affect reproductive success and breeding dispersal in a spatially structured amphibian population, the yellow-bellied toad, *Bombina variegata*. In forests exploited for timber, *B. variegata* breeds in early successional patches composed of waterbodies (e.g. ruts and residual puddles) resulting from logging operations (Cayuela, Lambrey, Vacher, & Miaud, 2015). First, we investigated how patch size affects the probability of breeding occurrence and the abundance of newly metamorphosed individuals (i.e. local juvenile production) between patches. As large breeding patches usually increase the chance of mate encounter (Gascoigne et al., 2009) and provide more breeding resources (Cushman, 2006), we predicted a positive relationship between breeding occurrence (i.e. presence of breeding indices), breeding success (i.e. presence and abundance of newly metamorphosed individuals) and patch size. In parallel, we also examined how the annual level of patch renewal through disturbance influenced breeding occurrence and success. By deepening ruts and increasing ground compaction (Ampoorter, Van Nevel, De Vos, Hermy, & Verheyen, 2010; Wronski & Murphy, 1994), the passage of skidders limits the natural silting of waterbodies and improves their water-holding capacity, which reduces the risk of a pond drying out and thus amphibian reproductive failure (Tournier, Besnard, Tournier, & Cayuela, 2017). Hence, we expected a positive relationship between breeding occurrence and success and the extent of the surface area disturbed in a patch each year by skidders. Second, we analysed how patch size and disturbance influence breeding dispersal between patches. We took advantage of recent developments in multievent capture–recapture models (Cayuela, Pradel, Joly, & Besnard, 2017; Cayuela, Pradel, Joly, Bonnaire, & Besnard, 2018) to examine this issue. As individuals are expected to adjust their dispersal decisions according to their fitness prospects in a given patch, we hypothesized that emigration probability would be lowest in large patches with a higher disturbance level where reproductive success is highest. For the same reason, we hypothesized that immigration to these patches would also be highest.

METHODS

Study Area and Data Collection

The capture–recapture (CR) study was conducted over a 9-year period (2000–2008) on a spatially structured population of *B. variegata* located in a woodland of northeast France (49.37°N, 4.83°E, elevation 200 m; Fig. 1). The woodland is a mixed forest covering approximately 7000 ha and is surrounded by intensively

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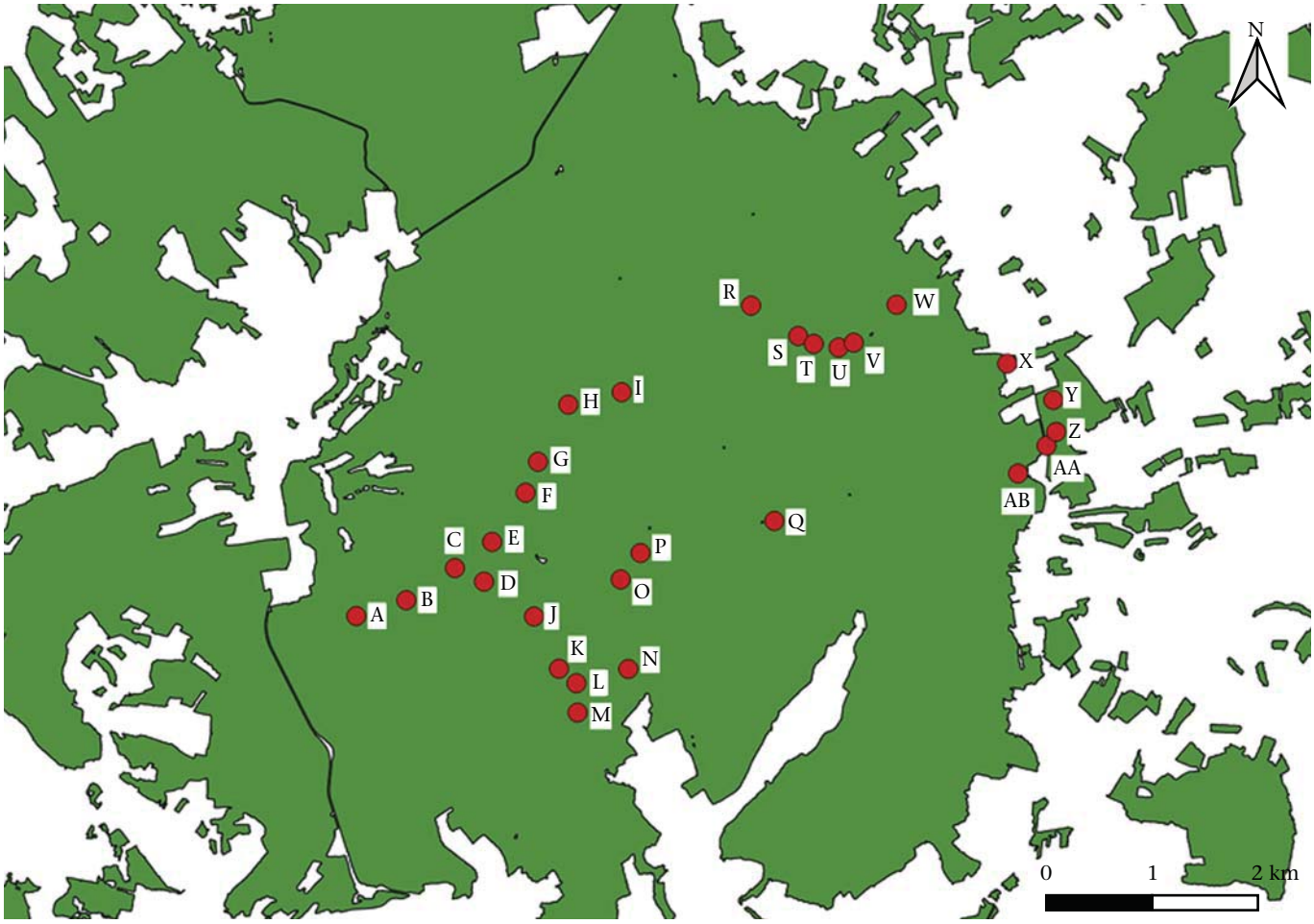


Figure 1. Map of the study area, showing the location (red dots) of the 28 breeding patches (i.e. group of ruts) within the woodland.

cultivated farmland. The nearest other *B. variegata* population to our study population is more than 20 km from the forest. The study population occupies 28 breeding patches (i.e. groups of ruts and puddles) in the study area. All the patches used by toads to reproduce were exhaustively sampled. The delineation of each patch was established using ArcGis 10.1 (ArcGis 10.1, Environmental Systems Research Institute, Redlands, CA, U.S.A.) to create polygons connecting the waterbodies located on the boundary of the pond network (i.e. the minimum convex polygon approach; see White & Garrott, 1991). As in previous studies of *B. variegata* (see Cayuela et al., 2016a), patches were assumed to differ based on a minimum distance of 100 m separating the boundaries of polygons. This distance was chosen since the between-pond movement in this species is usually less than 100 m (Beshkov & Jameson, 1980; Hartel, 2008). The median of the Euclidean distance between patches was 2458.83 m (minimum = 150.90 m, maximum = 6905.91 m). Patch size was calculated as the mean cumulative surface area of the ruts composing the patch (i.e. length × width of each rut) over the 9-year study period. The surface area of the 28 breeding patches varied widely, ranging from 2.50 m^2 to 107.67 m^2 (mean = 23.99 m^2, SD = 22.33 m^2). The patch disturbance level was evaluated by calculating the cumulative surface area of the waterbody disturbed by skidder passages during a breeding season divided by the patch's total water surface area (i.e. the percentage of the patch's total water surface area that was disturbed). This variable was recorded only during the last 2 years of the study. For that reason, the capture–recapture analyses related to the effect of patch renewal through disturbance were restricted to the 2007–2008 period. The proportion of the waterbody surface area disturbed by skidders in the 28 breeding patches varied widely, from 0% to 100% (2007: mean = 47%, SD = 46%; 2008: mean = 41%, SD = 47%). Prior to the analyses, we verified the collinearity between patch size and disturbance; the two variables were weakly correlated ($r = 0.15$). As well, the number of ponds in a patch and the percentage of disturbed area were very weakly correlated ($r = 0.06$). By contrast, patch size and the number of waterbodies in a patch were highly correlated ($r = 0.73$). Furthermore, we investigated how the number of adults in attendance in a breeding patch was related to patch characteristics (the analysis is detailed in Appendix 1). Zero-inflated Poisson regression models revealed that the number of adults increased with the size of the patch and the level of disturbance.

The capture sessions were carried out during the toad's breeding season (from late April to July) of each year. The number of capture sessions per year ranged from one in 2003 and 2004 to six in 2000 (for details of the number of capture sessions and the number of individuals captured each year, see Appendix 1). During each capture session, all the breeding patches were exhaustively surveyed. Toads were caught by hand or using a dipnet. The catching effort was performed in a waterbody several times and stopped when no new individual was detected. Based on the outcomes of previous studies on different *B. variegata* populations (Cayuela et al., 2016b), we assumed that toads became sexually mature at the age of 3 years, with a mean body length (snout–vent

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length) of 36 mm in males and 37 mm in females; smaller individuals were excluded from the analysis. The sex was assessed on the basis of strong forearms with nuptial pads in males. We identified each individual by the specific pattern of black and yellow mottles on its belly, recorded by photographs. To minimize misidentification errors, multiple comparisons of individual patterns were performed using the pattern-matching software ExtractCompare (Hiby & Lovell, 1990). ExtractCompare provides similarity scores between patterns scanned from photographs showing ventral patterns. During a visual confirmation step, the observer then validates the automatic matching returned by two algorithms, which further minimizes the risk of false rejection.

We surveyed breeding occurrence (i.e. presence of breeding indices) and success (i.e. presence and abundance of newly metamorphosed individuals) in 2007 and 2008. Two sampling sessions were performed annually in July and August to detect eggs, larvae and newly metamorphosed individuals. This sampling period was chosen to coincide with the period during which larvae and newly metamorphosed individuals occur. The searches for eggs, larvae and newly metamorphosed individuals were conducted during the day by visual encounter. The occurrence of eggs and tadpoles and the number of newly metamorphosed individuals were recorded.

Modelling the Influence of Patch Size and Disturbance on Breeding

To investigate the influence of patch size and disturbance level on breeding occurrence, we used multistate occupancy models (Gimenez et al., 2014; Nichols, Hines, Mackenzie, Seamans, & Gutierrez, 2007). The data from the relevant 2 years of the breeding survey (2007 and 2008) were compiled in a single data set; one site therefore had two annual replicates with two detection occasions (July and August) each. The year was included in the model as a group effect. By doing so, we allowed the state of the patch to vary between years. We considered three states: a site could be unoccupied for breeding (U), occupied with noneffective reproduction (i.e. presence of eggs and larvae without metamorphosis success: L) or occupied with successful reproduction (i.e. presence of newly metamorphosed individuals: M). The observations were coded as undetected (0), eggs and/or larvae detected (1) and newly metamorphosed individuals detected (2). Following Gimenez et al. (2014), the model was based on three types of information (the model matrices are provided in Appendix 1). (1) The vector of initial state probabilities contained two parameters of interest: the probability that a site is occupied with noneffective reproduction ($\psi 1$), and the probability that a site is occupied with successful reproduction ($\psi 2$). (2) The state–state transition matrix contained the transition probabilities, which were fixed at 1 in our study case; we did not model changes in the state of occupancy over time. (3) The field observation matrices allowed us to model the observation process conditional on underlying occupancy states. Two modelling steps were considered to highlight the successive processes of detection and breeding-state ascertainment. In the first matrix (Appendix 1), we introduced a set of intermediate observations: undetected (u), detection of eggs and larvae (l) and detection of newly metamorphosed individuals (m). This resulted in the consideration of two detection probabilities: one of eggs and/or larvae ($p1$) and the other of newly metamorphosed individuals ($p2$). The second matrix (Appendix 1) specified the probability of successful reproduction conditional on these intermediate observations. This parameterization was implemented in the E-Surge program (Choquet, Rouan, & Pradel, 2009). We ranked the models using the Akaike information criterion adjusted for a small sample size (AICc) and AICc weights. When the AICc weight of the best-supported model was less than 0.9, we performed model averaging. We tested our hypotheses from the general model, [ψ1,2(Di + Si), p1,2(Y)], which included three variables: the proportion of the surface area of a waterbody disturbed by skidders (Di, a continuous variable), the size of the patch (Si, a continuous variable) and a year effect (Y, a discrete variable with two modalities, 2007 and 2008). Owing to reduced statistical power (30 patches sampled over a 2-year period), the two patch-specific variables were included in an additive way in the model. For the same reason, we also considered an additive effect between two conditional occurrence probabilities (ψ1 and ψ2) and the variables. We tested all combinations of these variables, leading to the consideration of eight competing models (Appendix 1).

Then we conducted a second analysis to examine how patch size and disturbance influenced the number of individuals that successfully metamorphosed in the breeding patch. As newly metamorphosed individuals cannot be marked using a noninvasive method and leave the pond shortly after metamorphosis, we could not use density estimates based on capture–recapture or repeated count data. As the detection probability of newly metamorphosed individuals estimated by our multistate occupancy model was high (> 0.90, see 'Results'), we assumed that imperfect detection would not skew our inferences. To avoid the risk of double counting, we considered in our analyses the maximum number of newly metamorphosed individuals recorded in each patch during one of the two annual sampling sessions. Owing to the zero excess in the count data, we used zero-inflated Poisson (ZIP) regression models. First, we performed a preliminary analysis to investigate how the number of newly metamorphosed individuals was correlated with the number of adults in each patch and the density of adults per m^2 of patch. The number and the density of adults were corrected by dividing the number of captured individuals by the recapture probability (i.e. Horvitz-Thompson estimator) estimated by CR multievent models (see below): 0.45 in 2007 and 0.46 in 2008. The number of newly metamorphosed individuals (Ju) was treated as the response variable. In the Poisson regression part of the model, the number of adults (Ad), the density of adults (De), and the year (Y: 2007, 2008) were introduced as explanatory terms, resulting in the following general model (Ju ~ Ad + De + Y). The variables (Ad) and (De) were treated as continuous variables, were z-scored and were included in an additive way. We examined all the possible combinations of effects, resulting in eight competing models. The models were ranked using AICc and AICc weights. Normality of the residuals of the best-supported model was examined graphically using a quantile–quantile plot. Then we examined how newly metamorphosed individuals across patches (Ju) was correlated with patch size (Si) and disturbance (Di). We used the same modelling approach (i.e. ZIP models) as described above. The variables (Si) and (Di) and the year (Y: 2007, 2008) were incorporated as explanatory terms. The continuous variables (Si) and (Di) were z-scored. Moreover, as our preliminary analysis showed that the response variable (Ju) was strongly correlated with the number of adults (Ad) in patches, we introduced the variable (Ad) as an offset, leading to the following general model: [Ju ~ offset(log(1 + Ad)) + Di + Si + Y]. The offset variable was used to adjust for the local population size as recommended in Poisson models (Hutchinson & Holtman, 2005). From this model, we examined all possible combinations of effects.

Modelling the Influence of Patch Size on Dispersal

To test the effect of patch size on dispersal, we used CR multievent models recently developed by Cayuela, Pradel et al. (2017) and further extended by Tournier et al. (2017), which allow the estimation of movement rates between sites with differing characteristics. As with other multievent models, this model is composed of states and events (Pradel, 2005). Events correspond to

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field observations and are coded in an individual's capture history. These observations are related to the latent state (e.g. dead versus alive, resident versus disperser) of the individuals. Yet observations can carry a certain degree of uncertainty regarding this state. Multievent models aim to model this uncertainty in the observation process using hidden Markov chains.

Note that the effect of patch size and disturbance were analysed separately. Increasing the number of patch variables included in the model increases the number of states and state-state transitions; for n states, the number of transitions between states to be estimated is $n(n-1)$ and is thus a function of n^2. A large number of states and transitions makes model implementation very tricky, increases the issue of model convergence and reduces model stability. For this reason, we considered two distinct models, one for the effect of patch size and the other for the influence of patch disturbance.

The model used in Tournier et al. (2017) is based on 13 states (Table 1) that combine information about whether or not an individual occupies the same patch as on the previous capture occasion, whether or not the individual was/is captured at the previous and current occasion and the category of patch currently occupied. Note that in CR multievent models, patch characteristics cannot be introduced as continuous variables and are treated in a discrete way (Cayuela, Gillet et al., 2018; Cayuela, Pradel et al., 2017). The following codes are used: an individual that occupies the same patch as on the previous occasion is coded S for 'stayed' or if it occupies a different patch, M for 'moved'. These codes are prefixed by the previous capture status and suffixed by the current capture status (+ for 'captured', o for 'not captured'). In addition, we added a state designation to include the category of patch currently occupied: an individual can occupy one of two patch categories (s 'small' or l 'large'). A small patch ranged from 2.5 m^2 to 23 m^2 and a large patch from 23 m^2 to 108 m^2. We used the mean size of patches in our study system as the boundary between the two size classes. Five events were considered in the model: for an individual captured at t and $t-1$, a code of 1 or 4 was attributed if it did not change patch and was in patch category s or l respectively, and a code of 2 or 5 was attributed if it did change patch and was in patch category s or l respectively. For an individual not captured at $t-1$ and captured at t in patch category s or l, a code of 3 or 6 was attributed respectively. An individual not captured at t was given a code of 0. Note that in this model, the size of patch was assumed to be fixed over time. We made this assumption as the probability that a patch changes between states s and l was less than 0.001 at each time interval. By doing so, we avoided nonestimable transition probabilities and increased model stability. The model had a robust design structure (Pollock, 1982), i.e. several capture sessions performed within a year corresponded to secondary sessions and a set of yearly sessions corresponded to a primary period. This robust design structure allowed us to examine both intra-annual and interannual dispersal.

At its first capture, an individual could be in state oSs+ or oSl+. From this initial state of departure, the transition from the state at time $t-1$ to that at time t was updated through four successive modelling steps: (1) survival, (2) departure, (3) arrival and, finally, (4) recaptured or not (see Fig. 2). Following the convention set out in Souchay, Gauthier, and Pradel (2014), whenever the status in the state descriptor was updated to the situation at t, it became bold (and stayed bold throughout the following steps). First, the information about survival was updated; an individual could survive with a probability of ϕ or die with a probability of $1-\phi$ (Fig. 2), leading to a transition matrix with 13 possible states of departure and seven intermediate arrival states. Survival probability was set at 1 between secondary sessions. Second, departure was updated; an individual that survived between $t-1$ and t could leave its patch (designated s or l) with a probability of ψ or stay in the same patch with a probability of $1-\psi$ (Fig. 2). The departure probability could be dependent on the category of the patch (s or l). This resulted in a transition matrix with seven intermediate departure and 13 intermediate arrival states. Third, arrival was updated; an individual that left its patch could arrive in a small patch (s) with a probability of $1-\alpha$ or in a large patch (l) with a probability of α (Fig. 2). This led to a transition matrix with 13 intermediate departure states and 13 intermediate arrival states. Fourth, the recapture status of individuals was updated; an individual could either be captured with a probability of p or not captured with a probability of $1-p$ (Fig. 2), resulting in a transition matrix with 13 intermediate departure states and 13 arrival states at time t. The last component of the model linked events to states. In this specific situation, each state corresponded to only one possible event (Fig. 2).

The parameterization was implemented in the E-Surge program (Choquet et al., 2009), which provides advanced diagnostics of numerical convergence and adds the benefit of refining biological parameter estimates by detecting redundant parameters. As the information about patch size was recorded over the entire 9 years of the survey, the models were run using the complete data set (2000–2008). Competing models were ranked using AICc and AICc weights. When the AICc weight of the best-supported model was less than 0.9, we performed model averaging. The 95% confidence intervals, CIs, of model-averaged parameters were calculated using the parametric bootstrap method. Our hypotheses regarding recapture and state–state transition probabilities were examined

Table 1
The 13 states of the CR multievent models and their definitions

State	State description
oMs+	Captured at t in a small patch different from the one occupied at $t-1$ when not captured
+Mso	Not captured at t and in a small patch different from the one occupied at $t-1$ when captured
+Ms+	Captured at t in a small patch different from the one where captured at $t-1$
oSs+	Captured at t in the same small patch occupied at $t-1$ when not captured
+Sso	Not captured at t and in the same small patch where captured at $t-1$
+Ss+	Captured at $t-1$ and t in the same small patch
oMl+	Captured at t in a large patch different from the one occupied at $t-1$ when not captured
+Mlo	Not captured at t and in a large patch different from the one occupied at $t-1$ when captured
+Ml+	Captured at t in a large patch different from the one where captured at $t-1$
oSl+	Captured at t in the same large patch occupied at $t-1$ when not captured
+Slo	Not captured at t and in the same large patch where captured at $t-1$
+Sl+	Captured at $t-1$ and t in the same large patch
D	Dead

The state formulation includes four types of information: + = captured or o = not captured at previous occasion, S = stayed or M = moved, s = small patch or l = large patch, + = captured or o = not captured at current occasion. Note that the patch disturbance model used the same states as those presented here except that 's' (small) and 'l' (large) were replaced by l = low disturbance and h = high disturbance.

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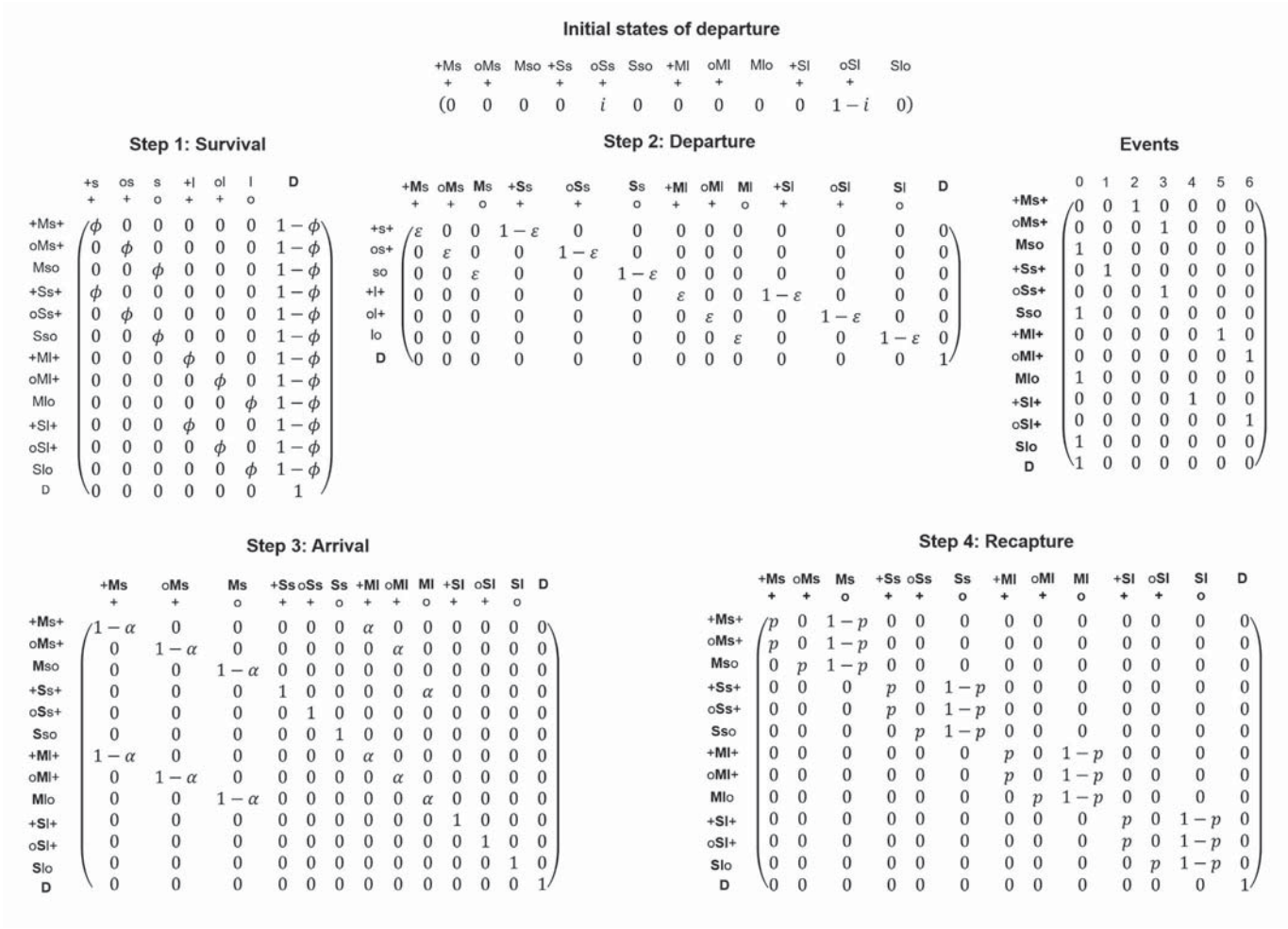


Figure 2. Modelling the influence of patch size: matrices of initial states of departure, state–state transitions and events (field observations). The definition of the states is provided in Table 1. Four state–state transition steps were considered in the model: survival probability ϕ (step 1), departure probability ψ (step 2), arrival probability α (step 3) and recapture probability p (step 4).

using the general model [ϕ(Si + S), ψ(Si + S), α(Si + S), p(Y + Si + S)], which included three effects: (1) patch size (Si), coded as states in the model; (2) group effect for sex-specific variation (S); and (3) year-specific variation (Y). As previous studies on this toad population have shown that recapture probability varies between years (Cayuela et al., 2016a, 2016b), we retained year-specific variation in all the models. From this general model, we tested all the possible combinations of effects, resulting in the consideration of 64 competing models (Appendix 2).

Modelling the Influence of Patch Disturbance on Dispersal

The effect of patch disturbance was evaluated using the model recently proposed by Cayuela, Pradel et al. (2018) to account for the possibility that a patch could change category (i.e. low ↔ high disturbance) between two capture occasions. In our study system, the probability of a patch change of category between 2 years was 0.57. We used the mean proportion of disturbed surface area as the boundary between the two classes. Low disturbance corresponded to patches with a lower proportion of the waterbody surface area disturbed by skidder passages (from 0% to 41%, the latter being the mean disturbance rate). High disturbance corresponded to patches with a higher proportion of the waterbody surface area disturbed by skidders (from 42% to 100%). This model was based on the same states (Table 1) and events as the previously described model; 13 states and seven events were thus considered. In contrast to the previous model, we also considered additional state–state transitions in the arrival matrix to update patch status (step 3, Fig. 3). In addition, we included the code l for 'low disturbance to patch' and h for 'high disturbance to patch'. The model had a robust design structure to examine both intra-annual and interannual dispersal.

At its first capture, an individual could be in state oSl+ or oSh+. Then the transition from the state at time $t-1$ to that at time t was updated through four successive modelling steps: (1) departure, (2) survival, (3) arrival and patch dynamics and, finally, (4) recaptured or not (Fig. 3). First, information about departure was modelled; an individual could move from a patch (designated l or h) with a probability of ψ or remain in the same patch occupied at $t-1$ with a probability of $1-\psi$. The departure could be made dependent on the category of patch occupied at $t-1$. This led to a transition matrix with 13 states of departure and nine intermediate states of arrival (Fig. 3). Second, survival was updated; an individual could survive with a probability of ϕ or die with a probability of $1-\phi$, resulting in a transition matrix with nine possible states of departure and nine arrival states. Third, arrival and site dynamics were modelled. When an individual remained in the same site, it could occupy a site that changed state ($l \leftrightarrow h$) between $t-1$ and t with a probability of α, or a site that remained in the same state with a probability of $1-\alpha$ (Fig. 3). When an individual moved, it could

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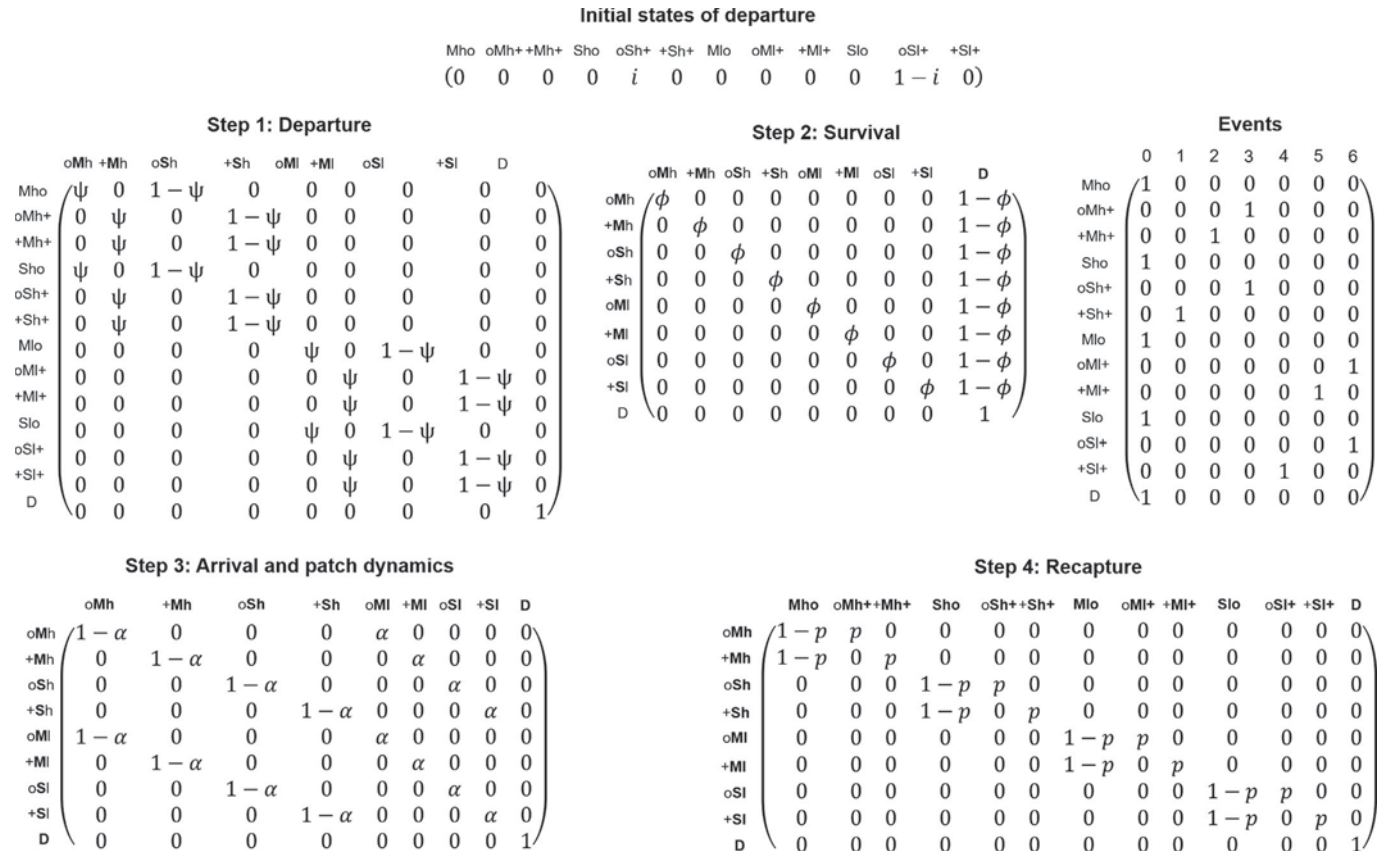


Figure 3. Modelling the influence of patch disturbance: matrices of initial states of departure, state–state transitions and events (field observations). The definition of the states is provided in Table 1. Four state–state transition steps were considered in the model: departure probability ψ (step 1), survival probability ϕ (step 2), probability of arrival and patch state change α (step 3) and recapture probability p (step 4).

arrive in a site of a different category (l or h) than the one previously occupied with a probability of α or in the same type of site with a probability of $1-\alpha$ (Fig. 3). This led to the consideration of a transition matrix with nine departure states and nine arrival states (Fig. 3). Fourth, recapture status was updated; an individual could be recaptured with a probability of p or missed with a probability of $1-p$. Recapture probability could depend on the patch category, leading to the consideration of a transition matrix including nine departure states and 13 arrival states (Fig. 3). The last component of the model linked events to states (Fig. 3).

The parameterization was implemented in the E-Surge program. As the information about patch disturbance was only recorded during the last 2 years of the survey, in this case the models were run using only the 2007–2008 data set. Competing models were ranked using AICc and AICc weights. We performed model averaging when the AICc weight of the best-supported model was less than 0.9 and used the parametric bootstrap method to calculate the 95% CI. Our hypotheses about departure ψ, survival ϕ, arrival α and recapture p were examined using the general model [ψ(Di + S), ϕ(S), α(Di + S), p(Y + Di + S)], which included three effects: (1) the patch disturbance level (Di), coded as states in the model; (2) group effect for sex-specific variation (S); and (3) year-specific variation (Y). As this analysis was based on a subset of data including only 2 years of study, we did not test the effect of disturbance on survival due to a lack of power. In all the models, the probability that a patch changed disturbance level depended on the site status at $t-1$. From the general model, we tested all the possible combinations of effects, resulting in the consideration of 32 competing models (Appendix 2).

Assessing the Effects of Patch Size and Disturbance on Arrival Probability

The conditional probability of arrival (i.e. depending on patch characteristics) estimated by the multievent CR models strongly depended on the quantity of patches of each category in the spatially structured population and the number of individuals in each patch that may reach these. For this reason, we examined patch size and disturbance by comparing the model-averaged conditional arrival probability to the probability of reaching a patch using a random dispersal hypothesis (i.e. the mean probability of arriving in a patch calculated from all the individuals occurring in all patches of the study area). As the number of males and females varied between patches, we calculated the expected random sex-specific probability. We assumed that the effect of patch size or disturbance was significant if the 95% CI of the conditional arrival probability did not overlap with the expected random probability. The percentage of deviation from the expected random probability was used to assess the influence of patch characteristics and to rank their effects on both sexes.

Ethical Note

The study was approved by two conservation agencies that have funded the research project, namely the Lorraine Direction Régionale de l'Environnement, de l'Aménagement et du Logement (DREAL), and the Agence de l'Eau Rhin-Meuse. Note that no permit number can be provided as the data were collected before the

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release of the ministerial order (February 19, 2007) establishing the conditions of demand and instruction of the capture of protected species. Instead, we provide a permit number delivered for similar surveys (capture–recapture method) performed in several populations of *B. variegata* in the Lorraine region from 2008 (arrêté no. 2008–2150).

In capture–recapture studies focusing on dispersal, all breeding sites in the study area need to be sampled exhaustively to detect dispersal events that are, by definition, rare (Cayuela, Rougemont et al., 2018). All the individuals are individually surveyed to obtain demographic and dispersal rates at the whole population level (Cayuela, Rougemont et al., 2018; Lebreton, Nichols, Barker, Pradel, & Spendelow, 2009). Despite this strong sampling effort, we believe our survey had limited implications for toads since (1) we used a less invasive method (i.e. photographs of the natural unique coloration patterns): available to identify and survey individuals; (2) we reduced as much as possible the time of handling (less than 2 min per individual); and (3) we released the individuals at their site of capture immediately after taking the picture. Furthermore, we assume that our sampling method did not negatively affect the population dynamics over the 9-year study period; in fact, the population size increased from 2006 (Appendix 2, Table 1). Note that the capture–recapture method is commonly used to survey spatially structured populations of *B. variegata* (Cayuela et al., 2016b, 2016a; Tournier et al., 2017), including in the context of conservation and reintroduction programmes (Cayuela, Gillet et al., 2018). To our knowledge, this kind of survey has never resulted in a population loss (see all the papers cited above). Furthermore, egg and tadpole detection, as well as juvenile counts, were performed without any handling (i.e. visual encounter). We are therefore confident that the study had limited implication for toad welfare and the long-term viability of the population.

RESULTS

Influence of Patch Size and Disturbance on Breeding

Multistate models revealed that the occurrence probability of noneffective reproduction was 0.10 (95% CI 0.04–0.23), whereas the probability of successful reproduction was 0.40 (95% CI 0.27–0.55); these estimates were extracted from a model with constant occurrence probability [ψ1,2(.), p1,2(Y)]. The detection probability of breeding indices (eggs and tadpoles) was 0.96 (95% CI 0.63–0.99); for newly metamorphosed individuals it was 0.93 (95% CI 0.83–0.97). The best-supported model was [ψ1,2(Si), p(Y)]; the complete model selection procedure is provided in Appendix 1. As its AICc weight was 0.58, we performed model averaging. Detection probability of noneffective reproduction was 0.96 (95% CI 0.60–0.99) in 2007 and 0.97 (95% CI 0.54–0.99) in 2008. Detection probability of successful reproduction was 0.91 (95% CI 0.76–0.97) in 2007 and 0.94 (95% CI 0.79–0.98) in 2008. More importantly, our analysis revealed that both noneffective and successful breeding probabilities were positively influenced by patch size (model-averaged slope: 3.00, 95% CI 0.71–5.41), whereas disturbance level had a marginal effect (model-averaged slope: 0.08, 95% CI −0.15–1.03).

The number of newly metamorphosed individuals in 2007 and 2008 varied from 0 to 73 from one patch to another (mean = 5.33, SD = 14.60). Our preliminary analysis revealed that the number and density of adults influenced the number of metamorphosed individuals in a patch. The best-supported ZIP model (Ju ~ Ad + De + Y) had an AICc weight of 0.99 (Appendix 1). It showed that the number of newly metamorphosed individuals was positively influenced by the number of adults recorded in the patch and negatively affected by the density of adults per m^2 of the patch (Fig. 4a and b). We then analysed the effects of patch size and

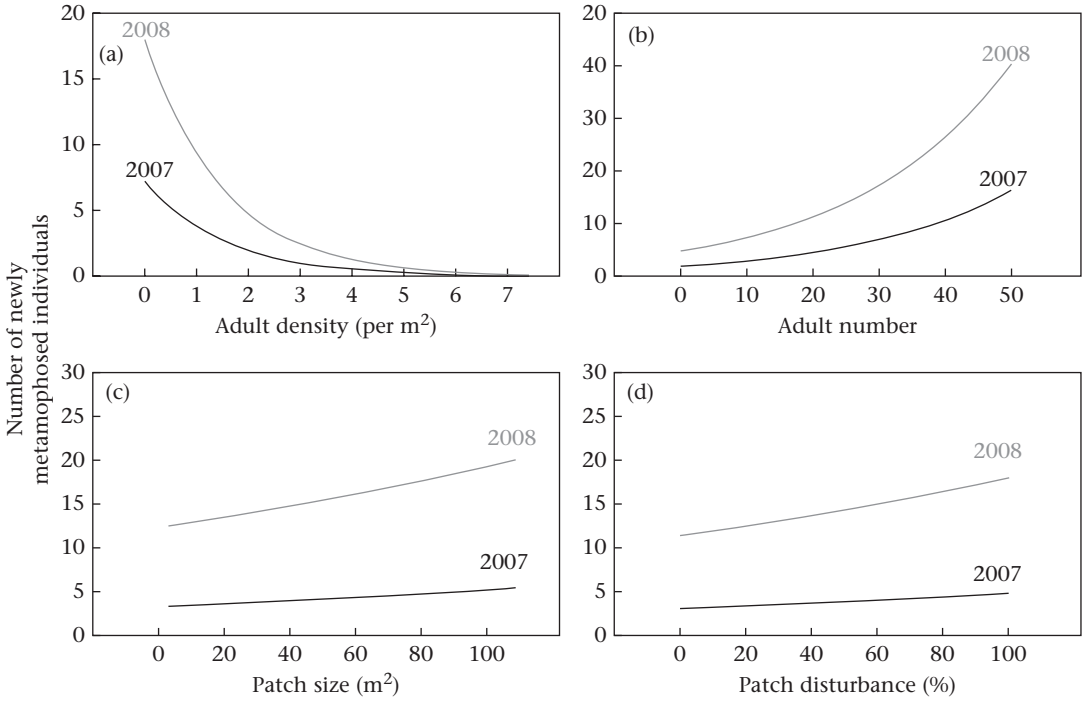


Figure 4. Influence of (a) the density and (b) the number of adults in attendance in a patch, (c) patch size and (d) the level of disturbance (the percentage of the patch's surface area disturbed by skidders) on breeding success, expressed by the number of newly metamorphosed individuals (in 2007 and 2008). The outputs of zero-inflated Poisson regression models are shown.

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disturbance on the number of newly metamorphosed individuals, taking the number of adults in the patch into account. The best-supported ZIP model [Ju ~ offset(log(1 + Ad)) + Di + Si + Y] had an AICc weight of 0.99 (see the complete model procedure in Appendix 1). The number of newly metamorphosed individuals was positively influenced by both patch size and patch disturbance (Fig. 4c and d). The number of newly metamorphosed individuals was also higher in 2008 than in 2007 (Fig. 4c and d). Note that these results were not affected when the variables 'Ad', 'Di', 'Si' and 'Y' were included in the binomial part of the model (see Appendix 1).

Influence of Patch Size and Disturbance on Dispersal

During the 9-year study period, we captured 744 toads. Of these, we identified 230 adults (120 males and 110 females). The number of individuals captured each year varied from 14 in 2004 to 103 in 2007 (for more details, see Appendix 2). We detected 64 dispersal events between successive capture sessions; 41 and 23 events were observed over the periods 2000–2005 and 2006–2008, respectively.

Concerning the influence of patch size on dispersal, the best-supported model was [ϕ(.), ψ(Si), α(Si), *p*(Si)]; the complete model selection procedure is provided in Appendix 2. As the AICc weight of this model was 0.13, we performed model averaging. Recapture varied according to patch size and between years: recapture probability was higher in small patches than in large ones. In small patches, recapture probability varied from 0.23 (95% CI 0.16–0.32) in 2003 to 0.59 (95% CI 0.51–0.66) in 2000, while in large patches it varied from 0.18 (95% CI 0.13–0.24) in 2003 to 0.50 (95% CI 0.44–0.57) in 2000. Sex-specific variation in recapture was marginal. In terms of survival, model-averaged estimates indicated that this did not vary according to patch size. Rather, the estimates suggested weak sex-specific variation in survival: males had a slightly lower survival probability (0.78, 95% CI 0.70–0.81) than females (0.80, 95% CI 0.76–0.86). More importantly, the analyses showed that dispersal depended on patch size (Fig. 5a). At both intra- and interannual levels, individuals had a higher probability of leaving a small patch than a large one. Intra-annually, the probability of an individual leaving a small patch was 0.19 (95% CI 0.14–0.27) in males and 0.16 (95% CI 0.10–0.21) in females; in contrast, in large patches it was 0.09 (95% CI 0.07–0.15) in males and 0.08 (95% CI 0.05–0.11) in females. We found the same pattern at the interannual level (Fig. 5). Furthermore, arrival probability also depended on patch size (Fig. 5b). Intra-annually, the proportion of individuals arriving in a large patch was 0.62 (95% CI 0.48–0.75) in males and 0.58 (95% CI 0.40–0.71) in females. At the interannual level, we detected a similar pattern: the proportion of individuals arriving in a large patch was 0.49 (95% CI 0.34–0.68) in males and 0.46 (95% CI 0.28–0.61) in females. These values were systematically far higher than those expected based on a random dispersal hypothesis (0.32 in males and females). The deviation of the estimated from the expected value was 94% in males and 81% in females at the intra-annual level; interannually, the deviation was 53% in males and 44% in females.

Concerning the influence of patch disturbance, the best-supported model was [ψ(Di), ϕ(S), α(Di), p(Y)]; the complete model-selection procedure is provided in Appendix 2. As the AICc weight of this model was 0.24, we performed model

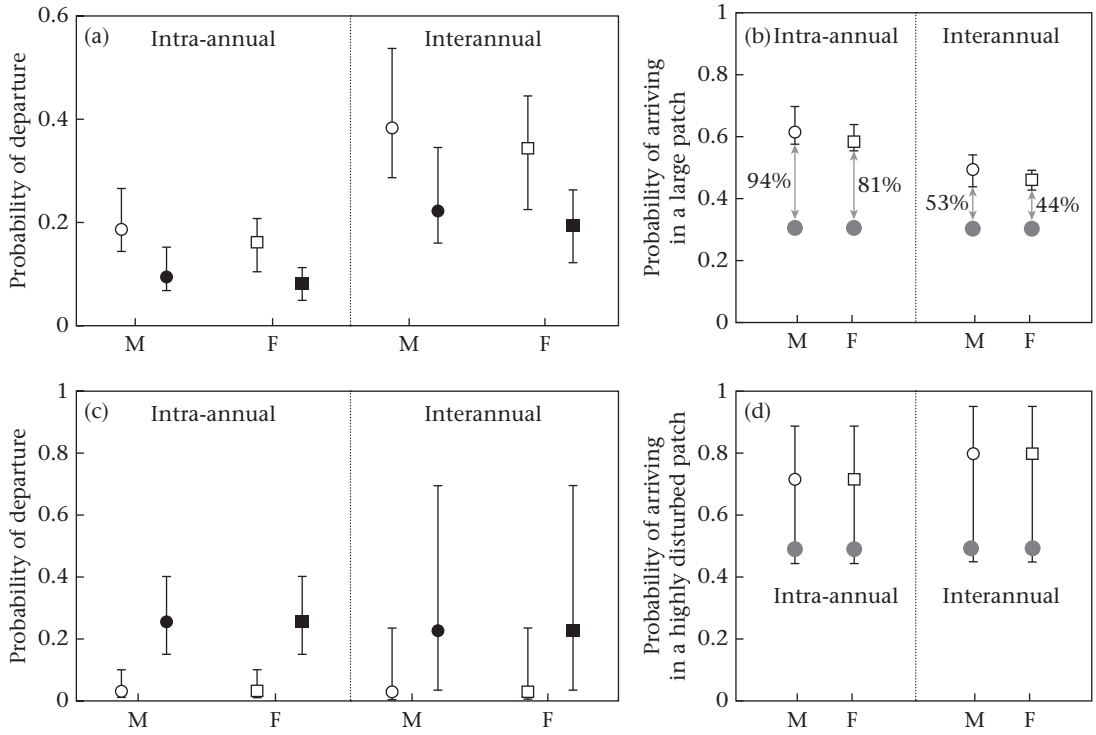


Figure 5. Influence of patch size and level of disturbance on dispersal of males (M) and females (F) intra-annually and interannually. (a) The departure probability of males (circles) and females (squares) in relation to patch size (empty circles and squares = small patch; full circles and squares = large patch). Error bars show the 95% CI. (b) The probability of arriving in a large patch (open circles) and the expected probability under a random dispersal hypothesis (grey circles). The percentages correspond to the deviation between the estimated and expected probabilities. (c) The departure probability of males (circles) and females (squares) in relation to the level of patch disturbance (empty circles and squares = patch with high disturbance; full circles and squares = patch with low disturbance). (d) The probability of arriving in a patch with high disturbance (open circles) and the expected probability under a random dispersal hypothesis (grey circles).

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averaging. The model-averaged estimates indicate that dispersal depended on the level of patch disturbance (Fig. 5c). Intra-annually, the probability of an individual leaving a patch with high disturbance was 0.03 (95% CI 0.01–0.10) in both males and females; in contrast, in patches with low disturbance it was 0.26 (95% CI 0.15–0.40) for both sexes. A similar pattern was detected at the interannual level. In contrast, arrival probability did not vary significantly according to patch disturbance (Fig. 5d). The 95% CI overlapped with the expected probability under random dispersal hypothesis. However, it is probable that this result is due to a lack of statistical power since the 95% CI was large (probably because we used a small subset for our analyses), while the deviation between estimated probability and expected probability (0.44 in males and females) was wide. Intra-annually, the proportion of individuals arriving in a patch with high disturbance was 0.71 (95% CI 0.44–0.88) in males and females. At the interannual level, the proportion of individuals arriving in a patch with high disturbance was 0.79 (95% CI 0.45–0.95) in both sexes. The deviation of the estimated from the expected value was 61% intra-annually; at the interannual level, the deviation was 80%.

DISCUSSION

Our findings revealed that the probability of successful reproduction of *B. variegata* increased with patch size. In addition, the number of newly metamorphosed individuals was positively influenced by patch size and the level of disturbance. Furthermore, the results showed that the patch-specific factors affecting breeding success also influenced breeding dispersal. Emigration probability was negatively influenced by larger patch size; in contrast, larger patch size positively influenced immigration probability. Equally, a higher level of breeding patch disturbance (measured by the percentage of surface area of the patch disturbed each year) had a strong negative influence on emigration probability.

Influence of Patch Size and Disturbance on Breeding and Fitness

The findings showed that the occurrence probability of newly metamorphosed individuals was higher in large patches than in small patches. We also found that the number of metamorphosed individuals increased with the number of adults in attendance in a breeding patch, which was positively correlated with patch size. Yet the analyses showed that the number of newly metamorphosed individuals still increased with patch size even after controlling for the number of adults in a patch. This indicates that patch size affects local breeding success regardless of breeder abundance. This might be explained in two ways. First, reproducing in a large patch with extensive breeding resources may reduce intraspecific larval competition and increase breeding success. However, an increase in reproductive success remains conditional on the local population density, since our results found that the number of newly metamorphosed individuals decreased with the density of breeding adults per m^2 (Appendix 1). A high density of adults in a patch is likely to increase larval density and competition, which negatively affects tadpole growth and survival (Jasieński, 1988). Second, large patches contain more breeding ponds than small ones. In *B. variegata*, females usually spread their egg capital over several clutches deposited in different waterbodies that often vary in temperature, hydroperiod and trophic resources (Barandun, Reyer, & Anholt, 1997). This egg-spreading behaviour is often regarded as a bet-hedging tactic to reduce the risk of reproduction failure in the face of hydric instability of waterbodies (Barandun et al., 1997; Buschmann, 2002).

The probability of the occurrence and the number of newly metamorphosed individuals increased with the proportion of the surface area of the waterbody disturbed by skidders; this increase was nevertheless marginal for the probability of successful reproduction, which may be due to the intrinsic roughness of the occurrence data, the limited survey length and the small number of breeding patches (28) in the study area. This result is congruent with previous studies highlighting that the occurrence of *B. variegata* reproduction is associated with aquatic habitats disturbed by human activity (Canessa et al., 2013; Warren & Büttner, 2008). In particular, Warren and Büttner (2008) found that *B. variegata* preferentially occupied and bred in waterbodies whose ground surface area disturbed by vehicle passage ranged from 40% to 100%. By deepening ruts and increasing ground compaction (Ampoorter et al., 2010; Wronski & Murphy, 1994), skidders limit the natural silting of waterbodies and increase their water-holding capacities, thus decreasing their risk of drying out. By reproducing in patches that include waterbodies with a longer hydroperiod, individuals can therefore mitigate the risks of breeding failure caused by desiccation, which is the main mortality factor at larval stage (Barandun & Rever 1997; Barandun et al., 1997).

Influence of Patch Size and Disturbance on Dispersal

We found that patch-specific factors influencing local breeding success also affected emigration and immigration probabilities. First, individuals were less likely to emigrate from large patches (where breeding success was highest) than from small ones; similarly, individuals were more likely to immigrate to large patches. Second, individuals had a lower probability of emigrating from patches experiencing a higher level of disturbance (defined by 42–100% of the patch's surface area disturbed annually by skidders), where breeding success was highest, than from patches with a low level of disturbance (0–41% of the surface area disturbed). The effect of disturbance was marginal on immigration probability. Collecting capture–recapture data over a longer survey period (e.g. 4–5 years) would certainly permit us to clarify the effect of disturbance on dispersal parameters and strengthen our conclusions about context-dependent dispersal.

Overall, the asymmetric dispersal rates reported in this study indicate that individuals adjust their dispersal decisions according to breeding patch characteristics, probably basing their choices on environmental and/or social signals that provide valuable information about local fitness prospects. This conclusion is in accordance with a recent study showing that *B. variegata* individuals were less likely to leave waterbodies where the risk of drying out is low, thus favouring successful and constant reproduction over time (Tournier et al., 2017). In anurans, individuals use olfactory cues to locate ponds and evaluate their quality for breeding (Semlitsch, 2008; Sinsch, 1990), behaviour that has also been observed in *B. variegata* (Cayuela, Lengagne, Joly, & Léna, 2017; Cayuela, Lengagne, Kaufmann, Joly, & Léna, 2016). This behavioural mechanism probably allows individuals to assess their chances of breeding success in a patch and then to decide where to breed.

Conclusion

The results of this study highlight that patch size and the level of disturbance affect the chances of reproductive success in *B. variegata*. They also suggest that breeders adjust their dispersal decisions according to local fitness prospects. In early successional organisms, a plastic response to dispersal is likely to permit rapid adjustment to progressive changes in environmental conditions resulting from the ecological succession process. This results in

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nonrandom dispersal between patches, which would be expected to have dramatic consequences on the demography of spatially structured populations by affecting local recruitment and population size. In addition, nonrandom dispersal is likely to drive the direction and intensity of gene flow and could thus influence evolutionary processes in a patch by affecting the effective population size, the effects of genetic drift and the effectiveness of selection. Future studies could help gain a better understanding of the eco-evolutionary dynamics shaping the demography and the evolution of early successional species.

Acknowledgments

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APPENDIX 1. ADULT ABUNDANCE, BREEDING OCCURRENCE AND BREEDING SUCCESS ANALYSES

Relationships Between Reproduction and Patch Size and Disturbance

To investigate the influence of patch size and disturbance level on breeding occurrence, we used multistate occupancy models (Gimenez et al., 2014; Nichols et al., 2007). We present the matrices of the model (Fig. A1) as formulated in Gimenez et al. (2014). The model selection procedure is presented in Table A1.

Relationships Between Adult Abundance and Patch Size and Disturbance

We used zero-inflated Poisson regression models to analyse how patch size and disturbance affected adult abundance. The number of adults captured annually in each patch was corrected by the recapture probability (i.e. Horvitz–Thompson estimator) estimated by CR multievent models for 2007 and 2008, i.e. 0.45 and 0.46, respectively. The number of adults recorded each year was treated as the dependent variable. In the Poisson regression part of the model, the patch size (Si), the proportion of waterbody surface disturbed by skidders (Di) and the year (Y; 2007, 2008) were introduced as explanatory terms (Count ~ Si + Di + Y). Si and Di were treated as continuous variables and were z-scored. The three explanatory variables were entered in the model in an additive way. We ranked models using AICc and AICc weights. Normality of the residuals of the best-supported model was examined graphically using a quantile–quantile plot.

The complete model procedure is provided in Table A2. The best-supported (Count ~ Si + Di + Y) had an AICc weight of 0.90. Our analysis revealed that adult number increased with patch size (slope coefficient: 0.39 ± 0.03) and disturbance (slope coefficient: 0.33 ± 0.04). Adult number was also slightly higher in 2008 (slope coefficient: 0.19 ± 0.07).

Relationships Between Successful Breeding and Patch Size and Disturbance

We analysed the influence of patch size and disturbance on the number of newly metamorphosed individuals using zero-inflated Poisson regression models. In Table A3, we present the model selection procedure. In Table A4, we compare the outputs of two models: a model including the following effects in the Poisson component only: offset(log(1 + Ad)) + Di + Si + Y; and another model in which these effects are incorporated in both the Poisson and binomial components of the model. Our results indicate that the effects of Di, Si and Y are nonsignificant in the binomial component of the model. They also indicate that the estimates of the Poisson component are not affected by the inclusion of these effects in the binomial part of the model.

We also investigated how adult number and density influenced the number of newly metamorphosed individuals using zero-inflated Poisson regression models (Table A5).

APPENDIX 2. CAPTURE-RECAPTURE DATA AND MODEL SELECTION PROCEDURES

In this Appendix, we present addition information about the capture–recapture survey (annual variation in numbers of captures, individuals identified and secondary capture sessions in the spatially structured population); see Table A6. We also provide the model selection procedure for the effect of patch size (Table A7) and disturbance (Table A8) on dispersal.

Table A1
Influence of patch size and disturbance on noneffective (i.e. egg and larvae without newly metamorphosed individuals) and successful breeding (newly metamorphosed individuals): model selection procedure

Model rank	Model	*k*	Deviance	AICc	*w*
1	ψ1,2(Si), *p*1,2(.)	6	190.51	203.60	0.58
2	ψ1,2(Si+Di), *p*1,2(.)	7	189.81	205.29	0.24
3	ψ1,2(Si), *p*1,2(Y)	7	190.32	205.79	0.19
4	ψ1,2(Si+Di), *p*1,2(Y)	8	189.62	207.54	0.08
5	ψ1,2(.), *p*1,2(.)	5	202.80	213.57	0.00
6	ψ1,2(Di), *p*1,2(.)	6	200.59	213.68	0.00
7	ψ1,2(Di), *p*1,2(Y)	7	200.39	215.86	0.00
8	ψ1,2(.), *p*1,2(Y)	6	202.60	215.69	0.00

The model includes four biological parameters: probability of noneffective reproduction ψ1, probability of successful reproduction ψ2, probability of detecting eggs and/or larvae *p*1 and probability of detecting newly metamorphosed individuals *p*2. *k* = number of parameters, deviance = residual deviance, AICc = Akaike information criterion adjusted for small sample size, *w* = AICc weights, Si = patch size, Di = proportion of waterbody surface disturbed by skidders, Y = year.

Table A2
Influence of adult number and density on the number of newly metamorphosed individuals (Count): model selection procedure

Model rank	Model	*k*	AICc	*w*
1	Count~Si+Di+Y	5	433.30	0.90
2	Count~Si+Di	4	437.67	0.10
3	Count~Si	4	500.85	0.00
4	Count~Si+Y	4	500.89	0.00
5	Count~Di+Y	3	609.43	0.00
6	Count~Di	3	613.12	0.00
7	Count~Y	3	690.97	0.00
8	Count~1	2	692.12	0.00

k = number of parameters, AICc = Akaike information criterion adjusted for small sample size, *w* = AICc weights, Si = patch size, Di = proportion of waterbody surface disturbed by skidders, Y = year.

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Table A3
Influence of patch size (Si) and disturbance (Di) on the number of newly metamorphosed individuals (Ju): model selection procedure

Model rank	Model	*k*	AICc	*w*
1	Ju~offset(log(1+Ad))+Di+Si+Y	5	413.89	0.99
2	Ju~offset(log(1+Ad))+Si+Y	4	423.17	0.01
3	Ju~offset(log(1+Ad))+Si	3	487.56	0.00
4	Ju~offset(log(1+Ad))+Di+Si	4	488.83	0.00
5	Ju~offset(log(1+Ad))+Di+Y	4	505.60	0.00
6	Ju~offset(log(1+Ad))+Y	3	507.79	0.00
7	Ju~offset(log(1+Ad))+Di	3	573.01	0.00
8	Ju~offset(log(1+Ad))	2	573.27	0.00

k = number of parameters, AICc = Akaike information criterion adjusted for small sample size, *w* = AICc weights, Ad = number of adults, Si = patch size, Di = proportion of waterbody surface disturbed by skidders, Y = year.

Table A4
Outputs of the zero-inflated models

Poisson component	Estimate	SE	*z*	*P*
Model with no effect on the binomial component				
Intercept	2.54	0.06	42.65	<0.0001
Si	0.39	0.03	14.67	<0.0001
Di	0.33	0.04	8.30	<0.0001
Y	0.19	0.07	2.52	0.01
Model with effect on the binomial component				
Poisson component				
Intercept	2.54	0.06	42.65	<0.0001
Si	0.39	0.03	14.67	<0.0001
Di	0.33	0.04	8.30	<0.0001
Y	0.19	0.07	2.52	0.01
Binomial component				
Intercept	−2.57	0.81	−3.17	0.001
Si	−0.65	0.91	−0.72	0.47
Di	0.30	0.52	0.57	0.56
Y	0.05	1.06	0.05	0.96

We compare the outputs of two models: a model including the following effects in the Poisson component only: offset(log(1+Ad)) + Di + Si + Y; and another model in which these effects are incorporated in both the Poisson and binomial components of the model.

Table A5
Influence of adult number (Ad) and density (De) on the number of newly metamorphosed individuals (Ju): model selection procedure

Model rank	Model	*k*	AICc	*w*
1	Ju~Ad+De+Y	5	397.63	0.99
2	Ju~Ad+Y	4	412.38	0.01
3	Ju~Ad+De	4	438.57	0.00
4	Ju~Ad	3	446.11	0.00
5	Ju~De+Y	4	499.32	0.00
6	Ju~Y	3	507.79	0.00
7	Ju~De	3	571.20	0.00
8	Ju~1	2	573.27	0.00

k = number of parameters, AICc = Akaike information criterion adjusted for small sample size, *w* = AICc weights, Ad = number of adults, De = adult density, Y = year.

Table A6
Annual variation in numbers of captures, individuals and secondary sessions identified in the spatially structured population

Year	Number of captures	Number of females identified	Number of males identified	Number of secondary sessions
2000	142	36	31	6
2001	195	44	47	4
2002	169	36	34	4
2003	37	12	18	4
2004	14	5	9	1
2005	16	7	9	1
2006	59	23	23	3
2007	176	43	60	3
2008	167	41	59	3

Table A7
Influence of patch size on dispersal: model selection procedure

Model rank	Model	*k*	Deviance	AICc	*w*
1	φ(.), ψ(Si), α(Si), *p*(Si+Y)	16	3749.97	3782.54	0.13
2	φ(S), ψ(Si), α(Si), *p*(Si+Y)	17	3747.98	3782.62	0.12
3	φ(.), ψ(Si+S), α(Si+S), *p*(Si+Y)	18	3746.70	3783.42	0.08
4	φ(S), ψ(Si+S), α(Si+S), *p*(Si+Y)	19	3744.75	3783.55	0.08
5	φ(.), ψ(Si), α(Si), *p*(Si+S+Y)	17	3749.10	3783.74	0.07
6	φ(S), ψ(Si), α(Si), *p*(Si+S+Y)	18	3747.38	3784.10	0.06
7	φ(Si), ψ(Si), α(Si), *p*(Si+Y)	17	3749.87	3784.51	0.05
8	φ(Si+S), ψ(Si), α(Si), *p*(Si+Y)	18	3747.80	3784.52	0.05
9	φ(.), ψ(Si+S), α(Si+S), *p*(Si+S+Y)	19	3745.87	3784.66	0.04
10	φ(S), ψ(Si+S), α(Si+S), *p*(Si+S+Y)	20	3744.18	3785.06	0.04
11	φ(Si), ψ(Si+S), α(Si+S), *p*(Si+Y)	19	3746.61	3785.40	0.03
12	φ(Si+S), ψ(Si+S), α(Si+S), *p*(Si+Y)	20	3744.60	3785.48	0.03
13	φ(Si), ψ(Si), α(Si), *p*(Si+S+Y)	18	3749.00	3785.72	0.03
14	φ(Si+S), ψ(Si), α(Si), *p*(Si+S+Y)	19	3747.22	3786.02	0.02
15	φ(.), ψ(Si), α(Si), *p*(Y)	15	3755.71	3786.21	0.02
16	φ(S), ψ(Si), α(Si), *p*(Y)	16	3753.70	3786.27	0.02
17	φ(Si), ψ(Si+S), α(Si+S), *p*(Si+S+Y)	20	3745.78	3786.66	0.02
18	φ(Si+S), ψ(Si+S), α(Si+S), *p*(Si+S+Y)	21	3744.05	3787.01	0.01
19	φ(.), ψ(Si+S), α(Si+S), *p*(Y)	17	3752.48	3787.12	0.01
20	φ(S), ψ(Si+S), α(Si+S), *p*(Y)	18	3750.47	3787.18	0.01
21	φ(.), ψ(Si), α(Si), *p*(S+Y)	16	3755.10	3787.67	0.01
22	φ(Si+S), ψ(Si), α(Si), *p*(Y)	17	3753.30	3787.94	0.01
23	φ(S), ψ(Si), α(Si), *p*(S+Y)	17	3753.32	3787.96	0.01
24	φ(Si), ψ(Si), α(Si), *p*(Y)	16	3755.43	3788.00	0.01
25	φ(.), ψ(Si+S), α(Si+S), *p*(S+Y)	18	3751.87	3788.58	0.01
26	φ(S), ψ(Si+S), α(Si+S), *p*(S+Y)	19	3750.08	3788.88	0.01
27	φ(Si+S), ψ(Si+S), α(Si+S), *p*(Y)	19	3750.10	3788.90	0.01
28	φ(Si), ψ(Si+S), α(Si+S), *p*(Y)	18	3752.20	3788.92	0.01
29	φ(Si), ψ(Si), α(Si), *p*(S+Y)	17	3754.82	3789.46	0.00
30	φ(Si+S), ψ(Si), α(Si), *p*(S+Y)	18	3752.93	3789.64	0.00
31	φ(Si), ψ(Si+S), α(Si+S), *p*(S+Y)	19	3751.59	3790.39	0.00
32	φ(Si+S), ψ(Si+S), α(Si+S), *p*(S+Y)	20	3749.72	3790.61	0.00
33	φ(.), ψ(.), α(Si), *p*(Si+Y)	15	3762.18	3792.68	0.00
34	φ(S), ψ(.), α(Si), *p*(Si+Y)	16	3760.18	3792.75	0.00
35	φ(.), ψ(S), α(Si+S), *p*(Si+Y)	17	3758.27	3792.91	0.00
36	φ(S), ψ(S), α(Si+S), *p*(Si+Y)	18	3756.30	3793.02	0.00
37	φ(.), ψ(.), α(Si), *p*(Si+S+Y)	16	3761.38	3793.95	0.00
38	φ(.), ψ(.), α(Si), *p*(Y)	14	3765.65	3794.09	0.00
39	φ(S), ψ(.), α(Si), *p*(Y)	15	3763.64	3794.14	0.00
40	φ(.), ψ(S), α(Si+S), *p*(Si+S+Y)	18	3757.48	3794.20	0.00
41	φ(S), ψ(.), α(Si), *p*(Si+S+Y)	17	3759.64	3794.28	0.00
42	φ(.), ψ(S), α(Si+S), *p*(Y)	16	3761.85	3794.42	0.00
43	φ(S), ψ(S), α(Si+S), *p*(Y)	17	3759.84	3794.48	0.00
44	φ(S), ψ(S), α(Si+S), *p*(Si+S+Y)	19	3755.78	3794.57	0.00
45	φ(Si), ψ(.), α(Si), *p*(Si+Y)	16	3762.15	3794.72	0.00
46	φ(Si+S), ψ(.), α(Si), *p*(Si+Y)	17	3760.10	3794.74	0.00
47	φ(Si), ψ(S), α(Si+S), *p*(Si+Y)	18	3758.24	3794.95	0.00
48	φ(Si+S), ψ(S), α(Si+S), *p*(Si+Y)	19	3756.24	3795.03	0.00
49	φ(.), ψ(.), α(Si), *p*(S+Y)	15	3765.04	3795.54	0.00
50	φ(S), ψ(.), α(Si), *p*(S+Y)	16	3763.26	3795.83	0.00
51	φ(.), ψ(S), α(Si+S), *p*(S+Y)	17	3761.24	3795.88	0.00
52	φ(Si+S), ψ(.), α(Si), *p*(Y)	16	3763.42	3795.99	0.00
53	φ(Si), ψ(.), α(Si), *p*(Si+S+Y)	17	3761.35	3795.99	0.00
54	φ(Si), ψ(.), α(Si), *p*(Y)	15	3765.52	3796.02	0.00
55	φ(S), ψ(S), α(Si+S), *p*(S+Y)	18	3759.45	3796.17	0.00
56	φ(Si), ψ(S), α(Si+S), *p*(Si+S+Y)	19	3757.45	3796.25	0.00
57	φ(Si+S), ψ(.), α(Si), *p*(Si+S+Y)	18	3759.57	3796.29	0.00
58	φ(Si+S), ψ(S), α(Si+S), *p*(Y)	18	3759.64	3796.35	0.00
59	φ(Si), ψ(S), α(Si+S), *p*(Y)	17	3761.71	3796.35	0.00
60	φ(Si+S), ψ(S), α(Si+S), *p*(Si+S+Y)	20	3755.72	3796.60	0.00
61	φ(Si), ψ(.), α(Si), *p*(S+Y)	16	3764.91	3797.48	0.00
62	φ(Si+S), ψ(.), α(Si), *p*(S+Y)	17	3763.04	3797.68	0.00
63	φ(Si), ψ(S), α(Si+S), *p*(S+Y)	18	3761.10	3797.82	0.00
64	φ(Si+S), ψ(S), α(Si+S), *p*(S+Y)	19	3759.26	3798.05	0.00

The model includes four biological parameters: survival ϕ, departure ψ, arrival α and the recapture *p*. *k* = number of parameters, deviance = residual deviance, AICc = Akaike information criterion adjusted for small sample size, *w* = AICc weights, Si = patch size, S = sex, Y = year.

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Table A8
Influence of patch disturbance on dispersal: model selection procedure

Model rank	Model	*k*	Deviance	AICc	*w*
1	ψ(Di), φ(S), α(Di), *p*(Y)	12	1101.42	1126.37	0.24
2	ψ(Di), φ(S), α(Di), *p*(S+Y)	13	1099.46	1126.57	0.22
3	ψ(Di), φ(.), α(Di), *p*(Y)	11	1104.52	1127.32	0.15
4	ψ(Di), φ(S), α(Di), *p*(Di+Y)	13	1101.40	1128.52	0.08
5	ψ(Di), φ(S), α(Di), *p*(Di+S+Y)	14	1099.41	1128.70	0.07
6	ψ(Di), φ(.), α(Di), *p*(S+Y)	12	1104.25	1129.20	0.06
7	ψ(Di), φ(.), α(Di), *p*(Di+Y)	12	1104.48	1129.44	0.05
8	ψ(Di+S), φ(S), α(Di+S), *p*(Y)	14	1101.22	1130.51	0.03
9	ψ(Di+S), φ(S), α(Di+S), *p*(S+Y)	15	1099.26	1130.74	0.03
10	ψ(Di), φ(.),α(Di), *p*(Di+S+Y)	13	1104.19	1131.30	0.02
11	ψ(Di+S), φ(.), α(Di+S), *p*(Y)	13	1104.32	1131.44	0.02
12	ψ(Di+S), φ(S), α(Di+S), *p*(Di+Y)	15	1101.22	1132.69	0.01
13	ψ(Di+S), φ(S), α(Di+S), *p*(Di+S+Y)	16	1099.23	1132.91	0.01
14	ψ(Di+S), φ(.), α(Di+S), *p*(S+Y)	14	1104.06	1133.35	0.01
15	ψ(Di+S), φ(.), α(Di+S), *p*(Di+Y)	14	1104.29	1133.58	0.01
16	ψ(Di+S), φ(.), α(Di+S), *p*(Di+S+Y)	15	1104.00	1135.48	0.00
17	ψ(.), φ(S), α(Di), *p*(Y)	11	1116.49	1139.29	0.00
18	ψ(.), φ(S), α(Di), *p*(S+Y)	12	1114.53	1139.48	0.00
19	ψ(.),φ(.), α(Di), *p*(Y)	10	1119.59	1140.26	0.00
20	ψ(.), φ(S), α(Di), *p*(Di+Y)	12	1115.66	1140.62	0.00
21	ψ(.), φ(S), α(Di), *p*(Di+S+Y)	13	1113.89	1141.01	0.00
22	ψ(.), φ(.), α(Di), *p*(Di+Y)	11	1118.94	1141.74	0.00
23	ψ(.), φ(.), α(Di), *p*(S+Y)	11	1119.32	1142.13	0.00
24	ψ(S), φ(S), α(Di+S), *p*(Y)	13	1115.87	1142.98	0.00
25	ψ(S), φ(S), α(Di+S), *p*(S+Y)	14	1113.91	1143.20	0.00
26	ψ(.), φ(.), α(Di), *p*(Di+S+Y)	12	1118.78	1143.73	0.00
27	ψ(S), φ(.), α(Di+S), *p*(Y)	12	1118.97	1143.92	0.00
28	ψ(S),φ(S), α(Di+S), *p*(Di+Y)	14	1114.92	1144.21	0.00
29	ψ(S), φ(S), α(Di+S), *p*(Di+S+Y)	15	1113.19	1144.66	0.00
30	ψ(S), φ(.), α(Di+S), *p*(Di+Y)	13	1118.30	1145.41	0.00
31	ψ(S), φ(.), α(Di+S), *p*(S+Y)	13	1118.71	1145.82	0.00
32	ψ(S), φ(.), α(Di+S), *p*(Di+S+Y)	14	1118.15	1147.44	0.00

The model includes four biological parameters: survival ϕ, departure ψ, arrival and patch dynamics α and recapture *p*. *k* = number of parameters, deviance = residual deviance, AICc = Akaike information criterion adjusted for small sample size, Si = patch size, S = sex, Y = year.

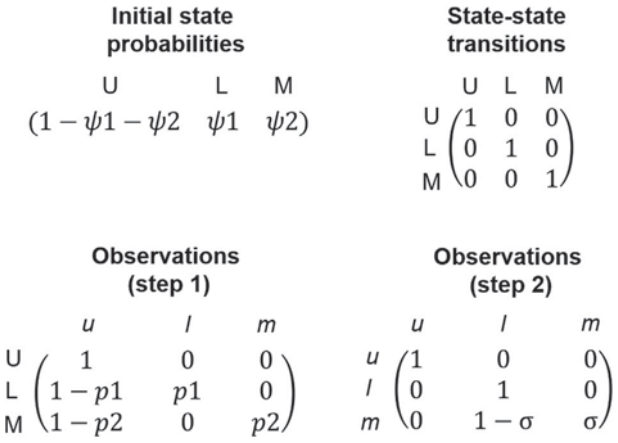


Figure A1. Modelling breeding success using occupancy models. The model is composed of three pieces of information: (1) initial states probabilities, which include the parameters of interest, ψ1 the probability of noneffective reproduction occurrence and ψ2 the probability of successful reproduction occurrence; (2) state-state transitions (probabilities set at 1); and (3) field observations (steps 1 and 2). Three states are considered in the model: a site can be unoccupied for breeding (U), occupied with a noneffective reproduction (i.e. presence of eggs and larvae, L) or occupied with a successful reproduction (i.e. presence of newly metamorphosed individuals, M). The field observations are: undetected (*u*), eggs and/or larvae detected (*l*) and newly metamorphosed individuals detected (*m*).

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Boualit, L., Pichenot, J., Besnard, A., Helder, Joly, P., Cayuela, H. (2019). Environmentally mediated reproductive success predicts breeding dispersal decisions in an early successional amphibian. Animal Behaviour, 149, 107-120. , DOI : 10.1016/j.anbehav.2019.01.008