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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, 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).

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.

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

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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, & Holooyak, 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 a higher diversity of species and 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; Kopecky, Vojar, & Denoel, 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 anthropogenic 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 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 (Amoorter, Van Nevel, De Vos, Henmy, & Verheyen, 2010; Wrósni & 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 (2000–2009) 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
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 m² to 107.67 m² (mean = 23.99 m², SD = 22.33 m²). 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 length).
length) of 36 mm in males and 37 mm in females; smaller indi-
viduals were excluded from the analysis. The sex was assessed on
the basis of strong forearms with nuptial pads in males. We iden-
tified 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 pat-
terns 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 meta-
morphosed 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, Mackenize, 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 meta-
morphosis success: L) or occupied with successful reproduction (i.e.
presence of newly metamorphosed individuals: M). The observa-
tions 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 in-
formation (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 ($p_1$), and the probability that a site is occupied with
successful reproduction ($p_2$). (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 suc-
cessive 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 ($p_1$) and the other of newly metamorphosed individuals ($p_2$). The second matrix (Appendix 1) specified the probability of
successful reproduction conditional on these intermediate obser-
vations. 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 aver-
aging. We tested our hypotheses from the general model,
$[p_1,2(\text{Di} + \text{Si}), \ p_1,2(Y)]$, which included three variables: the pro-
portion of the surface area of a waterbody disturbed by skidders
($\text{Di}$, a continuous variable), the size of the patch ($\text{Si}$, a continuous
variable) and a year effect ($Y$, a discrete variable with two modal-
ities, 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 ($p_1$ and $p_2$) 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 suc-
cessfully metamorphosed in the breeding patch. As newly meta-
morphosed 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 meta-
morphosed 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 m²
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 vari-
bles (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: [$Ju = \text{offset}(log(1 + Ad)) + Di + \text{Si} + Y$]. 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 com-
binations of effects.

Modelling the Influence of Patch Size on Dispersal

To test the effect of patch size on dispersal, we used CR multi-
event 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 char-
acteristics. 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 n2. 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 (S for ‘captured’, o for ‘not captured’). In addition, we added a state designation to include the category of patch previously occupied: an individual can occupy one of two patch categories (S ‘small’ or L ‘large’). A small patch ranged from 2.5 m² to 23 m² and a large patch from 23 m² to 108 m². 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 oM1 or oL1. 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) recapture 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 e or die with a probability of 1 − e (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 p or stay in the same patch with a probability of 1 − p (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 − a or in a large patch (L) with a probability of a (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 r or not captured with a probability of 1 − r (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., 2005), 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 AIC weights. When the AICc weight of the best-supported model was less than 0.9, we performed model averaging. The 95% confidence intervals, CI’s, of model-averaged parameters were calculated using the parametric bootstrap method. Our hypotheses regarding recapture and state–state transition probabilities were examined

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The state formulation includes four types of information: i = captured or o = not captured at previous occasion, S = stayed or M = moved, s = small patch or l = large patch, a = captured or o = not captured at current occasion. Note that the patch disturbance model used the same states as those presented here except that y (small) and Y (large) were replaced by l = low disturbance and h = high disturbance.
using the general model \( [\psi(S_i + S), \psi(S_i' + S), \alpha(S_i + S), \gamma(Y + S_i + S)] \), which included three effects: (1) patch size (S), 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 \( t \) 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 \( j \) or remain in the same patch occupied at \( t \) with a probability of 1 – j. The departure could be made dependent on the category of patch occupied at \( t \). This led to a transition matrix with 13 states of departure and nine intermediate states of arrival (Fig. 3).

When an individual moved, it could occupy a site that changed state (l ↔ h) between \( t \) and \( t \) with a probability of \( a \), or a site that remained in the same state with a probability of 1 – a (Fig. 3). When an individual moved, it could occupy a site that changed state (l ↔ h) between \( t \) and \( t \) with a probability of \( a \), or a site that remained in the same state with a probability of 1 – a (Fig. 3). When an individual moved, it could
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arrive in a site of a different category (l or h) than the one previously occupied with a probability of $x$ or in the same type of site with a probability of $1 - x$ (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 $\psi$, survival $\phi$, arrival $a$ and recapture $p$ were examined using the general model $\{j(Di + S), f(S), a(Di + S), p(Y + Di + S)\}$, 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

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 $\psi$ (step 1), survival probability $\phi$ (step 2), probability of arrival and patch state change $a$ (step 3) and recapture probability $p$ (step 4).

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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 *Bufo variegatus* 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 *Bufo variegatus* (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 \( p(1,2,\cdot) \). The detection probability of breeding indices (eggs and tadpoles) was 0.96 (95% CI 0.80–0.97); for newly metamorphosed individuals it was 0.93 (95% CI 0.83–0.97). The best-supported model was \( p(1,2,\cdot) \); 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 \( J_u \sim Ad + De + Y \) 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 m² of the patch (Fig. 4a and b). We then analysed the effects of patch size and

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**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.
disturbance on the number of newly metamorphosed individuals, taking the number of adults in the patch into account. The best-supported ZIP model \([\psi(S) \cdot \text{offset}(\log(1 + Ad)) + \text{Di} + Si + Y]\) 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 \([\psi(S) \cdot \text{offset}(\log(1 + Ad)) + \text{Di} + Si + Y]\); 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. 5). 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 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 \([\psi(Di) + \phi(S) + \alpha(Di) + \phi(Y)]\); the complete model-selection procedure is provided in Appendix 2. As the AICc weight of this model was 0.24, we performed model

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**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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The results showed that the 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 (Seminitsch, 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...
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 successive species.

Acknowledgments

We warmly thank all the fieldworkers who assisted in data collection. This research project was funded by the Lorraine Direction Régionale de l’Environnement, de l’Aménagement et du Logement (DREAL), the Agence de l’Eau Rhin-Meuse, the Conseil Régional de Lorraine, the Conseil Régional de Champagne-Ardenne, the Conseil Régional de Picardie, the Conseil Général de l’Aisne, the Conseil Général d’Ardèche, the Conseil Général d’Isère and the Communauté de Communes de l’Argonne Ardennoise (2CZA).

References

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.

Table A1

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>Deviance</th>
<th>AICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\phi(1,2)(p,1,2,1)$</td>
<td>190.51</td>
<td>203.60</td>
<td>0.58</td>
</tr>
<tr>
<td>2</td>
<td>$\phi(1,2,3)(p,1,2,1)$</td>
<td>189.81</td>
<td>205.29</td>
<td>0.24</td>
</tr>
<tr>
<td>3</td>
<td>$\phi(1,2)(p,1,2,2)$</td>
<td>190.32</td>
<td>205.79</td>
<td>0.19</td>
</tr>
<tr>
<td>4</td>
<td>$\phi(1,2,3)(p,1,2,2)$</td>
<td>189.62</td>
<td>207.54</td>
<td>0.08</td>
</tr>
<tr>
<td>5</td>
<td>$\phi(1,2,3)(p,1,2,1)$</td>
<td>202.80</td>
<td>213.57</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>$\phi(1,2,3)(p,1,2,2)$</td>
<td>200.59</td>
<td>213.68</td>
<td>0.00</td>
</tr>
<tr>
<td>7</td>
<td>$\phi(1,2,3)(p,1,2,2)$</td>
<td>200.39</td>
<td>215.86</td>
<td>0.00</td>
</tr>
<tr>
<td>8</td>
<td>$\phi(1,2,3)(p,1,2,2)$</td>
<td>200.60</td>
<td>215.69</td>
<td>0.00</td>
</tr>
</tbody>
</table>

The model includes four biological parameters: probability of nonselective reproduction $\phi$; probability of successful reproduction $\phi_s$; probability of detecting eggs and/or larvae $p_t$ and probability of detecting newly metamorphosed individuals $p_d$. $k$ = number of parameters, deviance $- \text{residual deviance}$, AICc $- \text{Akaike information criterion}$ adjusted for small sample size, $\text{w}$ = probability of detecting newly metamorphosed individuals.

APPENDIX 2. CAPTURE-RECAPTURE DATA AND MODEL SELECTION PROCEDURES

In this Appendix, we present additional 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 A2

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>$k$</th>
<th>AICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Count–Si + Di + Y</td>
<td>5</td>
<td>433.30</td>
<td>0.90</td>
</tr>
<tr>
<td>2</td>
<td>Count–Si + Di</td>
<td>4</td>
<td>437.67</td>
<td>0.10</td>
</tr>
<tr>
<td>3</td>
<td>Count–Si</td>
<td>4</td>
<td>500.85</td>
<td>0.00</td>
</tr>
<tr>
<td>4</td>
<td>Count–Si + Y</td>
<td>4</td>
<td>500.89</td>
<td>0.00</td>
</tr>
<tr>
<td>5</td>
<td>Count–Di + Y</td>
<td>3</td>
<td>609.43</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>Count–Di</td>
<td>3</td>
<td>613.12</td>
<td>0.00</td>
</tr>
<tr>
<td>7</td>
<td>Count–Y</td>
<td>3</td>
<td>690.97</td>
<td>0.00</td>
</tr>
<tr>
<td>8</td>
<td>Count–1</td>
<td>2</td>
<td>692.12</td>
<td>0.00</td>
</tr>
</tbody>
</table>

$k$ = 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.
We compare the outputs of two models: a model including the following effects in Table A6: morphosed individuals (Ju): model selection procedure

Table A4

<table>
<thead>
<tr>
<th>Poisson component</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model with no effect on the binomial component</td>
<td>Intercept</td>
<td>2.54</td>
<td>0.06</td>
<td>42.65</td>
</tr>
<tr>
<td>Si</td>
<td>0.39</td>
<td>0.03</td>
<td>14.67</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Y</td>
<td>0.01</td>
<td>0.02</td>
<td>4.67</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Model with effect on the binomial component</td>
<td>Intercept</td>
<td>2.54</td>
<td>0.06</td>
<td>42.65</td>
</tr>
<tr>
<td>Si</td>
<td>0.39</td>
<td>0.03</td>
<td>14.67</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Y</td>
<td>0.01</td>
<td>0.02</td>
<td>4.67</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

We compare the outputs of two models: a model including the following effects in the Poisson component only: morphosed individuals (Ju): model selection procedure

Table A5

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>k</th>
<th>AICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Ja-Ja</td>
<td>5</td>
<td>397.63</td>
<td>0.99</td>
</tr>
<tr>
<td>2</td>
<td>1-Ja</td>
<td>4</td>
<td>412.18</td>
<td>0.01</td>
</tr>
<tr>
<td>3</td>
<td>1-Ja</td>
<td>4</td>
<td>438.57</td>
<td>0.00</td>
</tr>
<tr>
<td>4</td>
<td>Ja-Ja</td>
<td>3</td>
<td>446.11</td>
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</tr>
<tr>
<td>5</td>
<td>Ja-Ja</td>
<td>4</td>
<td>499.32</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>Ja-Ja</td>
<td>3</td>
<td>507.79</td>
<td>0.00</td>
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<tr>
<td>7</td>
<td>Ja-Ja</td>
<td>3</td>
<td>571.20</td>
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<td>8</td>
<td>Ja-Ja</td>
<td>2</td>
<td>573.27</td>
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</tbody>
</table>

We compare the outputs of two models: a model including the following effects in the Poisson component only: morphosed individuals (Ju): model selection procedure

Table A6

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of captures</th>
<th>Number of females identified</th>
<th>Number of males identified</th>
<th>Number of secondary sessions</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>142</td>
<td>36</td>
<td>31</td>
<td>6</td>
</tr>
<tr>
<td>2001</td>
<td>195</td>
<td>44</td>
<td>47</td>
<td>4</td>
</tr>
<tr>
<td>2002</td>
<td>169</td>
<td>36</td>
<td>34</td>
<td>4</td>
</tr>
<tr>
<td>2003</td>
<td>37</td>
<td>12</td>
<td>18</td>
<td>4</td>
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<tr>
<td>2004</td>
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</tr>
<tr>
<td>2005</td>
<td>16</td>
<td>6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2006</td>
<td>59</td>
<td>23</td>
<td>23</td>
<td>3</td>
</tr>
<tr>
<td>2007</td>
<td>176</td>
<td>43</td>
<td>60</td>
<td>3</td>
</tr>
<tr>
<td>2008</td>
<td>167</td>
<td>41</td>
<td>59</td>
<td>3</td>
</tr>
</tbody>
</table>

The model includes four biological parameters: survival (S), departure (D), arrival (A) and the recapture rate (k) = number of parameters, deviance = residual deviance, AICc = Akaike information criterion adjusted for small sample size, w = AICc weights, AD = number of adults, DE = adult density, Y = year.
Table A8
Influence of patch disturbance on dispersal: model selection procedure

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\psi(D_1), \psi(S), \pi(D_1), p(Y)$</td>
<td>12</td>
<td>1101.42</td>
<td>1126.37</td>
<td>0.24</td>
</tr>
<tr>
<td>2</td>
<td>$\psi(D_1), \psi(S), \pi(D_1), p(S+Y)$</td>
<td>13</td>
<td>1099.46</td>
<td>1126.57</td>
<td>0.22</td>
</tr>
<tr>
<td>3</td>
<td>$\psi(D_1), \psi(\cdot), \pi(D_1), p(Y)$</td>
<td>11</td>
<td>1104.52</td>
<td>1127.32</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>$\psi(D_1), \psi(S), \pi(D_1), p(D_i+Y)$</td>
<td>13</td>
<td>1101.40</td>
<td>1128.52</td>
<td>0.08</td>
</tr>
<tr>
<td>5</td>
<td>$\psi(D_1), \psi(S), \pi(D_1), p(D_i+S+Y)$</td>
<td>14</td>
<td>1099.41</td>
<td>1128.70</td>
<td>0.07</td>
</tr>
<tr>
<td>6</td>
<td>$\psi(D_1), \psi(\cdot), \pi(D_1), p(S+Y)$</td>
<td>12</td>
<td>1104.25</td>
<td>1129.20</td>
<td>0.06</td>
</tr>
<tr>
<td>7</td>
<td>$\psi(D_1), \psi(\cdot), \pi(D_1), p(D_i+Y)$</td>
<td>12</td>
<td>1104.48</td>
<td>1129.44</td>
<td>0.05</td>
</tr>
<tr>
<td>8</td>
<td>$\psi(D_1+S), \psi(S), \pi(D_i+S), p(Y)$</td>
<td>14</td>
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The model includes four biological parameters: survival $\psi$, departure $\psi$, arrival and patch dynamics $\pi$ and recapture $p$. $k$ -- number of parameters, deviance – residual deviance, $\text{AICc} – $ Akaike information criterion adjusted for small sample size, $S_i$ – 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 state probabilities, which include the parameters of interest, $\psi$ the probability of non-efficace reproduction occurrence and $\psi2$ 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 non-efficace 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).