

Matrix permeability of agricultural landscapes: an analysis of movements of the common frog (*Rana temporaria*)

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The implications of habitat fragmentation go beyond changes in the size and composition of suitable habitat patches. In fragmented landscapes, “matrix permeability” influences the dispersal of organisms, thereby affecting the persistence of populations in such landscapes. We investigated the effect of habitat composition on the movement of adult and recently metamorphosed juvenile common frogs (*Rana temporaria*) emigrating from a pond in an agricultural landscape. One question driving our research was: do the numbers of captured individuals differ between habitat types? Such a difference would indicate avoidance of or preference for certain habitats. A subsidiary question was: does the response to landscape composition differ between adults and juveniles? We found significant differences in the numbers of frogs trapped in various habitat types. Adult and juvenile common frogs preferred extensive meadows and hedgerows above other habitat types. Arable land was the most avoided habitat type, but short-cut pastures and road verges were also avoided. For instance, almost 10 times more juveniles and four times more adults were caught in meadows than in arable land. Hedgerows were also frequented often, with four times more juveniles and 2.2 times more adults captured compared to arable land. Juveniles displayed more clear-cut preference and avoidance of habitat types than adults. These findings suggest that intensively farmed landscapes form a larger barrier for juveniles than for adults, from which we conclude that different life stages of the same species may react differently to matrix composition. The demonstrated influence of matrix composition on frog dispersal underlines the importance of having well-connected habitat networks to ensure the sustainability of amphibian communities in agricultural landscapes.

Key words: amphibians, behaviour, connectivity, dispersal, field experiment, habitat fragmentation, nature conservation

INTRODUCTION

In today’s agricultural landscapes, natural or semi-natural habitats have become scarce and fragmented. For many amphibian species, the fragmentation of breeding habitat leads to population decline (Sjögren Gulve, 1994; Vos & Stumpel, 1996; Hamer et al., 2002), resulting in a loss of species in isolated and small ponds. Another factor important for the occurrence of amphibians is the amount of suitable terrestrial habitat in the surroundings of the pond (Vos & Stumpel, 1996; Semlitsch, 1998; Pope et al., 2000; Mazerolle et al., 2005). Habitat fragmentation involves more than changes in the size and composition of suitable habitat patches. Indeed, we should expect the landscape matrix (i.e. the non-habitat surrounding suitable habitat patches; Wiens, 1995) to regulate amphibian movements (dispersal and seasonal migrations) and thus to be important for population persistence in fragmented landscapes. It has been suggested (Ricketts, 2001) that matrix permeability – the degree to which different land cover types facilitate or impede animal movements – might play an important role in the response of species to habitat fragmentation. In fragmented agricultural landscapes in which habitats have been replaced by intensively-farmed fields, residential areas and roads, the exchange of individuals depends on the distance between

suitable patches together with the matrix permeability: so-called “functional connectivity” (Taylor et al., 1993; With et al., 1997). There is growing empirical evidence that patches linked by landscape structures that are permeable to dispersers – “corridors” in the broadest sense (Vos et al., 2002) – are more often occupied (e.g. Dunning et al., 1995; Gonzalez et al., 1998), have a higher migration rate of individuals (e.g. Haas, 1995; Haddad, 1999; Tewksbury et al., 2002) and have higher population densities (Haddad & Baum, 1999).

If viable amphibian populations are to be maintained in agricultural landscapes, it is important to know to what extent amphibian dispersal is influenced by landscape composition. For instance, many amphibian breeding sites and surrounding terrestrial habitats in Europe and in large regions of North America have been converted into intensively-used cropland or pasture (Wilén & Frayer, 1990; Vos & Zonneveld, 1993; Gibbs, 2000). It seems likely that such open areas will be inhospitable to dispersing amphibians. Studies focusing on movements of individual amphibians suggest they prefer closed-canopy habitat types for dispersal and emigration (Semlitsch, 1981; Windmiller, 1996; deMaynadier & Hunter, 1999; Vos, 1999; Jehle & Arntzen, 2000; Rothermel & Semlitsch, 2002; Mazerolle & Vos, 2006). It seems likely that juveniles will be more dependent on closed-canopy habitat, as

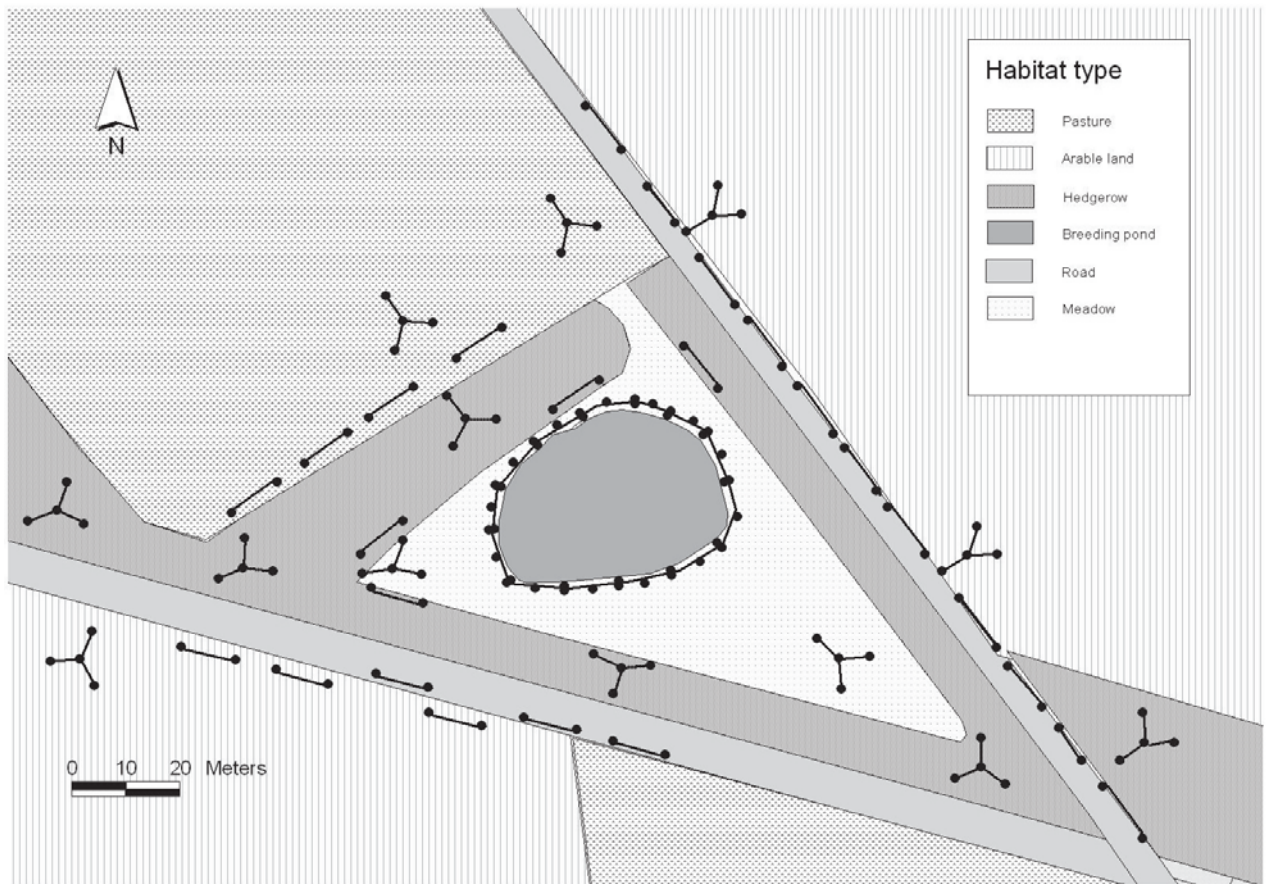


Fig. 1. The study area. The distribution of triangular and border arrays (see Fig. 2) is indicated.

compared to adults they are less mobile and lose more water through evaporation (Stebbins & Cohen, 1995). Although evidence is growing that the propensity of adults to disperse has often been underestimated (Perret et al., 2003; Smith & Green, 2005), it is the dispersal of juveniles that is especially important for the exchange between ponds (Gill, 1978; Breden, 1987; Berven & Grudzien, 1990). From this it follows that the factors determining dispersal success for juveniles may be critical in maintaining viable amphibian population networks.

The general question driving our study was: “How do juvenile amphibians respond to the composition of the agricultural landscape?” This topic has received little attention (but see Roethermel & Semlitsch, 2002). Being particularly interested in evidence for the avoidance of or preference for certain habitats, we posed two research questions: do the numbers of captured individuals differ between habitat types? And, does the response to landscape composition differ between adults and juveniles? In order to answer these questions we collected data on adult and recently metamorphosed juvenile common frogs (*Rana temporaria*) emigrating from a pond in an agricultural landscape in the Netherlands. *Rana temporaria* is common and widely distributed in Europe. Adults migrate to breeding ponds, lay eggs, and after a few weeks, return to their terrestrial habitats (Duellman & Trueb, 1986). The aquatic larvae remain in the water for 2–3 months, the rate of development depending on various factors (Laugen et al., 2003; Loman, 2004). After metamor-

phosis, the juveniles migrate from the wetland toward terrestrial habitats. The favoured terrestrial habitat consists of rough growth (e.g. tall grasses and high herbs), shrubs and bushes (Stumpel, 2004).

Though the common frog is considered a habitat generalist, able to subsist in agricultural landscapes, in recent decades the intensification of farming in the Netherlands has led to a major decline in its distribution and density (Bergmans & Zuiderwijk, 1986).

In our research we began by focusing on habitat selection by adults when migrating from a breeding pond, and then on habitat selection by post-metamorphic dispersing juveniles. To investigate relative avoidance of or preference for habitats, we tested whether the numbers of trapped individuals differed between components of the agricultural landscape. We also tested whether adults and juveniles responded differently to landscape composition. The agricultural habitats investigated were arable land, regularly mown grasslands, road verges, hedgerows and extensively managed meadows.

METHODS

The study area was located in the “Zuid-Eschmarke”, an agricultural landscape in the east of the Netherlands characterized by small fields, demarcated by hedges and hence referred to as “small scale” (by contrast with the “large scale” extensive open landscapes, where the view is unrestricted by hedges and thickets). Since the 1980s

Table 1. Overview of the number of arrays and pitfall traps placed in each habitat type.

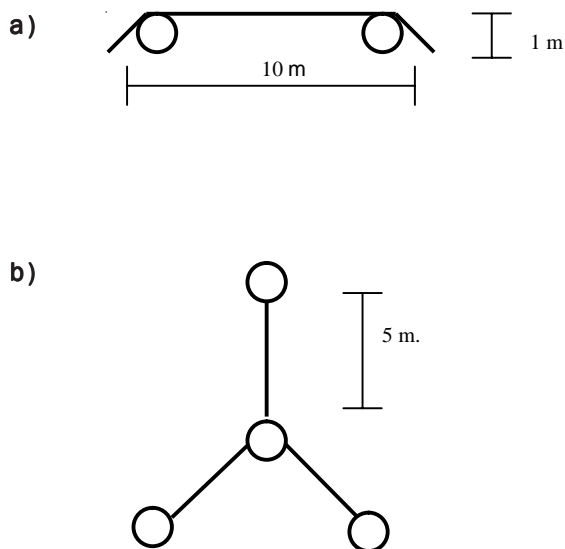
Habitat type	No. of triangular arrays	No. of border arrays	Total pitfall traps
Arable land	3	7	26
Hedgerow	6	6	36
Meadow	2	0	8
Pasture	2	4	16
Road verge	0	8	16
Total	13	25	102

many ponds and hedgerows in this landscape have been restored and are now managed by a cooperative of local farmers (STALES). We distinguished six habitat types in the study area: breeding pond, hedgerow, meadow, arable land, pasture and road verge (Fig. 1).

The breeding pond is 1500 m², with sloping banks and a maximum depth of approximately 2 m. It is in an extensively-managed meadow of tall grasses and herbs that is grazed by cattle for a few weeks every year. On three sides of the meadow are hedgerows (Fig. 1), each of different width: 20 m (NW), 10 m (S) and 3.5 m (NW). They consist of a tree layer (5–16 m high), a shrub layer, and a herb layer with variable cover. The vegetation in the nearby road verges is dominated by tall herbs and grasses; to the north-east is a maize field and to the south-west a field of winter cereal. The pastures are fertilized and mown regularly. The road in the north-west is 3 m wide and unpaved, whereas the road to the south is 4 m wide and paved; both have little traffic.

We erected a 50-cm-high plastic drift fence on wooden and metal stakes around the pond approximately 1 m from the water's edge. The bottom of the fence was in a trench 15 cm deep, to prevent individual frogs from getting through underneath. We installed 13 pitfall traps at 10 m intervals on both the inner and outer perimeters of the fence ($n=26$). The traps were 35 l plastic buckets (diameter 34.5 cm, depth 41.5 cm), sunk into the ground. A few centimetres of water and a piece of Styrofoam were placed in the pitfalls to prevent trapped amphibians from dehydrating. After the metamorphosis of the larvae, water was removed from the buckets to prevent drowning of dispersing juveniles.

In the surrounding landscape, 25 border arrays (Fig. 2a) were placed in different habitat types at a distance of 1 m from a habitat boundary as seen from the pond. Each border array consisted of two pitfall traps and a 10 m drift fence oriented towards the breeding pond. This set-up was to ensure that animals captured in a border array had recently moved from one habitat type to another. We also installed 13 triangular arrays (Fig. 2b) in the different habitat types, approximately 5 m from the transition between habitats. Each triangular array consisted of four pitfall traps connected by three 5 m drift fences. All pitfall traps in the surrounding landscape consisted of 10 l buckets, 30 cm in diameter and 35.5 cm deep. Table 1 and Figure 1 give an overview of the number of arrays and pitfall traps placed in each habitat type. From 20 March to 20 June

**Fig. 2.** Arrays: a) border array; b) triangular array.

2002, all pitfall traps were emptied daily, except during a 12-day period in April and a 22-day period in May, when amphibian activity was very low and so the traps were emptied every other day. In total, therefore, the number of trapping days was 76. For each individual captured, we recorded the trap number and age class: adult, sub-adult or juvenile (i.e. recently metamorphosed). Each frog was released on the other side of the border array or pond fence of capture, or in the case of triangular arrays, 1.5 m from the pitfall trap of capture.

In total, 481 adult common frogs were caught and individually marked in the inner-fence traps at the pond. Each frog was immobilized by hand and a sterile passive integrated transponder (PIT tag) was injected with a hypodermic needle into its lateral lymph sac. The wound was closed with Vet-Seal (B. Braun Medical AG, Emmenbrücke, Switzerland) to prevent infection and loss of transponder. The transponders (Trovan, Identify UK Ltd, Yorkshire, United Kingdom), cylindrical in shape, measured 11 × 2.2 mm diameter. Body length, weight and sex were noted. The study was conducted in accordance with Dutch legislation concerning the protection and welfare of vertebrate animals used for experimental and other scientific purposes. A permit was obtained for the marking of 500 adult frogs.

Weather data were obtained from the weather station of the KNMI (Royal Dutch Meteorological Institute, www.knmi.nl). The station is approximately 7 km north of the study area. We calculated the amount of rainfall (mm) during the period between trap visits. As the pitfalls were emptied daily, we summed the rainfall of the day of emptying and the preceding day. Similarly, for the few occasions on which traps were emptied after two days, we totalled the rainfall of the preceding three days.

Marked adult frogs were counted in 38 arrays for 76 days, giving a total of 2888 counts. A log linear regression model, which is a generalized linear model with Poisson distribution and logarithmic link function (McCullagh & Nelder, 1989), was used to investigate the effect of spatial

Table 2. Analysis of deviance for trapped marked common frogs.

a) Adults, using a log linear model with the Poisson distribution.

Effect	d.f.	Deviance change	Mean deviance	<i>P</i> value
+ Date	75	468.92	6.25	<0.001
+ Array type	1	15.47	15.47	<0.001
+ Distance exponential	2	39.83	19.91	<0.001
+ Habitat type	4	19.65	4.91	0.001
Residual	2805	463.61	0.17	

b) Juveniles, using a log linear model with the negative binomial distribution with aggregation parameter κ set to 0.62.

Effect	d.f.	Deviance change	Mean deviance	<i>P</i> value
+ Date	23	829.75	36.08	<0.001
+ Array type	1	177.50	177.50	<0.001
+ Distance exponential	2	87.95	43.98	<0.001
+ Habitat type	4	869.94	34.71	<0.001
Residual	881	2103.96	0.99	

Date: trapping date; array type: border array or triangular array; distance exponential: an exponential model in distance from the pond; habitat type: arable land, meadow, pasture, hedgerow or road verge.

and temporal features on captures. The relationship between the mean μ of the Poisson distribution and the effects was thus modelled by $\log(\mu) = \text{constant} + \text{temporal effects} + \text{spatial effects}$. Juvenile frogs were also counted in 38 arrays, but only for 24 days. The resulting 912 counts were heavily over-dispersed as compared with the Poisson distribution: the over-dispersion factor was 16. The juvenile counts were therefore analysed by means of a negative binomial distribution and a logarithmic link function. The negative binomial distribution has variance $\mu + \mu^2 / \kappa$ where μ is the mean of the negative binomial distribution and κ is the so-called aggregation parameter (McCullagh & Nelder, 1989; White & Bennetts, 1996). Significance of effects was assessed by a chi-square test for deviance differences. For the negative binomial model, this was done by fixing the aggregation parameter κ to the estimate for the model including all effects.

As we were especially interested in differences in the frogs' preference for or avoidance of habitat types, we tested for this after correcting for 1) differences between capture dates (which accounts for seasonal effects and weather conditions), 2) differences between border arrays and triangular arrays (to account for differences in array design and efficiency) and 3) differences due to the distance between the array and the breeding pond (as we expected that fewer frogs would be caught further away

from the pond). Pairwise ratios of the expected number of trapped frogs for the habitat types were calculated from the regression coefficients, and the significance of these ratios was assessed by means of pairwise testing.

In a second analysis, we tested whether temporal variation in the number of trapped frogs was related to the amount of precipitation. This was tested after correcting for all differences between arrays, which includes differences in array design and distance from the pond, and differences between habitat types.

The effect of distance from the pond and the effect of the amount of precipitation were both modelled by means of the exponential model $\alpha \cdot \beta^{**x}$ with parameters α and β and x denoting distance or rain. This model reflected our expectation that effects will be large for short distances and small amounts of rain, and that these effects reach a plateau for long distances and large amounts of rain.

RESULTS

Of the 696 adult frogs captured leaving the pond, 481 were marked. The sex ratio of the 481 individually-marked adults was biased towards males (3.2:1). Body length ranged from 45 to 76 mm, with the average being 60.7 mm ± 5.2 SD. Of the individuals marked at the pond, 377 (78%) were never caught in the traps in the surrounding landscape. The remaining 104 frogs were recaptured 141 times in the surrounding habitats (1 recapture: $n=75$; 2 recaptures: $n=23$; 3 recaptures: $n=5$; 5 recaptures: $n=1$).

The dispersal of newly metamorphosed juveniles started on 28 May 2002. From then until 20 June, we captured 41,905 juveniles leaving the pond and 14,251 juveniles in the surrounding landscape. The juveniles were too small to be fitted with passive integrated transponders. Thus, the figures only represent the number of captures, and not the actual number of juveniles captured. Not taking into account possible recaptures of the same individual, 34% of the juveniles dispersing from the pond were captured in the traps in the surrounding landscape.

The results of the log linear regression analysis for the number of marked adult frogs that were captured are given in Table 2a. All the added terms were significant. There were big differences between dates ($P < 0.001$), implying a large variation in the numbers of frogs caught per day. The number of frogs trapped in triangular arrays exceeded the number trapped in border arrays by an estimated factor of 1.53. The exponential model in distance fitted better than a quadratic model in distance. Estimates of the exponential model are given in Table 3. The exponential model is displayed in Figure 3; it shows that the number of captured frogs fell sharply a few metres from the pond. After correcting for the date, trap type and distance from the pond, there were still significant differences ($P=0.001$) between habitat types. Table 4a gives the pairwise ratios for the five habitat types. Most adults were found in meadows, and to a lesser extent in hedgerows; the habitat most avoided was arable land. The pairwise ratios of meadow compared to the other habitat types and the ratio between hedgerow and arable land were significantly different from 1 (Table 4a).

Table 3. Estimates and standard errors (in parentheses) of the parameters of the exponential model with distance and rain.

Parameter	Distance		Rain	
	Adults	Juveniles	Adults	Juveniles
α	2.55 (0.97)	1.51 (0.61)	-2.70 (0.35)	-2.05 (0.26)
β	0.90 (0.04)	0.93 (0.03)	0.82 (0.05)	0.83 (0.05)

A similar analysis, but now employing the negative binomial distribution, was performed on the number of trapped juveniles per array per day (Table 2b). Again, all effects were significant. The estimate of the aggregation parameter κ was 0.62 for the model with all effects. The number of juveniles caught in triangular arrays was an estimated 2.43 times higher than the number trapped in border arrays. The exponential model in distance fitted better than a quadratic model in distance; the relationship is displayed in Figure 3 and the estimates are given in Table 3. The number of juveniles trapped differed across habitat type ($P < 0.001$). All pairwise ratios differed significantly from 1, with the exception of captures in pasture compared to captures in arable land, and captures in pasture compared to captures in road verges (Table 4b). The estimated ratios for juveniles show similar but stronger preferences for and avoidances of habitat types compared to the ratios for adults, especially for preferring meadows and hedgerows and avoiding arable land.

In the second analysis, the number of trapped frogs was related to the amount of rain, after correcting for differences between traps. For both marked adults and juveniles the exponential model with amount of rain was significant ($P < 0.001$). Estimates of the exponential model are given in Table 3, whereas Figure 4 displays the estimated ratio as compared with no rain for both adults and juveniles. The number of frogs captured increased with increasing precipitation; the effect was stronger in adults than in juveniles.

Table 4. The estimated pairwise ratios of a) adult and b) juvenile common frogs for all pairs of habitat types. The left-hand number in the ratio corresponds to the habitat type in the far left column and the right-hand number to the habitat type in the top row. The ratios significantly different from 1 ($P < 0.05$) are asterisked.

Habitat type	Arable land	Meadow	Hedge-row	Pasture
a) Adults				
Meadow	4.30:1*	-		
Hedgerow	2.20:1*	0.51:1*	-	
Pasture	1.17:1	0.27:1*	0.53:1	-
Road verge	1.28:1	0.30:1*	0.58:1	1.09:1
b) Juveniles				
Meadow	9.59:1*	-		
Hedgerow	4.00:1*	0.42:1*	-	
Pasture	1.24:1	0.13:1*	0.31:1*	-
Road verge	1.41:1*	0.15:1*	0.35:1*	1.14:1

DISCUSSION

With regard to our first research question, our data showed that the numbers of captured frogs did indeed differ between habitat types and, as described above, we were able to demonstrate that the two preferred habitat types of adult and juvenile common frogs were extensive meadows and hedgerows. The least preferred habitat type was arable land, but mown pastures and road verges were also avoided. The answer to our second research question – on the possible difference in response to landscape composition from adults and juveniles – was also affirmative: juveniles had a stronger preference for the preferred habitats. Thus, though the number of adults caught in meadows was four times larger compared to arable land and 3.7 times larger compared to pasture, the comparable figures for juveniles were almost 10 times more juveniles captured in meadows compared to arable land and almost eight times more compared to pasture. A similar pattern was found in preference for hedgerows over arable land and pastures: captures of adult frogs in hedgerows were twice as high as captures of adult frogs in arable land or pasture, but four times more juveniles were captured in hedgerows compared to arable land and three times more juveniles were captured in hedgerows compared to pasture.

These results indicate that dispersing common frogs are influenced by the matrix composition. Their behaviour leads to uneven distribution of individuals over the landscape, which will result in differences in connectivity between ponds: ponds connected by very permeable habitat types will have a higher probability of exchanging individuals than ponds surrounded by unfavourable habitat.

Why were road verges avoided slightly less than arable land and pasture? It will be recalled that the roads were narrow (3–4 m wide) and one of the roads was unpaved. In contrast, the road verges consisted of a vegetation of tall grasses and herbs, comparable with the preferred meadow vegetation. The combination of narrow road plus well-structured road verge vegetation seems to be less unattractive than arable land and pasture. It is known that amphibians regularly cross much wider roads; in such cases, what negatively impacts on matrix permeability is not the frogs' avoidance of the road, but the fact that they are frequently killed by traffic (e.g. Hels & Buchwald, 2001; Mazerolle, 2003).

The stronger preference for and avoidance of habitat types exhibited by juveniles resulted in their distribution over the landscape being more skewed. The implication is that intensively farmed landscapes restrict the movement of juvenile frogs more than the movement of adult frogs.

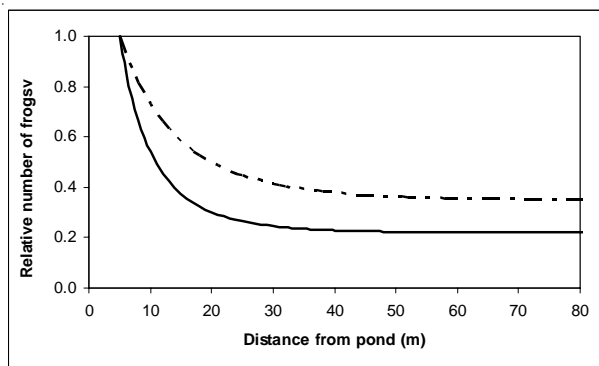


Fig. 3. The effect of distance from the pond on the relative number of trapped adult (solid line) and juvenile frogs (dotted line). The number at 5 m from the pond has been set at 1. For example, at a distance of 20 m from the pond, 0.32 times fewer adult frogs and 0.50 times fewer juveniles were caught compared with the number trapped at 5 m from the pond.

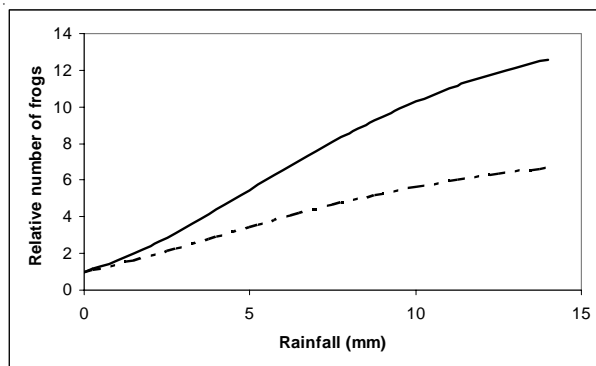


Fig. 4. The estimated ratio between number of trapped adults (solid line) and juveniles (dotted line) in relation to the amount of rainfall. For example, after 10 mm rainfall, 10.3 more adult frogs and 5.6 times more juveniles were caught compared with the numbers trapped after a dry period.

Thus, different life stages of the same species show different reactions to matrix composition, which means that conclusions based on the behaviour of one life stage cannot be extrapolated to another. For adults migrating after breeding, the landscape is not new. Furthermore, compared with the much smaller juveniles, adults are also potentially better able to perceive cues emanating from more remote habitats. This might influence decisions they make at boundaries, when they decide to cross open areas “knowing” these are not infinite.

If species are to be protected successfully, it is important to meet their requirements for the most critical stages in their life cycle. As juvenile amphibians are an important group in relation to recolonization (Gill, 1978; Breden, 1987; Berven & Grudzien, 1990), their successful dispersal is probably a key factor for their persistence in fragmented landscapes. Juveniles are present in high numbers; compared with adults, which show greater site fidelity, a larger proportion of juveniles disperses and they cover greater distances (Sinsch, 1990; but see Perret et al., 2003; Smith & Green, 2005).

One shortcoming of our statistical analysis could be that some individuals were captured more than once. If individual frogs do have specific habitat preferences, the results will be biased towards the preferences of the frogs that were caught more than once. We therefore tested whether the difference between habitat types was equal for adult frogs caught only once and adult frogs caught more than once. To do so, we defined an extra factor, “Recapture”, with levels “Once” and “Multiple”, and added this factor and its interaction with “Habitat type” to the analysis of deviance as in Table 2a. The interaction was far from significant ($P=0.423$). Interactions between Recapture and distance or amount of rain were not significant either. There is thus no indication that our conclusions are hampered by multiple recaptures. This conclusion does not necessarily also hold for the juvenile frogs; as noted earlier, adults and juveniles responded differently. We were unable to test for the possible influ-

ence of multi-captured individual juveniles, as juveniles could not be marked individually. However, we do expect the proportion of recaptured individual juveniles, and thus their possible influence on the outcome, to be smaller, as their capture period was much shorter (76 days for adults versus 24 days for juveniles).

It might be argued that the observed preference for and avoidance of habitat types is a result of the specific configuration of these habitats in the study area. In our analysis we did correct for differences in distance of the traps from the pond. Thus the preference ratios are estimates that assume that the habitat types were at the same distance from the pond. However, the possibility cannot be ruled out that the particular configuration of habitat types between the pond and the trap where an animal was caught influenced the probability of entering a particular trap. For instance, the estimates for road (i.e. the verge) and arable land are confounded, as it was not possible to reach arable land without first crossing a road. This means that the avoidance of arable land could partly be an avoidance of roads. Although there were many combinations of adjacent habitat types in the study landscape and these combinations were tested by installing several traps, in order to be able to extrapolate our findings to the matrix permeability of agricultural landscapes, more research needs to be done in different landscapes.

Though we have found a direct influence of the adjacent surrounding habitat types on movement paths of common frogs, it is possible that landscape characteristics other than the configuration of habitats might have influenced decisions about movement. It is known that amphibians use a multi-sensory orientation system that incorporates acoustic, magnetic, mechanical, olfactory and visual cues (see reviews in Sinsch, 1990, 2006).

The finding that both adult and juvenile activity was strongly correlated with the amount of precipitation leads to the conclusion that the permeability of the landscape improves when microclimatic conditions are favourable. We found that adults reacted more strongly than juve-

niles to the amount of rain and that the effect of rain levelled out after about 10 mm precipitation in the two-day period before trapping. The triggering of amphibian activity by precipitation is well known and is thought to be a reaction to their susceptibility to dehydration (Duellman & Trueb, 1986). We are unable to explain why adults rather than juveniles responded more strongly to the amount of precipitation. One would expect juveniles to respond more strongly to rain, as they are more vulnerable to dehydration (Stebbins & Cohen, 1995). It seems that what tip the scales towards movement are other factors that weigh differently for adults compared with juvenile frogs.

Several other amphibian species prefer closed-canopy habitat instead of open habitats, e.g. green frogs *Rana clamitans* (Lamoureux et al., 2002), juvenile wood frogs *Rana sylvatica* and spotted salamanders *Ambystoma maculatum* (deMaynadier & Hunter, 1999), crested newts *Triturus cristatus* and marbled newts *T. marmoratus* (Jehle & Arntzen, 2000), juvenile spotted salamanders and American toads *Bufo americanus* (Rothermel & Semlitsch, 2002) and juvenile common toads *Bufo bufo* (Mueller & Steinwarz, 1987). A radio-telemetry study on the tree frog *Hyla arborea* showed this species had a stronger preference for hedgerows and stronger avoidance of arable land compared to the common frog (Vos & Chardon, 1997; Vos, 1999); this provided evidence that species react differently to habitat composition in comparable landscapes. An earlier radio-telemetry study of movements of common frogs found that local movements were guided by drains and ditches, but long-distance migrations were not correlated with these elements (Seitz et al., 1992).

Among the factors that have been suggested to account for areas of intensive agriculture being less favourable for the movements of many amphibian species are scarcity of available water, scarcity of refuges, low food resources, toxicity from pesticide use and enhanced risk of predation (Ray et al., 2002). In particular, the risk of dehydration has been suggested as important for the avoidance of open habitat, where higher temperatures and low soil moisture may be limiting for amphibians. If the dehydration risk is paramount, juveniles should be more sensitive than adults because they have a bigger surface-to-volume ratio than adults (Stebbins & Cohen, 1995). An experiment with juvenile spotted and small-mouthed salamanders showed that their dehydration rate was quicker in open habitat than in forest (Rothermel & Semlitsch, 2002). Mazerolle and Desrochers (2005) found similar trends for *R. clamitans* subjected to dehydration on substrates in the presence and absence of cover. Another possible reason why juveniles are reluctant to cross open fields is that they move rather slowly.

Certain studies have found no influence of landscape composition on amphibian movement (Rosenberg et al., 1998; Joly et al., 2001). For instance, migrating California red-legged frogs (*Rana aurora draytonii*) typically moved overland in almost straight lines to target sites without noticeable regard for vegetation type or topography (Bulger et al., 2003). Obviously, amphibian movements are not always influenced by landscape com-

position. Whether matrix permeability depends on landscape composition depends on the interaction between species-specific traits and the characteristics of the particular landscape (Vos et al., 2002, 2005). With increasing intensification of land use, more species will become dependent on corridors of highly permeable habitat in order to cross an inhospitable matrix. The fact that even a species as widespread as the common frog is now declining, probably at least partly because of a matrix which impedes movement, is a strong argument for ensuring the protection of well-connected habitat networks for amphibian communities in agricultural landscapes.

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