

Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*)

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Abstract

The distribution pattern of the tree frog (*Hyla arborea*) in an intensively used agricultural landscape in Zeeland Flanders, was analyzed for effects of habitat fragmentation. The logistic regression models showed that the chance that a pond (potential reproduction site) was occupied by tree frogs depended on three isolation factors. The density of ponds within 750 m of the occupied pond was higher compared to ponds that remained unoccupied during the survey period. Additionally both the density of shrubs as well as the density of high herbs, two terrestrial habitat factors, was higher within 1000 m of occupied ponds. The explanatory value of two different types of isolation measures was compared with logistic regression analysis. It is discussed that 'Concentric isolation measures', which take size and distance of potential habitat patches in all directions into account, are expected to give a better description of isolation than the more often used 'distance from the nearest habitat patch'.

Introduction

Habitat fragmentation is being recognized as an important cause of loss of biodiversity in intensively used agricultural landscapes (see among others Opdam *et al.* 1993). With an increasing loss and disintegration of habitat, local populations will become smaller, and the frequency of interpatch dispersal will decrease. Depending on species characteristics and the stage of fragmentation, populations especially in small habitat patches, may go extinct, while the degree of isolation lowers the probability that unoccupied patches become recolonized (Verboom *et al.* 1993). If the process of fragmentation continues, opportunities for recolonization of empty patches will diminish and a species may eventually disappear from the region. Characteristically species whose distribution patterns are influenced by habitat fragmentation, are often absent in relatively small and isolated habitat patches. Effects of habitat size and isolation on the distribution of populations have been demonstrated for a variety of species of different species groups:

woodland birds (Opdam 1991; Askins *et al.* 1987) small mammals (Merriam 1988; Van Apeldoorn *et al.* 1992) butterflies (Harrison 1991; Hanski 1994), ground-dwelling invertebrates (Mabelis 1990). Furthermore, for amphibians, a group with relatively limited mobility and often dependent on natural elements in the agricultural landscape, effects of habitat fragmentation have been determined for several species: the pool frog (Sjogren 1988, 1991), the natterjack toad (Sinsch 1992). Moreover, Laan and Verboom (1990) found an effect on species diversity.

In habitat fragmentation studies, parameters that describe the spatial distribution of habitat, the isolation parameters: are often nearest neighbour measures (here called 'linear measures') e.g.: distance from the nearest suitable habitat patch (among others: birds: Müller 1982; Van Dorp and Opdam 1987; Soulé *et al.* 1988; butterflies: Thomas *et al.* 1992; amphibians: Dickman 1987; Wederkinch 1988; Laan and Verboom 1990) or the distance from the nearest occupied habitat patch or source patch (among others: birds: Fritz 1979; Van Dorp

and Opdam 1987; Soulé *et al.* 1988; butterflies: Harrison *et al.* 1988; Thomas and Harrison 1992; Thomas *et al.* 1992; amphibians: Sjogren 1991). However, we suggest that the distance from the nearest patch is an inadequate descriptor of the spatial relations between local populations. Being potential sources of dispersing animals all (occupied) habitat patches within a reachable distance contribute to the probability that a patch is being reached by a dispersing individual (Verboom *et al.* 1991; Hanski 1994). Isolation measures that take the total area of habitat in the patch surroundings into account are here called 'concentric isolation measures'. Few studies have considered concentric isolation measures: birds (Askins *et al.* 1987; Verboom *et al.* 1991); butterflies (Hanski 1994); amphibians (Loman 1988). A concentric isolation measure has the advantage that size and distance of potential habitat patches in all directions are taken into account. This is probably a more realistic description of isolation in relation to actual dispersal processes, presuming that dispersing animals have no foreknowledge of the direction of the nearest habitat patch and therefore leave in a random direction.

A second reason to prefer concentric isolation measures over linear measures is that they provide quantitative and spatially explicit information on the habitat requirements of species. This is important for the development of tools for nature conservation. In recent nature conservation policy plans in the Netherlands the problem of habitat fragmentation has been recognised. This has led to spatially explicit landscape plans in which sustainable ecological networks of core areas, nature restoration areas and interconnecting corridors have been designed (Min. LNV 1990). For the evaluation of these landscape plans, quantitative data on the amount of required habitat and the optimal spatial distribution of habitat of the target species are needed.

Our first objective in this study was to analyze whether the spatial characteristics of tree frog habitat play a role in explaining the distribution pattern of the tree frog in an intensively used agricultural landscape. The tree frog had declined considerably in number over the last decades (Borgula 1993) and it is one of the target species in nature restoration plans. There is a need for measurements by which

the effects of these plans can be predicted. The chance that a habitat patch is occupied by a local population of tree frogs is related to habitat quality, size and degree of isolation of the patch. Our second objective was to determine whether concentric isolation parameters give a better explanation of the distribution pattern than linear isolation measures. Finally, the translation of concentric and linear isolation measures into tools for landscape planning is discussed.

Study area

The study area is 250 km² and is situated in the western part of Zeeland Flanders (Fig. 1). The landscape mainly consists of arable lands. (Semi) natural vegetations can be found on dikes, in the coastal sand dunes and in meadows with cattle drinking ponds, the aquatic habitat used by tree frogs. The terrestrial habitat required by tree frogs consists of shrubs, bushes and vegetation of high herbs (Clausnitzer 1986; Stumpel 1993). The habitat patches form approximately 1.5% of the total landscape cover and are isolated from each other by intensively used agricultural land that is unsuitable for the species.

Methods

Presence and absence data of the tree frog were collected from 1981 to 1986 for 512 cattle drinking ponds. Tree frog presence was recorded by listening for calling males, (spontaneously or in reaction to tape-recorded mating calls) and by searching for eggs, tadpoles, juveniles and adults in the pond and the pond surroundings (see Stumpel 1987a for detailed information). The ponds were visited at least three times a year (in the years 1981–1983 and 1986) during the reproduction period. Since not all tree frogs call every night and because of the low chance of tracing animals in ponds with very low densities (Stumpel 1987a; Tester 1993) tree frogs may have been recorded erroneously as absent in ponds with very few animals. All occupied ponds were treated equally in further analysis, regardless of tree frog density or whether successful reproduction could be confirmed.

Zeeland Flanders

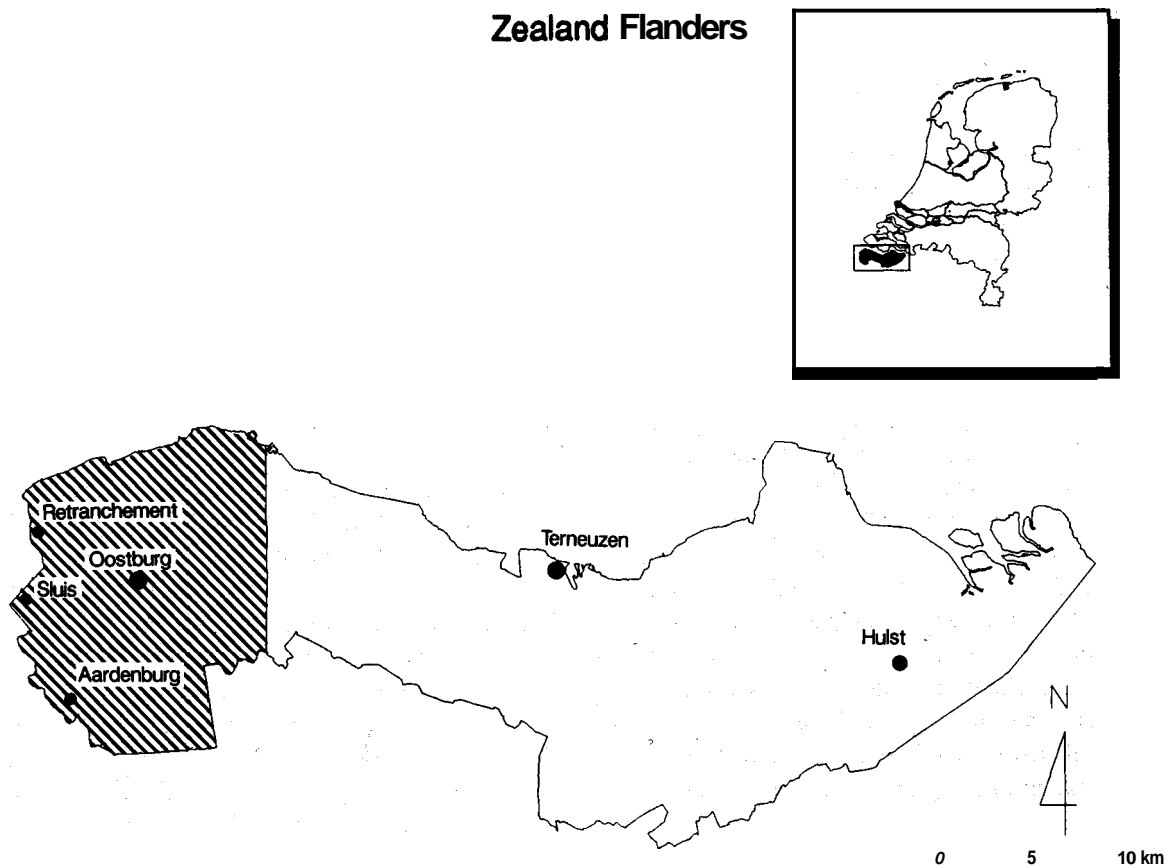


Fig. 1. The position of the study area.

In 1986, habitat quality parameters and pond area were measured, in a subset of 196 ponds (Table 1). The subset contained all 50 ponds where tree frogs were found in at least one year. As brackish water is an unsuitable habitat for reproduction (Stumpel 1987b; Grosse 1993), ponds with a chloride concentration higher than 500 mg/l were removed from the dataset. Habitat isolation measures were calculated for the complete data set of 512 ponds in the study area. This led to a total number of 187 ponds for analysis of which both habitat quality and isolation parameters were available. To test whether the subset was a representative sample of the variation in isolation, regression analysis was also carried out with the complete dataset of 512 ponds in the study area (see results).

In 1993 a survey of the terrestrial habitat in the study area was made. Two types of terrestrial tree frog habitat were distinguished: sites with a vegetation of high perennial herbs and sites with a devel-

oped shrub layer, such as hedgerows and wood fringes (Clausnitzer 1986; Stumpel 1993). For linear sites of high herbs only those elements with a minimum width of 5 m were taken into account. Based on a control of the vegetation map in the field from 1986 and considering the minimal width of the elements, we assumed that no substantial changes had taken place in the distribution pattern of these terrestrial habitats in the years between the tree frog inventory and the survey of the terrestrial habitat. Therefore, the data sets were analyzed together. The spatial configuration of water and land habitat was put in a geographic information system Arc-Info (Fig. 2).

The following measures for the isolation of the ponds were calculated. Linear variables: distance from the nearest pond and distance from the nearest occupied pond. Concentric variables were calculated in circles surrounding each pond with an increasing radius from 100, 250, 500, 750, 1000,

Table 1. Mean value and standard deviation of water quality variables, pond area and isolation variables.

Variables		Occupied ponds Mean \pm sd	Unoccupied ponds Mean \pm sd
Pond Variables			
PH	pH pond water	7.6 \pm 0.8	7.7 \pm 0.9
COND	Electrical Conductivity pond water (μ S/cm)	83.2 \pm 33.8	88.9 \pm 40.7
CHLOR	Chloride (mg/l)	51.9 \pm 37.4	65.6 \pm 64.3
COVER	Water Vegetation cover (%)	50% \pm 40%	20% \pm 30%
SHADE	Shaded pond area (%)	10% \pm 20%	20% \pm 30%
AREA	Pond area (m ²)	511 \pm 644	359 \pm 405
Linear Isolation Variables			
OCCDIST	Distance to nearest occupied pond (m)	390 \pm 606	1441 \pm 1088
PONDDIST	Distance to nearest pond (occupied or empty)	153 \pm 124	232 \pm 192
Circular Isolation Variables			
OCC100	Number of occupied ponds within 100 m	0.2 \pm 0.5	0.0 \pm 0.2
OCC250	ditto 250 m	1.0 \pm 1.1	0.2 \pm 0.6
OCC500	ditto 500 m	2.7 \pm 1.9	0.7 \pm 1.5
OCC750	ditto 750 m	4.8 \pm 3.2	1.7 \pm 3.1
OCC1000	ditto 1000m	6.3 \pm 4.3	1.7 \pm 3.1
OCC1500	ditto 1500m	7.0 \pm 4.5	2.6 \pm 3.7
OCC2000	ditto 2000 m	8.2 \pm 4.7	3.8 \pm 4.6
POND100	Total number of ponds within 100m	0.5 \pm 0.6	0.3 \pm 0.5
POND250	ditto 250 m	2.6 \pm 1.7	1.7 \pm 1.7
POND500	ditto 500 m	7.8 \pm 3.6	4.8 \pm 3.7
POND750	ditto 750 m	14.7 \pm 6.8	8.4 \pm 5.3
POND1000	ditto 1000m	20.9 \pm 10.4	12.7 \pm 7.5
POND1500	ditto 1500m	32.4 \pm 13.8	22.5 \pm 11.3
POND2000	ditto 2000 m	45.0 \pm 16.6	35.9 \pm 15.0
HERP100	Area of high herbs (ha) within 100m	0.20 \pm 0.41	0.61 \pm 0.18
HERP250	ditto 250 m	0.85 \pm 0.93	0.31 \pm 0.45
HERP500	ditto 500 m	2.03 \pm 1.51	0.90 \pm 0.95
HERP750	ditto 750 m	3.14 \pm 1.85	1.74 \pm 1.50
HERP1000	ditto 1000m	4.60 \pm 2.07	2.89 \pm 1.20
HERP1500	ditto 1500m	7.13 \pm 1.98	5.68 \pm 2.73
HERP2000	ditto 2000 m	10.66 \pm 2.70	9.62 \pm 3.17
SHRUB100	Area of shrubs (ha) within 100m	0.13 \pm 0.22	0.11 \pm 0.37
SHRUB250	ditto 250 m	0.76 \pm 1.01	0.39 \pm 1.12
SHRUB500	ditto 500 m	1.98 \pm 2.26	0.82 \pm 1.72
SHRUB750	ditto 750 m	3.52 \pm 3.22	1.40 \pm 2.32
SHRUB1000	ditto 1000 m	5.08 \pm 4.10	2.18 \pm 3.12
SHRUB1500	ditto 1500m	7.26 \pm 4.89	4.09 \pm 4.32
SHRUB2000	ditto 2000 m	9.75 \pm 5.56	6.45 \pm 5.15

1500 and 2000 m. In these zones the following variables were measured: total number of ponds (both occupied and unoccupied ponds), number of occupied ponds, area of high herbs and area of shrubs (Table 1).

The presence or absence data of tree frogs in a

pond were analyzed with logistic regression analysis, in which a pond was judged 'occupied' if in at least one out of six years, tree frog presence was recorded. An 'occupied' pond is also referred to as a 'tree frog pond'. Thus, we analyzed the spatial pattern of occupancy. The temporal pattern was

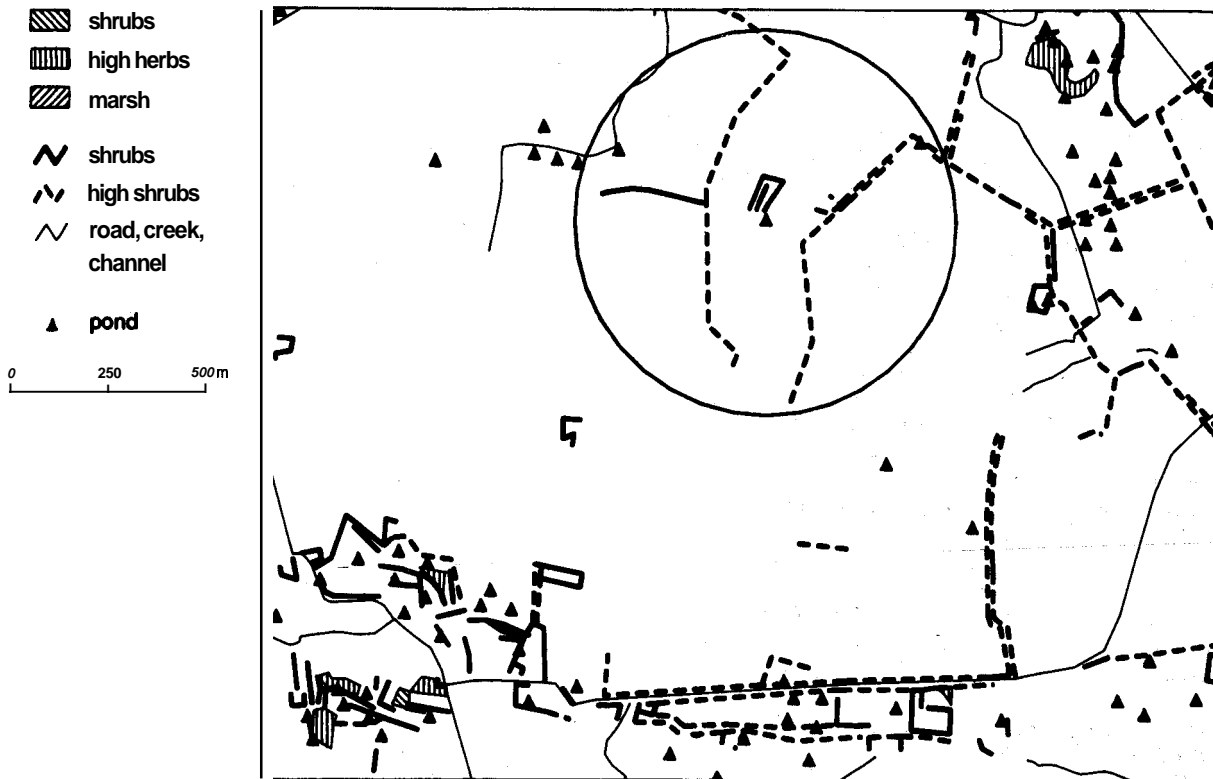


Fig. 2. Detail of the digitized landscape elements. The circle has a radius of 1000 m.

judged less informative because of potential variation in search intensity over the six years of study. The regression analysis was carried out in two stages. In the first stage only habitat quality parameter of the ponds were entered in the model in a stepwise fashion. In the second stage the model was extended with isolation parameters. Whether isolation parameters are additional explanatory factors to the habitat quality factors can be tested using this method (Van Apeldoorn *et al.* 1992). For each concentric isolation variable the optimal radius was determined by the variable with the highest explanatory value in the regression model, as judged on the basis of the deviance statistic (Jongman *et al.* 1987).

Results

During the six-year survey period 50 ponds were occupied by tree frogs in at least one year. Only a few ponds were occupied during the whole period.

The distribution pattern of occupied ponds is shown in Figures 3 and 4.

Analysis of the habitat quality variables revealed vegetation cover and electrical conductivity of the pond water as significant variables, while shading and acidity of the pond showed no effect (Table 1). A high coverage of the pond surface by aquatic vegetation had a positive effect on the occupation probability (COVER, $p < 0.001$, Table 2 model 1a). The vegetation mainly consisted of floating and submerged species: *Glyceria fluitans*, *Ranunculus aquatilis*, *R. baudotti*, *Lemna minor*, *Zannichellia palustris* and *Ceratophyllum submersum* (Stumpel 1987b). The second important variable was electrical conductivity, high values of which had a negative effect on the occupation probability of a pond (COND, $p < 0.01$, Table 2 model 1b). Although electrical conductivity of the water in agricultural landscapes is generally a measure for eutrophication, in Zeeland Flanders it is highly correlated with the concentration of chloride ions in the water ($r = 0.983$, $n = 187$, $p < 0.01$), caused by mixing

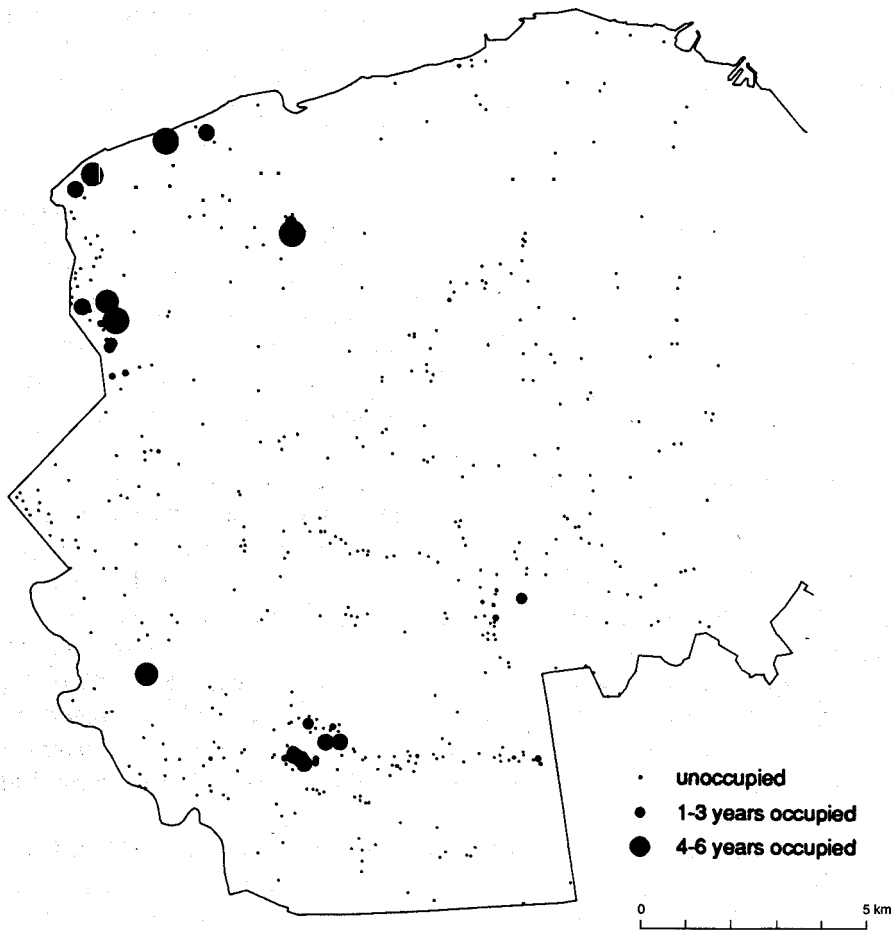


Fig. 3. Distribution pattern of ponds in the study area. The circle size is related to the number of years of occupancy in the period 1981–1986.

with salt water from flooding and seepage (Provinciaal Bestuur Zeeland 1993).

After accounting for habitat variation in the next stage of the analysis the variables related to habitat fragmentation and area were added to the model. Although occupied ponds were somewhat larger than unoccupied ponds (occupied ponds: mean $511 \pm 644 \text{ m}^2$, unoccupied ponds mean $359 \pm 405 \text{ m}^2$, Table 1), pond area was not a powerful explanatory variable in the model.

First, the linear isolation measures were added to the model. The linear variable 'distance from the nearest occupied pond' (OCCDIST) gave the best explanation of the occupation pattern ($p < 0.001$, Table 2 model 2a). The difference between unoccupied and occupied ponds regarding their distance from a tree frog pond is shown in Figure 4. As is

illustrated, nearly all occupied ponds were within 500 m from other occupied ponds, with a threshold value between 500 and 750 m. When the linear variable 'distance from the nearest pond' (occupied as well as unoccupied ponds, PONDDIST) was added to the model ($p < 0.01$, Table 2 model 3a), the explanatory value was lower than in model 2a. The variables OCCDIST and PONDDIST were correlated ($r = 0.351$, $n = 187$, $p < 0.01$) and therefore exchangeable in the model (Table 4).

The results of the analysis of the linear isolation variables on the complete dataset of 512 ponds showed a similar explanation of the occupation pattern (OCCDIST $p < 0.001$, PONDDIST $p < 0.001$). Therefore, it was concluded that the subset of 187 was a representative sample of the habitat fragmentation in the study area.

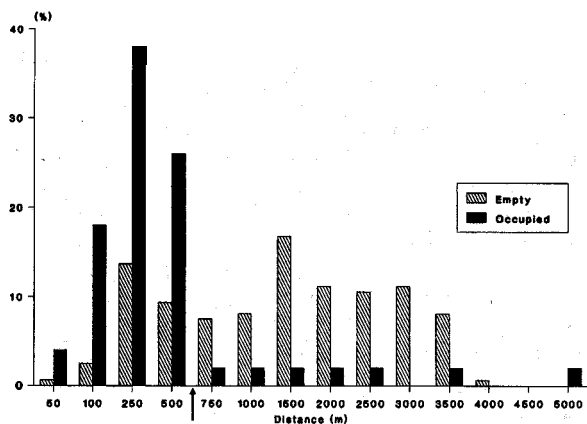


Fig. 4. Frequency distribution of the distance from the nearest occupied pond for occupied ($n = 50$) and unoccupied ponds ($n = 137$).

The optimal range of the concentric measures was determined by adding the concentric variables to the model separately with increasing ranges from 100 to 2000 m (Table 3). The optimal range varied between 750 m for ponds and 1000 m for the terrestrial habitat parts. To test whether concen-

tric isolation measures fit better than linear measures, their contribution as explanatory variables were compared. When the distance from the nearest occupied pond (OCCDIST) was replaced by the corresponding concentric variable 'the number of occupied ponds in a circle of 750 m' (OCC750) it gave about the same explanation (compare model 2a and model 4a, Table 2, R^2 adjusted of the total model **38%** respectively 37%). However, for the total number of ponds (both unoccupied and occupied) in a circle of 750 m (POND750), the concentric measure was an improvement compared to the linear variable (compare model 3a and model 5a, Table 2, R^2 adjusted of the total model **18%** respectively 29%). As was the case with the linear variables OCCDIST and POND750, the variables OCC750 and POND750 were also correlated ($r = \mathbf{0.804}$, $n = 187$, $p < 0.01$) and therefore exchangeable in the model (Table 4).

The concentric isolation measures of the two terrestrial habitat components, 'area of high herbs' and 'area of shrubs' had the highest explanatory value in a circle of 1000 m surrounding each pond (HERB1000, SHRUB1000, Table 3). When adding

Table 2. Selection of the logistic regression models. Significance levels of the last variable added to each model and R^2 adjusted of the total model are listed (for abbreviations see Table 1).

Habitat quality variables	Logistic regression models	Significance of the last variable	R^2 adjusted total model
	Linear and concentric isolation variables		
PH		ns	
CHLOR		ns	
SHADE		ns	
AREA		ns	
1a COVER		***	10%
1b COVER + COND		**	13%
2a COVER + COND	+ OCCDIST	***	38%
2b COVER + COND	+ OCCDIST + HERP1000	ns	
2c COVER + COND	+ OCCDIST + SHRUB1000	ns	
3a COVER + COND	+ POND750	**	18%
3b COVER + COND	+ POND750 + HERP1000	***	21%
3c COVER + COND	+ POND750 + HERP1000 + SHRUB1000	***	34%
4a COVER + COND	+ OCC750	***	37%
4b COVER + COND	+ OCC750 + HERP1000	ns	
4c COVER + COND	+ OCC750 + SHRUB1000	ns	
5a COVER + COND	+ POND750	***	29%
5b COVER + COND	+ POND750 + HERP1000	**	32%
5c COVER + COND	+ POND750 + HERP1000 + SHRUB1000	***	37%

ns not significant, ** $p < 0.01$, *** $p < 0.001$.

Table 3. Significance levels and deviances of the concentric isolation measures, added to the model with increasing ranges from 100 to 2000 m (for abbreviations see Table 1).

Habitat quality variables	Number of tree frog ponds	Number of ponds	Area of high herbs	Area of shrubs
COVER + COND +	OCC100 *** (12.4)	POND100 ** (7.4)	HERP100 ns (3.8)	SHRUB100 ns (0.0)
	OCC250 *** (23.0)	POND250 * (6.5)	HERP250 *** (16.6)	SHRUB250 ns (1.3)
	OCC500 *** (33.5)	POND500 *** (19.6)	HERP500 *** (21.4)	SHRUB500 ** (6.4)
	OCC750 *** (43.7)'	POND750 *** (29.8)'	HERP750 *** (21.1)	SHRUB750 *** (13.4)
	OCC1000 *** (39.7)	POND1000 *** (28.9)	HERP1000 *** (21.7)'	SHRUB1000 *** (15.2)'
	OCC1500 *** (31.7)	POND1500 *** (18.9)	HERP1500 ** (9.8)	SHRUB1500 *** (12.3)
	OCC2000 *** (26.0)	POND2000 *** (11.7)	HERP2000 ns (3.1)	SHRUB2000 ** (10.6)

ns not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; 'highest deviance.

Table 4. Correlation matrix of the model variables. ns not significant, * $p < 0.05$, ** $p < 0.01$ (for abbreviations see Table 1).

	COVER	COND	OCCDIST	PONDDIST	OCC750	POND750	HERP1000	SHRUB1000
COVER								
COND	-0.218 ns							
OCCDIST	-0.256 *	-0.168 ns						
PONDDIST	-0.103 ns	0.158 ns	0.351 **					
OCC750	0.143 ns	-0.060 ns	-0.624 **	-0.303 **				
POND750	0.090 ns	-0.168 ns	-0.546 **	-0.490 **	0.804 **			
HERP1000	0.029 ns	-0.034 ns	-0.539 **	-0.172 ns	0.508 **	0.465 **		
SHRUB1000	0.225 ns	0.023 ns	-0.374 **	-0.204 ns	0.419 **	0.260 *	0.107 ns	
	COVER	COND	OCCDIST	PONDDIST	OCC750	POND750	HERP1000	SHRUB1000

these terrestrial measures to the models that already included the linear or concentric tree frog ponds variables, the terrestrial variables added no further explanation (compare model 2b and 2c for the linear tree frog variable and model 4b and 4c for the concentric tree frog variable, Table 2). This can be explained by the high correlation of HERB1000 and SHRUB1000 with OCCDIST (respectively $r = 0.539$, $n = 187$, $p < 0.01$ and $r = 0.374$, $n = 187$, $p < 0.01$) and of HERB1000 and SHRUB1000 with OCC750 (respectively $r = 0.508$, $n = 187$, $p < 0.01$ and $r = 0.419$, $n = 187$, $p < 0.01$, Table 4). However, both the area of high herbs and the area of shrubs in a circle of 1000 m do add significantly to the model that already included the distance from the nearest pond (model 3b and 3c, R^2 adjusted of the total model 27% and 34%, Table 2) and to the model with the number of ponds in a circle of 750 m (model 5b and 5c, R^2 adjusted of the total model 32% and 37%, Table 2).

Discussion

The statistical models show that occupied ponds are less isolated than unoccupied ponds. The densi-

ty of both aquatic and terrestrial habitat was higher in the surroundings of occupied ponds compared to ponds that remained unoccupied in the six years of the survey period. The many ponds that remained unoccupied, the few ponds that were occupied during the whole survey period (Fig. 3) and the fact that occupied ponds were close to other occupied ponds are indications that the distribution pattern of the tree frog in Zeeland Flanders can be explained by habitat fragmentation.

When looking at the potential dispersal sources in the surroundings of a pond, the concentric isolation variable 'number of occupied ponds in a circle of 750 m' is no better explanation of the distribution pattern than the distance from the nearest occupied pond (compare model 2 and model 4, Table 2, R^2 adjusted of the total model 38% respectively 37%). The presence of at least one dispersal source within 500–750 m seems to be the deciding factor for the occupation chance. The fact that there can be more than one source in the pond's surroundings does not improve this chance. Sjogren (1988, 1992) also found that the distance from the nearest occupied pond was an important explanatory factor for the distribution pattern of the pool frog (*Rana lessonae*). The distances between ponds were larger in

the Swedish study area and the landscape between ponds mainly consisted of pine forest instead of arable land. When the actual sources are ignored and all ponds are taken into account, the concentric compared to the linear measure is an improvement (compare model 3 and model 5, Table 2, R^2 adjusted of the total model 18% and 29% respectively). Here the concentric measure is a standard for pond density. In population networks where continuous occupancy of ponds is rare, the overall pond density may be an important measure of the mean presence of dispersal sources over time.

The area of high herbs and bushes is regarded as an isolation variable. However, especially in the direct surroundings of the pond, it will also have a function as the terrestrial habitat part of a local population. In agricultural landscapes the terrestrial and aquatic part of the tree frog habitat are often separated, and the terrestrial habitat is spread over several linear elements. In this respect increasing distances between terrestrial and aquatic habitat will increase the probability of higher mortality rates during the terrestrial phase and seasonal migrations and therefore lower the survival probability of a local population. The amount of suitable terrestrial habitat surrounding the pond can also be regarded as a connectivity measure, which will increase the colonization probability of a pond. It is plausible that dispersal will be more successful in a landscape with a high density of suitable terrestrial habitat. The fact that the concentric measure over a distance as far as 1000 m, rather than 100, 250 or 500 m ranges, gives the highest explanation in the model (Table 3), is an indication of this last function. The range of the concentric isolation measures (750 m for ponds and 1000 m for terrestrial habitat) is an indication of the distance over which regular exchange among populations is possible.

The terrestrial habitat area has no significant effect when added to a model that includes the number of occupied ponds. This can be explained as follows: because the complete habitat of amphibians consists of an aquatic as well as a terrestrial part, the presence of occupied ponds in the neighbourhood automatically implies that suitable terrestrial habitat must be present. This is also indicated by the relatively strong correlation between these parameters (Table 4).

Pond area was only weakly correlated with tree

frog presence. However, in a fragmented landscape one would expect a correlation between patch size and occupation change (Levins 1970; Goodman 1987; Verboom *et al.* 1993). A positive effect of pond area on the occupation probability has indeed been demonstrated for several amphibian species (Loman 1988; Laan and Verboom 1990; Sjögren 1991). One possible explanation for the absence of such an effect is that the variation in pond size in the study area was too small (Table 1). Bronmark and Edenhalm (1994) found a negative correlation between the presence of fish and tree frogs, especially in ponds larger than 1000 m². Relatively strong predation pressure in large ponds could reduce the positive effect of pond size on tree frog presence. However this is not a plausible explanation for the lack of an area effect in this study, because only 13 ponds were larger than 1000 m², of which a relatively large number (50%) was occupied by tree frogs. An alternative explanation is that population size is determined not only by the aquatic habitat part but also by the suitable terrestrial habitat area. Although generally the size of the reproduction site is thought to be a limiting factor in amphibian populations (Wilbur 1987; John-Alder and Morin 1990), in an intensively used agricultural landscape the terrestrial habitat might be more determining. If the mortality in the terrestrial phase is high, due to unfavourable conditions, the carrying capacity of ponds will never be reached.

Each pond was treated as a separate potential site for a population. This simplification seems justified by the fact that even in clusters of ponds that are within 100 m of each other, in two-third of these clusters only one pond was occupied during the survey period. Still it is not possible to determine exactly the limits of a local population. In an extreme stage of habitat fragmentation a phase can be reached when habitat patches become so small that they can no longer contain a local population. If these small patches are close to each other, several patches will be used by one 'local population' and effects of habitat fragmentation will play a role on the individual level (Haila *et al.* 1993; Andrén 1994). This is probably the case in the metapopulation study on the natterjack toad (*Bufo calamita*) by Sinsch (1992). Based on the movements of individuals, clusters of 6 to 20 ponds were regarded as one local population. However, in this (Sinsch 1992)

study the distances between ponds were much smaller.

Potentials for application in landscape planning and evaluation

Based on the regression model, predictions can be made of the occupation probability of a pond given the amount of suitable terrestrial habitat and number of ponds in the pond's surroundings. Using these predictions, guidelines for the design of an 'optimal tree frog landscape' can be developed and different landscape planning scenarios can be compared (Vos 1993). Concentric isolation measures have better potentials for application compared to linear measures, because they can be translated into habitat density requirements such as 'pond density or shrub area per km²'. For application purposes, it is preferable to focus on the models with pond density (Table 4, model 5) rather than on the models with occupied pond density (model 4). New ponds can be created easily, while it is not possible to create 'occupied ponds', unless one considers the introduction of the target species. Of course it is essential that the target species already be present in the planning area, and that restoration plans are designed around these potential dispersal sources (Vos 1993). For the same reason, models including both terrestrial and aquatic habitat isolation variables (Table 2, model 5c) have better potential for application because in these models both essential habitat parts can be quantified. As discussed above, the variable 'presence of occupied ponds' is a combination of both suitable terrestrial and aquatic habitat in the ponds' surroundings, in which the contribution of the two components cannot be separated.

Towards further quantification of isolation parameters

The concentric measure of pond density in a zone of 750 m is a more powerful explanatory variable than the linear variable 'distance from the nearest pond'. A limitation of the concentric isolation measure is that all ponds in the circle contribute equally to the connectivity of a pond, regardless of their

actual distance. It is, however, a simplification to assume that potential dispersal sources at a distance of 750 m have the same impact as sources near the target pond. In addition, one would like to take into account the actual size of dispersal sources. A measure that takes these spatial characteristics into account is the isolation or connectivity measure used by Verboom *et al.* (1991) and Hanski (1994). In this measure, all (occupied) habitat patches are treated as potential dispersal sources, corrected for habitat size (as a measure of population size) and distance from the target patch. However, for ground dwelling species not only the distance but also the character of the intermediate landscape influences the isolation of a pond, as was indicated by the contribution to the model of the amount of suitable terrestrial habitat components in a circle of 1000 m surrounding a pond. For several species groups it has been demonstrated that corridors do have a positive effect on the dispersal of species (Bennet *et al.* 1994). In a 'complete' isolation measure, not only the distance but also the relative resistance of the landscape between ponds should contribute to the connectivity of a habitat patch.

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