A TEMPORAL AND SPATIAL COMPARISON OF THE MOVEMENTS OF THREE FROGS (GENUS *RANA*) AMONG FARM AND FORESTED LANDSCAPES IN THE ANNAPOLIS VALLEY, NOVA SCOTIA.

by

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TABLE OF CONTENTS

Chapter 1: Survey Study

Methods

Results

Chapter 2: Mark-recapture study

Chapter 3: Radio-telemetry study

LIST OF TABLES

Chapter 1. Survey study

Chapter 2. Mark-recapture study

Chapter 3. Radio-telemetry study

LIST OF FIGURES

Chapter 1.

Chapter 2.

Chapter 3.

ABSTRACT

The temporal and spatial movements of *Rana sylvatica* (wood frog), *Rana pipiens* (northern leopard frog) and *Rana clamitans* (green frog) was assessed at three scales (3 studies) in two landscapes, one dominated by forested habitat, the other by agriculture. The results of the three studies support the conclusion that specific elements within landscapes influence the movement of these three species to and from breeding sites.

Results of the seasonal survey (n=195 days) indicate that at a broad scale, temporal movement patterns are tri-phasic for all three species, with peak movements occurring in the spring, mid summer and early fall. The spatial movement patterns suggest that stream and riparian habitat impede movements to ponds in the non-forested landscape but facilitate movements in the forested landscape. The size of the frog contributes to the movement patterns observed.

Results of the mark-recapture study indicate that at a meso scale, the movements of frogs displaced within 300 metres from philopatric ponds (n=24 routes) are influenced by type of habitat. The data indicate that field habitat facilitates movement to ponds, and linear aquatic elements impede movements to ponds.

Results of the telemetry study using *R. clamitans* (n=32), indicate that at a fine spatial scale, the specific responses to different habitat types influences movement. Forested habitat, residential areas and linear aquatic elements impede movements (frogs remain in these habitats for extended periods of time) across the landscape. Fields with and without cover and roads facilitate movements (high rates of movement) across the landscape.

In all three studies, drainage ditches in the non-forested landscape appear to act as barriers to movement. Short term needs associated with dehydration are met, however, long term population persistence may consequently be compromised. Creating permanent aquatic sites from drainage ditches is proposed as a means of providing both short and long term resources for these frogs and other amphibians.

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GENERAL INTRODUCTION

Amphibians are speculated to be undergoing a more rapid and coordinated decline than any other set of organisms (McCoy 1994). One factor proposed to be influencing these declines is changing land use patterns in which urban and agricultural lands are replacing, isolating and fragmenting required resource habitats (Blaustein *et al.* 1993, Pechmann & Wilbur 1994, Johnson 1992, Saunders et al. 1991). For anurans (genus *Rana*), resource habitats can be associated with three distinct phases; aquatic sites for breeding, and aquatic or terrestrial sites for summer foraging and for over-wintering (Gilhen 1984, Wright & Wright 1949). The extent to which landscapes may influence anuran population persistence will depend on the specific habitat requirements of the individual species and the elements within a landscape mosaic (Berven & Grudzien 1990, Laan & Verboom 1990, Loman 1988).

A landscape mosaic is defined as the pattern of habitats or resource patches for an organism. Three elements are considered. The first is the composition or the types of resource patches occurring within a landscape. The second is the configuration or the relative positions of those patches within a landscape (Dunning *et al.* 1992). The third is the connectivity or the relative ability of animals to move through the landscape (Taylor *et al.* 1993). The following definitions for landscape terms have been borrowed from Danielson (1991).

1. Habitat is defined as a combination of biotic and abiotic features that provide a useful means of broadly classifying existing conditions into distinct types.

2. A landscape is defined as a large area that comprises more than one type of habitat distributed in numerous patches.
3. A patch is defined as an area, smaller than a landscape, that contains only one type of habitat.

The extent to which the resources required by anurans are isolated from one another is speculated to influence the long-term persistence of these species (Berven & Grudzien 1990, Laan & Verboom 1990, Loman 1988). The premise that isolated populations are more prone to extinction than non-isolated populations, stresses the importance of considering the spatial dynamics of anurans within landscapes (Sjögren 1991). The potential physiological constraints, relatively low mobility and site fidelity of anurans may limit their ability to recolonize areas after local extinction (Blaustein, Wake & Sousa, 1993). Consequently, it is important to identify the features within landscapes that may facilitate or impede the movement between required resource patches for these organisms, before populations become too isolated and prone to extinction.

Within landscapes, it is difficult to distinguish between individual anuran populations because of the continuous movements associated with the complex life histories. The most obvious congregation of anurans occurs during the breeding phase. Males generally arrive at the breeding site first and attract females by vocalization (Wright & Wright 1949). In this study, the mass congregation of individuals at breeding sites is used to define individual populations. I use the movement toward and away from the breeding sites to assess the influence of landscape structure on anuran movement dynamics within landscapes.

In this thesis, I explore the relationship between anuran movement patterns and landscapes altered by human activities. My objective is to assess the extent to which landscapes altered by habitat fragmentation influence the movements of *Rana sylvatica*, *Rana pipiens* and *Rana clamitans*. I compare the movement patterns in two landscapes; one dominated by forest habitat in which forest cover is continuous, the other dominated by agriculture in which forest cover is highly fragmented. Although all three species require an aquatic habitat for breeding, the resource requirements for both the summer foraging and over-wintering phases vary. In the case of *R. clamitans*, only aquatic habitats are required, however, both *R. pipiens* and *R. sylvatica* require terrestrial habitats (Gilhen 1984, Wright & Wright 1949). These different habitat requirements within and between species may provide insight into potential mechanisms influencing the movements of anurans, in general, across landscapes.

It is increasingly being recognized that patterns observed at the landscape scale result from processes occurring at finer spatial scales (Levin 1992, Wiens *et al.* 1993). To elucidate these processes and patterns, Wiens *et al.* (1993) proposes two features of individual behaviour that must be considered: movement and patch choice. In this thesis, I evaluate movement and patch choice using three approaches; a survey study, a mark-recapture study and a radio-telemetry study.

At a broad scale (Chapter 1), I surveyed the movement dynamics of *R. clamitans, R. pipiens* and *R. sylvatica* at twelve different breeding sites, six in each of two landscapes. Movements were quantified using the number of frogs trapped per habitat type. Three habitat types are represented; forested, field and stream-riparian habitat. The objectives at this scale were to define the temporal and spatial patterns of habitat use surrounding ponds for the three species. Mechanisms influencing the movement dynamics could not be assessed because only the capture point and not the starting point was known. The extent to which the starting point may influence the movement patterns observed in the survey was assessed using a mark-recapture study (Chapter 2).

In the mark-recapture study, I explore how the types of habitat occurring between the breeding site and the release site may influence movement within a landscape. These movement pathways provide generalizations of how landscape features influence the successful or unsuccessful return of frogs to ponds from which they were initially displaced. The extent to which the presence or absence of habitats may have influenced movements was assessed in a radio-telemetry study (Chapter 3).

In the radio-telemetry study, I explore how different types of habitat influence the movement behaviours of individual frogs. These fine scale movements have allowed me to identify habitats that facilitate movements and those that impede movements within the two landscapes.

The Survey study (Chapter 1) and the Mark-recapture study (Chapter 2) provide generalizations of trends in habitat use, and the Radio-telemetry study (Chapter 3) provides insight into specific habitat responses influencing those trends. By combining these three approaches, the terrestrial movements of anurans is reasonably well represented and from this, insights into conservation strategies are proposed.

Chapter 1

Survey Study

INTRODUCTION

The breeding migration of frogs (Genus *Rana*) has been well documented in the literature (e.g., Gibbons & Bennett 1974, Laan & Verboom 1990, Loman 1988, Merrell 1970, Reh & Seitz 1990). The interception of these movements using drift fencing and traps has provided scientists with the means to assess the population dynamics within and between species at breeding sites. Within species, Berven (1995, 1990) and Pechmann *et al.* (1989) have assessed age structure of populations. Across species, Gill (1978a), Hecnar & M'Closkey (1996), Jehle *et al.* (1995) and Laan & Verboom (1990) have assessed species diversity and community structure.

Other studies exploiting breeding migrations have shown that specific types of habitat (e.g., ravines and streams) are selectively chosen for movement to breeding sites (Seburn *et al.* 1997, Guttman *et al.* 1991 and Maynard 1934). This selective use of habitats stresses the importance of considering movement dynamics during migrations to required resources. The extent to which different types of habitats may facilitate or impede movements to breeding ponds may influence the age, sex and number of individuals and species breeding at one site.

To date, studies exploring the influence of landscape structure on anuran population dynamics have generally considered the relative isolation of breeding sites (Hecnar &

M'Closkey 1996, Laan & Verboom 1990, Reh & Seitz 1990, Sjögren 1994, Vos & Stumpel 1995). Within landscape features such as the distances and composition of habitat types between breeding sites have been used as measures of isolation. Although this allows us to make rough estimates as to the influence of landscapes on population structure, the mechanisms associated with the proposed isolation measures have not been assessed. Without some understanding of these processes, we risk inappropriately classifying features of landscapes as being either detrimental to or beneficial for the persistence of anuran populations.

Studies quantifying within habitat movements have generally been conducted during the summer foraging phase (e.g., Bellis 1962, Bellis 1965, Bennett *et al.* 1980, Hadden & Westbrooke 1996, Heatwole 1961, Dole 1969). These studies have provided assessments of fine scale movements within one type of habitat and one landscape. The influence of different habitat types and landscapes on the movement patterns of frogs is still relatively unknown (Loman 1990).

I am speculating that the extent to which landscapes are being modified by human activities (e.g. replacement of forest and stream-riparian habitat with cultivated fields and irrigation ditches) influences the migrations of anurans to breeding sites. Movements between required resources (e.g. to and from breeding sites) will reflect the structure of the landscape, that is the amount, type and placement of non-resource habitat through which the frogs must move. In order to elucidate the potential influence of different habitat types on the movement patterns of frogs migrating to breeding ponds, I studied anuran movement dynamics between two different landscape types, one dominated by forested habitat, the other dominated by agriculture.

To evaluate the effects of landscape structure on anurans in general, I monitored *Rana sylvatica, R. pipiens and R. clamitans*, each with different habitat requirements. *R. sylvatica*, locally known as the wood frog, is predominantly a terrestrial species, spending most of its time in forested habitat and only migrating to and from aquatic sites in the spring for breeding (Gilhen 1984). Movements toward and away from ponds for this species will predominantly be associated with the breeding phase. *R. pipiens*, known as the northern leopard frog, is also predominantly a terrestrial species, spending most of the summer foraging phase in field habitat, migrating to aquatic sites for both breeding and over-wintering (Gilhen 1984). Seasonal movements to and from ponds for this species will be associated with both breeding and over-wintering phases. *R. clamitans*, known as the green frog, is almost completely aquatic, spending all phases in and around ponds; this frog summer forages along the banks of aquatic sites never venturing far from aquatic habitat (Gilhen 1984). Seasonal movements for this species will be associated with all phases of the frog's life history. The extent to which the ponds are used by each species is expected to influence the temporal and spatial movement patterns around ponds.

The objectives of this survey are threefold. One, to assess the influence of landscape type on the distribution and numbers of the three ranid species at the breeding sites. Two, to assess the influence of habitat type within and between the two landscapes on the movement patterns at breeding sites. Three, to assess the influence of landscape and habitat on the temporal movement patterns at breeding sites.

METHODS

Sites. I used a series of twelve ponds, six ponds in each of two landscapes located in the Annapolis Valley, Nova Scotia, Canada. Each landscape represents a different intensity of agricultural activity. The forest dominated landscape consists of a mosaic of forest habitat interspersed with few orchards and agricultural fields (45° 11.2’, 64° 24.6’) (Figure 1a), and the agriculture dominated landscape consists predominantly of fields interspersed with isolated forest fragments (45° 06.7’, 64° 25.9’) (Figure 1b). The forest and agriculture dominated landscapes are 1.84 km and 1.42 km in diameter respectively and are approximately 15 km apart. All ponds within the study area were artificially created between 12 and 25 years ago for irrigation purposes. General pond features are outlined in Table 1.

Table 1. General pond features outlining size, depth, pH, presence of vegetation and use of pond in 1996 season.

landscape	**pond***	**perimeter (metres)**	**depth (metres)**	**pH**	**emergent vegetation**	**stream fed (?)**	**pond use**	**used for irrigation in 1996**
Non-Forest	D1	220	>3	—	yes	yes	Irrigation	no
Non-Forest	S1	224	>3	7.7	no	yes	pasture	no
Non-Forest	A1	382	>3	9.3	yes	yes	Irrigation	yes
Non-Forest	B1	87	1.6	6.9	yes	no	Aesthetic	no
Non-Forest	C1	139	>3	8	yes	no	Aesthetic	no
Non-Forest	D2	268	2	7.6	yes	yes	Irrigation	yes
Forest	W1	471	>3	8	yes	yes	Irrigation	no
Forest	W2	85	~3	7	no	yes	Irrigation	no
Forest	W3	305	>3	10	yes	yes	Irrigation	no
Forest	M1	163	2	9.4	yes	no	Irrigation	no
Forest	M2	353	>3	9	yes	yes	Irrigation	yes
Forest	M3	127	1.3	6	yes	no	Irrigation	no

***Alpha-numerical codes denote the last name initial of land-owner and the number of ponds used. For convenience, pond codes were not changed.**

Three main habitat types surround each pond; these consist of forest, field and stream-riparian vegetation. The forest habitat consists of mixed deciduous-coniferous forest. In the agriculture dominated landscape, forest habitat occurs predominantly as fence-rows and isolated forest fragments. In the forest-dominated landscape, the forest habitat is predominantly continuous. Field habitats include both abandoned and cultivated fields. Stream and riparian systems include streams with no vegetation, streams with vegetation (including drainage ditches) and permanently wet areas.

Fences and traps. Partial drift fences were initially set in the early spring at five to twenty metres from ponds depending on topography and the degree to which the ground was frozen. The minimum number of fences set per pond was dependent on the size of the pond and the number of habitat types surrounding each pond. In order to assess the influence of habitat on anuran movement, fences were selectively placed in each habitat type surrounding ponds. Table 2 indicates the type and amount (in metres) of habitat at each pond and the proportion of habitat fenced.

Fences were made of nylon mesh (donated by Weavex Inc., Kentville, N.S.) and chicken wire (for stream areas) 50-75cm high and 19-40 metres in length. Fences were buried two to five cm into the ground to prevent amphibians from crawling under the fence. Each fence included four side-flap pail-traps (Nadorozny & Barr 1997), with two traps set up on each side of the fence to isolate captures for animals moving toward the pond (habitat side of fence) from individuals moving away from the pond (pond side of the fence). The number of traps within each habitat type and each landscape is outlined in Table 2.

Table 2. Table indicating the perimeter of the ponds, perimeter of habitat type surrounding the pond, proportion of habitat fenced and the total number of traps per habitat type within each landscape. Perimeter values are in metres.

landscape **	**pond**	**perimeter (metres)**		**field (metres)**		**forest (metres)**		**Stream-riparian (metres)**	
		total	pro.fen	total	pro.fen	Total	pro.fen	Total	pro.fen*
NF	A1	382	0.366	297	0.228	30	1	55	0.763
NF	B1	87	0.402	49	0.387	38	0.421	0	---
NF	C1	139	0.553	101	0.386	38	1	0	---
NF	D1	220	0.336	137	0.270	0	---	83	0.445
NF	D2	268	0.414	125	0.264	103	0.368	40	1
NF	S1	224	0.241	188	0.148	0	---	36	0.722
NF	**total**	**1320**	**0.371**	**897**	**0.249**	**209**	**0.583**	**214**	**0.677**
NF	**number of traps**				**28**		**16**		**24**
F	M1	163	0.417	65	0	65	0.538	33	1
F	M2	353	0.331	144	0.187	160	0.256	49	1
F	M3	127	0.629	40	1	87	0.459	0	---
F	W1	471	0.276	125	0.312	275	0.116	71	0.830
F	W2	85	0.411	0	---	80	0.375	5	1
F	W3	305	0.239	53	0.698	214	0.088	36	0.472
F	**total**	**1504**	**0.334**	**427**	**0.311**	**881**	**0.223**	**194**	**0.840**
F	**number of traps**				**16**		**28**		**20**
TOTAL		**2824**	**0.351**	**1324**	**0.269**	**1090**	**0.292**	**408**	**0.754**

*pro.fen = proportion of perimeter fenced.
**Landscape type abbreviations: NF = Non-Forest, F = Forest

Collection of data. Data were collected between 18 April 1996 and 31 October 31 1996. Traps were monitored every day until 16 June 1996, after which traps were checked daily on rainy days, and every second day on drier sunny days. This range of dates ensured that movements associated with all seasonal phases of anuran life histories were recorded: breeding migrations, summer foraging movements and over-wintering migrations to and from ponds. Although a number of species of amphibians and reptiles were captured, data were only recorded for the three target species, *R. sylvatica*, *R. pipiens* and *R. clamitans*.

Each captured frog was first measured. I recorded snout-vent length, which is the total length from the tip of the snout to the posterior end of the urostyle (Force 1933) and size of tympanum (inner ear). Sex was then determined using guidelines followed in Gilbert *et al.* (1994) (*R. pipiens*), Bellis (1965) (*R. sylvatica*) and Martof (1953) (*R. clamitans*). Males were sexed based on the presence of thumb pads, vocal sacs, coloration of throat (for *R. clamitans*) or obvious vocalization. Females were sexed conservatively based on the absence of these secondary sexual characteristics. Many individuals could not be sexed due to the subjective nature of the techniques. Four classes of frogs were consequently identified; males, females, adults (sex questionable, most likely young adults) and juveniles (metamorphosed during the field season).

Toe clipping. Frogs were individually marked by toe clipping to ensure that individuals were not counted twice, and also for the mark-recapture study (Chapter 2). Each unique identification consisted of a combination of three toes; followed by a combination of four toes once all possible three toe combinations had been used. Combinations were determined by clipping only one toe from the front feet and two toes from the hind feet. These combinations were used to minimize the number of toes clipped and to facilitate identification in the field. Because males use their thumbs to clasp females during the breeding phase and to maintain consistency, thumbs were not clipped on either sex.

Toe clipping involved three steps. First, the toes were washed using 70% ethanol. Second, each toe was crushed just below the first joint using fine curved Kellys to stimulate the release of chemicals with coagulative properties from the skin that help to minimize bleeding (C. Harvey-Clark, personal communication). Toes were then clipped using surgical scissors. Bleeding was observed in approximately two percent of all frogs, but by the time the frogs were released, bleeding had completely stopped. The implications of toe clipping is discussed in Chapter 2 (Mark-recapture study).

Data analysis.

The temporal patterns of movement within and between the two landscapes are presented graphically by plotting the log of the ratio of movement towards versus away from the ponds.

Generalized linear models were fitted to two response variables. In the first model, I used the number of trapping events defined by the number of times one trap captured one or more frogs. The number of trapping events was used to account for potential lack of independence in the data. In some cases, males continued to call when captured, attracting females (observed pairs in amplexus in traps). Consequently, this resulted in an overestimate of captured frogs. One limitation to using the number of trapping events is that the potential differences in movement influenced by the size of the frogs are not considered. In the second model, I used the corrected number of captures for each species in three size classes. Size classes were determined by dividing the range of sizes within each species into three different size groupings. The total numbers of individuals captured were then fit into one of the three size categories; small, middle and large sized frogs.

The independent variables tested in the two models include the following five spatial parameters:

1. side of fence	movement towards, versus away from ponds may influence the choice of habitat used
2. habitat	one of three habitat types, forest, field or stream-riparian habitat

3. landscape	forested landscape versus non-forested landscape
4. pond(landscape)	to account for distribution of three species within the 12 ponds
5. habitat:landscape	if similar habitats are used differently across the two landscapes.

Generalized linear models. Both response variables, number of trapping events and corrected number of captures for the three species-size combinations are count data which are appropriately modeled as a Poisson distribution (StatSci 1995). Initial models were conducted using Poisson regressions. The link function between the mean value of the response variable (μ) and the linear predictor y is $y = \log(\mu)$, following the assumption that the variance (σ^2) is equal to the mean (μ) with the dispersion parameter $\phi = \{(\sigma^2) / (\mu)\} = 1$ (StatSci 1995). Overdispersion $\phi > 1$, or underdispersion $\phi < 1$ implies that the models are not well fit. The initial Poisson models indicated that the data were overdispersed and to account for this, I used the quasi-likelihood estimation, which allows one to estimate the parameters within the models without fully knowing the error distribution of the response variables, i.e., without specifying what the distribution function is (StatSci 1995). The link, ($y = \log(\mu)$) and variance ($(\sigma^2) = (\mu)$) functions are the only parameters required for fitting the models. The dispersion parameters for all models are included in the results.

RESULTS

Species Diversity. A comparison of the number of ponds used by the three species, *R. clamitans*, *R. pipiens* and *R. sylvatica* suggests that there is no significant difference in the number of ponds used between landscapes, $\chi^2 = 0.1875$, p-value = 0.6. All three species were captured at 70% of the ponds, *with Rana clamitans* being the only species to occur in all ponds in both landscapes (Table 3). A comparison of the overall number of individuals captured in both landscapes indicates that 50% of all captures were *Rana pipiens*, while *Rana clamitans* and *Rana sylvatica* represent 29% and 21% of the captured individuals respectively. The mean number of species, including both amphibians and reptiles captured at the six ponds in the non-forested landscape is 4.2 ± 0.6 whereas in the forest dominated landscape a greater diversity of 7.2 ± 0.7 species was observed (Appendix 1).

Table 3. Summary of the number of ponds occupied by each target species, uncorrected and corrected number of adults captured within each landscape.

landscape	**species**	**number of ponds occupied**	**Uncorrected number of captures**	**corrected number of captures**
Forest	*Rana clamitans*	6	23	58
Forest	*Rana pipiens*	6	71	232
Forest	*Rana sylvatica*	5	34	90
NonForest	*Rana clamitans*	6	53	174
NonForest	*Rana pipiens*	5	35	158
NonForest	*Rana sylvatica*	5	30	72

Temporal activity. All three target species were trapped moving toward and away from ponds from the early spring (April 18 1996) until the late fall (October 31 1996). Weekly moving averages of the ratio of frogs moving toward versus away from ponds show a tri-phasic movement pattern (Figure 2). Interestingly, these tri-phasic seasonal patterns suggest similar trends in pond use for all three species. Peak movements into ponds occurred in early spring, at mid summer and mid fall. In the spring, there appears to be an initial efflux from ponds for *R. pipiens* and *R. clamitans* followed by an influx toward ponds. This may reflect the movement away from over-wintering sites in the early spring followed by the movement toward breeding ponds for these two species. For *R. sylvatica*, the movement away from ponds may reflect after breeding migrations, assuming that movement toward ponds occurred before the traps were completely set up.

The temporal movement at ponds also reflect differences within species. *R. pipiens* was the most continuously active species throughout the season. *R. sylvatica* was the least observed species moving at ponds and *R. clamitans* fell in between these two. A greater proportion of *R. clamitans* were captured moving toward ponds than away from ponds, whereas for the other two species, numbers appear balanced, with equal numbers moving toward and away from ponds throughout the season. For *R. clamitans*, this may represent dispersal toward permanent aquatic sites.

A comparison of the movement patterns between the two landscapes suggests that frogs generally moved less in the non-forested landscape (greater number of weeks with no movement detected) (Figures 3a, 3b and 3c). It also appears that there is a time lag (offset in most cases by one week) between movements in the non-forested landscape and in the forested landscape. This is more apparent at the beginning of the season, when the thawing of both ground and ponds in the more sheltered forested landscape may delay the onset of movement. Also of interest is the movement of *R. clamitans* at the end of the season. In the non-forested landscape, frogs are predominantly moving toward ponds, presumably for over-wintering, whereas in the forested landscape, this same species is moving away from ponds, suggesting that sites other than ponds may be used for over-wintering.

Within habitat differences. The vegetation surrounding each pond consists of different proportions of the three habitat types, field, forest and stream-riparian vegetation. As a consequence, the sampling intensity within each habitat type is potentially correlated to the different proportions of habitat and to the number of traps occurring within each habitat type. I used a χ^2 test (test of independence) to determine if the distributions of species across the habitat types was significantly different from the distribution of the traps within the three habitat types. The test determines if there is any association in the form of statistical dependence between the two variables, the number of traps per habitat type and the number of individuals captured per habitat type. The results suggest that the distribution patterns across the different habitat types are significantly different from the distribution patterns of traps within each habitat type (Table 4).

Table 4. Corrected number of adults captured and number of trapping events for each species in each landscape and type of habitat including number of traps per habitat type and proportion of habitat. Results of the χ^2 test indicating that the distribution of each species caught in the three different habitat types is not correlated to the distribution of the traps within each habitat type.

Landscape features				**corrected number of captures**			**number of trapping events**		
Site*	**Habitat**	**traps**	**habitat**	*clam.*	*pip.*	*sylv.*	*clam.*	*pip.*	*sylv.*
NF	Field	28	0.318	108	73	29	21	19	7
NF	Forest	16	0.074	44	76	37	19	7	17
NF	Stream	24	0.076	22	9	6	16	7	2
F	Field	16	0.151	1	59	8	1	20	4
F	Forest	28	0.312	35	106	51	14	26	11
F	Stream	20	0.069	22	67	31	13	38	11
χ^2 values testing correlation between number of traps and number of trapping events per species within each habitat type							12.178	19.840	16.876
$P(\chi^2)$							**0.0324**	**0.0013**	**0.0047**

Abbr.; clam. = *R. clamitans*, pip.= *R. pipiens*, sylv.= *R. sylvatica*.
•NF= NonForest landscape, F= Forested landscape.

Trapping events. The results of the generalized linear models comparing the influence of habitat and landscape across the three target species suggest three things. One, the type of habitat had a significant effect on the mean number of trapping events for only one species, *R. sylvatica*, and $p < 0.001$. Two, the type of landscape had a significant influence on the mean number of trapping events for all three species, $p < 0.001$, $p = 0.004$ and $p < 0.001$ for *R. sylvatica*, *R. clamitans* and *R. pipiens* respectively (Table 5). Three, there is a significant interaction effect between landscape and habitat type on the mean number of trapping events for *R. clamitans*, $p = 0.003$ (Table 5). The interaction plot suggests that stream and riparian habitat are used differently within the two landscapes. In the forested landscape, more trapping events occurred in the stream-riparian habitat, whereas in the non-forested landscape, the opposite was observed (Figure 4c). A similar pattern in stream-riparian habitat use was observed for *R. sylvatica* and *R. pipiens*, however, these trends were not significant (Figures 4a and 4b).

Table 5. Comparison between species, using a quasi-likelihood model to determine the influence of pond, habitat type and landscape type on the number of trapping events.

		SPECIES								
		R. sylvatica			***R. pipiens***			***R. clamitans***		
Source	**df**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**
side of fence	1	2.25	3.00	0.09	10.95	9.13	**0.00**	1.44	0.93	0.33
Habitat	2	15.24	10.13	**0.00**	2.26	0.94	0.39	1.85	0.59	0.55
Landscape	1	1.13	1.50	0.22	10.28	8.57	**0.00**	29.56	19.01	**0.00**
pond (landscape)	10	33.57	4.46	**0.00**	47.42	3.95	**0.00**	64.69	4.16	**0.00**
habitat:landscape	2	0.92	0.61	0.54	9.03	3.76	**0.03**	1.41	0.45	0.63
ϕ		0.752			1.199			1.554		

All P(F) values in **bold** denote significant effects in models.

ϕ Dispersion parameter

Size. Because the size and species of frog may influence movement patterns (Cushing 1992, Martof 1953, Thorson & Svihla 1943, Bellis 1962, Schmid 1965); I analyzed the effects of habitat and landscape on trapping events using three species-size class combinations. For my purposes, the effect of size was not considered independently of species; to do otherwise would have introduced a number of confounding factors. These are identified as within species differences. Species-size categories include potential differences associated with the developmental stage of the frog and differences associated with timing of movement. If sizes were linked across species, a within species term would have to be included in the models. Because of the small number of individuals captured and the unbalanced number of captures in some of the size-species categories, I have chosen to consider only within species differences. Plots of the species-size combinations suggest that there are differences in the size structure of the captured populations at the landscape level (Figures 5a, 5b, 5c). In the forested landscape, all three species indicate similar sized distribution patterns; the smallest frogs are the least abundant size class, the middle sized frogs are the most abundant size class and the largest size frogs fall in between these two. In the non-forested landscape, the largest frogs are in greatest abundance, followed by the middle-sized frogs and then the smallest sized individuals. These trends are most pronounced in *R. clamitans* (Figure 5c). To test the potential effects of landscape type on the species-size distribution, I conducted a series of generalized linear models for each species-size class combination.

No consistent trends were found within species or across the different size classes (Tables 6,7,8). However, a number of significant effects were observed. For *R. clamitans* and *R. pipiens*, the habitat type influenced the number of captures for all age classes (Tables 6, 7), whereas for *R. sylvatica*, only the middle sized frogs were significantly influenced by type of habitat (Table 8). The type of landscape significantly influenced the number of recaptures for both large and middle sized *R. clamitans*, for middle and small sized *R. pipiens* and for small sized *R. sylvatica*. There is a significant interaction effect between habitat and landscape on the middle and small sized *R. clamitans*, middle sized *R. pipiens* and small sized *R. sylvatica*.

Table 6. Comparison between the three size classes for *R. clamitans* using a quasi-likelihood model to determine the influence of pond, habitat and landscape elements on the corrected number of captures.

					Frog Size					
			Large (3)			***middle (2)***			***small (1)***	
Source	**Df**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**
side of fence	1	0.43	0.15	0.69	34.75	17.6	**0.00**	1.39	2.13	0.14
habitat	2	34.64	6.00	**0.00**	13.05	3.31	**0.03**	11.22	8.56	**0.00**
landscape	1	60.16	20.84	**0.00**	8.55	4.34	**0.03**	0.04	0.07	0.78
pond (landscape)	10	75.52	2.61	**0.00**	49.71	2.52	**0.00**	70.48	10.76	**0.00**
habitat:landscape	2	7.89	1.38	0.25	30.16	7.67	**0.03**	6.28	4.79	**0.00**
ϕ		2.887			1.966			0.654		

Table 7. Comparison between the three size classes for *Rana pipiens* using a quasi-likelihood model to determine the influence of pond, habitat and landscape elements on the corrected number of captures.

					Frog Size					
		large (3)			***middle (2)***			***small (1)***		
Source	**df**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**
side of fence	1	0.14	0.04	0.83	0.02	0.00	0.93	2.56	0.59	0.44
habitat	2	60.78	9.24	**0.00**	18.21	2.94	**0.05**	33.09	3.85	**0.02**
landscape	1	3.84	1.16	0.28	30.25	9.79	**0.00**	63.53	14.79	**0.00**
pond (landscape)	10	185.39	5.63	**0.00**	235.99	7.64	**0.00**	78.11	1.81	**0.06**
habitat:landscape	2	2.66	0.40	0.66	27.81	4.50	**0.01**	0.31	0.03	0.96
ϕ		3.289			3.087			4.295		

Table 8. Comparison between the three size classes for *Rana sylvatica* using a quasi-likelihood model to determine the influence of pond, habitat and landscape elements on the corrected number of captures.

Frog Size										
		large (3)			***middle (2)***			***small (1)***		
Source	**df**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**	**Deviance**	**F**	**P(F)**
side of fence	1	4.82	1.24	0.26	3.78	2.65	0.10	1.20	0.94	0.33
habitat	2	7.70	0.99	0.37	79.41	27.8	**0.00**	4.85	1.90	0.15
landscape	1	0.77	0.19	0.65	0.92	0.64	0.42	7.17	5.63	**0.01**
pond (landscape)	10	97.98	2.52	**0.00**	134.55	9.43	**0.00**	30.53	2.39	**0.01**
habitat:landscape	2	11.26	1.44	0.23	2.14	0.75	0.47	8.26	3.24	**0.04**
ϕ		3.884			1.426			1.272		

DISCUSSION

The specific habitat requirements and the temporally separated breeding phases for the three species, *R. sylvatica, R. pipiens and R. clamitans* suggest that movement patterns among species should vary both spatially and temporally. In this study, the movement patterns among species differ spatially, but do not appear to differ temporally. All three species demonstrate a similar temporal tri-phasic use of the ponds (Figure 2), with peak movements being associated with breeding, summer foraging and over-wintering phases. For *R. clamitans,* the most aquatic of the three species studied, this trend makes intuitive sense since this species spends most of its life around the pond (Gilhen 1984). However, for *R. pipiens* and *R. sylvatica,* this trend suggests movement occurring at ponds outside of the expected breeding phase for *R. sylvatica* and breeding and over-wintering phases for *R. pipiens* (Gilhen 1984). The movement peaks for these two species in the middle of the summer possibly reflects excursions and summer foraging behaviour of adults away from typical terrestrial habitats. Dole (1965) and Heatwole (1961) have observed such movements in *R. pipiens* and *R. sylvatica* respectively. The extent to which different sized individuals may be contributing to the tri-phasic nature of the movement distributions needs to be considered. For example, larger individuals moving toward and away from ponds during the breeding and over-wintering phases may be interspersed with sexually immature smaller frogs dispersing to new habitats mid summer as well as potentially searching for over-wintering sites later in the fall.

The distribution of *R. sylvatica* within the non-forested landscape may be indicative of such exploratory behaviours. *R. sylvatica,* characterized as a forest dwelling species (Gilhen 1984), was captured less often (5/6 ponds) in the forest-dominated landscape than in the non-forested landscape (6/6 ponds)(Table 4). Although *R. sylvatica* were captured in all six ponds in the non-forested landscape, in four of the ponds, fewer than five individuals were captured per pond, whereas only two ponds had fewer than five in the forest dominated landscape (Appendix 1). Potential factors influencing this trend between the two landscapes are the relative isolation of over-wintering sites to breeding sites (Loman 1988), the density and availability of temporary breeding sites and the species diversity within the ponds (influencing the amphibian community structure at ponds). Although the influence of species diversity was not tested on the relative proportions of the three target species, a greater diversity of species was found in all six ponds in the forested landscape (7 species) than in the non-forested landscape (4 species)(Appendix 1).

A comparison of the temporal activities and the number of trapping events between the two landscapes suggests that two of the three species of frogs, *R. pipiens* and *R. sylvatica* were more abundant in the forest dominated landscape whereas *R. clamitans* was more abundant in the non-forested landscape (Figures 3a, 3b and 3c). For *R. clamitans* and *R. pipiens,* a significant effect of landscape type on the number of trapping events was detected, $p<0.001$ for both species (Table 5). The extent of these movements is speculated to be influenced by two factors, one, the specific terrestrial resource requirements of the individual species and two, the proximity of the terrestrial resource habitats to ponds. This appears to be the case for *R. pipiens* and *R. sylvatica*, which require terrestrial resource habitats that are more abundant in the forested landscape; highly saturated soil areas within fields (Dole 1965) and forested habitat (Heatwole 1961, Bellis 1962, Bellis 1965) for these two species respectively. Only for *R. sylvatica* was a significant effect detected for habitat type on the number of trapping events $p<0.001$ (Table 5). Under a similar habitat configuration (forested habitat along ponds), Heatwole (1961) observed comparable movements for *R. sylvatica*.

Rana clamitans however; is predominantly an aquatic species (Martof 1953), and may be less dependent on the diversity of terrestrial habitats surrounding ponds. This would explain the greater abundance of this species in the non-forested landscape. The non-specific terrestrial resource requirements of this species may explain the non significant effect of habitat type on the number of trapping events $p=0.39$, (Table 5). Of interest, is the significant interaction effect between habitat and landscape, $p= 0.003$ for this species. A plot of this interaction indicates that in the forested landscape, the greatest proportion of *R. clamitans* was captured in the stream and riparian habitat, whereas in the non-forested landscape, these same habitats indicate the least amount of movement activity (Figure 4c). These same trends, although not significant, were observed for both *R. sylvatica* and *R. pipiens* (Figures 4a and 4b).

The movements at the end of the season for *R. clamitans* differ between the two landscapes (Figure 3c). During the fall, this species generally moves toward ponds for over-wintering (non-forested landscape), however, the movements indicate that a greater proportion of the frogs were moving away from ponds (forested landscape) suggesting that they may be over-wintering elsewhere. Both *R. pipiens* and *R. clamitans* have been known to use streams and river beds for over-wintering sites (Martof 1953, Cunjak

1985). These habitats are found in the forested landscape, and are much less abundant in the non-forested landscape.

A comparison of the size distributions for each species between the forested and non-forested landscapes suggests that the type of landscape has a significant effect on the size structure of the populations at ponds, $p(\chi^2=19.915) < 0.001$, $p(\chi^2=36.730) < 0.001$ and $p(\chi^2=6.367) = 0.04$ for *R. clamitans*, *R. pipiens* and *R. sylvatica* respectively (Figures 4a, 4b and 4c). In the forested landscape, numbers for the three size categories indicate that the smallest frogs are the least abundant, the middle sized frogs are the most abundant and the largest sized frogs fall in between these two size classes. In the non-forested landscape, the largest sized frogs do not show this same trend, but represent the most abundant size category across all three species. Intuitively, the smallest sized frogs represent sexually immature individuals not yet breeding but potentially dispersing to new aquatic sites. Therefore, movement toward ponds would occur infrequently and numbers caught should reflect this. The largest sized frogs are expected to be less abundant than the middle sized class reflecting typical anuran population dynamics where the larger sized frogs are also the oldest frogs and are therefore less abundant than younger frogs. Numbers of frogs caught should also reflect this. Such a pattern is observed in the forested landscape, however, the sizes of the individuals caught in the non-forested landscape do not reflect this. These differences in size structured trends are probably influenced by elements within the different landscapes.

A comparison of the regression models for each species-size combination indicates that a significant interaction effect between habitat and landscape was detected for all species. However, these significant effects were only observed within specific size classes (middle and small sized *R. clamitans*, middle sized *R. pipiens* and small sized *R. sylvatica*) (Tables 6,7 and 8). Significant habitat effects were detected for all species-size combinations for *R. pipiens* and *R. clamitans* and for middle sized *R. sylvatica*. Significant landscape effects were detected for large and middle sized *R. clamitans*, middle and small sized *R. pipiens* and small sized *R. sylvatica*. The inconsistency in significant effects of landscape elements within the different size classes suggests that within species, different mechanisms may be influencing movements associated with the different size classes. Proposed different movement behaviours may include such factors as individuals migrating to a breeding site in their first year (dispersing to a new breeding site) compared to individuals migrating to philopatric ponds in their second and older years. From this, two hypotheses are proposed. One, the developmental stage of the frog may influence the familiarity the frog may have moving to ponds, i.e., philopatric returns versus first year dispersers, is influencing movement behaviours. Two, the starting location of the frog, which can also be associated with the developmental stage of the frog is influencing movement behaviours. Consequently, to compare the use of habitats surrounding ponds, some indication of where the frogs are coming from should be assessed. In the following chapter, I displace frogs in order to assess how the initial location may influence their movement towards ponds (Chapter 2).

A number of conclusions can be drawn from this survey. All three species of anurans studied have a tri-phasic seasonal movement pattern toward and away from ponds within the forested and non-forested landscapes. There is a greater amount of movement activity within the forested landscape than the non-forested landscape. All species were found in a minimum of five and a maximum of six ponds within the two landscapes. *R. sylvatica* and *R. pipiens* are more abundant in the forested landscape whereas *R. clamitans* is more abundant in the non-forested landscape. The type of landscape and type of habitat significantly influence movements, however, the size of the frog appears to influence the relative significance of habitat type on movement. Although all three species require aquatic habitats in which to breed, *R. clamitans* (aquatic species) appears to be more restricted in movements at ponds than *R. pipiens* and *R. sylvatica*. The use of terrestrial summer habitats is thought to account for these differences.

Figure 1a). Forested landscape (45° 11.2' N, 64° 24.6' W) in the Annapolis Valley indicating the names and locations of the ponds used in the survey study (W1, W2, W3, M1, M2 and M3). Letters preceded by an '*' indicate release sites referred to in Chapter 2.

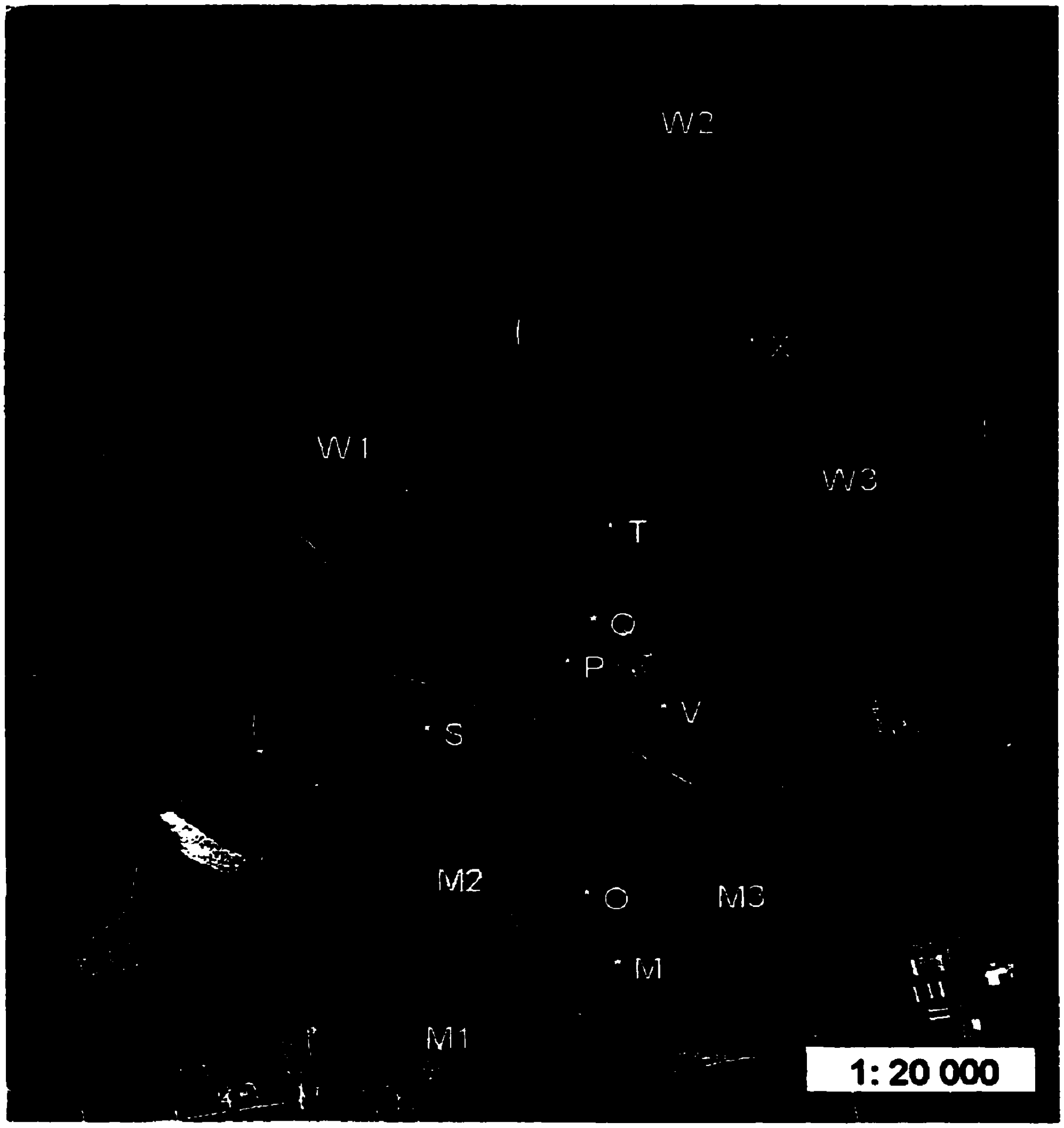

W2
X
W1
W3
T
Q
P
V
S
M2
O
M3
M
M1
1: 20 000

Figure 1b). Non-forested landscape (45° 06.7' N, 64° 25.9' W) in the Annapolis Valley indicating the names and locations of the ponds used in the survey study (D1, S1, A1, C1, B1 and D2). Letters preceded by an '*' indicate release sites referred to in Chapter 2.

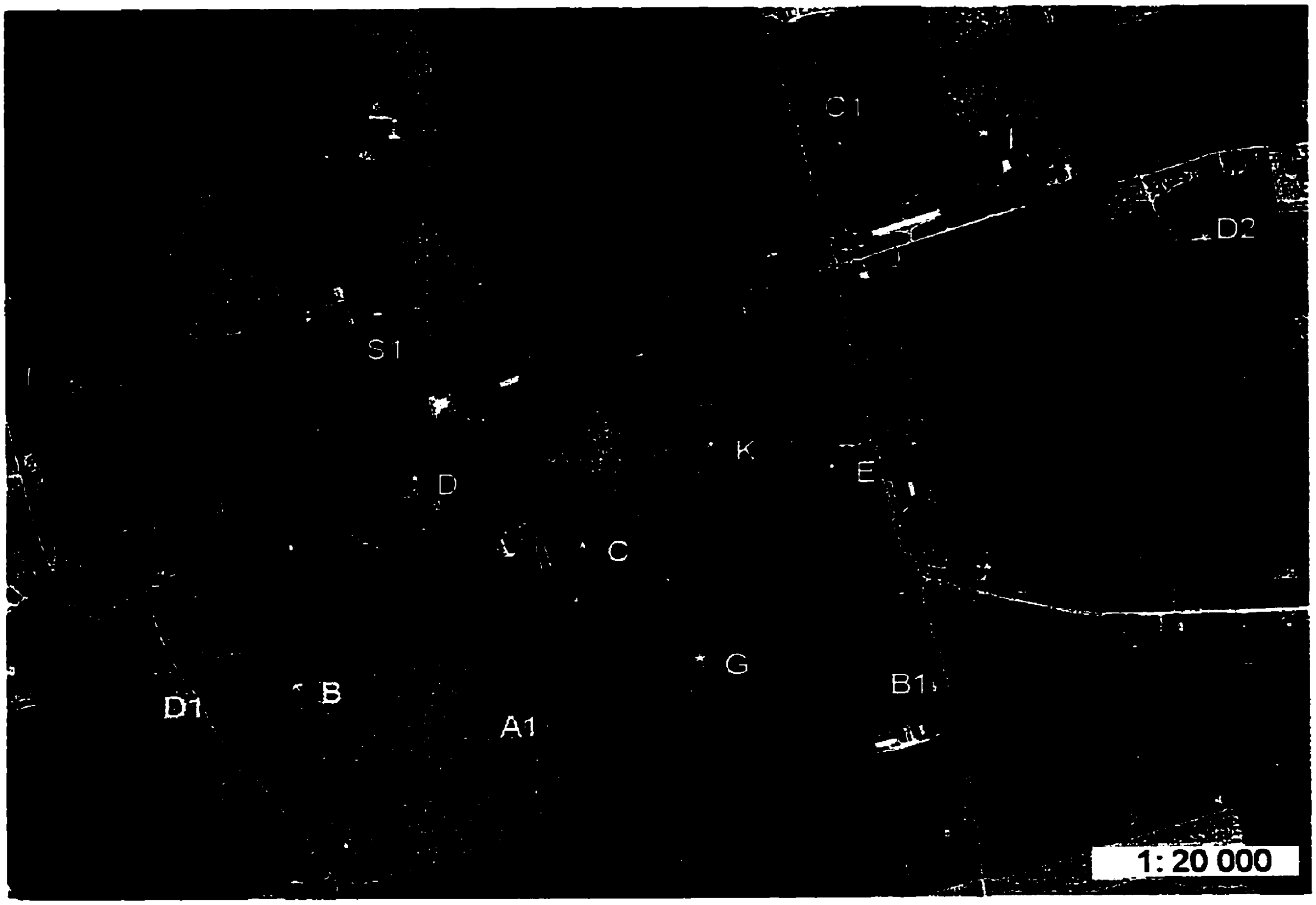
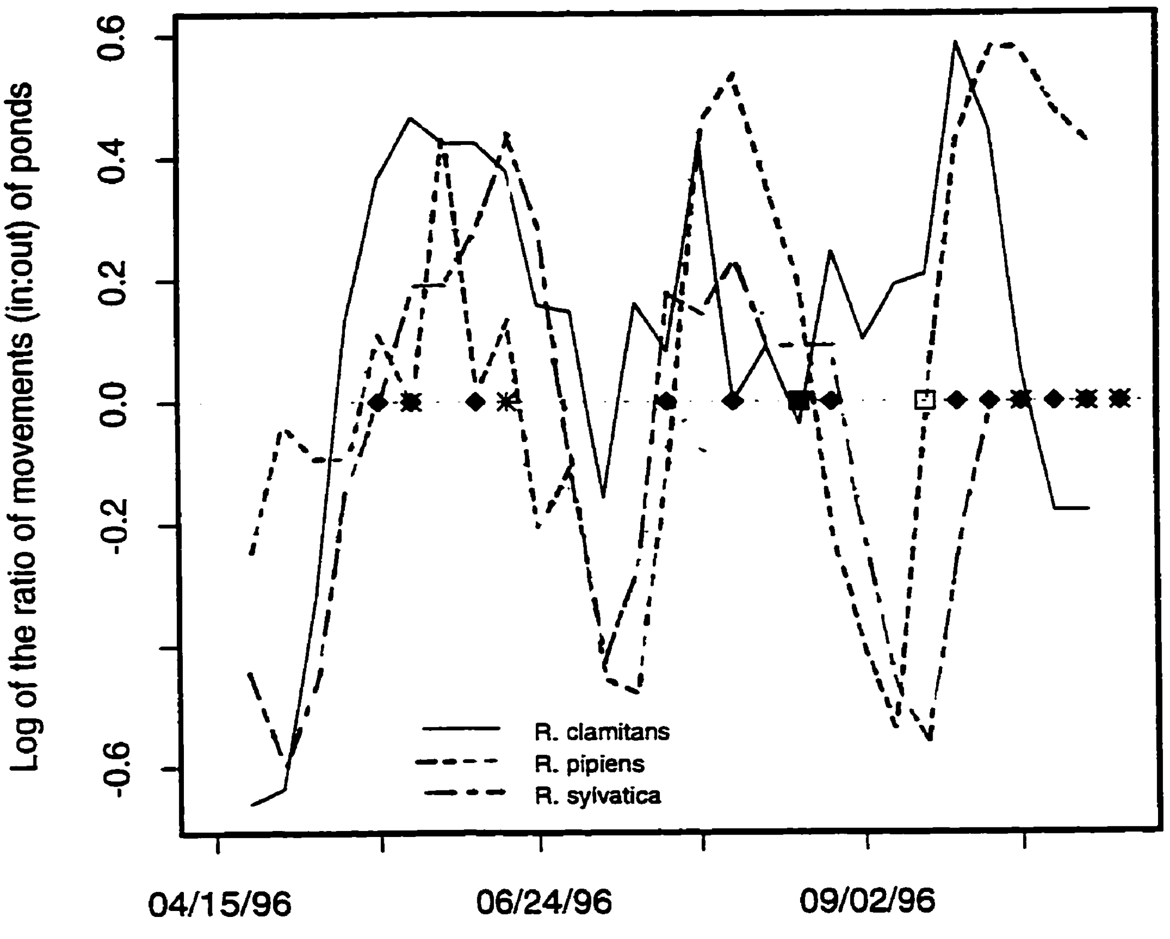

C1
D2
S1
K
E
D
C
G
B1
D1
B
A1
1: 20 000

Figure 2. Temporal movement patterns using a three week moving average of the log of the ratio of movements toward, versus away from ponds for *R. clamitans*, *R. pipiens* and *R. sylvatica*.

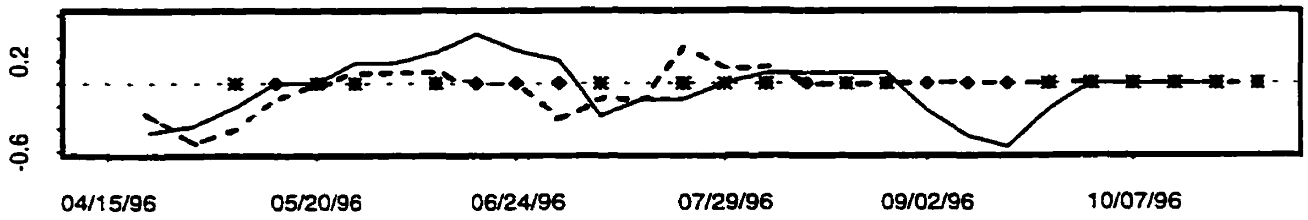
Values are pooled across the two landscapes. All values on the zero line denote weeks during which *R. clamitans* (✻) *R. pipiens* (☐) and *R. sylvatica* (◆) were not captured. Values above the zero line denote an influx of movement and values below the zero line denote an efflux of movement. The patterns indicate a tri-phasic oscillation.



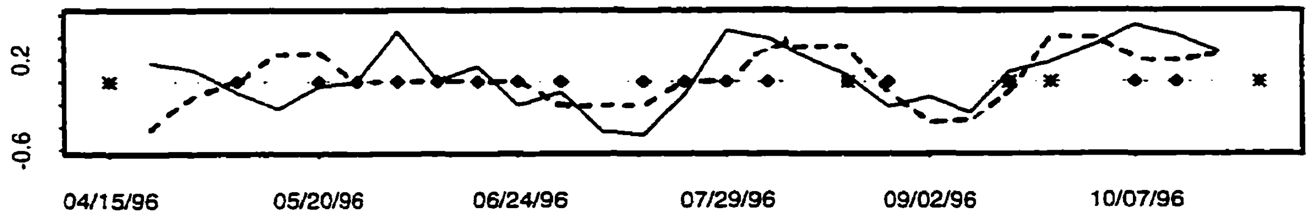
Weekly intervals from 18 April to 31 October 1997

Figure 3. Temporal movement patterns using a three week moving average of the log of the ratio of movements toward, versus away from, ponds between the forested and non-forested landscapes for *R. sylvatica* (a), *R. pipiens* (b) and *R. clamitans* (c). All values on the zero line denote weeks during which no frogs were captured in the forested (✱) and non-forested (◆) landscapes. Values above the zero line denote an influx of movement and values below the zero line denote an efflux of movement.

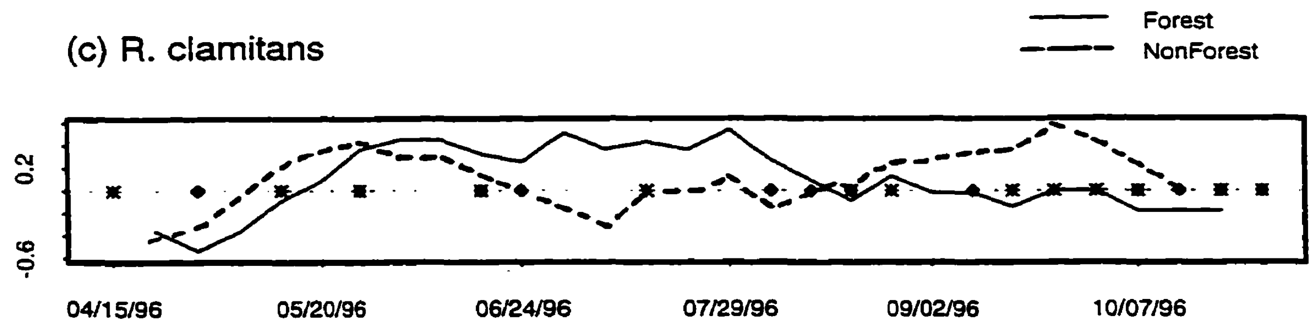
(a) R. sylvatica



(b) R. pipiens



(c) R. clamitans



Weekly intervals from 18 April to 31 October 1997

Figure 4. Interaction plot indicating the mean number of trapping events per habitat and landscape type for (a) *R. sylvatica*, (b) *R. pipiens* and (c) *R. clamitans*. Each line represents the response to the different landscape type: ——— for the Non-Forest landscape (NF) and - - - - - - for the Forest landscape (F). Each species denotes a similar response to both field and forest habitat in the two landscapes but a different response to the stream habitat. For all three species, the mean number of trapping events is lowest in the stream habitat in the NF landscape but highest in the F landscape.

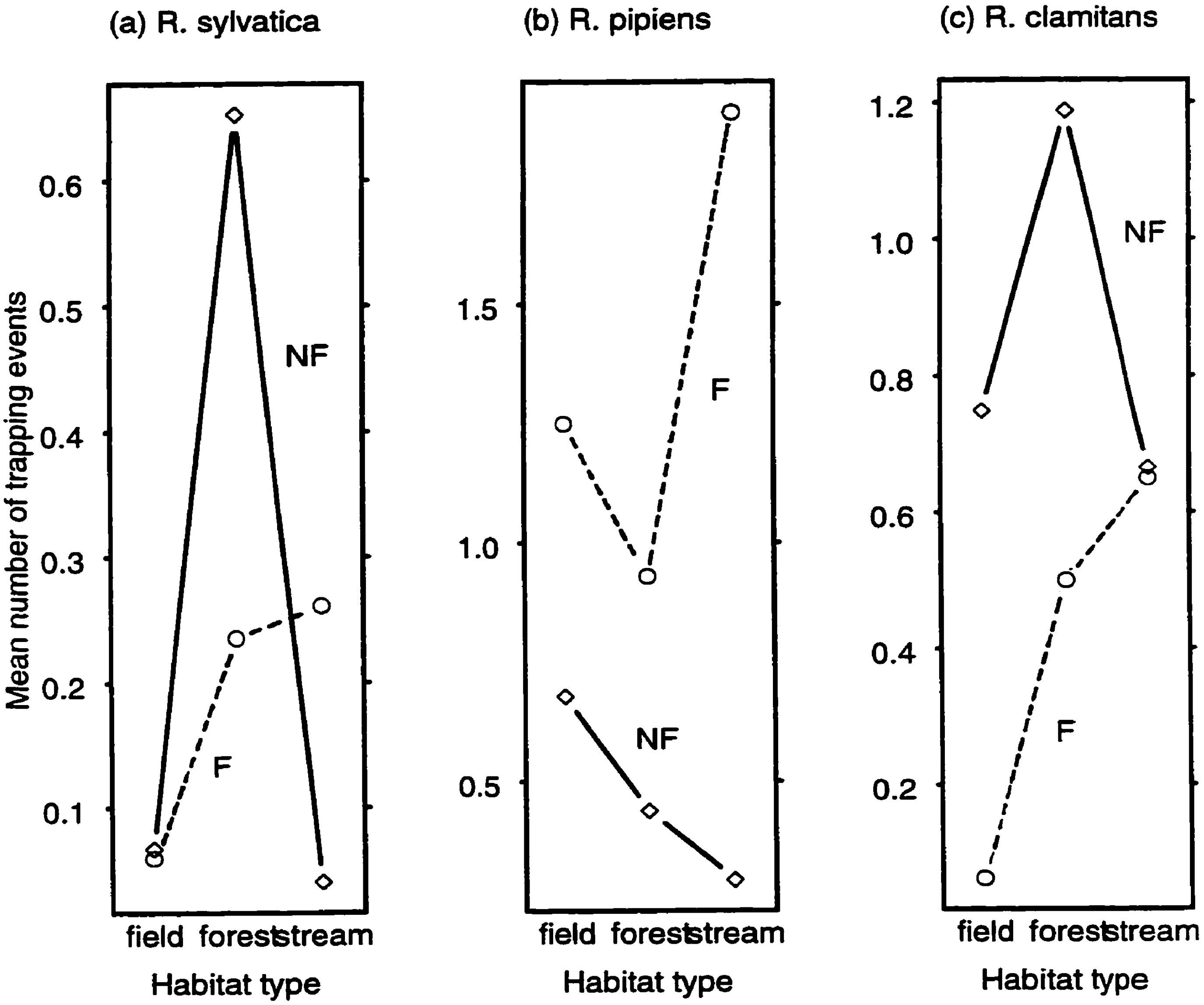
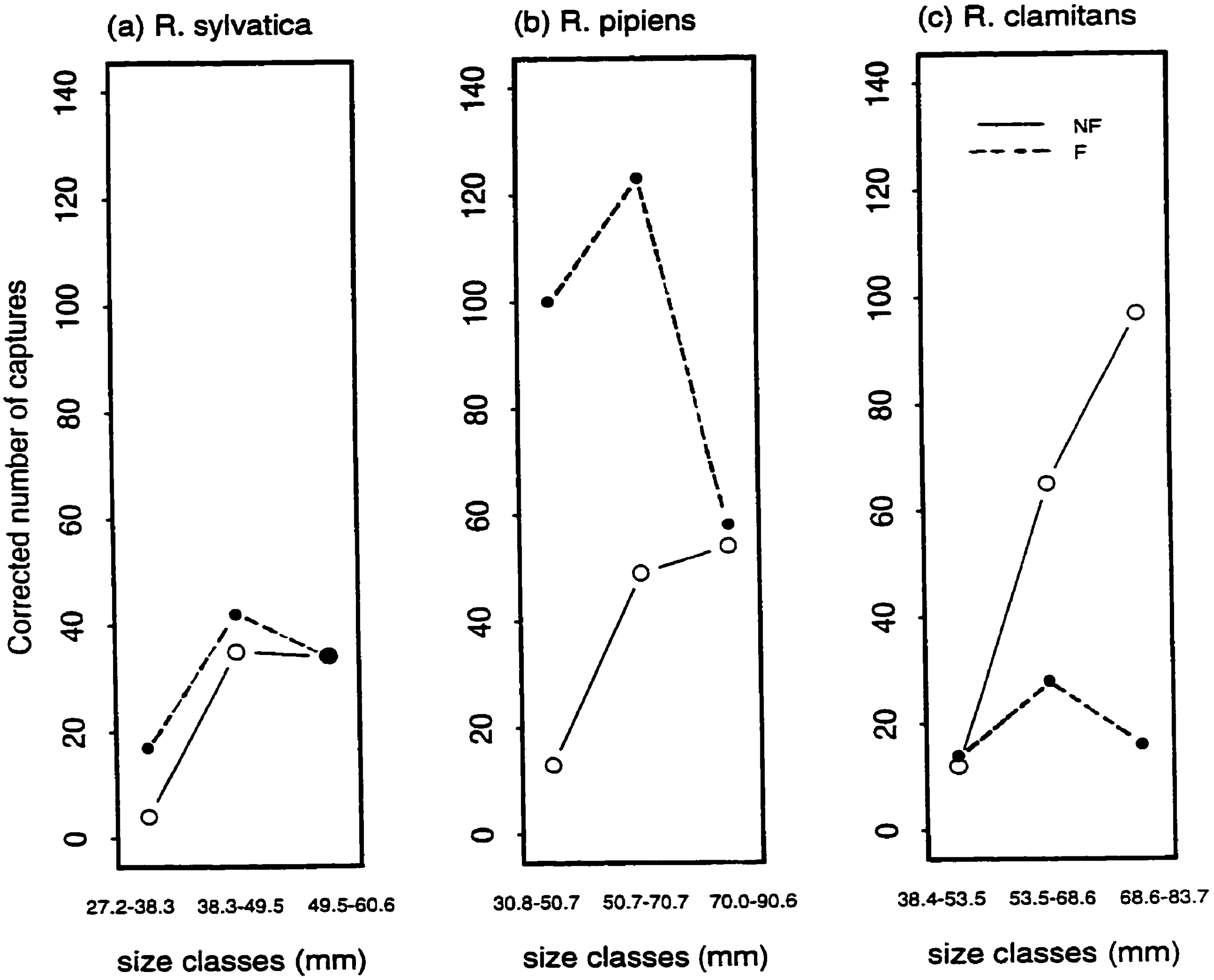

(a) R. sylvatica
(b) R. pipiens
(c) R. clamitans
Mean number of trapping events
0.1
0.2
0.3
0.4
0.5
0.6
NF
F
field
forest
stream
Habitat type
0.5
1.0
1.5
F
NF
field
forest
stream
Habitat type
0.2
0.4
0.6
0.8
1.0
1.2
NF
F
field
forest
stream
Habitat type

Figure 5. Plots of the corrected number of captures for each species-size class combinations; *R. sylvatica* (a), *R. pipiens* (b) and *R. clamitans* (c) in the NF (———) and F (- - - - - -) landscapes. Total numbers are n=72 and 90 for *R. sylvatica*, n=158 and 232 for *R. pipiens* and n=174 and 58 for *R. clamitans* in the NF and F landscapes respectively.


(a) R. sylvatica
(b) R. pipiens
(c) R. clamitans
Corrected number of captures
0
20
40
60
80
100
120
140
NF
F
27.2-38.3
38.3-49.5
49.5-60.6
30.8-50.7
50.7-70.7
70.0-90.6
38.4-53.5
53.5-68.6
68.6-83.7
size classes (mm)
size classes (mm)
size classes (mm)

Appendix 1. Uncorrected number of individuals captured including both adults and juveniles for all species of amphibians and reptiles caught at the twelve ponds in both the forested and non-forested landscapes.

Landscape	**Non-Forest**						**Forest**					
	pond											
species	A1	B1	C1	D1	D 2	S1	M1	M2	M3	W1	W3	W2
Rana sylvatica	3	19	8	1	1	1	9	8	119	1	19	0
Rana pipiens	7	0	19	74	10	7	118	300	62	150	25	3
Rana clamitans	9	34	94	5	23	12	39	21	10	67	23	9
Rana catesbeiana	0	0	1	0	0	0	0	0	0	0	1	0
Bufo americanus	15	0	0	10	47	2	0	0	0	0	0	0
Hyla crucifer	1	6	0	1	0	0	1	2	2	9	9	0
Ambystoma maculatum	0	0	0	0	0	0	14	60	61	85	38	13
Notophthalmus viridescens	0	0	0	0	0	0	15	16	27	294	6	0
Chrysemys picta	1	0	0	0	0	0	0	2	0	1	0	0
Thamnophis sirtalis	0	0	0	0	0	0	0	1	1	0	4	0
no. species	5	3	4	5	4	4	6	8	7	7	8	3
x and σ	4.2 ± 0.6						6.5 ± 3.5					
x and σ (excluding W2)**	-------						7.2 ± 0.7					

**W2 excluded because the water temperature for this pond was ~ 15°C cooler than all other ponds.

Appendix 2. Size and distribution of corrected number of individuals per size class (from large 3 to small 1) at each pond for each of the three species, *R. clamitans*, *R. pipiens* and *R. sylvatica*.

		Rana clamitans			***Rana pipiens***			***Rana sylvatica***		
site	**pond**	**3**	**2**	**1**	**3**	**2**	**1**	**3**	**2**	**1**
NF	A1	10	21	0	0	4	3	3	3	1
NF	B1	28	10	0	0	0	0	18	23	3
NF	C1	5	2	0	10	17	0	6	6	0
NF	D1	13	0	0	33	20	4	0	0	0
NF	D2	19	12	10	0	4	6	0	3	0
NF	S1	22	20	2	11	4	0	7	0	0
NF	**total**	**97**	**65**	**12**	**54**	**49**	**13**	**34**	**35**	**4**
F	M1	7	6	2	1	18	12	5	5	4
F	M2	1	3	0	7	23	8	6	0	9
F	M3	0	5	2	0	1	1	5	9	0
F	W1	0	11	0	38	81	33	0	0	0
F	W2	6	3	10	0	0	8	0	0	0
F	W3	2	0	0	12	0	38	18	28	4
F	**total**	**16**	**28**	**14**	**58**	**123**	**100**	**34**	**42**	**17**

Chapter 2

Mark-recapture Study

INTRODUCTION

One approach to assessing the ability of amphibians to move through landscapes is by conducting mark-recapture studies. Mark-recapture studies provide an indirect technique for quantifying organism movement by assessing the overall displacement of an organism between the point of release and recapture (Turchin et al. 1991). Such experiments have provided information on the philopatric nature of frogs (Oldham 1967, Dole 1968, Dole 1972, Gill 1978b, Berven & Grudzien 1990, Guttman et al. 1991, Heusser 1960, Wassersug 1973), the home ranges of many species of amphibians (Martof 1953, Heatwole 1961, Dole 1965, Bellis 1965) and the seasonal and temporal fluctuations of breeding populations (Berven 1990, Gill 1978a, Jehle *et al.* 1995, Pechmann *et al.* 1989, Berven 1995). At large spatial scales, these studies demonstrate the temporal fluctuations of breeding communities within a pond (Hecnar and M'Closkey 1996), the breeding success within ponds (Pechmann *et al.* 1989) and the effects of isolation on dispersal abilities (Vos and Stumpel 1995). At small spatial scales, the distances moved by individuals have provided information on local feeding behaviours (Dole 1965), territorial responses influencing movement (Martof 1953), and the ability of displaced frogs to relocate their initial capture sites (Dole 1968, Dole 1972, Oldham 1967). What has not been studied is the influence of different habitat types on the movement behaviours of anurans. More specifically, the influence of intervening habitats on the movement patterns of individuals migrating to breeding, summer foraging and over-wintering sites is not known. These processes are speculated to occur at the meso level within landscapes, where the type, position and amount of habitat will influence the movements of individuals. Because anurans are a group of organisms with a relatively limited mobility (Vos & Stumpel 1995), the extent to which required resource patches are isolated from one another will influence their movement behaviours across the landscape (Loman 1990, Laan & Verboom 1990, Sjögren 1991). Studies have indicated that a number of landscape features may influence anuran migrations to required resource patches. *R. sylvatica* and *Ambystoma maculatum* (Guttman et al. 1991) have been observed to selectively move via ravines as they migrate to breeding sites. Species such as *Bufo americanus* (Maynard 1934) and *R. pipiens* (Seburn *et al.* 1997) have also been observed to move via stream systems. These studies suggest that movement between required resource sites may be directed by landscape features. One of the consequences of anthropogenic activities is the depletion and replacement of forest and stream-riparian habitat with cultivated fields and irrigation ditches. To what extent have these 'replacement habitats' influenced anuran movements? The objective of this study is to assess the influence of various landscape elements on the philopatric behaviour of adult frogs moving to a required resource, the breeding pond.

To assess the influence of landscape structure on the movements of anurans, I experimentally manipulated three species of frogs by releasing them at fixed distances away from ponds in two different landscapes; one dominated by forest habitat where forest cover is continuous, the other by agriculture, where forest cover is highly fragmented. The forested landscape consists predominantly of forests with stream systems and riparian vegetation. In the agriculture dominated landscape, the forests, streams and riparian systems have been replaced with fields and a network of irrigation ditches. By selectively choosing the release sites, I was able to specify *a priori* the starting location of the frogs. This allowed me to compare routes from the release sites (starting point), to the philopatric ponds (end point). A comparison could then be drawn between the routes for which frogs successfully returned to ponds and those for which frogs did not. The implication is that the differences in land use patterns across the two landscapes will reflect differences in anuran movement patterns. I hypothesized that the type of landscape would influence the proportion of frogs successfully returning to philopatric ponds, and that the differences observed at the landscape level are influenced by the types and amount of vegetation along a route.

METHODS

Data set. All adult *Rana sylvatica*, *R. pipiens* and *R. clamitans* captured in the side-flap pail traps in the survey conducted from April 18, 1996 to October 31, 1996 were used in the mark-recapture study. The seasonal extent of this study consequently included all movements associated with breeding, summer foraging and over-wintering migrations to and from ponds. For *R. sylvatica*, movements toward and away from ponds during the breeding phase are considered, for *R. pipiens*, movements toward and away from ponds during the breeding and over-wintering phases are considered, and for *R. clamitans*, movements are associated with all phases of the frog's life history.

Toe clipping. Refer to Toe clipping Section in Chapter 1 for protocol (pg. 13).

Implications of toe clipping. Studies documenting the impact of toe clipping on the survivorship and movement behaviours of frogs are limited. However, the findings proposed by Clarke (1972) suggest that toe clipping does influence the recapture rates of *B. woodhousei*. Clarke showed that as the number of cut toes increased, the proportion of recaptures decreased. In order to minimize the potential influence of toe clipping on the proportion of frogs recaptured, I minimized the number of toes cut by only cutting a minimum of one toe and a maximum of two toes from the front feet and maximum of two toes from the hind feet. Unlike Martof (1953), I did not cut more than four toes in order to minimize potential effects on survivorship. The proportion recaptured in this study denotes a similar trend to the proportion of frogs returning to ponds in the radio-telemetry study (Chapter 3). In this study (mark-recapture), 19 (corrected captures) of 228 initially released frogs successfully returned to a pond, denoting an 8.3% recapture rate. In the radio-telemetry study, three of the 32 frogs tracked and toe-clipped returned to a pond denoting a 9.3% return rate. Of the 29 remaining, all but three had died, and these three were eaten by animals. This suggests that toe clipping has not compromised the survivorship. The influence of toe clipping on movement is more difficult to assess. Because most of the recaptures were initially caught in the early spring, all individuals had a left front toe clipped. This is presumed to create a temporal effect and the influence of having clipped a right front toe versus a left front toe can not be explored. There is no observable trend in the pattern of toe clipping in the hind feet for individuals recaptured. This suggests that the movement behaviours of the frogs although potentially compromised are consistent for all toe clipped individuals.

Sexing frogs. In order to consider the potential influence of sex and reproductive state of the frogs on movement, all frogs captured were sexed. Refer to Sexing frogs section in Chapter 1 for protocol.

Release sites. The extent of philopatric behaviour for displaced frogs appears to be influenced by the distance at which frogs are released from the pond. However, the displacement distances proposed in the literature are variable; one km for *R. pipiens*, Dole (1968) and between 548 metres and greater than two km for *R. clamitans* (Oldham 1967). In this study, marked animals were displaced at two different distances from their philopatric ponds in order to consider the effect of distance on philopatric behaviour. A short distance release site (200 - 300 meters) and a long distance release site (600 - 800 meters) were selected for each of the twelve ponds in the two landscapes. Each release site was equidistant from the pond in which the frog was initially captured (philopatric pond) and to a neighbouring pond (non-philopatric pond). By having release sites equidistant from two or more ponds, any variation associated with distance is minimized and the influence of habitat on movement can be explored.

All adult frogs caught on a daily basis were released on a daily basis at either a short or long release site. The number released at each site was determined by numbers initially caught, with equal numbers released at each site.

Data analyses. Numbers recaptured were divided by the numbers initially released in order to obtain the proportion recaptured per release site. In all but one case, recaptures (eight of nine) were released at the short (200-300 meters) release sites, and therefore, only routes from short release sites were quantified and used in the model. Routes from release sites to philopatric and non-philopatric ponds are characterized by the presence or absence of linear aquatic elements (including drainage ditches and streams) and linear roadways, and the type and proportion of habitat along a route. The types of habitat include;

1. field, including both fields covered with vegetation (crops), and fields without cover (ploughed fields).
2. forest, including continuous forest, forest fragments and fence-rows.
3. wet habitat, including riparian vegetation, streams and drainage ditches.

4. residential areas.

A binomial regression model was used to test the effects of proportion of habitats and presence or absence of linear elements within routes, on the proportions recaptured. The terms in the model were tested against a χ^2 distribution.

RESULTS

Of 228 frogs released in this study, 9 individuals were recaptured, with approximately equal numbers caught in each landscape (Table 1). A significant effect of landscape type was detected, P(4.100) = 0.04, on the proportion of *R. sylvatica* recaptured, with the highest proportion occurring in the non-forested landscape (Table 1). The proportion of *R. pipiens* recaptured was approximately the same in both landscapes. *R. clamitans* was the least caught species in this study.

Table 1. Number of frogs released (rel), corrected number of frogs recaptured (rec) and proportion of frogs recaptured (pro) on per species and per landscape basis. Results of χ^2 test indicating if numbers recaptured in forested landscape are significantly different from numbers recaptured in non-forested landscape.

Species	***R. clamitans***			***R. pipiens***			***R. sylvatica***			**Total**		
Landscape	rel	rec	pro	rel	Rec	pro	rel	rec	pro	rel	rec	pro
non forest	50	2	0.04	35	3	0.09	25	6	0.24	110	11	0.10
Forest	22	0	0.00	68	8	0.12	28	0	0.00	118	8	0.17
Total	**72**	**2**	**0.03**	**103**	**11**	**0.11**	**53**	**6**	**0.11**	**228**	**19**	**0.08**
χ^2 test	0.0126			0.022			4.1002			0.3244		
$P(\chi^2)$	0.8821			0.9107			**0.0429**			0.569		

Of the 113 frogs released at short distances (200-300 meters) and 115 frogs released at long distances (600-800 meters) from ponds, eight of the nine recaptures were from the short distance release sites (Table 2). Tables 3a and 3b outline the numbers caught and released from each pond, the numbers released at each release site and the proportions recaptured at each pond. Figures 1a and 1b demonstrate the spatial distribution of release sites to each other and to other ponds as well as the straight line routes from the release sites to the ponds along which frogs successfully returned. Differences between numbers recaptured between the two landscapes within each distance class were not significant, p=0.80 and p=0.94 for short and long release sites respectively (Table 2).

Table 2. Summary of the number of frogs released and the uncorrected number of frogs recaptured at short and long distances within each landscape. Influence of landscape on the number of frogs recaptured in each distance class is tested using a χ^2 test for assessing association between the two distributions.

landscape	**Short**		**long**	
	Released	recaptured	released	recaptured
non-forested	54	4	54	0
forested	59	4	61	1
Total	113	8	115	1
proportion recaptured	0.071		0.009	
χ^2 value	0.060		0.004	
$P(\chi^2)$	0.80		0.94	

Philopatric behaviour of frogs. In 7 out of 8 cases, frogs returned to the same pond when released within 300 meters of the pond at which they were initially captured. In only two cases did frogs return to a different pond; one was released 600 metres from the pond and returned to an alternate pond located within 300 meters of the release site, and in the other case, the frog was released within 300 meters of the initial pond, but was recaptured at a pond more than one km away (Table 4).

For individuals recaptured, the rates of movement per day suggest that frogs initially caught moving into ponds, once released, generally traveled at a faster rate than frogs initially moving out of ponds (Figure 2a). The side of fence on which the frogs were initially caught may be indicative of the physiological state of the frog, i.e., gravid, non-gravid for females and the breeding state of males. Although the sample sizes are small, the data suggest that gravid females generally moved at a faster rate than males, and males generally moved at a faster rate than the non-gravid females (Figure 2b). Although these movement rates must be interpreted cautiously, they are suggestive that certain physiological mechanisms may be influencing the movements of frogs within a landscape.

Table 3. Proportion and number of frogs displaced and recaptured at two distance classes; short distances (a), 200-300 metres and long distances (b) 600-800 metres in the two landscapes.

(a)

landscape*	pond from which frogs released	release site	numbers released	numbers recaptured	return to same pond?	proportion recaptured
NF	A1	D	5	0	N/A.	0.00
NF	B1	G	14	2	yes, yes	0.14
NF	C1	I	12	2	yes, no	0.17
NF	D1	B	8	0	N/A.	0.00
NF	D2	I	9	0	N/A.	0.00
NF	S1	D	4	0	N/A.	0.00
F	M1	M	12	3	yes, yes, yes	0.25
F	M2	S	11	0	N/A.	0.00
F	M3	V	6	0	N/A.	0.00
F	W1	S	13	1	yes	0.08
F	W2	X	2	0	N/A.	0.00
F	W3	T	9	0	N/A.	0.00

NF=Non-Forest, F=Forest.

(b)

Landscape	pond from which frogs released	Release site	numbers released	numbers recaptured	return to same pond?	proportion recaptured
NF	A1	E	3	0	N/A.	0.00
NF	B1	D	16	0	N/A.	0.00
NF	C1	C	11	0	N/A.	0.00
NF	D1	C	9	0	N/A.	0.00
NF	D2	K	7	0	N/A.	0.00
NF	S1	E	8	0	N/A.	0.00
F	M1	Q	14	0	N/A.	0.00
F	M2	T	13	0	N/A.	0.00
F	M3	X	5	0	N/A.	0.00
F	W1	O	15	1	no	0.07
F	W2	P	4	0	N/A.	0.00
F	W3	S	10	0	N/A.	0.00

Table 4. Landscape, species, date initially captured (date cap.) and recaptured (date recap) and time difference in days between captures, philopatric nature of frog, distance moved by frog and rate of movement between release site and pond of recapture.

Landscape	**Species**	**date cap.**	**date recap**	**time (days)**	**same pond**	**same trap**	**distance (m)**	**rate (m/day)**
NF	*R. clamitans*	7/16/96	7/29/96	13	yes	no	300	23.1
F	*R. pipiens*	7/16/96	8/16/96	31	yes	no	140	4.5
F	*R. pipiens*	6/5/96	6/10/96	5	yes	no	220	44.0
F	*R. pipiens*	4/22/96	6/2/96	41	yes	yes	220	5.4
F	*R. pipiens*	4/25/96	5/2/96	7	yes	yes	300	42.9
F	*R. pipiens*	5/2/96	5/6/96	4	no	N/A.	140	35.0
NF	*R. pipiens*	5/3/96	5/18/96	15	yes	no	290	19.3
NF	*R. sylvatica*	4/18/96	4/21/96	3	yes	no	300	100
NF	*R. sylvatica*	4/22/96	7/20/96	89	no	N/A.	1100	12.4

A comparison of the proportion of individuals recaptured at philopatric ponds initially displaced to short release sites indicates that the type and proportion of habitat along a route will influence the movement patterns observed. Based on the results of a stepwise regression using a binomial model, the proportion of field habitat had a significant effect on the movement of frogs to philopatric ponds (p=0.0550, Table 5). Within both landscapes, the proportion of frogs recaptured at ponds appears to increase as the proportion of field habitat within a route increases (Figure 3a). In contrast, it appears that as the proportion of both forest and aquatic habitats within a route increases, the number of frogs recaptured at the pond decreases (Figures 3b, 3c). Roadways appear to influence somewhat the movement patterns of the frogs. The presence of streams and drainage ditches does not appear to facilitate the movement of frogs from the release sites to philopatric ponds. The proportion of frogs recaptured at ponds is greater in the absence of both these linear elements along the routes (Figures 4a, 4b). I emphasize the influence of linear aquatic elements or drainage ditches on impeding the movements of frogs. I observed R. *clamitans* and *R. pipiens* at a drainage ditch release site up to two months after the frogs had been initially released (personal observation). The animals occupied different territories along the drainage ditch and had not moved even after periods of heavy rain.

Table 5. Results of the binomial model testing the effects of intervening habitats within routes from release sites to philopatric ponds using the proportion of frogs recaptured.

Terms	Df	D	Resid df	Resid D	$P(\chi 2)$
Null model			12	16.01	
Percent field	1	3.68	11	12.32	0.0550
Presence road	1	0.82	10	11.51	0.3654
Presence aqua*	1	0.00	9	11.50	0.9436
Landscape	1	2.53	8	8.97	0.1114

Terms added sequentially (first to last)
*Presence aqua=aquatic systems

DISCUSSION

The objective of this study was to assess how various landscape features influenced the return of adult frogs to philopatric ponds from which they were initially displaced. Out of a possible 24 release sites (twelve sites in each landscape), only five sites had recaptures, three of which had more than one recapture (Tables 3a and 3b). The multiple recaptures observed at three of the sites do not fully reflect the numbers initially released, suggesting that certain elements within the landscapes may be facilitating the movement of the frogs.

The reproductive state of the animal is a potential factor influencing the pattern of movements observed. Although no distinction was made between frogs initially caught in traps moving toward versus away from ponds, the frogs moving toward ponds when released generally moved at a faster rate than frogs moving away from ponds (Figure 2a). The assumption is that frogs moving toward ponds are pre-breeders and frogs moving away from ponds are post-breeders, implying that the reproductive state of the frogs is influencing their movements. The trends in the data, although not significant, suggest that gravid females generally move at a faster rate than males, and males moved at a faster rate than the non-gravid female (Figure 2b). Consequently, the final destination of the frogs may be influenced by their reproductive state, thereby influencing the time the frogs spend within terrestrial habitats. Turchin (1991) suggests that the speed of movement is a response of organisms to environmental heterogeneity, and for the non-reproductive frogs, the time elapsed between release and recapture sites may reflect the behavioural responses of these animals as they explore different terrestrial habitats. Dole

(1965) found that exploratory excursions by adult frogs do occur, and that these excursions help the frog to establish familiarity with the environment (Dole 1965). One of the limitations of this study is that the movement within specific terrestrial habitats cannot be ascertained.

The distance at which frogs were released from ponds had a significant effect on the proportions recaptured. Eight of the nine individuals recaptured were released at short distances (200 - 300 meters) from ponds, and of these eight, seven returned to the same pond (Tables 3a 3b), two of which were recaptured in the same trap (Table 4). Such philopatric behaviour has been observed among a number of different amphibian species including *R. clamitans* (Oldham 1967), *R. sylvatica* (Berven & Grudzien 1990, Guttman et al. 1991), *R. pipiens* (Dole 1968), *N. viridescens* (Gill 1978), and *Bufo americanus* (Dole 1972). In other displacement studies using *R. pipiens* (Dole 1968) and *R. clamitans* (Oldham 1967), the frogs were able to orient in the direction of the pond from which they were initially captured, at distances ranging between 400 and 800 metres. At distances beyond 800 metres, frogs were unable to do this. My results do not necessarily agree with the distances proposed by Dole and Oldham. Different criteria were used to assess the return to ponds and this may support our different conclusions. In the studies by Dole and Oldham, orientation in the direction of the ponds was used, whereas, I used a successful return to the pond. However, I propose that the differences between these studies are influenced by the structure of the landscapes between the release sites and the philopatric pond of the frog. Loman (1990) proposed that the characteristics of the habitats crossed would influence the distances frogs are able to move across the landscape.

To assess the influence of landscape structure on the movement behaviours between the release sites and ponds at which recaptured, only routes with release sites at short distances from philopatric ponds were included in the analyses. Considering that most of the recaptures were at the short distance, this seemed a reasonable criterion on which to base the analysis. The model suggests that a high proportion of field habitat between a release site and a pond will facilitate the return of the frogs to their aquatic sites (Table 5). Routes with a high proportion of field have a greater number of recaptures (Figure 3a), whereas routes with a high proportion of forest or wet habitat appear to negatively influence movements to aquatic sites (Figures 3b and 3c). The responses of the frogs to the specific types of habitat need to be explored more fully.

Other landscape elements potentially affecting frog movements are the presence of drainage ditches, streams and roads. Although these variables were not significant in the models, more frogs were recaptured in the absence of these linear systems (Figures 4a and 4b). The presence of roadways have been shown to reduce the size of breeding populations as a consequence of the high proportion of frogs killed by autos, especially during the breeding season (Fahrig *et al.* 1995, Mader 1984). In this study, fewer autos travel along roadways in the forested landscape than on the roads in the non-forested landscape. I speculate that the difference in traffic intensity will influence the size structure of the frog populations within each landscape. The greater proportion of large versus smaller sized adult frogs observed in the survey study (Chapter 1) support the conclusion that the death toll on dispersing young adults is high. Where the roadways are less traveled, as in the forested landscape, the smaller sized frogs are in greatest abundance. I conducted a survey during the rainy evening of July 29 1996 along the roadways in the agriculture dominated landscape and found that all three species were observed moving in this habitat (unpublished). *R. sylvatica* (n=4) and *R. clamitans* (n=6) were the most abundant species on the road (only 1 individual of *R. pipiens* was observed). Mortality rate of all observations was 70%. This suggests that in the agricultural landscape, roadways do have a negative effect on the movement on frogs.

In both landscapes, the effects of streams and drainage ditches appear to impede frog movements to ponds (Figure 4b), however I propose that the reasons are other than those observed in the road systems (associated with mortality). Frogs released within drainage ditches and at streams appear to remain in these habitats for extended periods of time. I have observed *R. clamitans* establishing territories and remaining in pools of water within the drainage ditches at my release sites in the agriculture dominated landscape. I have also observed *R. sylvatica* (radio-telemetry; personal observation) remaining in the bottom of the drainage ditch where the ground was moist during dry sunny periods and move up along the bank of the drainage ditch but not leaving the area during rainy periods. This suggests that drainage ditches are acting as a resource habitat for these frogs.

Are frogs that remain in drainage ditches and at streams able to meet all of their resource requirements within these habitats? One of the objectives of this study was to determine how frogs respond to landscape structure as individuals migrate to breeding sites. If frogs stop moving when they encounter a drainage ditch or a stream system, will they successfully breed in these habitats? I believe that drainage ditches in the agriculture dominated landscape may not provide resources available to frogs in stream systems in the forested landscape. Ability to successfully breed may be one of them. Over-wintering success may be another. For example, *R. pipiens* (Cunjak 1986) and *R. clamitans* (Martof 1953) have been observed to over-winter in stream systems and move into ponds for breeding in the spring. I do not think that the drainage ditches in the agriculture dominated landscape are able to provide an over-wintering resource. Frogs that attempt to over-winter in drainage ditches face several challenges. One challenge is to avoid the mowing of vegetation in drainage ditches, another is to be able to find a suitable over-wintering location in the drainage ditch, and another challenge is a delayed over-wintering migration from a drainage ditch. The similar behavioural responses of frogs in these two similar and yet different resource habitats may result in significant differences observed at the population level. The differences in the size structures of the breeding populations in the two landscapes do support the above conclusion.

Although the recapture success in this study was low, and consequently, the results must be interpreted cautiously, a number of trends suggest that landscape structure does influence the movements of frogs returning to philopatric ponds. A high proportion of field habitat in the routes between the release sites and aquatic sites appears to facilitate the return to ponds. However, a high proportion of forest and wet habitat along a route appears to impede the return to philopatric ponds. The presence of the linear elements-roads, streams and drainage ditches- also appear to impede the return to philopatric ponds. Although these findings provide generalizations about landscape use, the limitations of this study are that the behavioural mechanisms responsible for the observed displacements are not known. A radio-telemetry study (Chapter 3) was initiated to explore the influence of specific habitat types on the movement of frogs across a landscape.

Figure 1a). Spatial distribution of the release sites (*T, *Q, *P, *S, *M, *O and *X) to each other and to the ponds (M1, M2 M3, W1, W2 and W3) in the Forest landscape. Routes along which frogs returned to a pond are marked in white.

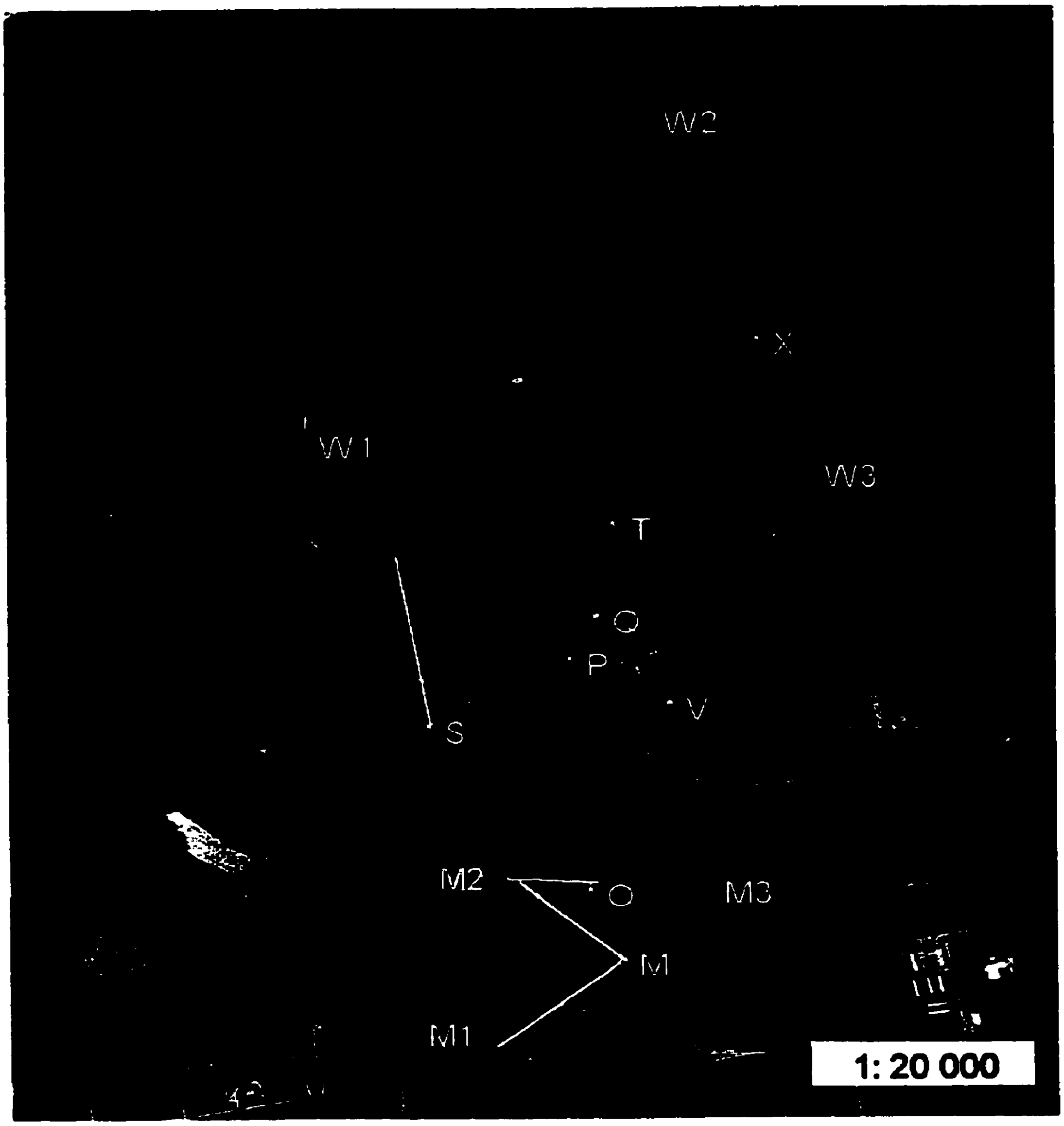

W2
X
W1
W3
T
Q
P
V
S
M2
O
M3
M
M1
1: 20 000

Figure 1b). Spatial distribution of the release sites (*B, *D, *C, *K, *G, *E and *I) to each other and to the ponds (D1, A1, S1, C1, B1 and D2) in the Non-Forest landscape. Routes along which frogs returned to a pond are marked in white.

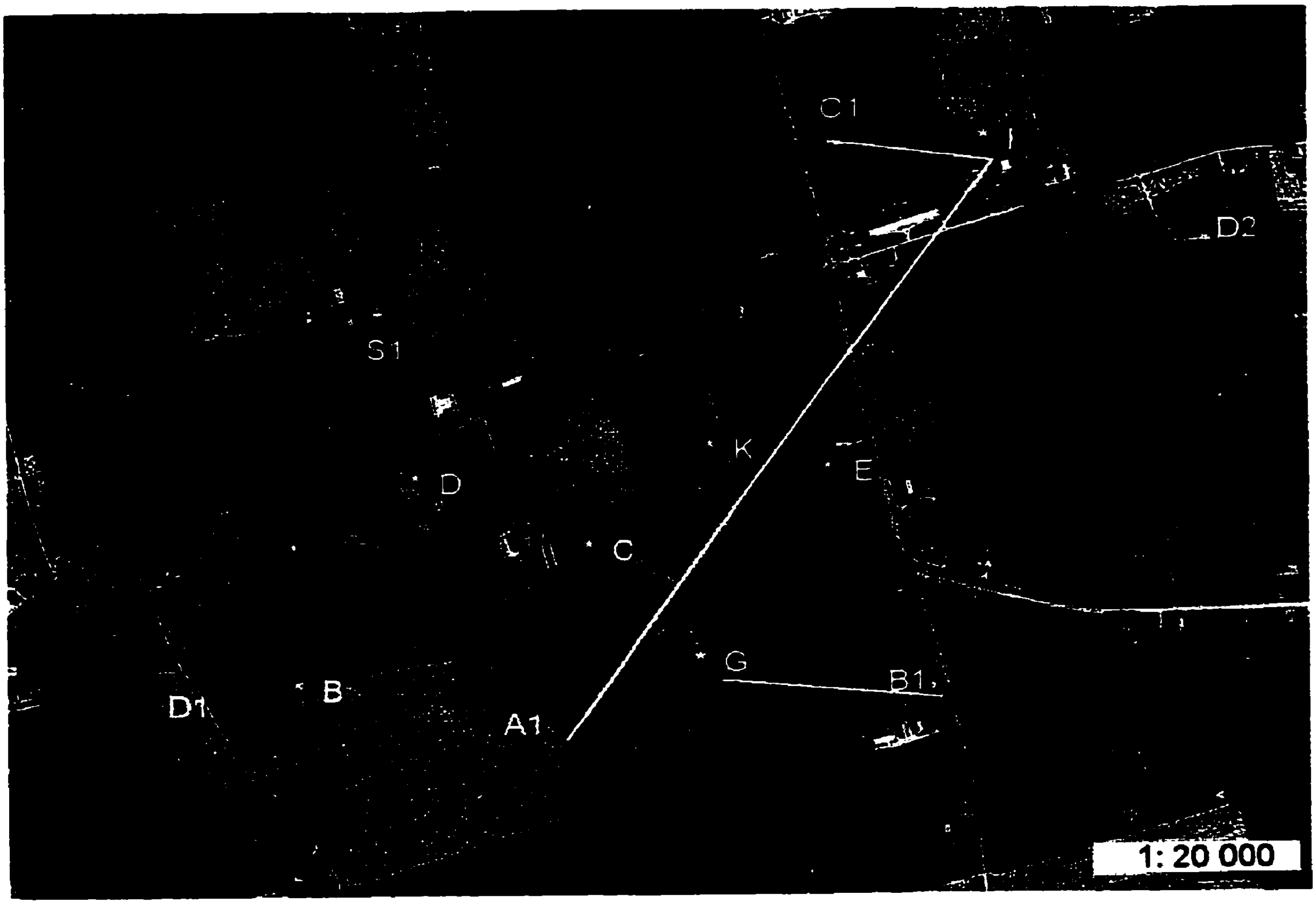

C1
D2
S1
K
E
D
C
G
B1
D1
B
A1
1: 20 000

Figure 2. A box plot comparing the rate of movement (metres/day) between frogs (a) initially captured moving toward ponds (habitat) and frogs moving away from ponds (pond), and (b), rates of movement between gravid females (n=5), a non gravid female (n=1) and potentially breeding males (n=3). The white bar within each bar denotes the median value, the outline of the box denotes the quartile range, the whiskers denote 95% confidence intervals and the lines above and below the boxes denote outliers in the data.

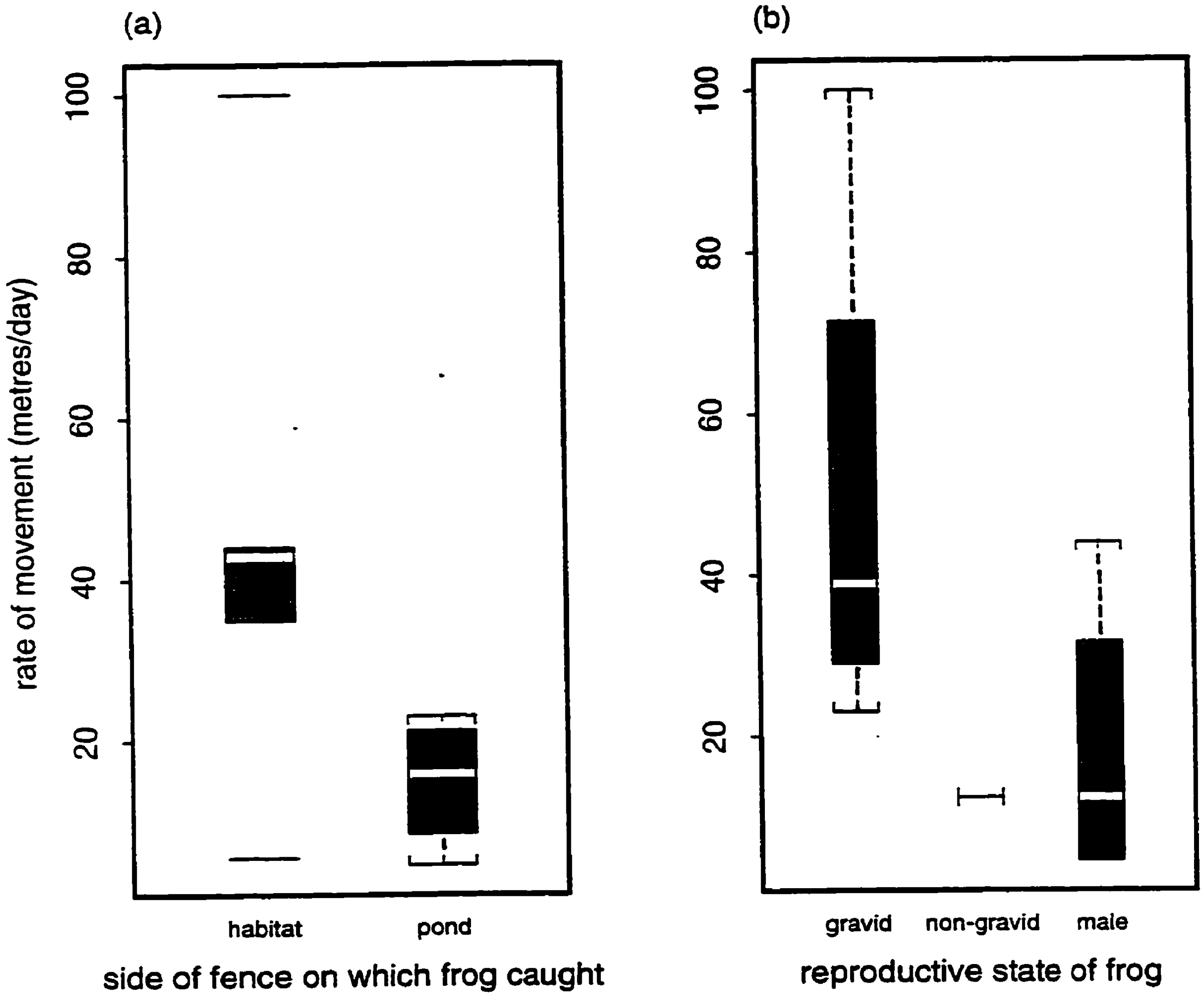

(a)
rate of movement (metres/day)
100
80
60
40
20
habitat
pond
side of fence on which frog caught
(b)
100
80
60
40
20
gravid
non-gravid
male
reproductive state of frog

Figure 3. A scatter plot of the proportion of frogs recaptured plotted against
the proportion of field habitat along a philopatric route (a),
the proportion of forested habitat along a philopatric route (b)
and the proportion of aquatic habitat along a philopatric route (c)
in the Forest (◆) and Non-Forest(□) landscapes.

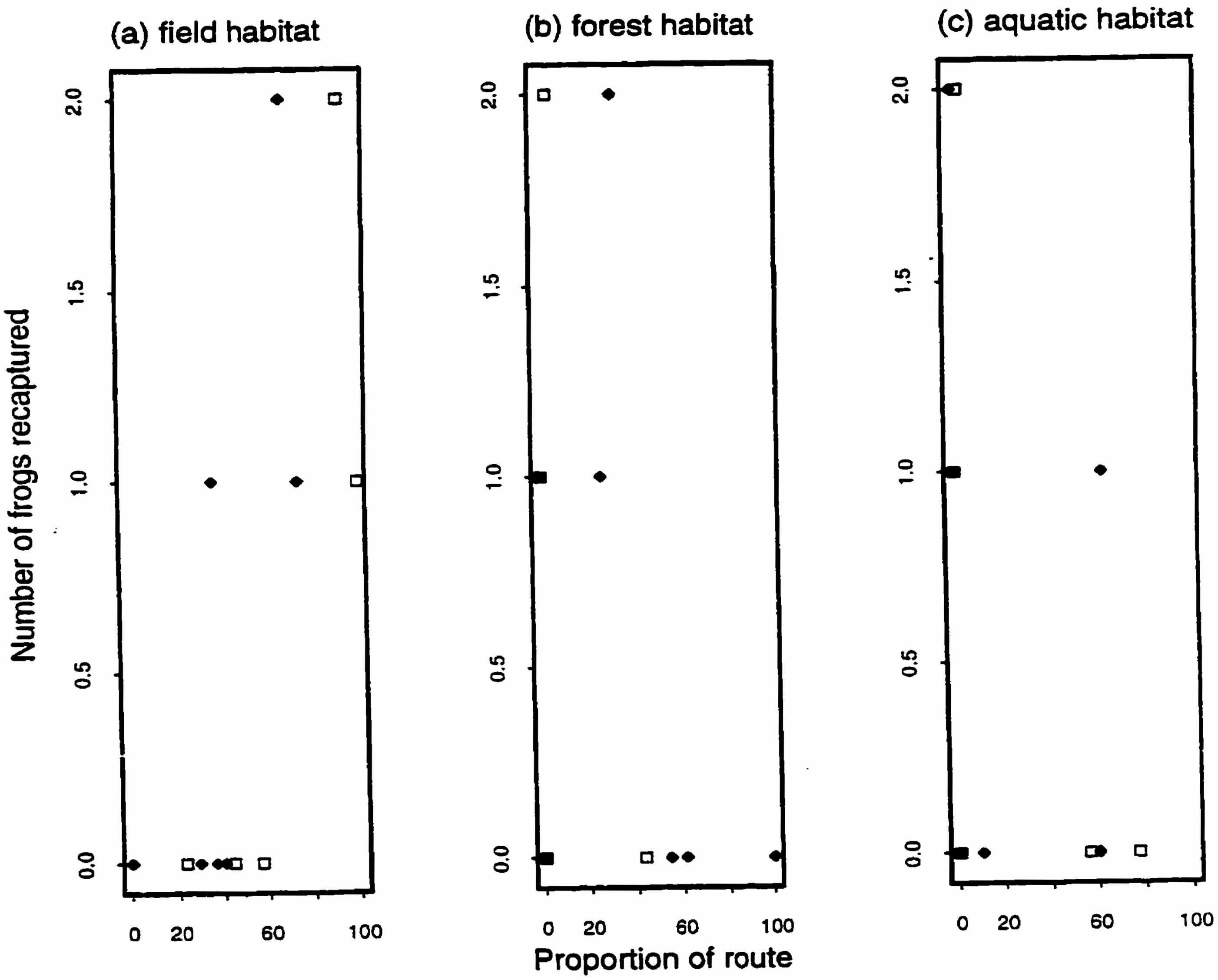
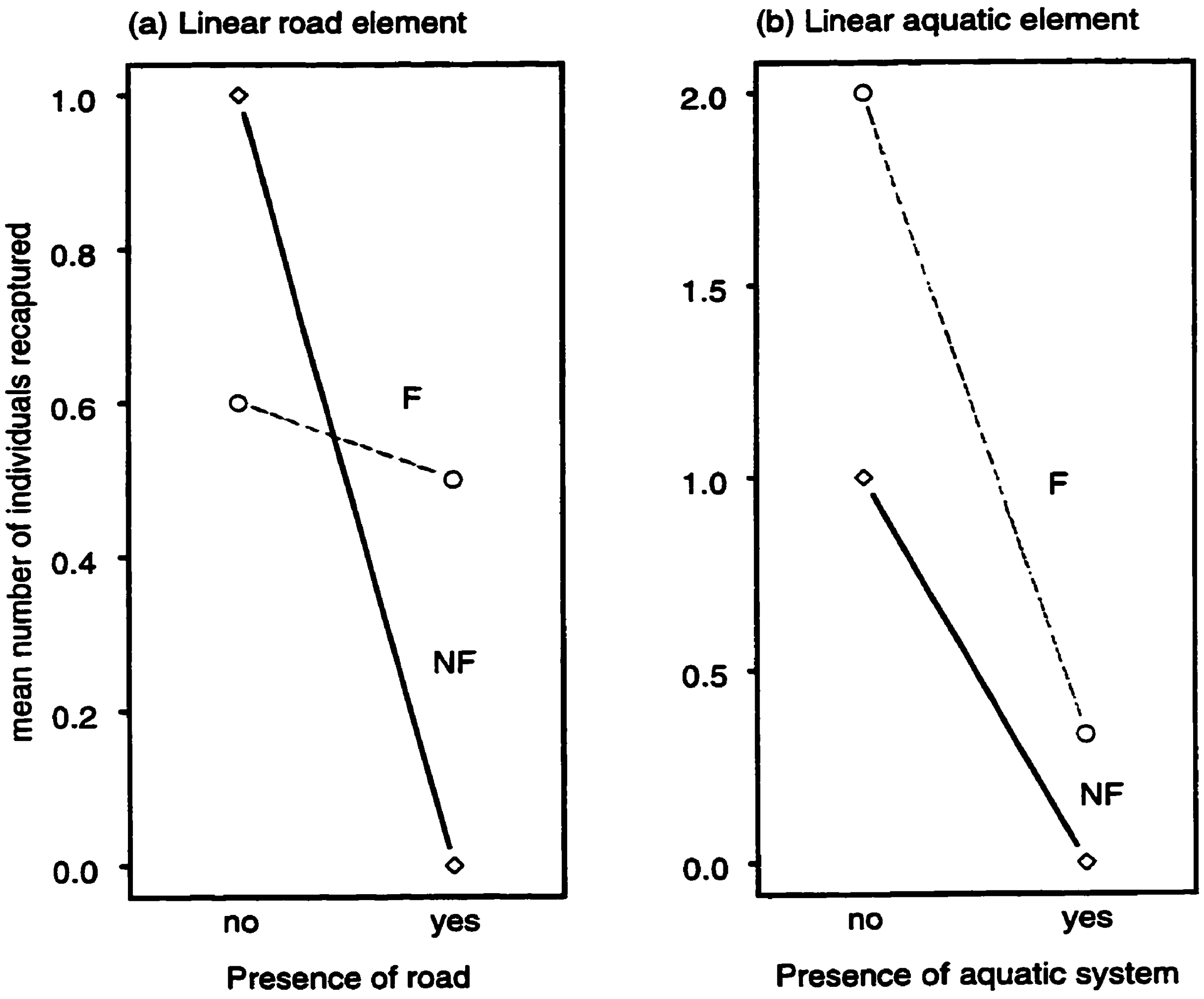

(a) field habitat
(b) forest habitat
(c) aquatic habitat
Number of frogs recaptured
0.0
0.5
1.0
1.5
2.0
0
20
60
100
Proportion of route

Figure 4. Interaction plots indicating the mean number of individuals recaptured between the presence of roadways and landscape type (a) and the presence of linear aquatic elements and landscape type (b). The frogs recaptured at ponds did cross roadways in the Forest landscape, but did not do so in the Non-Forest landscape. In both Non-Forest and Forest landscapes, the presence of linear aquatic elements reduced the mean number of individuals recaptured.


(a) Linear road element
(b) Linear aquatic element
mean number of individuals recaptured
1.0
0.8
0.6
0.4
0.2
0.0
F
NF
no
yes
Presence of road
2.0
1.5
1.0
0.5
0.0
F
NF
no
yes
Presence of aquatic system

Chapter 3

Radio-telemetry

INTRODUCTION

Anurans have complex life histories which necessitates migrations between habitats with different ecological properties (Reh & Seitz 1990). At the landscape level, the movement dynamics within habitats separating required resource patches (for breeding, summer foraging and over-wintering) needs to be evaluated. It is suggested that animals respond to landscape structure at fine spatial scales, e.g., their movements within an hour or a day (Wiens *et al.* 1993) and that movements assessed at this level may provide insight into landscape movement dynamics.

Although small scale movement studies using anurans have been limited, the works of Tracy and Dole (1969) using *B. boreas* and Dole (1965, 1968, 1972) using *R. pipiens* and *B. americanus* have pioneered our current knowledge of anuran movement dynamics at fine spatial scales. The main objective of their work was to assess the extent to which these animals were capable of returning to their philopatric ponds after being displaced. Tracy and Dole monitored the movement of their animals using a bobbin and thread as a trailing device. They were able to determine that individuals displaced up to one km from their philopatric pond were able to orient in the direction of the pond, with movements potentially triggered by both olfactory and ocular senses. The movements between the release sites and recapture sites revealed that *R. pipiens* spent approximately five percent of their time moving, generally during rainy evenings. Although not explicitly stated, the movement studies are assumed to have been conducted during the summer foraging phase of *R. pipiens*; in meadows and forested habitat. What these studies fail to explore are the movement dynamics across a range of habitat types within a given landscape.

As frogs move across the landscape during seasonal migrations, the likelihood of encountering appropriate habitat, prey or predators will be influenced by the characteristics of the different habitat types within the landscape (Wiens *et al.* 1993). Modifications to landscapes as a result of intensive agricultural practices have potentially isolated breeding and over-wintering sites from summer foraging sites. Isolation may occur because of a decrease in the number of available breeding sites, or, by the replacement of forest and stream habitats with fields and irrigation ditches. Although large scale studies suggest that the composition and amount of habitat will influence the distribution of breeding populations at ponds, the mechanisms influencing within habitat movements have not be evaluated. My objective is to assess the influence of different habitat types on the movements of *R. clamitans* in two different landscapes. One is dominated by forested habitat, where forest cover is continuous and the other is dominated by agriculture, where most of the forest and stream systems have been replaced with fields and irrigation ditches.

The results of the survey (Chapter 1) and mark-recapture (Chapter 2) studies suggest that anurans do selectively chose habitats to move through as they migrate to the breeding sites. However, the paths to the ponds are unknown. The goal of this study is to explore these pathways by assessing movements within the different habitat types from the same release points used in the mark-recapture study (Chapter 2). Because *R. clamitans* are predominantly an aquatic species and have a late summer breeding phase (occurring at the same time as this study), they were a model organism for this study. I exploited their tendency to return to permanent aquatic sites in order to assess within habitat movements. My objectives were threefold;

1. to assess the influence of release habitat on the total distances moved,
2. to assess the influence of release habitat on the net displacement, and
3. to assess the influence of the different habitat types on rates of movement.

Combining the above three objectives allowed me to assess the connectivity of the landscapes by defining habitats, which facilitate and habitats which impede movements toward ponds.

METHODS

Landscapes. This study was conducted within the same two landscapes used in both the survey study (Chapter 1) and the mark-recapture study (Chapter 2). I used a subset of the same release sites used in the mark-recapture study (Chapter 2) in order to maintain continuity between the two manipulated studies. Links can then be made between the movements observed in the telemetry study (this Chapter) and the mark-recapture study (Chapter 2). For a description of the landscapes, see Chapter 1, and for a description of release sites, see Chapter 2. Movements were tracked within six habitat types;

1. field with cover (including oat fields, barley fields and potato fields),
2. field with no cover (fields recently ploughed),
3. residential areas (including any type of urban development, i.e., landscaped lawns, junkyards),
4. linear aquatic elements (including streams and irrigation ditches),
5. roads (including dirt roads and highways) and
6. forests (including continuous forest and forest fragments such as fence-rows).

Frogs. For this study, *R. clamitans* were used. Working with this species provided several advantages; one, adult *R. clamitans* are predominantly an aquatic species, and spend most of their lives in and around ponds. Consequently, if displaced from a pond, they are expected to return to it. Two, *R. clamitans* have a relatively late breeding season (occurring simultaneously with this study), and by using only females of this species (many of which were gravid), I assumed that movements would be similarly directed towards an aquatic site during the breeding phase.

Eight *R. clamitans* were collected on the first day of each experiment (four residents and four foreigners). Frogs were collected from ponds during the day and searches continued into the evening if necessary. Once caught, frogs were weighed (to ensure that the transmitter weighed less than three percent of body weight) and toe clipped (for future identification in case transmitter harness slipped off). Chapter 1 provides the protocol for the toe clipping technique. Frogs were then fitted with a harness and transmitter. Two different size transmitters were used, 1.8 grams on larger frogs and 1.5 grams on smaller frogs. Transmitters were purchased from Holohil Inc. in Ottawa Ontario. Transmitter frequencies ranged from 150.102 to 150.690 Mg Hz. 150 Mg Hz was chosen as the optional range because it allowed for the detection of frogs moving into aquatic habitats. The harness attaching the transmitter to the frog consisted of a band made of polyethylene tubing (0.95 mm outside diameter and 0.65 mm inside diameter) fitted around the waist of the frog and secured to the transmitter. Bands were held firmly in place using a fly-line eyelet. Barbs on the fly-line eyelet acted as a hook connecting the two ends of the tubing. This allowed for individual frogs to be fitted with a harness of an appropriate size. P. Bartlet (Iowa State U., unpublished) developed the protocol followed. In the field, a Yaggi two-way antenna was used to locate the frogs. Tracking on flat terrain was possible up to one km, and in hilly terrain, tracking was more limited, ranging between 200 and 500 meters.

Release of frogs. Four experiments were conducted in total. This consisted of two experiments per landscape (initial experiment and replicate), all separated temporally. Frogs were released in two habitat types, field and forest (sites T and X for field and forest respectively in the forest dominated landscape, and site I and K for field and forest respectively in the agriculture dominated landscape). For each experiment, approximately one hour was required to track the four individuals released at each release site and to get from one site to the other. Tracking occurred over a six-day period. See Table 1 for list of dates (start and finish), landscape and release sites and distances of release sites to ponds.

Tracking. Tracking consisted of two components, four day tracking from sunset to sunrise, (~ 8:30pm to ~6:00 am) with readings every two hours, and two day tracking with readings once per day. The first component (first four days) was to observe specific responses to the different habitat types within the landscape and the second component (last two days) was to allot enough time to allow frogs to return to a pond. In the recapture study (Chapter 2), the minimum number of days required to return to a pond was approximately 3-6 days.

Once an individual was located to within five meters, a flag was placed near the location of the frog. During the next tracking session, the flag was used as a reference point. At the end of the six-day tracking period, flag locations were georeferenced using a GPS, downloaded onto a computer, and differentially corrected to within a five-metre resolution. Distances between successive moves were then calculated. From these distances, I obtained values for rates of movement per habitat type (meters per hour), total distances moved, (adding distances between consecutive moves) and net displacements (straight-line distances from release points to recapture points). The ratio of net displacements to total distances moved was calculated as a measure of tortuosity in the pathways.

Data sets. I assessed the influence of habitat on movements using four movement indices. My four response variables are; total distances moved, net displacement, ratio of net displacement to total distance moved and rates of movement. I used total distances moved and net displacements to assess the extent of activity across the different habitats within the landscapes. I used the ratio of net displacement to total distance moved to assess the degree of tortuosity or linearity within the pathways. Lastly, I used rates of movement to assess the movement pathways within the different habitat types.

The following Independent variables were used in the models.

1. Release habitat.	Habitat in which frogs were released, either field habitat or forest habitat. In both forested and non-forested landscapes, the field habitat consisted of potato fields with potato plants measuring approximately 50 cm in height.
2. Landscape.	Landscape represents either the forested landscape or the non-forested landscape in which frogs were released.
3. Habitat.	One of six habitats found within each landscape mosaic. Habitat types include; forest, field with cover (potato, oat and barley fields

and abandoned fields), field without cover (ploughed fields), roads, residential and linear aquatic elements including streams, irrigation ditches and riparian vegetation.

4. Release date (meso scale analyses) and relative humidity(fine scale analysis).

   To account for variation associated with temporal seasonal effects, a release date term was included in the meso scale models, and for the fine spatial scale model, a relative humidity term (rh.min) was used. This served to account for variation in climatic conditions and potentially soil moisture conditions throughout the duration of the study.

5. Days moved. The total number of days frogs moved, (n=5 or 6 days) was also included in the meso scale models to account for variation in distances moved as a function of total time spent in the field.

6. Class of frog. The extent to which a frog may be familiar with the landscape, i.e., class of frog being either a resident (from the same landscape in which released or foreigner (not from the same landscape), may influence the movement behaviours within each landscape.

Table 1. Start and finishing dates, the class of frog (res.=resident, for.=foreigner), release landscape, site and habitat of release, and the distance to closest pond from release sites for the tracking of *R. clamitans*.

date of experiments	Class of frog from ponds:		release landscape	release site	release habitat	distance to closest and (philopatric) pond
	Res.	for.				
07/30 - 08/05	W1	C1	F	T	field	280 (W1)
07/30 - 08/05	W1	C1	F	X	forest	290, 550(W1)
08/13 - 08/19	W1	B1	F	T	field	280 (W1)
08/13 - 08/09	W1	C1	F	X	forest	290, 550(W1)
08/19 - 08/25	W1	C1	NF	I	field	290 (C1)
08/19 - 08/25	W1	C1	NF	K	forest	500 (C1)
08/25 - 08/31	W1	B1	NF	I	field	850 (B1)
08/25 - 08/31	W1	B1	NF	K	forest	550(B1)

RESULTS

Of the 32 female *Rana clamitans* released with radio transmitters, 27 were successfully followed for the six consecutive days (Tables 3a, 3b). Of the five not tracked, two had slipped out of their harness, the third could not be located (either the transmitter failed, the frog quickly moved out of tracking range or was predated upon), the fourth was accidentally killed while being tracked and the fifth was eaten by a cat. Four of the five were lost within the first two days, whereas the fifth was tracked until the end of the fourth day. The data for the fifth frog are presented; however, they are not used in the statistical analyses.

Of the 27 individuals tracked for the six consecutive days, three located a pond, and a fourth (without a transmitter) was recovered in a trap at the pond. All frogs (two of which were residents, the other a foreigner) that successfully located ponds were released at the field release site in the forested landscape (site T) (Table 2). Frogs at this site also demonstrated the highest net displacements (Table 3a). Frogs released at both the forest and field release sites (K and I respectively) in the non-forested landscape demonstrated similar net displacements to each other, but shorter net displacements than the field release site in the forested landscape (site T). Frogs released at the forest release site (X) had the shortest net displacements. Distances moved at and away from release sites are presented in Figures 1a through 1d. Although the frogs locating ponds generally moved the greatest distances (distances ranging between 280 and 309 meters), the data suggest that some frogs which did not locate ponds, moved similar, and in some cases, longer distances (distances ranging between 318 - 612 meters), (Tables 3a, 3b). A comparison of the distances moved between frogs returning to ponds and frogs not returning to ponds but travelling similar distances, showed that residents had net displacements greater than foreigners but the foreigners moved total distances greater than the residents (Figures 7a and 7b). The ratio of the net displacement to total distance moved is only suggestive of a difference in movement responses between the residents and foreigners and between the two landscapes (Tables 3a, 3b).

Table 2. Summary of proportion of frogs successfully returning to ponds from the field and forest release sites in each landscape. Frogs for which transmitters were lost have been subtracted from the initial four released to give the number remaining in terrestrial habitat.

landscape	release habitat	frog class	proportion returned to pond	number returning to pond	number remaining in terrestrial habitat
forest	field	resident	1.00	2	0
forest	field	foreigner	0.33	1	2
forest	forest	resident	0.00	0	4
forest	forest	foreigner	0.00	0	3
non-forest	field	resident	0.00	0	3
non-forest	field	foreigner	0.00	0	4
non-forest	forest	resident	0.00	0	4
non-forest	forest	foreigner	0.00	0	4

Table 3. Summary of the movement results for telemetry sessions in forested (a) and non-forested (b) landscapes. Total distances moved, net displacements (net displ) and the ratio of net displacement : total distance moved (nd: ds) are presented based on pond from which frog was initially taken, release site and habitat in which released, and habitat in which recaptured.

3a Forested landscape

Dates of telemetry sessions	pond of capture	release site	release habitat	frog	habitat in which recaptured	distance moved in m	net displ in m	ratio nd : ds
30/07 - 07/08	W1	X	forest	◊	orchard	40.55	28.88	0.71
30/07 - 07/08	W1	X	forest	O	stream	27.52	9.22	0.34
30/07 - 07/08	C1	X	forest	◆	stream	89.31	79.67	0.89
30/07 - 07/08	C1	X	forest	●	disappeared	----	-----	----
30/07 - 07/08	W1	T	field	◊	pond	445.45	308.54	0.69
30/07 - 07/08	W1	T	field	O	trans. off*	----	-----	----
30/07 - 07/08	C1	T	field	◆	side of road	274.04	152.88	0.56
30/07 - 07/08	C1	T	field	●	forest	270.12	152.74	0.57
13/08 - 19/08	W1	X	forest	◊	stream	156.74	103.00	0.66
13/08 - 19/08	W1	X	forest	O	sub terrain	27.81	26.99	0.97
13/08 - 19/08	B1	X	forest	◆	forest	41.95	20.56	0.49
13/08 - 19/08	B1	X	forest	●	forest	29.63	15.45	0.52
13/08 - 19/08	W1	T	field	◊	trans. off*	----	-----	----
13/08 - 19/08	W1	T	field	O	pond	305.19	289.83	0.95
13/08 - 19/08	B1	T	field	◆	field	318.03	313.61	0.99
13/08 - 19/08	B1	T	field	●	pond	443.66	279.83	0.63

* trans. off = transmitter fell off.

Table 3b Non-forested landscape

Dates of telemetry sessions	pond of capture	release site	release habitat	frog	habitat in which recaptured	distance moved in m	net displ in m	ratio nd : ds
19/08 - 25/08	C1	K	forest	◊	drain ditch	153.93	123.99	0.81
19/08 - 25/08	C1	K	forest	O	field	63.32	31.39	0.50
19/08 - 25/08	W1	K	forest	◆	drain ditch	117.36	117.36	1.00
19/08 - 25/08	W1	K	forest	●	field	611.94	100.83	0.16
19/08 - 25/08	C1	I	field	◊	stepped on	----	-----	----
19/08 - 25/08	C1	I	field	O	eat by cat	145.07	108.06	0.74
19/08 - 25/08	W1	I	field	●	field	198.95	179.44	0.90
19/08 - 25/08	W1	I	field	●	drain ditch	247.00	78.93	0.32
25/08 - 31/08	B1	K	forest	◊	drain ditch	243.78	211.51	0.87
25/08 - 31/08	B1	K	forest	O	drain ditch	133.20	122.28	0.92
25/08 - 31/08	W1	K	forest	●	drain ditch	139.53	118.35	0.85
25/08 - 31/08	W1	K	forest	●	drain ditch	382.53	188.35	0.31
25/08 - 31/08	B1	I	field	◊	residential	52.35	39.5	0.75
25/08 - 31/08	B1	I	field	O	residential	35.72	35.32	0.99
25/08 - 31/08	W1	I	field	◆	residential	53.33	39.5	0.74
25/08 - 31/08	W1	I	field	●	drain ditch	364.72	115.74	0.32

Symbols in the frog columns of Tables 3a and 3b denote residents (hollow symbols) and foreigners (solid symbols) within the two landscapes in which frogs were tracked. The same symbols are used in the plots of the frog routes (Figures 2b, 2c, 3b, 3c, 4b, 4c and 5b, 5c).

Meso scale effects. I tested the hypothesis that the habitat and landscape in which the frogs were released would influence movement across the landscape. The results suggest that the release habitat influences both total distances moved and net displacements; $p<0.001$ and $p<0.001$ for total distance moved and net displacement respectively (Table 4). A significant interaction effect between habitat and landscape was also detected; $p<0.001$ and $p<0.001$ for total distance moved and net displacement respectively (Table 4). The significant interaction effects appear to be influenced by the forested habitats within each landscape (Figure 6). In the non-forested landscape, the forest patch is a fence-row one tree wide (release site K) whereas in the forested landscape, the forest patch is approximately thirty trees wide (site X). Although a one tree wide fence-row is not usually identified as a forest patch, it does represents woody vegetation which is becoming increasingly scarce in the non-forested landscape. All frogs released in the fence-row left that habitat within the first six hours whereas only one frog released in the forest habitat in the forest landscape left the habitat, moving into an orchard in the direction of the pond from which it was displaced. Neither release habitat nor landscape significantly influenced the degree of tortuosity (ratio net displacement : distance moved) within the routes (Table 4). However, the class of frog does appear to influence the degree of tortuosity within the pathways, $p=0.18$ (Table 4). A comparison between net displacements and total distances moved suggests that class of frog has a significant effect on the total distances moved, $p=0.0446$ (Table 4). Foreigners, although exhibiting net displacements less than residents, generally moved greater total distances (Figure 7).

The pathways observed at each release site provide insight into some of the differences in the movement patterns (Figures 2b, 2c, Figures 3b, 3c for the forested landscape, and Figures 4b, 4c, Figures 5b, 5c for the non-forested landscape, field and forest release sites respectively).

Table 4. Models from regressions indicating the influence of the release habitat and interaction between release habitat and landscape on the three response variables: the sqrt (total distance moved (meters)), sqrt (net displacement (meters)) and the ratio of net displacement to total distance moved (net.displaced:dist.moved). Variation associated with release date, number of days moved and class of frog were accounted for before testing for the influence of the landscape elements.

		sqrt (total distance moved)			sqrt (net displacement)			net diplaced:dist.moved		
terms	Df	D	F	Pr(F)	D	F	Pr(F)	D	F	Pr(F)
release date	3	17.85	0.34	0.79	5.33	0.24	0.86	0.08	0.40	0.76
days moved	1	77.23	4.41	**0.05**	30.97	4.20	**0.05**	0.00	0.09	0.76
class of frog	1	80.83	4.62	**0.04**	7.87	1.06	0.31	0.13	1.93	0.18
rel. habitat	1	144.04	8.23	**0.00**	129.50	17.57	**0.00**	0.02	0.30	0.59
rel. h.: land*	1	203.72	11.65	**0.00**	171.58	23.28	**0.00**	0.03	0.42	0.52
residuals	19	332.24			139.98			1.32		

* rel.h.: landscape denotes the interaction between release habitat and landscape.

Pathways. For two of the residents in the forested landscape at the field release site, a dirt road facilitated their return to their philopatric pond (Figures 2b, 2c). The one non-resident locating the pond moved in a direct line through an oat field from the release point to the pond (Figure 2c). Although the influence of frog class on directionality has not been tested statistically, the residents generally moved in the direction of the pond, whereas the direction of the foreigners appears to be more random (Figures 2 through 5).

The frogs appeared to initially explore the surroundings around the release site before moving greater distances away from the release points. At the forest release site in the forest landscape (Figures 3b, 3c), frogs generally located the nearby stream and did not venture far from it. Only one individual (resident) left the forest-stream habitat moving into the nearby orchard. The movement direction of this individual was toward the pond of initial capture. One resident located a network of underground pathways and spent most of the tracking time underground.

In the non-forested landscape, frogs were unable to successfully locate a pond over the six days. However, one resident was within 100 meters and headed in the direction of the pond from which it was initially captured. A significant difference between these two landscapes is the presence of drainage ditches in the non-forested landscape. Eight of the sixteen frogs located a drainage ditch and remained in this habitat until the end of the tracking period (Figures 3b, 3c, Figures 4b, 4c). At the field release site, four of the eight frogs remained in residential habitat (one of which was eaten by the cat). At the forest release site, two of the eight frogs took shelter under dried clumps of earth in the ploughed field, one remaining for one day and the other for two days. Both days were sunny (+25 °C ambient temperatures) and frogs moved once the sun had set. The resilience of *R. clamitans* in such potentially desiccating conditions is impressive.

The pathways outlined above suggest that residents demonstrate different movement patterns than did the foreigners. The foreigners appear to move in a more exploratory circular fashion whereas the residents appear to be more directed in their movements.

These patterns are habitat specific; with movement in fields demonstrating the trends described whereas the response to drainage ditches, streams and forested habitat appears to be similar within the two classes of frogs.

The effects of habitat on movement rates were assessed using a repeated measures analysis accounting for variation within and across all frogs. The results suggest that the type of habitat significantly influenced the rates at which the frogs moved, $p<0.001$ across all frogs, and $p=0.06$, within consecutive moves of individual frogs (Table 6). The effects of relative humidity on the movement rates indicates the reverse trend, highly significant within consecutive moves for individuals, $p<0.001$, and marginally significant across all frogs, $p=0.08$ (Table 6). The interaction between relative humidity and habitat type has a marginally significant effect on rates of movement both within (within consecutive moves for individuals) and across frogs, $p=0.08$ in both cases. The interaction between relative humidity and landscape type has a significant effect on within frog rates of movement, $p=0.03$. The three way interaction between relative humidity, habitat type and landscape type also has a significant effect on within frog rates of movement, $p=0.02$. The implications of these results are twofold. One, the variation within consecutive moves by frogs is influenced by a combination of landscape elements and changing relative humidity. Secondly, the variation in movements across all frogs, after accounting for within frog differences, are also significantly influenced by landscape elements and changing relative humidity.

Movement within the six different habitat types in the two landscapes suggests a behavioural response of frogs to these habitats. Upon entering a particular habitat, frogs either continuously moved through the habitat or stopped moving. Drainage ditches, forest habitat and residential areas appear to impede the movement of frogs (high proportion of observations with no movement), whereas roads tend to strongly facilitate movement (Table 5). In between these two extremes, frogs alternated between moving and stopping in both fields with cover and those without (ploughed fields). The stopping frequency and rates of movement suggest a similar pattern in habitat use. Habitats with a high stopping frequency demonstrate slow rates of movement (drainage ditches, forest and residential habitats) and habitats with a low stopping rate indicate high rates of movement (roads) with fields being intermediary between these two (Table 5, Figure 8).

Table 5. Summary table indicating the total number of observations, the number and proportion of observations with no movement within the six main habitat types in the Forest and Non-forest landscapes pooled for all *R. clamitans*, n=32.

Habitat	**total number of obs.****	**number of obs. with no movement**	**proportion of obs with no movement**
drainage ditch	43	41	0.95
forest •	128	109	0.85
residential	58	47	0.81
field - cover *	134	63	0.47
field - no cover	26	11	0.42
road	18	1	0.06

• the habitat types for the release sites in the two landscapes are included in this table, explaining the high total number of observations.

**obs. = observations

Table 6. Model from repeated measures analyses relating the log (movement rate (meters/hour) to the habitat and landscape, accounting for variation within consecutive moves of frogs before assessing the influence of landscape elements on movement rates.

	Error: within frogs				Error: frog			
Terms	Df	SS	F	Pr(F)	Df	SS	F	Pr(F)
rel. hum.	1	9.09	7.45	**0.00**	1	4.66	3.37	0.08
Habitat	5	13.14	2.16	0.06	5	79.04	11.45	**0.00**
Landscape			----	----	1	5.37	3.89	0.06
rel. hum.: habitat	5	11.92	1.96	0.08	5	16.91	2.45	0.09
rel. hum: landscape	1	5.67	4.65	**0.03**	1	1.48	1.07	0.31
habitat: landscape	3	5.33	1.46	0.23	3	11.76	2.84	0.07
rel. hum:hab:land	2	5.79	2.38	0.09	2	4.00	1.45	0.27
residuals	143	174.36			13	17.95		

rel.hum = minimum relative humidity,

rel. hum:hab:land = minimum relative humidity : habitat : landscape interaction

____marginally significant values

DISCUSSION

In this study, the use of telemetry provides insight into the movement patterns of female *R. clamitans* within and across six different habitats in two landscapes. Within habitat movement rates (fine spatial scale) suggest that *R. clamitans* are influenced by the habitat type, $p=0.06$ and $p<0.001$, within consecutive moves per frog and across all frogs respectively (Table 6). The total and net distances travelled by *R. clamitans* suggest that the structure of the landscape (based on the release site and landscape in which released) influences the ability of the frogs to return to ponds (Table 2). Two non-landscape elements of comparable importance are; the degree to which the frogs are familiar with the surrounding landscape (class of frog, Table 4), and the influence of the daily minimum relative humidity on movement rates (Table 6).

The extent to which anurans are able to tolerate desiccation has been proposed to influence their terrestrial movements (Thorson & Svihla 1943). The movements of *R* significantly influenced by the minimum daily relative humidity (Figure 9). This suggests that for *R. clamitans*, the best physical environmental indicator influencing the terrestrial activities of this species is the daily minimum relative humidity below which movement appears to be hindered. Other studies using *R. sylvatica* (Bellis 1962, Heatwole 1961), and *R. pipiens* (Dole 1965) have correlated frog activities with the onset of rainfall and high humidity levels. The differences in the physical factors observed may be associated with the different tolerances to desiccation between these species. *R. pipiens* and *R. sylvatica* have been shown to have similar tolerances to desiccation whereas for *R. clamitans* the tolerance to desiccation is much lower (Schmid 1965).

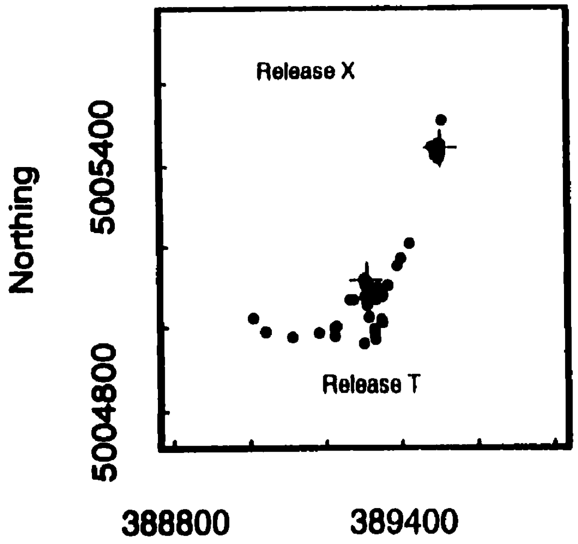
The degree to which a frog is familiar with an area has a significant effect on the total distances moved within a landscape (Table 3). Individuals displaced into the foreign landscape generally moved greater distances than residents displaced within the same landscape, $p<0.001$ (Figure 7a). This effect was not observed using net displacements, $p=0.31$ (Table 4, Figure 7b). This suggests that although the foreigners covered more territory, the distances between the release sites and recapture points did not significantly differ between the residents and foreigners. The inability of both residents and foreigners to locate ponds at three of the four release sites suggests that although initial responses to movement between these two groups may differ, their overall responses to the landscapes were similar (Table 1). However, the individuals locating the pond at the field release site in the forested landscape included both residents and foreigners, suggesting similar behavioural responses to the habitats between the release site and pond. If the pathways are compared, both residents moved along a curved dirt road to get to the pond whereas the foreigner moved through a field (Figures 3a, 3b). This may be indicative of familiarity within the landscape that the residents would have and the foreigner would not. Dole (1965) and Martof (1953) observed that both *R. pipiens* and *R. clamitans* explored their surroundings during rainy nights. This form of exploration may have provided the residents at the field release site in the forested landscape with the necessary environmental cues to direct their movements. This suggests that there is a selective use of habitats for movement by the frogs. Personal observations of frogs moving along the dirt road indicated that these individuals took refuge in a nearby field (< 10 meters) away from the road during the day only to return to the road at night.

The stopping frequencies of *R. clamitans* appear to be highly influenced by the different habitats between the release sites and the ponds. Stopping frequencies were high in drainage ditches, streams and residential areas (rock gardens, landscaped lawns) (Table 5). Of the 27 frogs recaptured, 11 were located in either drainage ditches or streams, suggesting that upon encountering these wet linear habitats, frogs remained there until recovered on the last tracking day. This suggests that these habitats may be providing the frogs with the necessary resource requirements (moisture and food) that will impede their movements to a pond. Movement detected along these habitats was minimal, strongly suggesting that they are not used for movement but as a refuge. Frogs moving along roadways exhibited the fastest rates of movement, >60 metres / hr (Figure 8) and only in one instance was a frog on a roadway in the same location for two consecutive readings (Figure 2b). Frogs moving in fields with and without cover spent approximately half their time moving (Figures 4b, 4c, 5b and 5c). In the field without cover (at site K), two foreigners remained in this habitat throughout the day hidden under clumps of dry earth and only left their refuge over the course of the following evening in one case, and two evenings in the other. These frogs survived days of +25°C ambient temperatures suggesting certain resilience to desiccating conditions. Although rates of movement were similar between the two types of fields, frogs in the fields without cover tended to move in a direct line whereas those in the fields with cover displayed a circular outward radiating pattern. All but one of the covered habitats consisted of potato fields and it is hypothesized that the movement patterns observed within the potato fields is the result of a potential search for food. Because potato fields are highly sprayed with insecticides, food resources may be limited in this habitat. This would suggest that frogs, which generally feed passively (sit still and use tongue to capture insects as they fly by) (Dole 1965, Martof 1953), may actively search for food in a habitat in which food resources may be scarce.

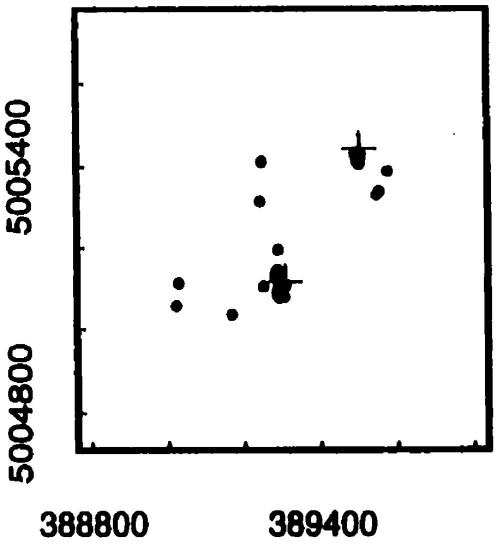
These findings suggest that the habitats within a landscape influence the movements of *R. clamitans* across the landscape. The similar responses of the frogs to the drainage ditches in agriculture dominated landscapes and streams in forest dominated landscapes needs to be considered further. The high stopping frequency and slow movement rates in drainage ditches and forest habitats, and the influence of the minimum daily relative humidity on rates of movement suggest that the physiological hydrated state of the frogs may be influencing the behavioral response of these animals as they move across the landscape.

Figure 1. Spatial extent of movements for radio tagged *R. clamitans* at the release sites for the four tracking sessions. Movements in the Forest landscape during tracking session 30/07 to 07/08 are presented in (a), during tracking session 13/08 to 19/08 are presented in (b). Movements in the Non-Forest landscape during tracking session 19/08 to 25/08 are presented in (c) and during tracking session 25/08 to 31/08 are presented in (d). All plots are in a one-km by one-km grid using UTM Easting and Northing coordinates in Zone 21. (+) symbol denotes release location in relation to distances moved.

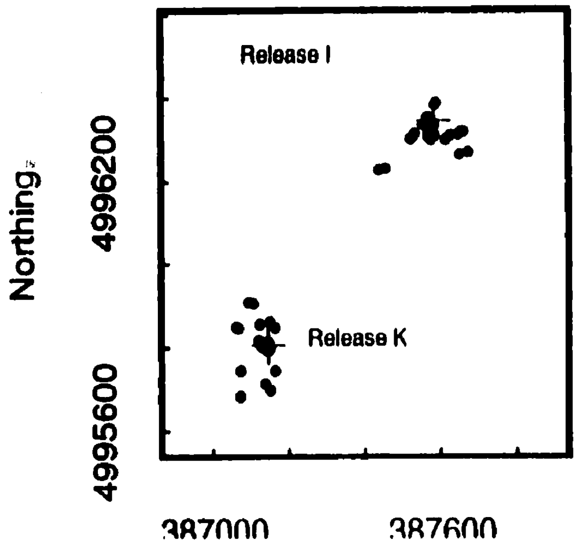
(a) Forest landscape 30/07 - 07/08



(b) Forest landscape 13/08 - 19/08



(c) Non-forest landscape 19/08 - 25/08



(d) Non-forest landscape 25/08 - 31/08

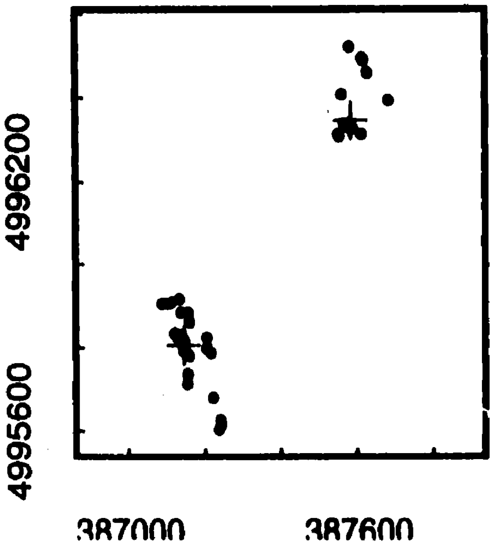
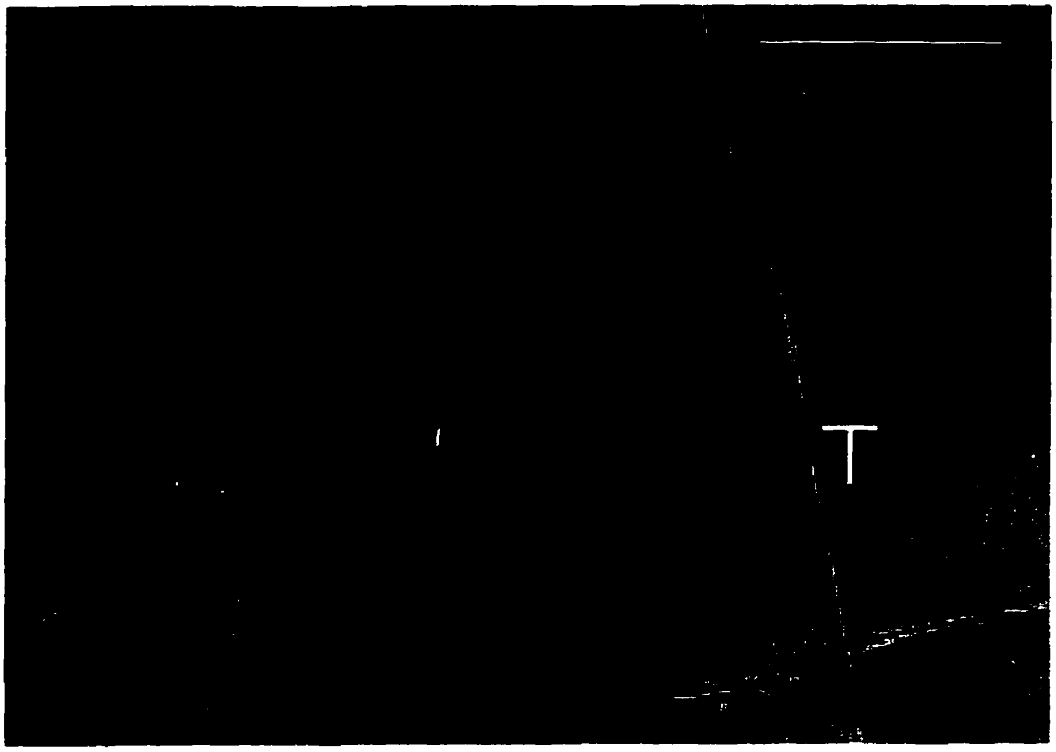
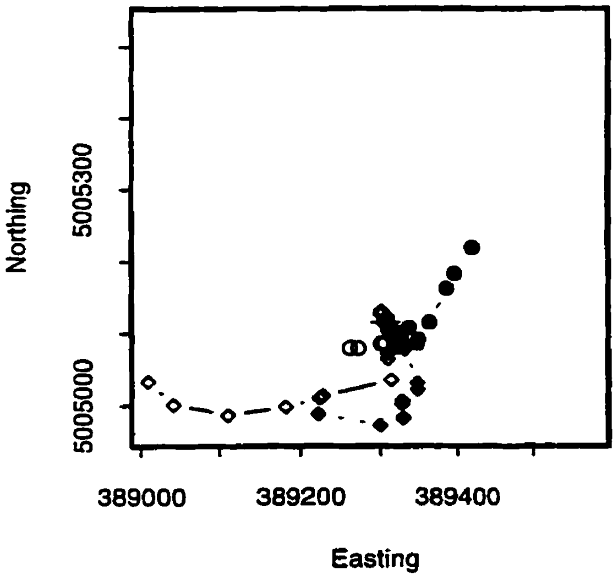


Figure 2. Graphical presentation of movement pathways for frogs released at site T in the Forest landscape. The different habitat types at site T are depicted in the aerial (a) and can be matched to the pathways taking the different scaling factor into account. The scale of the bar in the aerial is 85 metres. Cross bars in Figures 2(b) and 2(c) denote the release point, site T, and the curved pathways represent movements following the gravel roadway. Open symbols denote residents of the landscape and solid symbols denote foreigners.



(b) Release site T in forest landscape
date: 30/07-07/08



(c) Release site T in forest landscape
date: 13/08-19/08

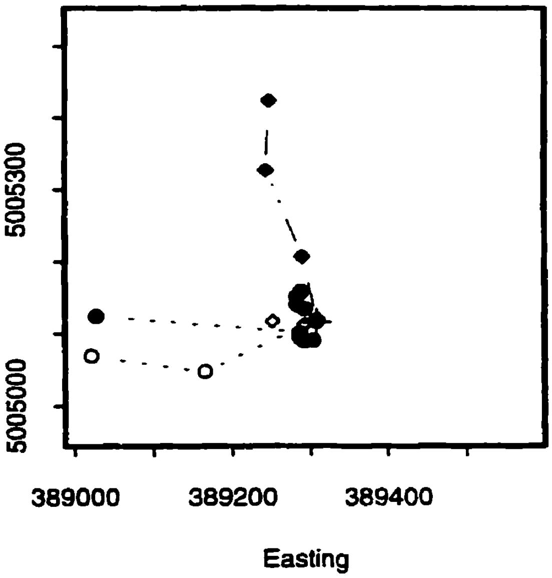
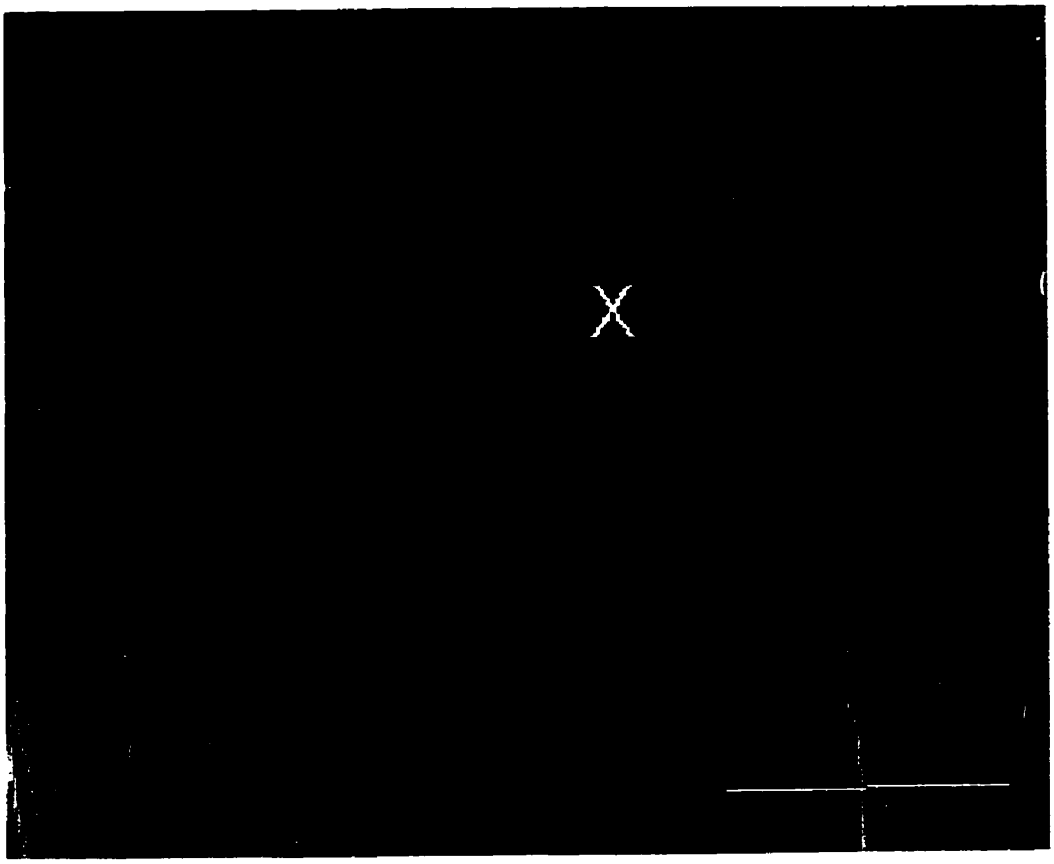
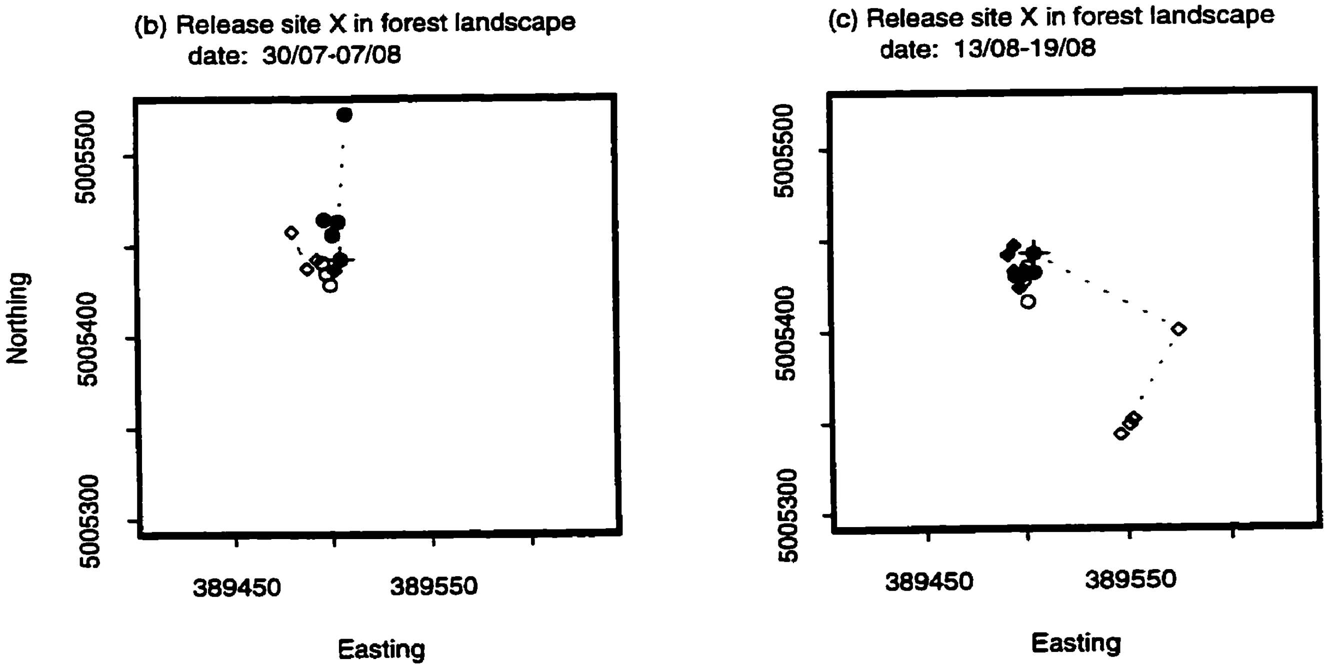


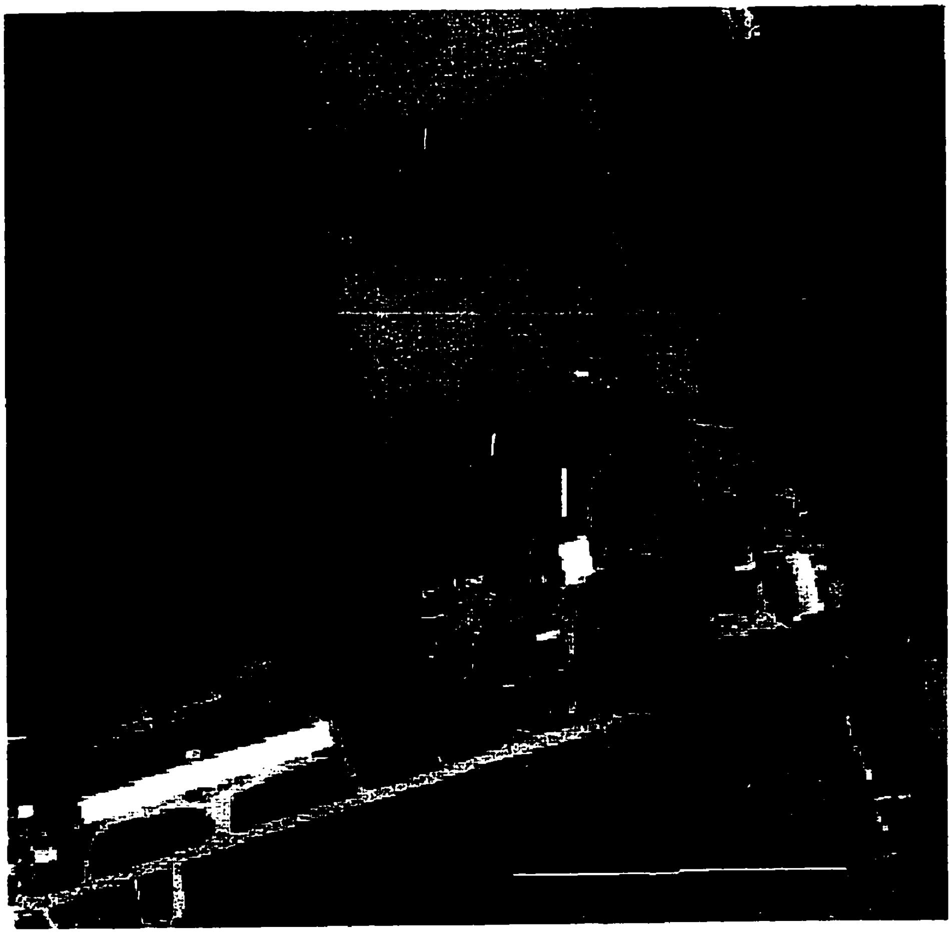
Figure 3. Graphical presentation of movement pathways for frogs released at site X in the Forest landscape. The different habitat types at site X are depicted in the aerial (a) and can be matched to the pathways taking the different scaling factor into account. The scale of the bar in the aerial is 90 metres. Cross bars in Figures 3(b) and 3(c) denote the release point, site X. At this release site, frogs tended to remain relatively stationary; little movement was observed. Open symbols denote residents of the landscape and solid symbols denote foreigners.



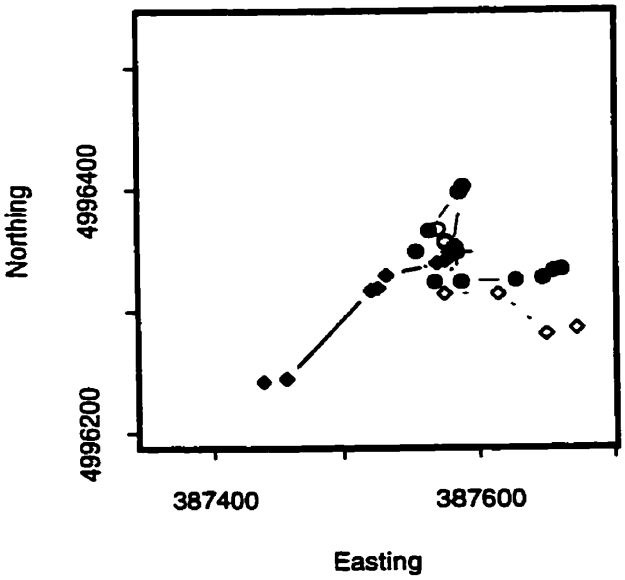

(b) Release site X in forest landscape
date: 30/07-07/08

(c) Release site X in forest landscape
date: 13/08-19/08

Figure 4. Graphical presentation of movement pathways for frogs released at site I in the Non-Forest landscape. The different habitat types at site I are depicted in the aerial (a) and can be matched to the pathways taking the different scaling factor into account. The scale of the bar in the aerial is 130 metres. Cross bars in Figures 4(b) and 4(c) denote the release point, site I, with movements appearing constrained by the presence of residential buildings and drainage ditches. Open symbols denote residents of the landscape and solid symbols denote foreigners.



(b) Release site I in non-forest landscape
date: 19/08-25/08



(c) Release site I in non-forest landscape
date: 25/08-31/08

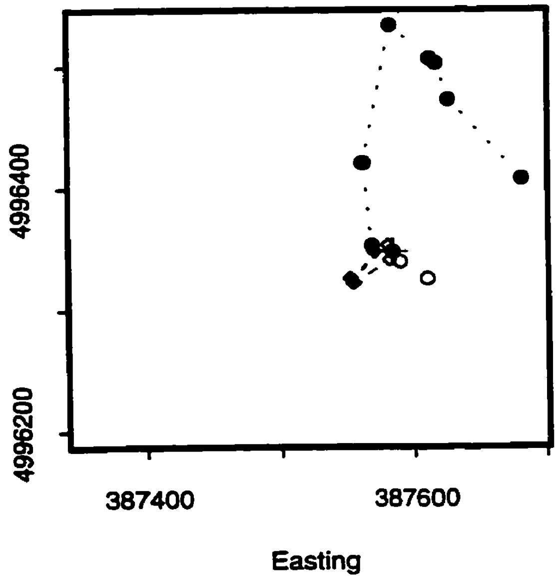
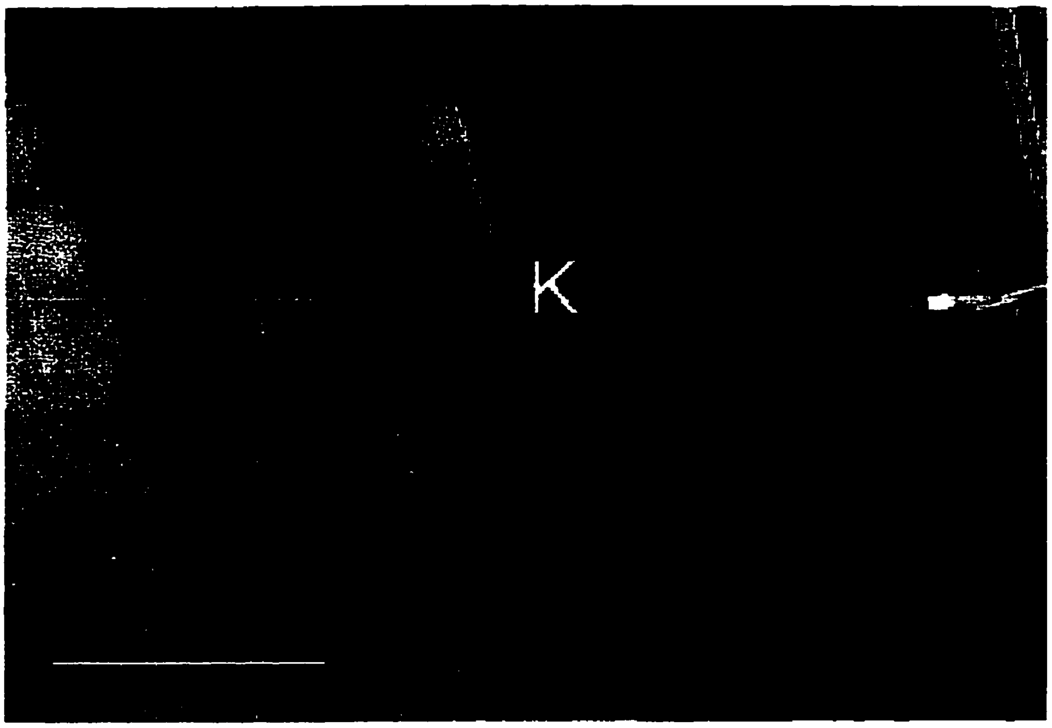
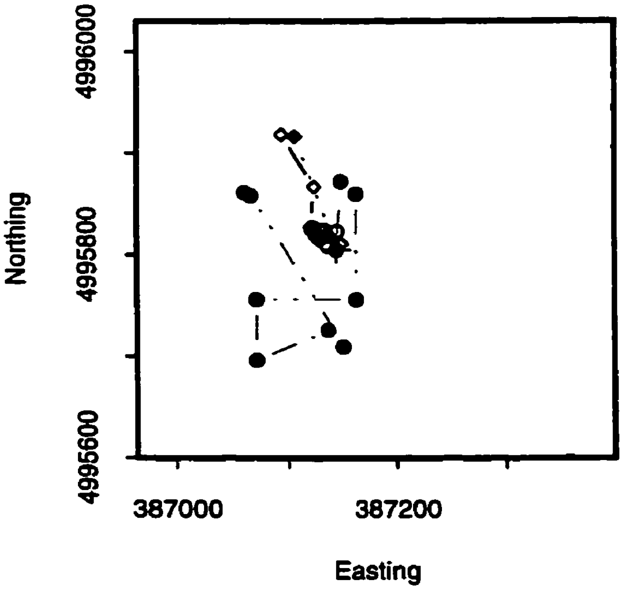
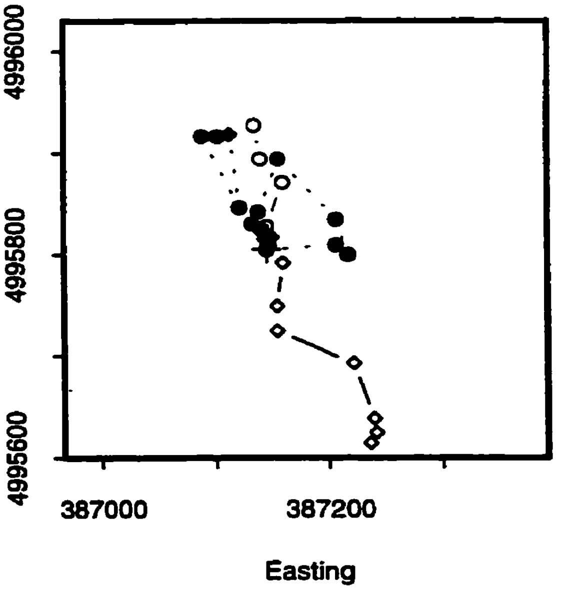


Figure 5. Graphical presentation of movement pathways for frogs released at site K in the Non-Forest landscape. The different habitat types at site K are depicted in the aerial (a) and can be matched to the pathways taking the different scaling factor into account. The scale of the bar in the aerial is 170 metres. Cross bars in Figures 5(b) and 5(c) denote the release point, site K, with movements appearing constrained by the presence of drainage ditches. Open symbols denote residents of the landscape and solid symbols denote foreigners.





(b) Release site K in non-forest landscape
date: 19/08-25/08



(c) Release site K in non-forest landscape
date: 25/08-31/08

Figure 6. Plot of the interaction between habitat and landscape on the total distance moved by *R. clamitans* after the six day tracking period. The forested habitat in the Forest landscape indicates minimal distances moved whereas the forested habitat (fence-row) in the Non-Forest landscape indicates greater amounts of movement.

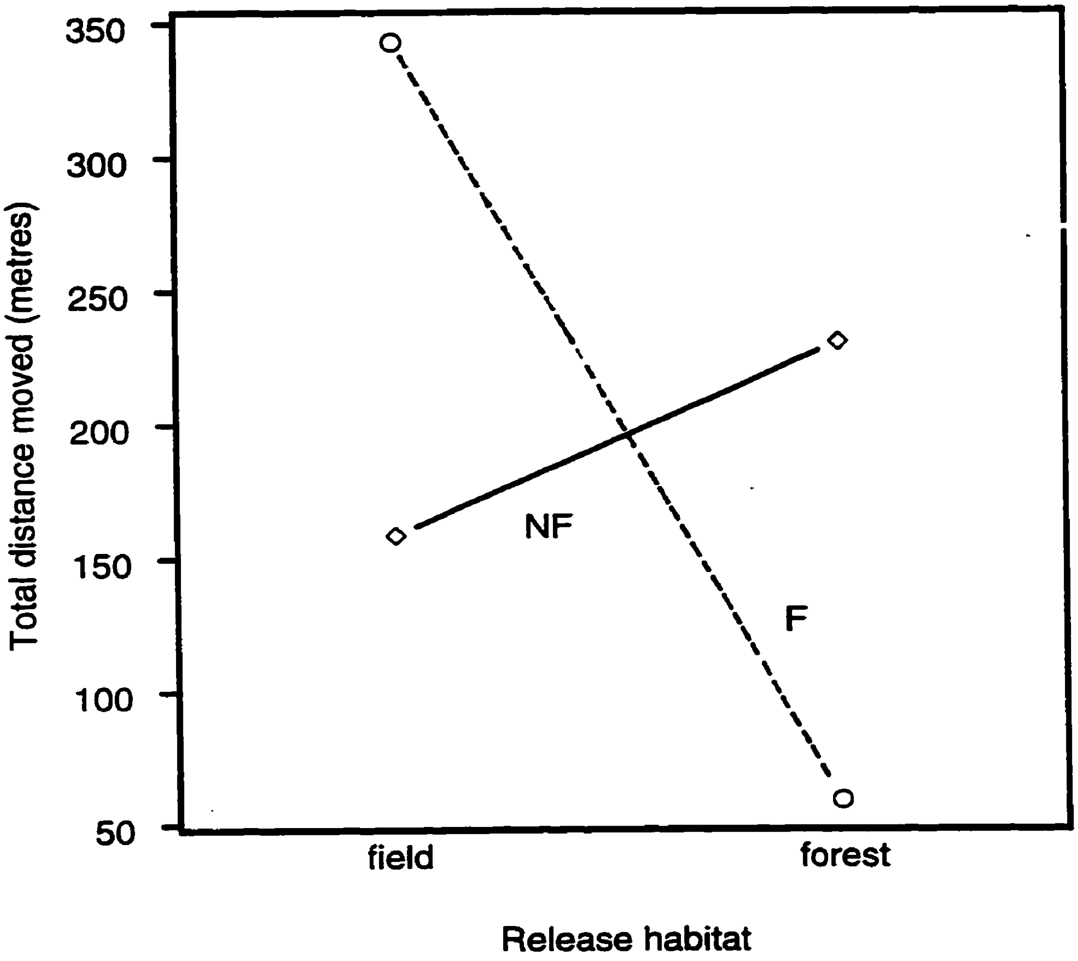

350
300
250
200
150
100
50
Total distance moved (metres)
NF
F
field
forest
Release habitat

Figure 7. Boxplots indicating the influence of class of frog; foreigner or resident, on the total distances moved (a), on the net displacements (b) and on the ratio of net displacement to total distance moved. For both total distances moved and net displacement, foreigners moved on average, the greatest distances. The ratio of net displacement to total distance moved (c) indicates that residents on average will move in a more direct line (mean closer to 1).

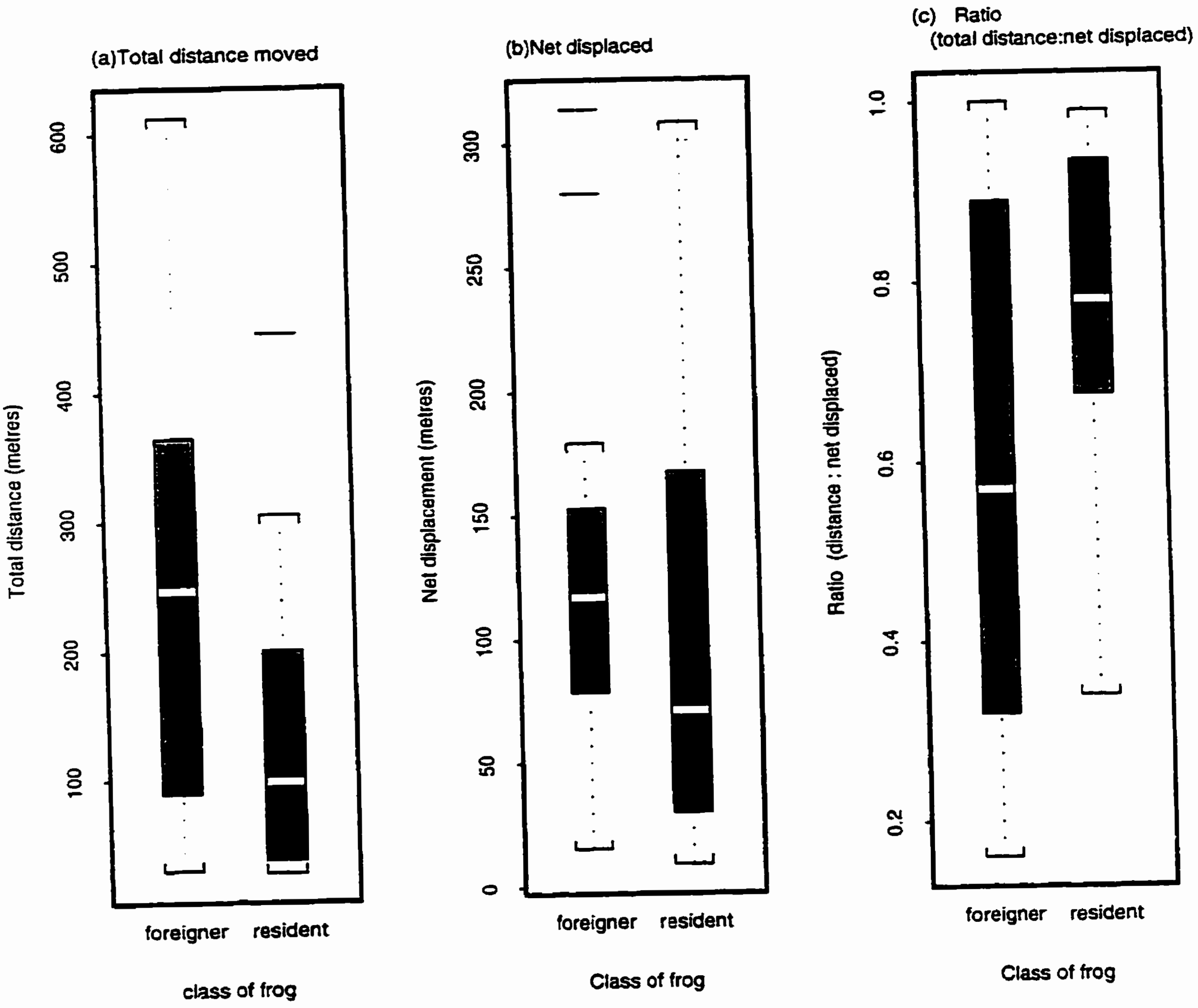

(a)Total distance moved
Total distance (metres)
100
200
300
400
500
600
foreigner
resident
class of frog
(b)Net displaced
Net displacement (metres)
0
50
100
150
200
250
300
foreigner
resident
Class of frog
(c) Ratio
(total distance:net displaced)
Ratio (distance : net displaced)
0.2
0.4
0.6
0.8
1.0
foreigner
resident
Class of frog

Figure 8. Boxplot indicating the influence of habitat type on rates of movement. Frogs moving through roads, fields with and without cover demonstrate the highest rates of movement and frogs moving through drainage ditches, forested habitat and residential areas demonstrate the lowest rates of movement

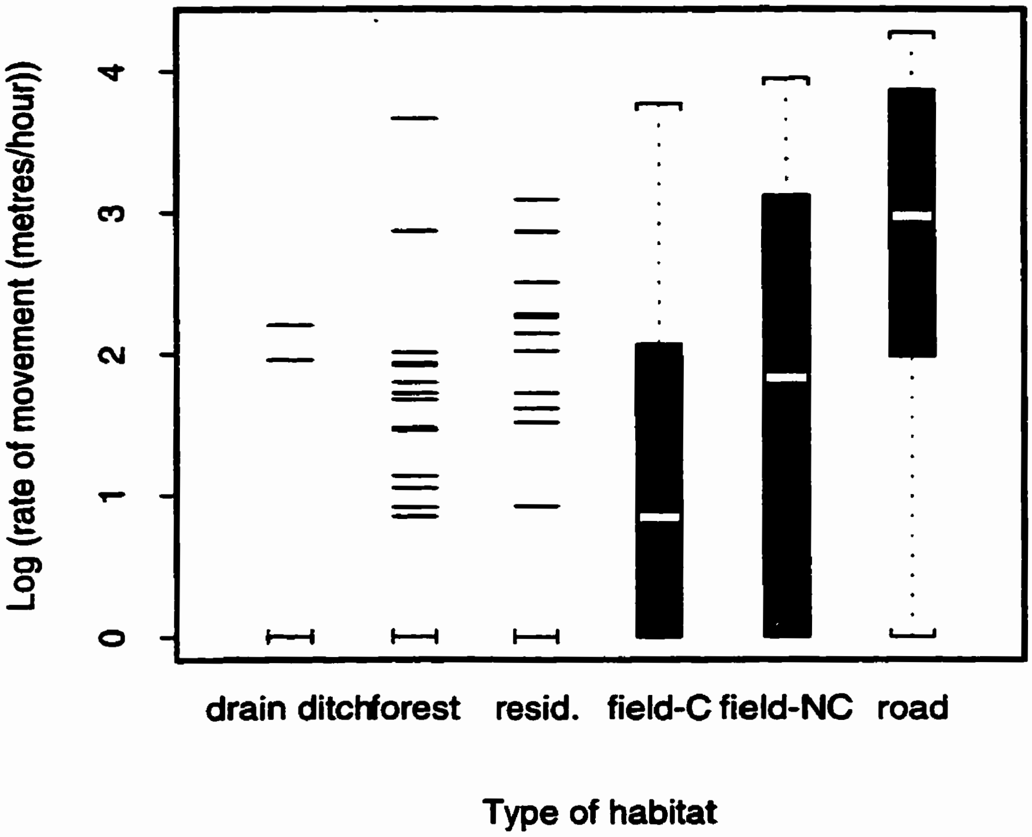
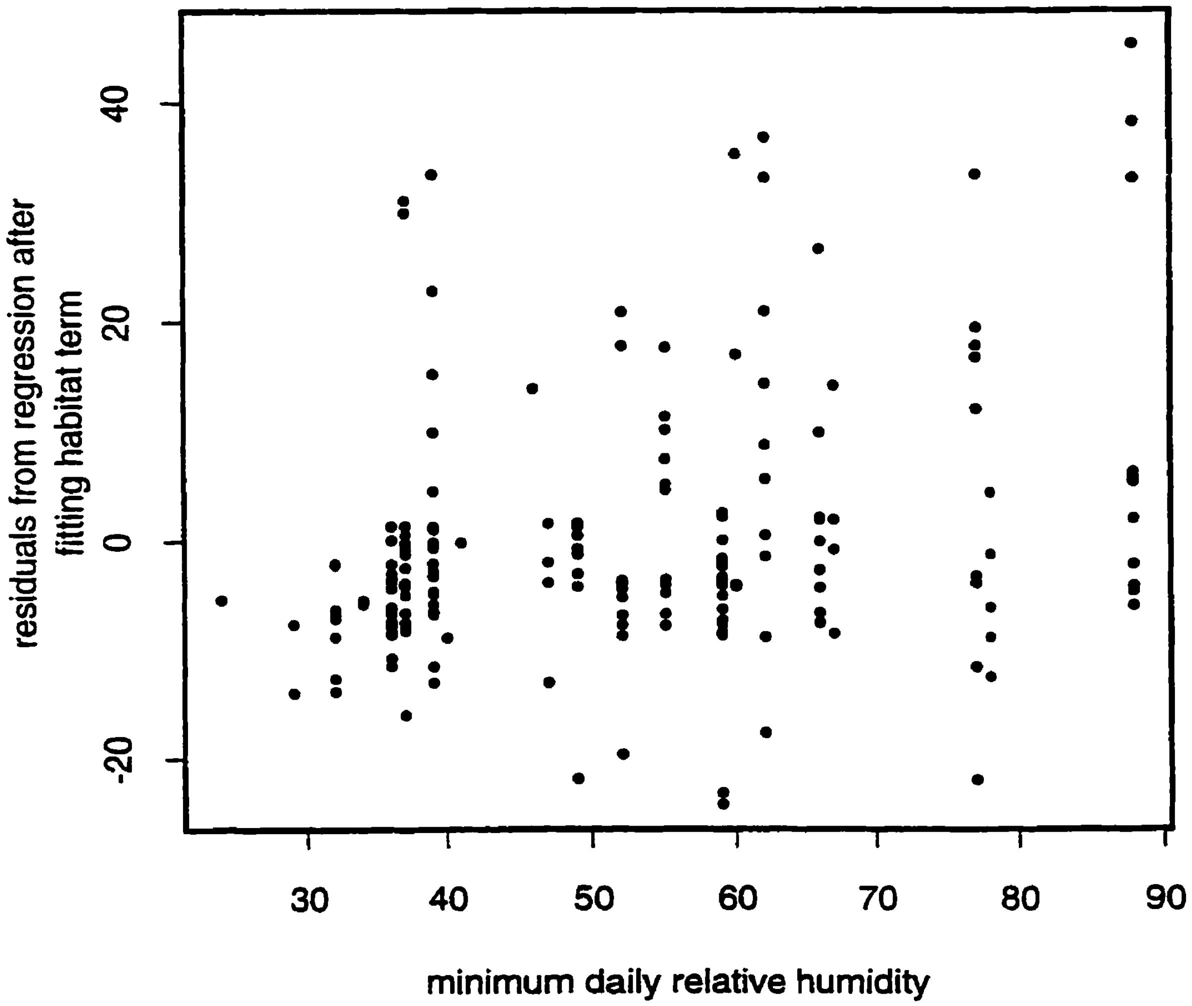

Log (rate of movement (metres/hour))
0
1
2
3
4
drain ditch
forest
resid.
field-C
field-NC
road
Type of habitat

Figure 9. Plot indicating the influence of minimum daily relative humidity on the residuals of the rates of movement after fitting the influence of habitat using a linear regression. The influence of the minimum daily relative humidity on the rate of movement is only marginally detected.


residuals from regression after
fitting habitat term
-20
0
20
40
30
40
50
60
70
80
90
minimum daily relative humidity

GENERAL DISCUSSION

I used a hierarchical approach to assess the movement dynamics of *Rana sylvatica*, *R. pipiens* and *R. clamitans* at breeding ponds in two different landscapes; one dominated by forested habitat, the other by agriculture. Three studies form the hierarchy. The survey study (Chapter 1) provides a generalized view of the seasonal and spatial distribution of individuals moving toward or away from breeding ponds in three habitat types; field, forest and stream-riparian vegetation. The mark-recapture study (Chapter 2) provides generalizations on landscape structure elements that influence the success of individuals returning to their philopatric ponds. The influence of intervening habitats between the release site and recapture point was assessed by comparing the pathways between successful and unsuccessful returns to philopatric ponds. The radio-telemetry study (Chapter 3) provides insight into the behavioural responses of the frogs to the six different types of habitat found within the two landscape mosaics. A distinction was made between habitats which facilitate or impede the movement of frogs across the landscape.

A number of conclusions are drawn from the survey study. A greater amount of movement activity was observed in the forested landscape. This reflects that within this landscape, the proximity and types of habitats surrounding ponds may be more conducive to movements at the ponds. Heatwole (1961) demonstrated that the presence of an aquatic site in a forest patch prompted the movement of *R. sylvatica*. As the pond dried up during the summer, this species followed the receding water line. A greater number of *R. sylvatica* and *R. pipiens* were captured in the forested landscape, whereas a greater number of *R. clamitans* were captured in the non-forested landscape. This may reflect the specific terrestrial habitat requirements for both *R. sylvatica* and *R. pipiens* whereas *R. clamitans* is predominantly an aquatic species and therefore less reliant on the diversity of terrestrial habitat.

All three species of anurans demonstrated a tri-phasic seasonal use of ponds, suggesting that ponds are used for more than breeding. Movement peaks were detected at ponds in the spring, mid summer and early fall. I expected the aquatic species *R. clamitans* to display such a trend, however, both semi-terrestrial species *R. pipiens* and *R. sylvatica* demonstrated this trend as well. The seasonal activities observed are probably influenced by both the size and stage of the frogs (i.e., breeding adults during breeding and potentially over-wintering migrations; sexually immature first and second year olds dispersing to new aquatic sites during the summer). Similar age specific movement patterns have been proposed for *Ascaphus truei*- the pacific tailed frog (Daugherty & Sheldon 1982).

An assessment of the size distributions within each species indicated that large frogs of all three species were in greater numbers in the non-forested landscape, with fewer large frogs being found in the forested landscape. This trend suggests that different factors are influencing the population size structures of these populations within the two landscapes. Although it is not known whether this is occurring in the terrestrial or aquatic phase, it is probable that terrestrial movement is influencing these trends. The significant influence of the type of habitat on the movements of all size classes for both *R. clamitans* and *R. pipiens* toward and away from ponds suggests that the structure of the landscape may be contributing to the observed size structure of the two populations. Within each species, the influence of landscape and habitat-landscape interactions suggests that landscape features consistently influence no single size class. The combination of seasonal trends in movement and changing environmental conditions such as soil moisture and vegetative cover may be masking potential movement trends associated with different stage structured movements, i.e., breeding migrations, summer dispersal and over-wintering migrations. In order to consider these elements, the mark-recapture study provided a fixed starting point from which pathways within landscapes could be assessed.

The results from the mark recapture study identified a number of key points not clarified in the survey study. Frogs displaced to short distances (200-300 metres) from philopatric ponds represented all but one of the recaptures at ponds. This suggests that movement toward ponds at the survey level may have been highly influenced by the extent to which frogs were isolated from the ponds. In this study distances between 600 and 800 metres significantly isolated frogs from their philopatric ponds. My distance estimates compared to the work of Dole (1965) and Oldham (1967) seem quite conservative--the distances at which the frogs in their studies were isolated from philopatric ponds ranged between 1.0 and 3.2 km. In this study, it was found that the probability of a successful return to a pond was greatest when the proportion of field habitat along a route was high. Reh & Seitz (1990) similarly found that the presence of field habitat significantly influenced the movements of *R. temporaria* between ponds. A large proportion of forested or wet habitat along a route, however, decreased the probability of returning to a pond. The presence of linear elements, such as roadways, streams and ditches also appeared to decrease the rate of recapture at ponds. This contradicts findings by Reh & Seitz (1990) who proposed that the presence of linear aquatic elements facilitated the movements of *R. temporaria* between ponds. My findings suggest that the type of habitat has a significant influence on the movement dynamics of these species across the landscape. However, the mechanisms influencing the behavioural responses are not known. To assess the influence of specific habitat types on these trends, movement within specific habitats was explored by using radio-telemetry.

Movement within specific habitat types was evaluated by considering the following three movement responses; rates of movement within specific habitat types, total distances moved between a release point and the recapture point, and the net displacements between the release and recapture points. Total distances moved and net displacements were both significantly influenced by the landscape and habitat in which frogs were displaced. Comparable to the generalizations made in the mark-recapture study, field habitat facilitated movements whereas forest and wet habitat impeded movements to philopatric ponds. Rates of movement within the different habitats suggest similar responses; linear aquatic elements such as drainage ditches and streams, and sheltered forests impede movements, and fields with and without cover and roads facilitate movement. Based on these findings, movement toward ponds would therefore be facilitated by the presence of dry and exposed habitats such as fields and roads and impeded by the presence of wet and sheltered habitats such as drainage ditches, streams and forests. Of concern is that the three species of frogs studied did not move out of habitats which impeded their movements, but remained there for the duration of the telemetry study, and in many cases for the mark-recapture study. For species that require breeding, summer foraging and over-wintering sites, these 'stopping' habitats may hinder their ability to persist.

All three studies suggest that the linear aquatic elements, in the form of drainage ditches and streams impede movements to breeding ponds. In the telemetry study, individuals entering drainage ditches or streams, generally remained in this habitat for the duration of the tracking period. The mark recapture study indicated that the routes which facilitated movements to philopatric ponds did not consist of drainage ditches or streams. The survey data suggest that in the forested landscape, a greater proportion of captures occurred in stream habitat, however, in the non-forested landscape, fewer individuals were captured in streams and drainage ditches.

The specific behavioural responses of the three species, *R. clamitans*, *R. pipiens* and *R. sylvatica* to the different habitat types may have significant implications in the persistence of these species within the two landscapes. The extent to which the linear aquatic elements may trap individuals moving to breeding, summer foraging or over-wintering sites in the non-forested landscape may account for the differences in the size structure of the populations in the non-forested landscape compared to the forested landscape. Similarly, the presence of roadways may equally contribute to the difference in the size structure of the two landscape populations. The rationale is that the young of the year are more physiologically constrained than larger frogs (which have a lower surface area to volume ratio than smaller frogs) influencing their movements as they disperse from their larval ponds. Consequently, the movements across terrestrial habitats for individuals with considerable physiological constraints and low mobility suggests that the extent to which frogs can tolerate potentially desiccating conditions may be influenced by the specific habitat types they encounter. My work suggests that in a landscape mosaic where most of the habitat consists of field, anuran movements to ponds is facilitated, however, when aquatic elements are introduced, movements to ponds are hindered. The implication is that frogs will take refuge in drainage ditches and streams in the short term, but may remain in these habitats in the long term. The success of breeding and over-wintering in such habitats has not been assessed however, *R. sylvatica* has been observed to unsuccessfully breed in drainage ditches. The role of these aquatic habitats in conjunction with surrounding terrestrial habitat needs to be more thoroughly considered in light of the physiological capabilities of the frog. Because these animals may spend a significant amount of time in linear aquatic elements in order to compensate for physiological constraints, the influence on the population structure of these species does not look promising.

The major conclusion from this thesis is that drainage ditches appear to be detrimentally influencing the persistence of anuran populations in landscapes altered by human activities. Frogs take refuge in this habitat and our objectives should be to ensure that these animals are capable of meeting both breeding and over-wintering requirements. The question proposed is whether we can alter drainage ditches to provide these resources or to ensure the movement of anurans to more appropriate sites. In landscapes that have been altered by human activities, the number of breeding sites available to frogs are reduced from what they once were. In light of this, it may be advantageous to create new sites for these animals. Drainage ditches that are already acting as refugia can be altered to provide a more permanent resource. Lining drainage ditches with semi-permeable to impermeable clay bottoms may help to retain water in these habitats. Also, during the summer months, many farmers irrigate their crops and some of this water could potentially be used to ensure breeding success. Approaches to ensure over-wintering success will be species dependent; *R. clamitans* and *R. pipiens* requiring aquatic habitat and *R. sylvatica* requiring terrestrial habitat. These modifications to drainage ditches should increase the number of resource sites available to anurans, enhancing the ability of these species to persist.

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