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Population Ecology of the Western Chorus Frog,

Pseudacris triseriata.

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requirements of the degree of Master of Science

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Abstract

The relationship between habitat preferences and rates of dispersal and directional orientation across different vegetations was investigated using captures from an array of drift fences for *Pseudacris triseriata*, at a breeding pond near Boucherville, Quebec. Growth rates for juveniles were similar across the study area, suggesting that food was not limiting and movement is related to habitat preference. Frog residence time in habitat enclosures, and between fence arrays was significantly longer for frogs in humid prairie vegetation compared to those in shrubby vegetation. The number of frogs caught per metre of fence in humid prairies was also on average higher than either shrubby or arid prairie vegetations. Together both migration rates and captures per metre of fence suggest that the preferred habitat for *P. triseriata* is humid prairie vegetation (e.g. *Phalaris* grass). Target-oriented dispersal may explain why similar numbers of *P. triseriata* were captured in both shrubby and humid prairie vegetation, despite the perceived preference for humid prairies over shrubby vegetation. The continued persistence of this population appears to be based on the recruitment of juveniles from the larval stage, and is also sensitive to the fecundity of the first time breeders.

Résumé

Le rapport entre la préférence d'habitat et les degrés de dispersion et l'orientation directionnelle à travers différentes végétations ont été étudiés en utilisant des captures d'une rangée de clôtures de déviation pour *Pseudacris triseriata*, à un étang de reproduction près de Boucherville, Québec. La croissance des jeunes était semblable à traver le secteur d'étude, suggérant ainsi que la nourriture n'est pas limitée et que le mouvement a été lié à la préférence d'habitat. La durée de la résidence des grenouilles dans des clôtures d'habitat et entre les rangées de barrière était sensiblement plus longue en végétation de prairie humide qu'en végétation composée d'arbustes. Le nombre de grenouilles attrapé par mètre de clôture dans les prairies humides était plus élevé que celui en végétation d'arbustes ou en prairie aride. Ensemble, le degré de migration et les captures par mètre de clôture suggèrent que l'habitat préféré du *P. triseriata* est la végétation en prairie humide (par exemple, herbe de *Phalaris*). La dispersion orientée selon la cible peut expliquer pourquoi des nombres semblables du *P. triseriata* ont été capturés en végétation de type arbuste et en prairie humide, en dépit de la préférence perçue pour celle en prairie humide. Le succès de cette population semble être basé sur le recrutement des jeunes dès le stade de têtard et est également relié à la fécondité des rainettes qui se reproduisent pour la première fois.

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Introduction

Conservation of declining species requires that we know what habitats are critical to the species survival. The critical habitats may change from location to location but some understanding of what a species needs, and can use, are important to understanding the ecology of the species of concern and in so knowing can we then begin to work towards their conservation.

Amphibians and especially anurans may have an important role in transferring energy from their aquatic breeding pools to the terrestrial system. Reduction or elimination of the energy transfer is likely to affect the ecosystem. As such, amphibians are receiving considerable attention as possible indicators of ecosystem deterioration (Wake 1991; Beebee 1996; Alford and Richards 1999). A better understanding of the ecology of amphibians, the health of their populations and the connections between amphibians to the rest of their ecosystem might give insight both into the conditions and potential causes of their decline and their potential as indicators for ecosystem decline.

In Quebec, *Pseudacris triseriata* has been designated as threatened due to apparent reductions in the number and sizes of their populations. *Pseudacris triseriata* is an amenable species to work with because it breeds annually in discrete and identifiable habitats that can be located by listening for chorusing males, and because evidence indicates that they do not disperse very far (Kramer 1974; Smith 1983). Ascertaining why this species is declining in Quebec might help to address questions about how and why species may become endangered and diminish in both abundance and range.

The Western Chorus Frog, *Pseudacris triseriata*, is a small tree frog whose range extends from Oklahoma to South Dakota in the west and to southern Quebec and northern New York in the east with a disjunct portion in New Mexico and Arizona (Platz 1989). Seemingly a habitat generalist, they were probably originally most abundant in savannah and grassland ecosystems (Bleakney 1959), whereas today they occur in many habitat types. The most frequently encountered situation is in a field in early to mid succession, usually former farmland, with sparse tree and shrub cover and shallow marshes (Briston and Kissell 1996; Conant and Collins 1991). The status of *P. triseriata* is secure in North America, but within the northeast of its range extending into southern Quebec and Vermont, the populations are locally threatened. Choruses of *P. triseriata* announcing the beginning of spring in many areas within its range have gone silent. Bider and Matte (1991) claim that *P. triseriata* is the most rare amphibian in Quebec. The apparent sudden disappearances, not only from the periphery but also from within *P. triseriata*'s range have yet to be adequately explained.

The principles determining species ranges and abundances, and distributions within those ranges, are unclear. History and happenstance may have determined where species are today. Knowing why species are where they are, can we then begin to understand why they are absent in a vicinity, and why they decline?

Current species ranges are often a poor reflection of historic ranges. Hecnar and M'Closkey (1996, 1998) show that amphibian communities in southwestern Ontario have lost more species in areas with longer exposure to European settlement. Much of what was suitable habitat has been altered, cleared or become a barrier to dispersal, thus isolating populations. Additionally, some barriers to dispersal have been removed, allowing species to invade new ranges of which some have reduced or eliminated species native to that area (e.g. Lampreys among other aquatic species in the Great Lakes, and Brown tree snakes on Guam to name two).

The persistence of isolated populations depends greatly upon the local dynamics within patches. The success of species in those patches, in turn, is dependent upon their ability to persist or be re-colonized in the face of perturbations (Tilman 1994). Drawing from Tilman's work we may assume that some species are better at persisting in a single location but are poor colonizers whereas others are good colonizers but have unstable populations. In the face of environmental and habitat changes, a balance between colonization and persistence is necessary depending upon conditions in a constantly changing landscape. Those species that are on the extremes of the persistence or colonization spectrum risk being isolated or too dispersed to persist in the face of perturbations and habitat loss, accentuated via the Allee effect of negative density dependence (as per Tilman 1994). In low density populations, failure to locate mates, and inbreeding, can result in further negative growth, thereby further reducing the population and can eventually cause its local extinction (Leibhold and Bascompte 2003).

Physiological and phylographic boundaries ultimately determine the global range of a species. The distributions and ranges of species result from regional and local processes. Biogeographical and historical processes acting at larger spatial scales control the regional presence or absence of a species in that landscape (Cornell and Karlson 1997) whereas local processes, which include competition, predation, resource availability and local abiotic conditions, determine the species' presence and abundance within a habitat. A combination of local abundance and recruitment supply individuals who may disperse into the regional landscape composed of a mosaic of suitable, marginal, and undesirable habitats. Species that are mobile can access more isolated and distant patches of habitat while those with limited dispersal depend upon closely linked patches of suitable habitat (Haddad 1999). It is commonly believed that species with greater mobility are likely to be less affected by fragmentation and habitat alteration. Gibbs (1998), however, demonstrated the opposite in that woodland amphibian species with high mobility and complex habitat needs were more likely to suffer local extinction when habitats become fragmented than species with limited dispersal and simple habitat needs. Re-colonization of sites within the region depends upon the species' ability to disperse and recruitment within that locality. The heterogeneity of patches permits species to be locally abundant in one patch while, in others, they may flounder or crash. The ability of a species to re-colonize patches where crashes occur may allow a species to persist in marginal patches. The overall persistence of a species at a regional scale thus is a result of the dynamics of extinction, colonization, and migration among local populations (Gilpin and Hanski 1991).

What we know about Pseudacris triseriata

The Western Chorus Frog is a secretive species, rarely seen after its breeding season. What is known or inferred about *P. triseriata* habitat is that the frogs prefer humid grassy fields, near shallow temporary ponds with relatively few aquatic predators. The frogs are found in mostly open habitats, with low canopy cover such as landscapes in early succession (Bleakney 1959; Constible et al. 2001; Kramer 1978; McLeod and Gates 1998; Morin 1983; Pearman 1995; Skelly 1995b; Smith and Smith 1952).

Pseudacris triseriata is found in temperate climates where breeding occurs soon after or during the spring thaw, with breeding populations sometimes reaching over a thousand individuals. Females can lay eggs in several masses with the total number in the range of 72 to 1000 (Smith 1990; Whitaker 1971), with significant variation from localities and across their distribution (Kramer 1978; Smith 1990; Whitaker 1971). Breeding generally occurs in quiet waters, temporary ponds, ditches and water holes, which are generally associated with farm landscapes (Bleakney 1959; Daigle 1997; Kramer 1978). Breeding does occur, but with reduced success, in more permanent water bodies that contain greater densities of amphibian larvae predators (Morin 1983; Pearman 1995; Skelly 1995a).

Pseudacris triseriata appear to have poor dispersal (Tordoff 1976, Tordoff and Pettus 1977), and are rarely seen more than 100 m from a pond (Smith 1983). The limited dispersal behaviour of chorus frogs creates dependence upon closely situated ponds for continued persistence. Despite the limited dispersal of a majority of the population, Desroches et al. (2001) reported movement as far as 275 m from the current study's breeding pond and Spencer (1964) reported individuals of the boreal chorus frog, *Pseudacris maculata*, moving up to 685 m, which may be important for maintenance of metapopulations.

Pseudacris triseriata's critical habitats appear to be variable and depend on the setting. The uncertainty of their dispersal ability, which seems underestimated (compare Smith 1983; Tordoff et al. 1976; and Tordoff and Pettus 1977 versus Spencer 1964), may result in greater home ranges for *P. triseriata* than normally believed. Dispersal may be mediated by local factors such as location of suitable hibernacula, and summer foraging or refuge areas.

Possible reasons for their decline

Historical accounts of *P. triseriata* (Bleakney 1959), suggest that the northeastern limit of its range was the St. Lawrence River valley around Montreal. Bleakney (1959) concluded that both the Ottawa and St. Lawrence River posed significant barriers to *P. triseriata* dispersal. The other barriers to Western Chorus Frog distribution in the area are the mountain regions to the east and west of the valley where no populations can be found, and the agricultural lands along the shores of the river that are tilled and drained leaving no suitable habitats (Bleakney 1959). Bonin and Galois (1994) suggest that deforestation of the St. Lawrence created favourable conditions for the establishment of the species during European colonization. The subsequent succession of those landscapes, like in southern Ontario (Hecnar and M'Closkey 1996, 1998), has caused the extirpation of open habitat species, such as *P. triseriata*, in landscapes in mid to late succession.

Succession at sites results in ponds becoming enclosed by forest canopies, reducing hydroperiods, and causing changes to the microbial community and productivity of ponds that can reduce or eliminate recruitment of individuals into the surrounding population (Skelly et al. 1999; Skelly and Meir 1997). The hydrology of a breeding site influences which species are likely to persist (Hecnar and M'Closkey 1996; Kolozsvary and Swihart 1999). Farming and urban developments can cause changes in the hydrology of ephemeral ponds, reducing hydroperiods of breeding ponds, thus reducing or eliminating recruitment and further diminishing populations.

The limiting factors that determine a species' persistence or demise are the abundance of resources, population demographics and the habitats critical to the species. The critical habitat for a pond-breeding frog is composed of the required breeding sites, terrestrial foraging habitat and, in the case of temperate-region species, over-wintering hibernacula (Beebee 1996). Critical to its survival is how and when the animals use those habitats.

The expansion of farming and encroachment of urbanization is certainly eliminating populations of *P. triseriata*. The anthropogenic impacts may also alter or eliminate essential habitats within sites that *P. triseriata* uses throughout the season, diminishing populations. The role of land use change is clear in disturbed areas, but declines may be occurring even in apparent undisturbed areas. Other mechanisms proposed as causing amphibian declines include environmental fluctuations, increased use of pesticides and toxic chemicals, infectious diseases and invading species (Collins and Storfer 2003). These mechanisms alone or acting in synergism may also be responsible for *P. triseriata* population declines.

Competition between *P. triseriata* and invading native species has been implicated in the decline and disappearance of populations of Western Chorus frogs. Western Chorus frogs do co-exist with other amphibian species in the same breeding pool. Investigations into larval communities, though, revealed existence of weak interspecific competition between *P. triseriata* and *Pseudacris crucifer* (Skelly 1995a, 1996, 1997; Van Buskirk 1988). *Rana sylvatica* is another frog mentioned as a potential competitor to the *P. triseriata,* and is implicated in the disappearance of the introduced populations of *P. triseriata* in Newfoundland (Maunder 1983).

Pseudacris triseriata tadpoles have rapid growth rates and a reduced time to metamorphosis compared to both *P. crucifer* and *R. sylvatica* allowing them to be more competitive in temporary ponds (Skelly 1995a). In comparison to *P. crucifer*, *P. triseriata* are less successful in permanent ponds as their tadpole mortality is high in permanent water bodies. A trade-off exists for *P. triseriata,* whose larval activity is greater than that of *P. crucifer*, allowing them to acquire more resources and grow faster, but at the cost of increased predation (Bridges 2002). Many of the aquatic predators use movement and mechanosensory means to detect prey, resulting in increased predation of chorus frog larvae (Skelly 1995a; Wassersug and Sperry 1977). The density and types of predators increase with the permanence of the pond, with more and larger predators occurring in permanent water bodies (Skelly 1992, 1995a; Smith 1983; Woodward 1983). The increased risk of predation not only reduces the activity of *P. triseriata,* reducing growth rate, but mortality can be so high as to eliminate recruitment in permanent ponds.

The different distributions and ranges of *P. triseriata* versus *P. crucifer* appears to be explained by differential susceptibility to pond permanence and predator compositions found in the gradient of ephemeral to permanent ponds (Skelly 1995a, 1996, 1997). Relatively few *P. triseriata* populations occur near permanent ponds, while greater proportions and abundances can be found near temporary bodies of water, whereas the opposite is true of *P. crucifer* (Pearman 1995; Skelly 1995a, 1996). Similarly, species in the *Litoria* genus, in Australia, show similar patterns of distributions for species with dissimilar larval activity (Skelly 1997). *Pseudacris triseriata* larvae show plasticity in their behaviour in response to presence of predators by reducing activity but at the cost of growth rate, which may increase the period of susceptibility to size dependent predators, further reducing recruitment (Skelly 1995a, 1997; Travis 1981). In larger ponds, heterogeneity of microhabitats within the pond could create refuges from predators, creating a patchy distribution of larvae within the pond, allowing successful recruitment in ponds with many aquatic predators.

Success of amphibian populations, which have complex life cycles, is dependent upon successful recruitment into each of several life stages. *Pseudacris triseriata* has four life stages, adult, egg, larval and a froglet or juvenile period before they reach sexual maturity. Skelly (1995a, 1996, 1997) has shown that the larval stage of *P. triseriata* can be an important mechanism controlling the distribution of the species across a pond permanence and predation gradient. The larval stage is the first bottleneck for recruitment. The survivorship of larvae to metamorphosis determines the starting number of metamorphs. Segregation of tadpoles might reflect interspecific competition, responses to local conditions or presence of predators. The distribution and abundance of larval amphibians within a pond may affect health of individuals, determine growth rates, and ultimately size at metamorphosis (Skelly 1995a; Smith 1983, 1987, 1990; Sredl and Collins 1991).

What we know little or nothing about

Little is known of the postmetamorphic ecology of the Western Chorus Frog. We have an idea of the success of *P. triseriata* larvae in temporary ponds versus more permanent ponds, larvae success in absence of aquatic predators (e.g. Skelly 1995a, 1996, 1997; Smith 1983, 1987), use of cryoprotectants for freeze-tolerance in adults (Jenkins and Swanson 2000; Miller and Packard 1977), and relative status of populations (*ie.* Daigle 1997), but little has been done to determine their ecology (Whitaker 1971). An investigation into the selection of habitats at each life stage of *P. triseriata*, by means of looking at the directional orientation of migration patterns and the distribution of abundances in the available habitats, use of over-wintering habitats, and breeding behaviour will reveal some of the postmetamorphic ecology of the Western Chorus Frog.

Pseudacris triseriata is a secretive animal, rarely seen outside of the breeding season, and is difficult to find in the field due to its camouflage and burrowing habits (Kramer 1973). In addition, the chorus frog is too small for affordable tracking devices. These two properties require new techniques to observe the behaviours of chorus frogs outside of the breeding season.

Caldwell (1987) demonstrated success in using a drift fence with *Pseudacris ornata* and *P. nigrita* to determine abundance of breeding populations. An array of two drift fences around a breeding pond was used to determine the dispersal patterns of *P. triseriata*. The migration patterns of adults and young of the year caught immigrating and emigrating from the breeding pond and outer fence, if different from random, would suggest orientation behaviour by chorus frogs (Dodd and Cade 1998). Orientation could suggest active selection of habitats or target oriented homing towards suitable foraging or over-wintering habitats (Sjogren-Gulve 1998). Orientation may be by use of cues to orientation like the sun or by stellar navigation or rheotaxis (Phillips and Sexton 1989; Stenhouse 1985). To determine the habitat preferences of the *P. triseriata* we need to determine how much time it spends in the habitats available.

Habitat complexity and differences may be important to anurans for foraging, thermoregulation, protection against desiccation and predation. Amphibians are often associated with leaf litter, ground cover and soil moisture and density changes in relation to the availability of these resources and the physiological and behavioural requirements of the species (Constible et al. 2001). Rothermel and Semlitsch (2002) showed that juvenile amphibians are capable of detecting and avoiding unfavourable habitats, preventing demographic drain in emigrating juveniles away from a breeding pool.

Dispersal determines the structure of metapopulations (Hecnar and M'Closkey 1996), affecting gene flow and the maintenance of sink populations. Movement away from habitat that is unsuitable or is of low quality, dispersal during times of stress (Parris 1998), or migration in search of suitable hibernacula are all types of dispersal that shape the ecology of the Western Chorus Frog. Individuals finding themselves in habitats of poor-quality should try to leave and those in high-quality habitats should remain (Winker et al. 1995). Therefore, if dispersal is related to habitat quality or suitability, animals finding themselves in unsuitable habitat should disperse out of it. There should be a relative rate of dispersal associated with different habitat types, depending on the selection preference of the species. To test for habitat preferences in *P. triseriata*, residence time in different habitat enclosures would permit insight into the needs of the frog at different times. In the case of the Western Chorus Frog residence time is expected to be short in unsuitable habitat, longer in marginal habitat, and longest in suitable and preferred habitats.

Little is known about the natural conditions of *P. triseriata* hibernation. Ectotherms in temperate zones contend with low temperatures during winter. Amphibians survive cold temperatures via freeze-tolerance and or hibernation in places protected against the cold. Some anurans hibernate in the water of a pond or lake, others dig into the soil or use tunnels or burrows (e.g. *Pseudacris streckeri illinoensis*), and others still hide under leaf litter to avoid adverse environmental conditions (Irwin et al. 1999; Holenweg and Reyer 2000; Pinder et al. 1992; Tucker et al. 1995; Tucker 2000). Only incidental accounts of chorus frogs found in ant colonies (Carpenter 1983) and occasional discovery under logs (Froom 1982) are available as descriptions of hibernacula for *P. triseriata*. The Western Chorus Frog is freeze-tolerant and might show similar behaviour to other hylids such as *Pseudacris crucifer* whom is also freeze-tolerant or, such as *Acris crepitans*, a terrestrial hibernator, and choose areas that provide protection from the elements. When the temperature drops in the fall, the Western Chorus Frogs should search out areas where leaf litter is sufficient to insulate them against the cold of winter during their hibernation.

The success of the juvenile stage is dependent upon the ability of froglets to secure sufficient resources and find suitable hibernacula to survive the winter. Rapid growth can increase the likelihood that individuals reach sexual maturity earlier but, in addition, successful over-wintering depends upon stored reserves to effectively hibernate which is related to the body size (Jenkins and Swanson 2000).

Growth of froglets is dependent upon food availability and environmental conditions. Christian (1982) showed that for *P. triseriata* food is not limiting, as they tend to select larger more efficient foods despite the greater abundance of smaller foods. If prey abundance is equally distributed or not limiting across all habitats, then significant differences between growth rates in different habitats would be due to different costs in those habitats. A comparison of size of young of the year across habitat types may show that there are added benefits or costs to certain habitat types.

Ecological sensitivity analysis

Lastly, to determine the stability of the study population, monitoring survival at each stage, either through inference or direct observation, permits the construction of a stage-structure model with which sensitivity and elasticity analyses can be conducted. Sensitivity analysis determines the impact of the survival, recruitment, and fecundity on the per capita growth rate, λ. The sensitivity of each stage is likely to be different as each stage may respond differently to biotic and abiotic factors and the influences one stage has on the next. The increased sensitivity of one stage may determine the ultimate success of the population.

Pseudacris triseriata is a short-lived species, whose success in the larval stage has been shown to determine its distribution within parts of its range (Skelly 1995a, 1996, 1997). Depending upon the contribution of the two succeeding stages, fluctuations in the recruitment from the larval stage may be the most important determinant of population growth and thereby population persistence.

Objectives

The roles of breeding, migration and dispersal, larval distribution, recruitment, survival and habitat selection of *Pseudacris triseriata* were investigated to determine the critical habitats of *P. triseriata*. A comparison with two other species, *P. crucifer* and *R. sylvatica*, found at the same breeding site provided the ability to determine whether observations were specific selection responses of *P. triseriata* to availability of habitats or related to landscape effects of the site.

Due to the difficulties in capture and unknown ecology of the species, a single breeding pond was chosen to concentrate efforts. By concentrating on the migrations of frogs at a single pond, a good picture of habitat selection, growth rate, dispersal and survivorship was compiled.

Materials and Methods

Site description

The study site was located on private lands in a landscape of agricultural fields, wood lots and abandoned fields in different stages of succession on the southern shore of the St. Lawrence River near Boucherville, Quebec (46°36'24" N - 73°23'34" O). A paved road through the area, provided access to the study site, and may have contributed to mortality of migrating amphibians. On the northern side of the road, near the study site, were two cornfields and a small cattle pen. The southern side of the road was a mixture of woodlots, fields in crop rotation and abandoned fields in early succession. During the spring several temporary ponds were situated in depressions in the fields, of which one was chosen as the study pond. The pond was chosen for its ease of access, simple perimeter, and abundance of Western Chorus frogs. Permission for access was obtained from the owner for the duration of the study.

The study pond (Figure 1) was 70 m by 55 m and, at its greatest extent, rarely deeper than 25 cm. The pond was ephemeral, as melting snow and rainfall filled the pond in the spring and by mid summer no surface water remained. The pond itself, lay in a depression into which fed three agricultural drainage ditches and, out of which water drained on the western side of the pond. Within the pond were willow (*Salix sp.*), ash (*Fraxinus sp.*), and American Elm (*Ulmus Americana*) trees. Duckweed (*Lemna minor*), reed canary grass (*Phalaris arundinacea*), and purple loosestrife (*Lythrum salicaria*) dominated the muddy waters of the pond.

The area surrounding the pond was once cultivated but is now fallow. The vegetation on the northern side of the pond consisted mainly of grassy plants dominated by goldenrod (*Solidago sp.*), berry plants (*Rubus alleghenienses, R. strigosus*), and other dry meadow species hereafter referred to as "arid prairie" vegetation. The paved road passed through the field 20 m from the pond. Shrubby plants such as meadowsweet (*Spiraea latifolia*), and wild sarsaparilla (*Aralia nudicaulis*), dominated the eastern side of the pond with hawthorns (*Crataegus sp.*) along the edges of the drainage canal, and a few poplar (*Populus sp.*) and birch trees (*Betula sp.*). The south of the study site was divisible into three vegetative sections. One was mostly goldenrod (arid prairie), the other shrubs (e.g. *S. latifolia* and *A. nudicaulis*) and the third a mix of trees whose understory was dominated by ferns (*Onoclea sp.*) and sarsaparilla. The southwestern corner of the area was a large wet depression that consisted almost entirely of reed canary grass with a few small willow trees hereafter referred to as "humid prairie" vegetation. A drainage ditch bordered by willow and elm trees on the western side of the pond gave way to canary grass in the wet depressions and became arid prairie vegetation further on.

The study pond was host to eight breeding amphibians, two snake species, several migratory and resident birds, small mammals, and many invertebrates. The amphibians breeding at the pond were: *Pseudacris triseriata; Pseudacris crucifer; Rana sylvatica; Rana pipiens; Rana clamitans; Hyla versicolor; Bufo americanus* and *Ambystoma laterale*. The two species of snakes found at the pond were the eastern garter snake (*Thamnophis sirtalis*) and the redbelly snake (*Storeria occipitomaculata*). In the early spring, several migratory ducks (*Anas platyrhynchos*) and Canadian geese (*Branta canadensis*) could be found feeding in the pond during the Western Chorus Frog breeding season. On several occasions I saw an American bittern (*Botaurus lentiginosus*) patrolling the waters. In addition there were numerous other birds present during the season such as redwing blackbirds (*Agelaius phoeniceus*), common starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), sparrows, and finches.

Survey methods

A drift fence was erected around the breeding pond (the "pond fence") to monitor migration of the breeding amphibian populations at the pond. The fencing material was transparent polythene mounted on a wooden frame with the base wrapped around a wooden bar and buried under the soil to keep the plastic taut. The fence was approximately 75 cm high, 25 cm higher than Caldwell's (1987), which was presumed to be of sufficient height to prevent chorus frogs from climbing over. The frame of the fence was already in place but when originally constructed it was built prior to the melting of the snow. As a result the southwestern corner of the pond was not contained within the pond fence. Extensive flood plains developed in that quadrant and in and around drainage canals that intersected the study pond, preventing complete containment of the pond within the pond fence. In the second year of the study, four metres of the plastic fence were replaced with a screen netting to allow water to circulate between the pond and the drainage area in the southwestern corner.

A second fence, the "outer fence", was erected 50 m from the pond fence, though was only 13 m from the pond where the road passed nearby. The outer fence was 471 m long and approximately 25 cm high, depending on the substrate, with a rope backbone stapled to wooden stakes at approximately 2 m intervals. It was designed to retard the frogs but not to stop them. As such, a certain proportion of frogs were expected to elude capture and not be reflected in the totals. In some locations, where water currents were too high, the fence was not buried so as to let water pass. The number of frogs eluding capture was assumed to be relative to the number reaching the fence.

Initially, minnow traps were placed around the exterior of the pond fence to capture incoming frogs. The traps were placed approximately every 6.25 m (35 traps over 223.2 m of fence). Each trap was placed in a depression lined with plastic to help preserve some moisture for amphibians caught. However *P. triseriata* were smaller than the openings in the mesh and use of the traps was discontinued after April 19, 2002. A second trap was designed using plumbing tubes with funnels attached at either end. The second trap had limited success and was discontinued. Due to incidental mortality of amphibians and small mammals the year prior to this study (Desroches et al. 2001), pitfall traps were not used. The final trap method consisted of cover boards placed next to the fence (Heyer et al. 1994), expecting that amphibians would use them for cover.

Each fence was initially divided into 35 sections, one for each trap with corresponding sections on the outer fence. Directional arms (1 m long fence sections perpendicular to the main fence) were placed on either side of the drift fence to replace the traps, on both the pond and outer fence, reducing the number of sections to 12 sections labelled A to L (Figure 1). The directional arms were used to contain the amphibians within that section.

Frogs were marked to monitor dispersal and to facilitate enumeration. Ott and Scott (1999) suggest that the ideal tag should not affect survivorship or behaviour, be permanent, unique, easily seen and implemented, and limit handling. Toe clipping was the most cost effective and fastest means of marking *P. triseriata*. Toe-clip marks are permanent even one to two years after metamorphosis in *P. triseriata* (Nicole M. Gerlanc pers. comm.; Smith 1987). A prior study (Desroches et al. 2001) conducted an individual marking scheme that was discontinued due to concerns about the number of toes removed given the large population at this site (three or more toes as N was greater than 900) and the potential increased mortality of removing many toes. Marking schemes changed during the two years of the study. In 2002 adults entering the pond were given a day specific mark of one toe, excluding the thumbs or the 4 toes on the rear legs. Following breeding migration all unmarked adults were marked as LR5 (code as per Donnelly et al. 1994). Postmetamorphic individuals prior to sexual maturity will be referred to as young of the year or as froglets. Froglets were initially not marked in the first three weeks from the first metamorphosing individual but young of the year caught after July 15 2002 were given a site-specific mark (two toes – LF3 and LR5). In 2003, two sets of different directional marks consisting of a combination of two-toe clips were given to adults and young of the year so as to distinguish between sections, age groups and study years. Froglets were not marked before July 7 of 2003 because their toes were too small to effectively remove the digits.

Fence surveys were conducted twice daily, or more during peak migration periods. Morning surveys were conducted between 6 and 9 AM, and night surveys began around sunset and continued until exhaustion of either the frogs or the researcher. Surveys consisted of one or more researchers checking one side of the fence for amphibians, identifying and marking all frogs if appropriate and releasing them on the other side of the fence. Immigrating individuals were not marked at the outer fence to reduce handling time and behaviour modification.

In 2002, other researchers at the site placed captured *P. triseriata* in cages, one for each section, and held them in captivity up to 24 hours until they could be measured, checked for diseases, marked and then released (J.-F. Desroches and M. Ouellet pers. comm.). Young of the year exiting between June 25 and July 10 of 2002 were subjected to the same protocol of capture, captivity up to 24 hours, measurement and release. I witnessed one release of young of the year that were supposed to exit the southeastern corner but, when released, oriented and swam toward the pond fence instead of southeast. Martin Ouellet (pers. comm.) confirmed the presence of chytrid fungus, with 38% of individuals checked showing evidence of infection. These procedures were abandoned in

2003 but there was a high likelihood that these procedures may have affected survival, spread of disease, and orientation behaviour in 2002.

Climate variables recorded in 2003 included air temperature with use of a data logger on the pond fence (iButton by Dallas Semiconductor Corporation), precipitation with use of a rain gauge, and cloud cover estimated at time of survey. Climate variables were not recorded in 2002, with the exception of precipitation starting September 11. In addition water temperature was recorded at three locations and depth of pond at four locations in the pond in 2003.

Dispersal patterns and distributions

The directional orientation patterns of adults and young of the year migrations across the twelve sections were tested against a random normal distribution to determine if there was directionality to the migration patterns. Distributions were analyzed using Rao's spacing test as a special case of empirical coverage permutation test (Mielke 1988). For distributions with a single mode the average direction $\bar{\phi}$, vector length r, and angular deviation s (circular standard deviation) were calculated. Vector length and angular deviation were corrected for grouping (see Batchelet 1981; Zar 1998).

Comparisons of directional orientation distributions were performed using a multi-response permutation procedure (MRPP) for univariate grouped data that compares treatment groups, analogous to a one-way analysis of variance. Analyses were performed using BLOSSOM Version W2001.08d National Biological Survey (Slauson et al. 1991).

To account for the potential influence of unequal lengths of some sections, the number of captures per metre of fence in each section were tested against the null hypothesis of no difference in mean captures per metre of fence across the three vegetations: shrub, arid and humid prairies. If habitat selection occurs during migration to or from the pond and outer fences, then the number of captures per metre would be higher for those vegetations which are preferred, as individuals in unsuitable vegetation/habitat would be expected to try and leave it in search of suitable/preferred habitat. Where appropriate, data from different migration patterns were pooled to determine if general patterns emerged.

Habitat preferences – residence time enclosure experiments

To determine which habitats *P. triseriata* preferred, experimental tests were designed and conducted in habitat enclosures I called "frog races". The "frog races" measure residence time of individuals released therein. For individuals released in unsuitable habitats, residence time was expected to be short compared to individuals released in suitable or preferred habitats. The construction of the habitat enclosures was identical to that of the outer fence, with a height of about 30 cm, in a circle with a radius of two metres, nearly half of the daily average movement of adults (3.5 m/day - Kramer 1973). Eight wooden stakes to provided support to the circle. A nylon cord added additional support and allowed attachment of plastic creating a lip as the plastic was folded over the cord, which may have prevented the escape of individuals. Pitfall traps were installed near each of the stakes to capture enclosed individuals and were checked every 12 hours to prevent death of captured individuals.

Enclosures were constructed in four different "natural" habitats: forested, humid prairie, shrubby, and arid prairie meadows. Two replicates of each were constructed, one near the pond and the other more than 50 m from the pond fence (Figure 1). Forested enclosures contained or were constructed near trees, as the root systems of some trees prevented the fence from being buried. In addition to the "natural" habitat enclosures, two enclosures were constructed in which the vegetation was removed ("de-vegetated"). One de-vegetated enclosure was placed in the humid prairies and the other in the arid prairies. The enclosure experiments were similar to those used by Rothermel and Semlitsch (2002) except that my design was circular allowing individuals to chose an orientation. The lack of options for the frogs in Rothermel and Semlitsch's experiment might have precluded low rates of movement in unsuitable habitats, whereas the 360° choice in a short circular enclosure was designed to prevent reversals and provide accurate measures of dispersal in both preferred and unsuitable habitats.

Depending on the availability of frogs, 10-15 individuals were released in the centre of each enclosure, to prevent density-mediated dispersal, and recaptures were made at the edge of the enclosure with the aid of pitfall traps. Time to reach the finish line or edge was recorded to give a measure of dispersal rate over the terrain or habitat type. The first race of each season had no marking, but in subsequent races one toe was removed to distinguish between the earlier race and other individuals that may have entered into the enclosure from the surrounding areas. A typical race was conducted over four days in at least four enclosures simultaneously. Only a proportion of individuals were caught in each race, preventing races being run back to back. Replication of treatments for both adults and juveniles was intended but due to the limited number of adults that exited the pond, adults were only tested once in the four habitats in 2003 (n = 5 in each enclosure). Young of the year, though abundant in early summer, were infrequent late in the summer and only two races were run each year. Five "frog races" were run over the two-year study: four races involving young of the year, two in each year, and one involving post-breeding adults in 2003.

The enclosures experiment tested whether both, residence time (hours until capture), and proportion of chorus frogs reaching the fence in each enclosure were equal across the different vegetation and unsuitable de-vegetated enclosures. Residence time would be expected to be lowest in unsuitable habitats (e.g. De-vegetated enclosures) compared to natural habitats and, in addition, if there were differences in residence times between natural habitats it would indicate preference of certain vegetation types. Greater proportions of individuals should be caught in unsuitable habitats and fewer caught in suitable natural habitats as residence time increases with preference.

Habitat preferences – residence time between the pond and the outer fence

Similar to the habitat enclosure experiment above, mark-recapture data was analyzed over discrete intervals to gauge the residence time of young of the year emerging from the pond in the different vegetation types present as they dispersed and were recaptured at the outer fence. The inability to mark emerging young of the year during the first two to three weeks after metamorphosis, due to their fingers being too small and flexible to cut cleanly, resulted in different cohorts of dispersing froglets each year (unmarked and marked). Once the toes of individuals were large enough to clip, the marked cohort period started. As few young of the year left the pond after it dried and reluctance to change marking schemes, only two cohorts were created each year. In 2002 the unmarked cohort could not be compared to the others as my replacement, during my absence, was instructed only to check two sections of the outer fence per visit due to the abundance of young of the year emerging from the pond. In total three groups of cohorts were monitored as they dispersed across the twelve sections, providing replication within cohort periods. These marathon-like races allowed frogs to disperse in their chosen settings and could be used to support results from the enclosures.

Each of the twelve sections was categorized by the prevailing vegetation present. The four habitat types tested in the enclosure experiments, humid prairie, arid prairie, shrubby and woody vegetation, were used to estimate the proportion of the arc length that each vegetation occupied. The shrubby and woody habitats were too intermingled to easily separate the two, and so were pooled together. Three vegetation categories were used to classify the sections: shrubby with woods, humid prairie, and arid prairie near the road. The resulting classification was arid prairie near road (sections A B J K and L), shrubby/woody (E F G H and I), with humid prairie composed of sections C and D. Section G was grouped in the shrubby/woody type due to the 50% presence of shrubby vegetation and similarity of capture rates with shrubby sections on either side. Section I was classified as shrubby due to the proportion of shrubby habitat near the pond fence and not the outer fence.

Each race was analyzed separately to compensate for potential changes in preferences as seasons changed and any potential influence that marking had on dispersal. Analysis of variance was performed with habitat as the factor and proportion of released individuals caught in each section as the dependent variable. The null hypothesis tested was: if vegetations were equally preferred then the proportion captured would be equal across vegetation type, with the expectation that unfavoured vegetations would have lower rates of recapture. Post hoc comparisons of the differences between treatments were done using Tukey multiple comparison tests if the results of the ANOVA were significant or revealed a trend in the data. The three periods analyzed were July 15 to August 7 2002 (marked 2002); June 26 to July 18 2003 (unmarked 2003); and July 8 to July 31 2003 (marked 2003). Additional analyses were done with shorter intervals to determine if random movement may increase with time, masking any initial preferences.

Analyses were redone for the two cohorts in 2003, with metres per day as the dependent variable tested against the null hypothesis of equal rates of movement across vegetation types. Residence time was expected to be higher in preferred vegetations and so should have a corresponding moderate rate of dispersal between the two fences. The average rate of movement for individuals in each section was given by the distance to the outer fence in each section divided by the number of days to reach the outer fence. Due to the distribution of captures being bimodal and few recaptures in some sections; only the first five captures in each section were used for both cohorts.

Hibernation

Drift fence arrays ("hibernation fences") were installed and operational after the soil thawed, potentially missing early captures, in 2003. Hibernation fences were 15 m long with three in a row radiating away from the outer fence (Figure 1). The first fence was 15 m from the outer fence, the second 30 m and the last 60 m from the outer fence. The furthest fence was approximately 110 m from the pond.

Hibernation fences were monitored twice daily in the course of outer fence surveys for the first eight days of spring migration in 2003. The placement of fences in a row allowed the distance to potential hibernation sites from the pond to be estimated for those caught, but eliminated replication required for analysis of variance. The distribution of the number adults caught in each fence array was tested against a random distribution . The directional orientation of adults entering from the outer fences was compared to that of adults expected given the relative proportion of young of the year exiting the outer fence the previous year, using the MRPP described earlier, to determine if success of hibernation reflected habitat choice or if over-winter survival was non-random.

Larval distribution

Four different habitats with amphibian larvae existed within the perimeter of the pond fence (Figure 2): submerged vegetation, emergent vegetation, open water, and woody emergent vegetation (trees). The submerged vegetation was identified as water with living vegetation that rarely broke the water's surface. The emergent vegetation habitat was composed mainly of tall reed canary grasses in standing water. The open water habitat had little to no vegetation below the surface of the water. The woody emergent vegetation consisted of mainly shrubby willow trees and some elm trees in standing water. Larval sampling was conducted on June 24, 2003.

Each habitat was divided into 1 m^2 quadrats. Within the pond fence were areas of moist soil and vegetation without standing water, which were excluded from the sampling even though they may have had standing water earlier in the spring. The number of quadrats sampled was chosen based upon habitat size and time to conduct the surveys. Quadrats were randomly selected according to a random number table, with rejection occurring if there was no water to sample, or if it was within five metres of another sample so as to reduce the influence on larvae in those areas (Shaffer et al. 1994). The number of samples per habitat did not reflect their respective areas, but more samples were taken in larger habitats to increase the likelihood of accurately depicting larval distributions within those areas. The number of samples taken from each habitat and the total area of the habitat in parentheses were: two in the submerged vegetation (75 m^2); six in the emergent vegetation (825 m^2); three from the open water (109 m^2); and five from the woody emergent vegetation (582 m^2).

The method for sampling was tested two days prior to determine efficiency and to practice the technique. Materials used included a butterfly net with a long handle, a bucket of pond water and a small aquarium net. The frame of the net was straightened to increase the length of the frame touching the substrate. The quadrat to be sampled was approached very slowly to minimize larval flight. The net was placed on the substrate and then swept approximately one metre along the bottom of the pond, and then brought back upon itself three times for a total of four sweeps. The contents of the net were then placed into the bucket of water and the vegetation carefully removed. After the vegetation was removed, larvae were removed with an aquarium net and tadpole species were identified. In addition to amphibian species, the number of insect predators were counted and categorized into dragonfly larvae (suborder Anisoptera), damselfly larvae (suborder Zygoptera), and other predatory insects such as beetle larvae (e.g. *Dytiscus sp.*). After the sample was completed, the depth of water sampled was measured.

Small and large belostomatids (*Lethocerus americanus*) were seen in the pond preying on tadpoles but were not captured during sampling. Conversely, backswimmers (family Notonectidae) were caught but not recorded, as I was not aware that they preyed upon tadpoles until some time after the sampling. Other species observed at the study site and known to be predators of larvae and small frogs included adult *Dytiscus sp.* seen in and around the pond, *Ambystoma lateral* larvae, an American bittern, robins, *Thamnophis sirtalis*, and Odonata larvae (Kieseeker 1996; Matthews and Pettus 1966; Pearman 1995; Skelly 1995a; Smith 1983; Wassersug and Sperry 1977).

The average abundances of tadpoles (#/m^2) in 2003 were tested against the null hypothesis that abundances were equally distributed across microhabitats sampled, with respect to presence and absence of larval predators, and equally distributed across pond depths. The abundance of tadpoles was expected to be unequally distributed given the non-random directional orientation of emerging juveniles in 2002, which suggested that tadpoles might be concentrated in certain pond microhabitats or areas contributing to the non-random orientation of emigration.

Young of the Year Growth

Froglet snout to vent length (SVL) was measured to the nearest 1mm, as it was the easiest of measurements and directly proportional to individual size. Measuring of young of the year began shortly after the first emerged from the pond, and was repeated weekly. Due to variable numbers of exiting young of the year, I tried to measure the first five individuals per section, though this was not always achieved. In sections with many young of the year, more than five were measured in the first three weeks. The SVL of emerging young were compared, testing for uniform size across sections.

The approximate shape of the growth rate for young *P. triseriata* was determined by comparing the SVL of young of the year measured exiting the pond fence June 30, 2003 to those young exiting the outer fence in following weeks. Both a linear and quadratic regression was performed to estimate the shape of the growth curve. To establish if growth rates were different among sections the slope and intercepts and their associated standard errors for the twelve linear regressions were compared to each other using the Students' t-test, resulting in 56 comparisons among the twelve sections.

Individual frogs were not monitored due to the absence of marking and the absence of recaptures once individuals exited the outer fence. The inability to follow individuals through the repeated measures obscures the relationship of growth but, as most unmarked individuals left the pond within 12 days of the first released, and only 31 of the 587 individuals included in measures were marked, we can be relatively confident in the relationships discovered. From what we know of frog growth cycles, two periods of growth should occur. One rapid growth stage for young frogs until they reach sexual maturity, and another slower growth stage after the frogs reach sexual maturity.

By the end of the season many young of the year were of adult size and showed secondary sex characters such as yellowing of the throat in males, and presence of developing eggs in the ovaries in females. At the end of the summer, adults re-emerged and the ability to discriminate the difference in age class was based on size. Those individuals below the adult length were recorded as juveniles and the others as unmarked adults (adult SVL was established at 24.0 mm for males and 25.0 mm for females, and was adjusted to 25.0 mm for both sexes in September as young of the year were approaching 24 mm in length).

Survivorship

Survivorship of adults during the breeding period was approximated as the number of adults exiting the pond divided by the number that immigrated to the pond in the spring (as per Berven 1990; Caldwell 1987). Similarly the survivorship of young of the year during the season was approximated as the number of young of the year reaching the outer fence divided by the number that exited the pond.

Survival during the larval period was not explored but the number of eggs laid, the number of larvae present and their survival to metamorphosis was estimated. Pettus and Angleton (1967) suggest that there is a linear relationship between the number of eggs produced per female and their SVL (figure 1 in Pettus and Angleton 1967). The slope of the regression line for the lower elevation population given was $\beta = 47.3$ ($t = 3.66$, $p < 0.01$, Pettus and Angleton 1967). The regression constant was interpolated to be –685. Given the current population's average female SVL of 25.48mm (2001 average Desroches and Ouellet pers. comm.) the regression estimates that an average female should have 520 eggs. The estimated number of eggs was within the range for the species (e.g. 455.5 eggs ± 46.6 SE for females of 24.1 mm ± 0.66 SE, Pettus and Angleton 1967; or 373 to 983 eggs with a mean of 642, Whitaker 1971). Egg survival to hatching was determined as the average from estimates of hatching success (from Howard et al. 2002; Kramer 1978; McCallum and Trauth 2001; Pettus and Angleton 1967; and Starnes et al. 2000), and the standard deviation was calculated from the same estimates. The average hatching success calculated from the above sources was 73.4% (± 15.3 SD). Given the estimated number of eggs produced per average female and average hatching success, each female in the population would produce 382 (± 80 SD) viable larvae. Survival to metamorphosis was estimated as to the number of young of the year exiting the pond during a given year divided by the product of the number of viable larvae per female and the number of females breeding in the pond.

Survival of young of the year was determined by estimating the number of young of the year surviving the summer, as the sum of those reaching the outer fence, and the number of young of the year entering the pond late in the summer (last two months), divided by the total number of young of the year exiting the pond that year. The likelihood of underestimating survival was high given that individuals likely escaped capture at the outer fence and not all young of the year were likely to exit the outer fence. Due to the absence of data collection from the outer fence in 2002 during July 1-10 comparison of survival between years were not performed as many young of the year were likely missed exiting the outer fence in 2002.

Sensitivity analysis

To uncover potential vulnerabilities of *P. triseriata* at this and other ponds, sensitivity and elasticity analyses were applied to survival estimates. A female-based stage-structured matrix was constructed for *P. triseriata*. Vital-rate data used to parameterize the matrix were from survival estimates from the current study population and from the literature (see above). Four stages were used to construct the matrix:

$$A=\begin{bmatrix} F_{egg} & F_{larvae} & F_{juv} & F_{adult} \\ P_{egg\rightarrow larvae} & P_{larvae\rightarrow larvae} & 0 & 0 \\ 0 & P_{larvae\rightarrow juvenile} & P_{juv\rightarrow juv} & 0 \\ 0 & 0 & P_{juv\rightarrow adult} & P_{adult\rightarrow adult} \end{bmatrix}$$ where F_x is the fertility of the stage,

and $P_{x\rightarrow y}$ is the probability of individuals surviving to the next stage or remaining within a stage and "juv" are pre-sexually mature juveniles.

Sensitivity analysis was used to estimate how small changes in fertility and survival affect population growth when the other elements in the matrix were held constant. Elasticity analysis (Caswell 2000, de Kroon et al. 2000; Biek et al. 2002) was performed to estimate the effect of a proportional change in the vital rates on population growth. Both sensitivity and elasticity matrices were calculated using EXCEL spreadsheets (©Microsoft). Those stages with the greatest sensitivity and elasticities would identify those stages that are likely of importance to the maintenance or recovery of *P. triseriata* populations. The reliability of the results is uncertain, as data to parameterize the matrix is limited to only one or two years of collection.

Other species

The presence and activity of the other amphibians at the study site were recorded. The detail of observations was not as explicit as for *P. triseriata* in 2002, but was equivalent in 2003. The additional effort to include other species was minimal as they were present during the fence surveys, and had to be moved regardless. The opportune collection of data permitted comparisons between those species and *P. triseriata.*

The directional orientation for both immigration and emigration of two other amphibians, *Rana sylvatica* and *Pseudacris crucifer*, were compared to those of *P. triseriata* distribution patterns. Data from many individual *P. crucifer* and *R. sylvatica* had to be dropped from analyses in 2002, as no direction was recorded with their movement. Only those data with recorded directions were used in comparisons. Comparisons with less than 15 individuals in one group were not significant, as that essentially constitutes testing against a random normal distributions equivalent to Rao's spacing test that was already analyzed. Differences between species likely reflect differences in habitat preferences between those species (Dodd and Cade 1998).

Analyses of larval abundance for *P. crucifer* and *R. sylvatica* among pond microhabitats, presence of predators, and depth of water were performed within sampling plots. Multiple correlations were performed to determine if tadpole abundances between species were related. Interspecific competition might be responsible for potential spatial segregation of larvae in different habitats if observed (as per Morin and Johnson 1988; and Skelly 1995a).

Results

Breeding behaviour

Breeding activity in both years started shortly after the snow melted (April 8 in 2002 and April 19 in 2003). *Pseudacris triseriata* was the first amphibian seen in both years of the study, with *Rana sylvatica* and *Pseudacris crucifer* emerging a day later (Table 1). Migration began as air temperatures rose above 5°C, and increased with temperature ($p = 0.0002$ from regression of *P. triseriata* movement on average temperature Figure 3a). Prolonged warmer temperatures in 2002 resulted in earlier migration, whereas average temperatures in 2003 did not remain above 5°C until April 19. The regression of movement on rainfall (Figure 3b) showed no significant relation ($p = 0.31$), with movement occurring in the absence of rainfall.

Pseudacris triseriata peak migration occurred soon after migration began - four days in 2002 and six days in 2003 (Figures 4 and 5). The average breeding date was estimated as two days after the peak migration (April 14 2002 and April 22 2003). *Pseudacris triseriata* breeding behaviour (calling and immigration) persisted longer in 2003 (2003 - April 19 – May 18; versus 2002 – April 9 – April 18), whereas, in 2002 breeding was rapid, coincident to a period of cold weather followed by snow accumulation after which no further breeding behaviour was observed. The operational sex ratio of breeding *P. triseriata* was biased towards males (61.6% in 2003 and 58.4% in 2002), and deviated significantly from 1:1 ($\chi^2 = 52.1$ in 2002 and $\chi^2 = 21.1$ in 2003 each with 1 df; $p < 0.0001$ for both). Of the *P. triseriata* population greater than two thirds immigrated to the pond from greater than 50 m (1246 of 1068 in 2002 and 453 of 630 in 2003).

The abundance and behaviour of calling males made locating individuals near impossible. Those males observed calling, or located and not seen, called from within or near clumps of dead reed canary grass, with a few individuals seen calling in open water amongst submerged vegetation.

Larval stage

Although I did not search specifically for chorus frog egg masses, two *P. triseriata* eggs masses were found in 2002 next to the exterior of the pond fence loosely attached to grass just below the surface of the water. The only *P. triseriata* egg mass that I came across in 2003 was again next to pond fence on the exterior, below the water surface attached to grassy vegetation. The egg mass was held together by a viscous jelly. No attempts to count the eggs were made, and the mass was moved into the pond to avoid stepping on it at a later date.

The date when tadpoles first were seen was not noted in either year. The first metamorphs to exit the pond fence each year were at night on June 23 in 2002, and in the morning of June 25 in 2003. After the first metamorphs emerged, a large emigration began. In 2002, within three days of the first emergence, more than 500 individuals exited the pond per day for ten days (Figure 6). Peak emergence occurred June 27 2002 and emigration continued into early October. In contrast, rarely more than 200 froglets exited the pond per day in 2003 (Figure 7) with multiple peaks of emigration observed with the last individual exiting the pond fence August 26 2003.

The pond dried on August 1 in 2001, July 15 in 2002, and July 4 in 2003. The observed hydroperiod was 98 days in 2002, and 85 in 2003. In absence of rain, the depth of the pond steadily decreased, in 2003 (Figure 8), either through the soil or via the agricultural drainage ditches. Tadpole stranding was common before the drying date as small shallow pools were formed as the water level decreased. Emigration of young of the year continued even after the pond dried both years. In 2002, 9086 *P. triseriata* young of the year emerged from the pond, while only 2862 emerged in 2003. Despite the differences in total number of young exiting the pond fence, significantly more exited after the pond dried ($\chi^2 = 4.6$, 1 df, $p = 0.032$) in 2003 (n = 1369) than in 2002 (n = 1259).

Dispersal pattern and distributions

Migration to and from the breeding pond was non-random with respect to direction for *P. triseriata*, regardless of sex, stage or year ($p < 0.0001$ for Rao's spacing test for all distributions except young of the year pond entry 2002 where $p = 0.0042$).

Adult *P. triseriata* immigration (Figure 9) was largely from the southwest, with the peaks of immigration from the humid prairies and shrubby areas, and relatively few migrating individuals from the northern half of the study site (across the road). More individuals arrived at the pond fence, n = 215, than the outer fence, n = 115, from northern directions, either avoiding capture at the outer fence, or emerging between the two fences. Adult emigration from the pond and outer fence was bimodal both years (Figure 10), with peaks to the southwest humid prairies and arid prairies in the southeast.

Pseudacris triseriata young of the year emigration started at the end of June and continued into October. Emigration of *P. triseriata* young of the year from the pond, changed from month to month both years (Table 2). Similarly the emigration patterns of young of the year at the outer fence changed from month to month each year. Young of the year emigration patterns (Figure 11) were different than those of adults (Figure 10). The differences were not only due to the abundance of emigrating young of the year, but in 2002 young of the year dispersal was mainly to the east towards the formerly flooded shrubby area. While in 2003, young of the year dispersal was bimodal with peaks to the southwest and to the east not seen in adults.

Immigration of adults and young of the year differed in 2003 (Table 3), with adults entering from the southwest while young of the year entered from the north ($p < 0.0001$ for both pond and outer fence immigrations, Figures 9 and 12). Adult *P. triseriata* immigrated to the pond from the shrubby and humid prairies in the southwest both years in spite of differences in outer fence entry distributions. Comparisons could not be performed in 2002, as there were only five young of the year entering the pond and three entering the outer fence. More *P. triseriata* young of the year re-entered the pond from the northern arid prairies than any other sections.

Adult *P. triseriata* post breeding emigration was similar both years ($p = 0.13$), with migration towards both the humid and arid prairies (Figure 10). Adult *P. triseriata* emigration was different in comparisons with that of young of the year, as young of the year moved more toward the east than did adults (Figure 11). Between year comparisons of *P. triseriata* young of the year were also significantly different ($p < 0.0001$). Adult *P. triseriata* emigration showed similar bimodal dispersal towards the humid and arid prairies both years ($p = 0.13$), while adult and young of the year emigration patterns deviated significantly in within year comparisons (Table 3). Young of the year emigration patterns were significantly different between years, with many more young of the year exiting to the east in 2002 (Figure 11).

Adult immigration did not mimic the orientation pattern of young of the year emigration at the outer fence the preceding year ($p = 0.0037$). The directional orientation of adult migration to the pond changed, as the population migrated from the outer fence to the pond fence (Figure 9, Table 4). When the entire population was considered, there was no clear similarity between pond entry and pond exit in either year, although with directional marking of adults in 2003, it was possible to show that the emigration of marked adults was not different from the distribution of marked adults entering the pond ($p = 0.15$). The same comparison, between pond entry and pond exit within the sexes, shows that both males and females in 2003, exited the pond in a similar pattern as they entered (Table 5). Adult emigration from the pond in 2002 was similar to the exit pattern at the outer fence ($p = 0.20$), though in 2003 the same comparison reveals differences in exit patterns between the two fences ($p = 0.014$). The difference between emigration patterns between the two fences remains when fence years were pooled and compared together ($p = 0.042$).

No comparison between the sexes of adult *P. triseriata* within years showed differences in the emigration patterns ($p > 0.05$, Table 5 and Figure 13). Comparisons of immigration patterns between the sexes revealed differences in outer fence entry patterns ($p = 0.006$ and 0.015 in 2002 and 2003), while the immigration pattern at the pond was similar in 2003 ($p = 0.55$) but differed in 2002 ($p < 0.0001$).

In comparisons between years within sexes (Table 5), male emigration patterns were similar between years ($p > 0.05$ for both fences), as was immigration to the pond but not to the outer fence ($p = 0.45$ pond fence; and $p < 0.0001$ outer fence). Female immigration differed between years on both fences ($p = 0.014$ pond; and $p = 0.001$ outer fence), while emigration patterns were similar between years ($p > 0.05$ for both fences).

The similarity of emigration patterns of adults from the pond fence to the outer fence, in 2002, might indicate a straight-line migration route. Those young of the year reaching the outer fence in 2003 with directional marks showed a similar straight-line emigration pattern between the two fences ($p = 0.95$, $n = 104$), but when all young of the year were compared the two patterns were significantly different ($p < 0.0001$).

Since several sections were of differing lengths, the mean number of frogs per metre of fence was compared among vegetation types for each fence (Figure 14). Each fence was analyzed separately due to the reduction in circumference and not migrants from the outer to the pond fence. When all adult individuals moving to and from the pond or outer fence were pooled, the mean number of captures per metre of fence was significantly different across vegetation types (pond $F_{2,45} = 6.5$, $p = 0.0034$; outer $F_{6.7} = 6.7$, $p = 0.0027$; Figure 14). There were significantly fewer adult *P. triseriata* caught per metre of pond fence in the arid prairies ($\bar{x} = 1.00 \pm 0.42$ SE) when compared to either the shrubby or humid prairie vegetations (arid versus shrub $p = 0.025$, arid versus humid $p = 0.0067$), while the mean number of adults per metre of fence did not differ between the humid prairie ($\bar{x} = 3.55 \pm 0.67$ SE) and shrubby ($\bar{x} = 2.63 \pm 0.42$ SE) areas of the pond fence. Similarly, the number of adult captures per metre of the outer fence in the arid prairies ($\bar{x} = 0. \pm 0.22$SE) was significantly lower than that in the humid prairies ($\bar{x} = 1.80 \pm 0.35$ SE), while the mean number of adults captured per metre in the shrubby sections of the outer fence ($\bar{x} = 0.96 \pm 0.22$ SE) was not significantly different than either those in the arid or humid prairies but was intermediate between the two.

The numbers of young of the year per metre of fence were only compared across vegetation types for emigrations at both the pond and then outer fences (Figure 14), due to the difference in abundance of young of the year exiting both fences in 2002 and 2003 (9086 vs. 2862 at the pond and 694 vs. 1603 at the outer fence). The number of young of the year returning to the pond or outer fence was too low in 2002 (pond = 5; outer = 3) and in 2003 (outer = 88; pond = 155) to perform reliable comparisons. The number of young of the year exiting both the pond and outer fences was significantly different per metre of fence across the vegetation types (Pond 2003 - $F_{2,9} = 5.9$, $p = 0.023$; Pond 2002 - $F_{2,9} = 6.0$, $p = 0.022$; Outer 2003 - $F_{2,9} = 6.4$, $p = 0.018$; Outer 2002 - $F_{2,9} = 14.7$, $p = 0.0015$). Multiple comparisons revealed that more young exited per metre of pond fence in shrubby sections in 2002 ($p < 0.05$) and in 2003 ($p < 0.05$), while all other comparison were not significantly different from each other. The number of young exiting the outer fence per metre was significantly greater in humid prairies compared to arid prairie sections in both 2002 ($p < 0.01$) and 2003 ($p < 0.05$). Similarly more young exited the outer fence in shrubby sections than arid sections in 2002 ($p < 0.01$), but not in 2003. If more captures per metre of fence within a vegetation type suggest use of that habitat, then both humid and shrubby vegetations were used more than the arid prairies.

Habitat preferences – enclosure experiments

The enclosure experiments measured residence time and proportion of individuals captured across four different vegetations and de-vegetated enclosures. A lower proportion of captures and relatively longer residence times compared to other enclosures would indicate preference for one vegetation over another. There were significant differences in proportion of captures among the six treatments ($F_{5,22} = 2.7$; $p = 0.047$, Figure 15a). Pooling de-vegetated enclosures increased the significance among treatments ($F_{4,23} = 3.6$; $p = 0.021$) with significantly more individuals reaching the perimeter of the de-vegetated enclosures than in the humid prairie enclosures ($p = 0.019$ Tukey multiple comparison). All other comparisons were not significant. When only "natural" enclosures were considered, the differences between vegetations were reduced below significance ($F_{3,16} = 2.6$; $p = 0.089$), but still suggested that residence time was less in both the forested and shrubby enclosures than the humid and arid prairie habitats as the mean number of individuals caught was higher in the forested ($\bar{x} = 3.92 \pm 0.96$ SE) and shrubby enclosures ($\bar{x} = 3.72 \pm 0.96$ SE) than in the arid ($\bar{x} = 1.92 \pm 0.96$ SE) and humid prairies ($\bar{x} = 0.70 \pm 0.96$ SE).

Repeating the analysis considering hours until capture likewise shows that the rates of movement were different among enclosure treatments ($F_{4,92} = 3.5$; $p = 0.011$, Figure 15b). The longest residence times were observed in the humid prairie enclosures, with the average capture occurring in 50.3 hours after release (± 7.33 SE; n = 5 individuals over all trials). Residence time was significantly longer in the humid prairie enclosures ($0.009 \leq p \leq 0.021$ – Tukey tests) than in the de-vegetated ($\bar{x} = 23.9 \pm 2.53$ SE; n = 42), shrubby ($\bar{x} = 24.4 \pm 3.67$ SE; n = 20) and arid prairie enclosures ($\bar{x} = 22.8 \pm 4.94$ SE; n = 11), but residence time in humid prairies was not significantly different than that in the forested enclosures ($\bar{x} = 31.1 \pm 3.76$ SE; n = 19; $p = 0.14$ – Tukey test).

Residence time shows that though few individuals were caught in the arid prairies, they moved faster than those in the humid prairies ($p = 0.021$) and as fast as those in the other enclosures ($0.67 \leq p \leq 1$, Tukey multiple comparison tests). The humid prairie enclosures showed that fewer individuals were caught and they had the longest residence time within enclosures when compared to other vegetations suggesting that the humid prairie is the preferred vegetation for young of the year.

Without replication, analysis of variance could not be performed on the adult enclosure trial. Of the five adults per enclosure released, two were caught in each of forest, shrub, and prairie enclosures, while only one was caught in the humid prairie enclosure. There was no difference in the number of individuals caught but the dispersal rate of captured individuals was significantly different across the enclosures when tested against the average time until capture of adults within enclosures ($\chi^2 = 7.9$, 3 df, $p = 0.047$). Two adults were caught within 27 hours of release in the forest enclosures (one 17 hours later, and another 27 hours after release), while the only other enclosure with a capture within the first 27 hours was the arid prairie with one (27 hours after release). The other captures occurred 42 hours after the start of the trials.

Habitat preferences – between fence residence time

The cohorts of marked and unmarked young of the year exiting the pond fence and dispersing towards the outer fence were divided into release periods and long and shorter recapture periods. The release periods for each cohort was ten days, and the recapture periods for "long races" was 22 days after the first released and 13 days after the last released, whereas for "short races" the recapture period was only four days after the last released which is a period of 14 days from the first released.

The "long races" revealed no significant differences in the proportion of captures across the vegetations (Figure 16a-c). Though, in 2002 there was a slight trend (Figure 16a) that differences existed among vegetation types ($F_{2,9} = 3.9$; $p = 0.060$), with more captures in humid than arid prairies ($p = 0.053$) and slightly more when compared against shrubby sections ($p = 0.10$). "Short races" in 2003 revealed differences between vegetations for the unmarked young of the year ($F_{2,9} = 16.3$; $p = 0.001$, Figure 16f), with greater captures in shrubby sections than both arid prairies ($p = 0.001$) and humid prairies ($p = 0.082$), but the short races revealed no differences in the 2002-marked cohort ($F_{2,9} = 2.2$; $p = 0.17$, Figure 16d). The proportion caught in the three cohorts were significantly different from each other, with 52.5% of individuals reaching the outer fence in the 2003-

unmarked cohort, compared to 14.7% in the 2003-marked cohort and 3.3% in the 2002-marked cohort ($F_{2,35} = 43.1$; $p < 0.0001$).

The migration rates of the marked individuals appear to be slower than that of unmarked young of the year ($t_{118} = -1.74$, $p = 0.085$), regardless of vegetation type when only the first five individuals captured in each section are considered (Figure 17a). Comparing the rates of movement within cohorts across vegetation types in 2003 (Figure 17b), showed significant differences in rates of movement across vegetations in both the unmarked ($F_{2,57} = 278.9$; $p < 0.0001$), and marked cohorts ($F_{2,57} = 71.9$; $p < 0.0001$). Both cohorts separately show that the rate of movement for young was fastest in shrubby sections, then humid prairies, and slowest in arid prairies (Figure 17b). The first five unmarked young of the year had an average migration rate of 7.22 m/day (± 0.194 SE, $n = 25$) in shrubby sections, 5.06 m/day (± 0.307 SE, $n = 10$) in humid prairies sections and 1.25 m/day (± 0.194 SE, $n = 25$) in the arid prairies, all of which were significantly different from each other ($p < 0.0001$, Tukey tests). Similarly, the migration rates of marked individuals showed significantly different rates of migration between vegetation types with average rates of movement of 1.65 m/day (± 0.238 SE) in arid prairie meadows near the road, 3.99 m/day (± 0.377 SE) in humid prairie sections and 5.69 m/day (± 0.238 SE) in shrubby sections ($p < 0.0001$ except comparison between shrubby and humid $p < 0.001$, Tukey multiple comparison tests).

Hibernation

The hibernation fences were not all buried in the ground by the time the first immigrating adults were caught. Some adults may have escaped capture during this period. Only 20 chorus frogs were caught in the twelve fences (Figure 18a). Ten were caught in the humid prairie fence array, while five were caught in each of the shrubby and arid prairie meadows, with no *P. triseriata* captures in the forest array during the first eight days of immigration. The analysis revealed that *P. triseriata* the number caught in each vegetation was significantly different than that expected if random, with more captures made in the humid prairies than any other vegetation ($\chi^2 = 10.0$, 3 df, $p = 0.018$). One adult male *P. triseriata* was caught in the forest array on May 1, but he remained in the water that had accumulated in that area to call. Inclusion of this one individual reduced the significance of the χ^2 test but still suggests a non-random emergence pattern with more individual emerging from humid prairies than expected by chance and fewer than expected, or no individuals emerging from forested areas ($\chi^2 = 7.8$, 3 df, $p = 0.051$).

The directional orientation of young of the year exiting the outer fence in 2002 (Figure 11) and that of adults entering the outer fence after hibernation in 2003 (Figure 9) the following year, were significantly different ($p = 0.037$). Proportionately more adults came from sections C F J K and L which were predominantly arid and humid sections, while proportionately more young went to sections A B E G H and I, which were mostly shrubby vegetation sections (Figure 18b). Overall more adults immigrated after hibernation from humid sections C and D (34.3% in 2002 and 26.3% in 2003), and shrubby sections E and F (39.0% in 2002 and 36.6% in 2003) than any other sections, with only 13.4% (2002) and 12.1% (2003) of adults immigrating to the outer fence from the arid sections next to the road. Survival may have been different across the sections and would account for a change in the distribution of adults returning after hibernation. Grouping sections by vegetation type, similarly, revealed that the number of adults returning after hibernation does not reflect the proportion of emigrating young of the year to those vegetation types from the previous year ($\chi^2 = 11.7$, 2 df, $p = 0.0029$; Figure 18c), as survival is likely non-random with respect to vegetation type. If the directional orientation of young at the outer fence represents the choice of over-winter habitat (humid prairie and shrubby vegetation), it does not reflect the success of over-winter survival, as fewer adults return from the shrubby sections and more return from the humid and arid prairies than expected.

Larval distribution

Analysis of the abundance of tadpoles in the four different microhabitats found in the pond revealed no differences in *P. triseriata* tadpole abundances across habitats (Figure 19a). The emergence pattern of *P. triseriata* metamorphs was not explained by the abundance of larvae in the different vegetation habitats, as the tadpoles were equally distributed across pond habitats ($F_{3,12} = 0.15$; $p = 0.930$), they did not segregate with the presence of dragonfly larvae ($F_{1,14} = 0.38$; $p = 0.546$, Figure 19b) nor with pond depth (four depth classes $F_{3,12} = 0.024$, $p = 0.995$; two depth classes $F_{1,14} = 0.069$, $p = 0.797$, Figures 19c-d).

Growth of Young of the Year

The analysis of variance in SVL for the first froglets to emerge from the pond in 2003, showed no variation among sections ($F_{11,129} = 0.561$; $p = 0.857$), and that the average size was 1.088 cm (± 0.067 SD) regardless of where they exited.

Linear and quadratic regressions were fitted to the size versus time data (Figure 20) of young of the year that exited the pond fence and reached the outer fence. The linear regression suggests that if growth were constant, young would grow at 0.158 mm/day (± 0.0003 SE). As growth rates are expected to change as frogs reach maturity, a quadratic regression shows approximately the biological tendency of a gradual change in growth rates as frogs reach maturity. The quadratic regression fits the data better than the linear regression ($R^2 = 0.89$ versus $R^2 = 0.86$), accounting for the change in growth rates. When treated separately, the linear regressions of young of the year growth over time were not significantly different in slope or intercepts between sections ($p > 0.05$, Student's t-test), suggesting that growth rates were similar across vegetation types.

Survivorship

Survivorship of adults over the breeding period was different in the two years of the study (Table 6). Breeding females had better survival than males in both years (36.2% vs. 26.9% in 2002, Yates corrected $p = 0.0023$ using a 2×2 contingency table; and 49.7% vs. 25.4% in 2003, Yates corrected $p < 0.0001$). Between years comparison showed no difference in male survival ($p = 0.64$), but female survival improved in 2003 ($p = 0.0049$). Adult over-winter survival was 2.6% (8 recaptures in 2003, from 304 survivors of 2002). As adult over-winter survival was low, the large adult populations were a result of successful recruitment at the larval and young of the year stages.

Larval survivorship was estimated as the number of young of the year exiting the pond divided by the number of larvae produced in a given year. The number of larvae produced was estimated by the number of eggs produced per SVL of females given the regression estimated from figure 1 in Pettus and Angleton (1967) multiplied by the average female SVL of 25.48 mm for this population. The number of eggs produced per breeding female predicted was 520, which would give an estimated 147,000 viable larvae (± 9209 SE) in 2002, and 89,770 (± 5621 SE) in 2003. The numbers of young of the year emerging from the pond were 9086 in 2002 and 2862 in 2003. Larval survivorship was greater in 2002 with 6.2% surviving versus 3.2% in 2003 ($p < 0.0001$). The greater survival was attributed to the longer hydroperiod in 2002.

Survival of young of the year during the season was significantly different ($p < 0.0001$) between the two years of the study (7.7% in 2002 versus 59.7% in 2003), although many young of the year may have been missed during the ten days when only two sections of the outer fence were checked per day in 2002 as mentioned above. Survival from metamorph to breeding adult for marked young of the year from 2002 was estimated to be 1.1% (20 of 1818 marked young returned in 2003). The overall survival from metamorph to breeding adult could not be estimated, as unmarked young from 2002 could not be distinguished from other unmarked adults.

Survival analysis of marked versus unmarked individuals revealed that there may be an increased mortality and reduced mobility of marked individuals. Survival of breeding adults was not significantly different between marked and unmarked adults in 2003 ($p = 0.10$) but there was a trend toward greater mortality of marked individuals (21.2% survival of marked versus 27.4% of unmarked). Proportionally fewer marked young of the year reached the outer fence, than unmarked individuals (14.5% versus 52.2% for cohorts in 2003). Similarly, significantly more unmarked than marked young of the year were caught at least twice in either year of the study (with 24.9% of 8990 unmarked versus 5.8% of 2958 marked young, $p < 0.0001$). Between year comparisons of survival for both marked and unmarked individuals were significantly lower in 2002, but within year comparisons of survival estimates were significantly lower for marked young of the year (Yates corrected $p < 0.0001$). Estimates for recaptures of unmarked young of the year assumes that there were few unaccounted young of the year that were not marked, which was reasonable given that all moist areas outside of the pond were dry before metamorphosis could have occurred in 2003. It is unclear whether survival is affected by marking young of the year, as the reason that few marked-young returned the following year was not determined (either mortality, or they had not reached maturity).

Sensitivity analysis

The transition matrix $A = \begin{bmatrix} 0 & 0 & 24.716 & 8.30 \\ 0.734 & 0 & 0 & 0 \\ 0 & 0.0469 & 0.0798 & 0 \\ 0 & 0 & 0.0951 & 0.0284 \end{bmatrix}$ was constructed from vital rates (Table 7) estimated from the study and the literature. The population growth rate, λ, was 0.984 at the stable stage distribution. The corresponding sensitivity matrix revealed that the tadpole to juvenile stage caused the greatest change to λ with a sensitivity of 6.73 (Figure 21). The elasticity analysis revealed that both the egg to tadpole and tadpole to juvenile transitions had the greatest elasticities ($e_{ij} = 0.321$ for both), while the elasticity of juvenile fertility was nearly as high ($e_{ij} = 0.310$). The greatest elasticities identify those stages that have the greatest impact on the population growth rate. From both the sensitivity and elasticity analysis, the recruitment from the aquatic stages of development appears to have the greatest impact on the growth rate of this population.

Other species present

Aside from *P. triseriata*, five other anurans were successful in recruiting individuals during the study period (Table 8). *Bufo americanus* was not successful in recruiting young in 2002, but a few young of the year were found in 2003. *Hyla versicolor* (*n* = 1 caught) and *Ambystoma laterale* (*n* = 5) successfully recruited a few individuals in 2002, and none in 2003 despite presence of larvae in the pond. *Hyla versicolor* tadpoles (*n* ~ 50) were rescued from diminishing pools and reared at home in 2003, of which 27 young were later released. Successful recruitment of young of the year was observed for both *R. sylvatica* and *P. crucifer* in both years (*R. sylvatica n* = 1776 and 227; and *P. crucifer n* = 1465 and 926, in 2002 and 2003 respectively). No success was observed for *Rana pipiens* even though calls were heard both years. *Rana clamitans* eggs and larvae were observed in 2002, but pond drying prevented recruitment, and no calls were heard in 2003 despite presence of individuals. Operational sex ratios within all populations in either one or both years deviated from 1:1 (Table 9).

Peak migration of the early spring breeders, *P. crucifer* and *R. sylvatica*, occurred three to five days after their migration began, similar to *P. triseriata* (Figures 22 and 23,

Table 1). Similar to *P. triseriata*, the bulk of *P. crucifer*, *R. sylvatica*, and *B. americanus* adults immigrated from areas outside of the outer fence (Table 10). The climbing ability of *H. versicolor* masked what proportion migrated from outside the outer fence (50 m).

Similar to *P. triseriata*, migration patterns of adult and young of the year *R. sylvatica* and *P. crucifer* were significantly non-random both years ($p < 0.0001$ for Rao's spacing test for all distributions with more than 15 individuals, except *P. crucifer* adult outer exit, $p = 0.0019$; and *R. sylvatica* adult pond exit, $p < 0.001$ all from 2002).

Significant differences existed in comparisons of directional orientations of migrants between species, including *P. triseriata*, at both the pond and outer fences (Tables 11 and 12). Comparison of adult species immigration patterns (Figure 24), both at the outer and pond fences differed for all species ($p < 0.001$). However, young *P. triseriata* and *P. crucifer* both re-entered the pond from the northern arid prairies in 2003 ($p = 0.47$). Pond emigration directional orientations did not differ significantly among species in 2002 ($p = 0.56$, $n = 364$), though, when all individuals were accounted for in 2003, significant differences in post breeding emigration from the pond were revealed ($p = 0.0044$, $n = 875$, Table 12).

Outer fence adult emigration patterns (Figure 25) in general were different between species ($p < 0.0001$ for comparison of all species in 2003, Table 12), with the exception of the comparison of *P. triseriata* versus *P. crucifer* in 2003 ($p = 0.095$). Between species comparisons of young of the year emigration patterns were similar for *P. triseriata* and *P. crucifer* in 2002 (Figure 26), but divergent in 2003 (Figure 27). *Pseudacris triseriata* had a large peak towards the east while *P. crucifer* peak emigration was to the southwest. Few wood frogs made it to the outer fence in 2003, likely biasing comparisons between them and other species to appear similar.

Larval distributions patterns (Table 13) of *R. sylvatica* (Figure 28) and *P. crucifer* (Figure 29) were similar to those of *P. triseriata* (Figure 19). The abundance of *R. sylvatica* tadpoles (Figure 28) was not dependent upon type of vegetation ($F_{3,12} = 0.33$; $p = 0.80$), or presence of dragonfly larvae ($F_{1,14} = 0.87$; $p = 0.36$), but was more abundant in water deeper than 15 cm ($F_{1,14} = 4.8$; $p = 0.046$). On the other hand, there was indication that *P. crucifer* tadpoles were segregated across habitats ($F_{3,12} = 3.2$; $p = 0.062$). Mean abundance of *P. crucifer* tadpoles was greater in the submerged vegetation compared to the other habitats (Figure 29)- results of Tukey multiple comparison tests $p = 0.044$ for submerged versus woody emergent vegetations, $p = 0.097$ for submerged versus emergent and $p = 0.18$ for submerged versus open water habitat). There was little indication that *P. crucifer* tadpoles segregated with depth of water ($F_{1,14} = 1.7$; $p = 0.21$) or presence of dragonfly larvae ($F_{1,14} = 0.43$; $p = 0.52$; Figure 29b-d).

Correlations between larval species revealed positive relationships between larval abundance of *P. triseriata* with both *P. crucifer* and *R. sylvatica* ($p = 0.033$ and $p = 0.078$ respectively, Pearson's correlation), but *P. crucifer* and *R. sylvatica* larval abundances were not correlated ($p = 0.76$).

Discussion

Breeding behaviour

Breeding populations were composed almost entirely of new adults each year. There were eight adults from the 2002-marked cohort and one from the 2001-marked cohort that returned in 2003. This suggests that *P. triseriata* generally only breeds once in their life, which is similar to *P. ornata* and *P. nigrita* (Caldwell 1987). Young of the year marked in 2002 returned as adults in 2003 (20 individuals, 16 males), showing that individuals are capable of maturing and participating in breeding within one year. Similarly, Smith (1983) found that 67% of young of the year mature in their first year, and the other 37% mature their second.

It is likely that energy stores are low after managing to survive the winter. Therefore it is reasonable to conclude mortality occurs during the breeding period as a result of low energy stores and evidenced by the reduced number of emigrants from the pond after the breeding period. Energetic costs are high during breeding (Caldwell 1987), and the potentially short supply of prey may prompt consumption of skin and vegetation (Whitaker 1971) that may be insufficient to sustain individuals during the breeding period. Mortality over the breeding period was higher in males than females. Inter-sexual differences point to different costs of breeding and the potential visibility of males to auditory and visual predators. Male survival was constant between years at 26.3%, while female survival improved in 2003 from 36.2% to 49.7%. Differences in between year survival of females is likely a result of the long freezing that interrupted the breeding period in 2002. Jenkins and Swanson (2000) showed that freeze and thaw cycles can deplete glycogen stores, and females in breeding behaviour are likely to have exhausted their stores after a long winter.

The same pattern of enhanced female survival was observed for *P. crucifer* in 2003. The two congeneric species had similar population survival rates both years, but their survival was less than that of *R. sylvatica*. Male and female *R. sylvatica* survival was similar at 53% and 57% for males and females respectively in 2003. Berven (1990), similarly, found no differences in male and female breeding survival for *R. sylvatica*. The increased survival of wood frogs may be due to a condensed breeding period and larger size of wood frogs in comparison to the two *Pseudacris* species. Caldwell (1987) suggests that length of breeding period is directly related to survival, and it seems plausible that individual size is related to energy stores for breeding. Thus wood frogs that have a shorter breeding period and would have greater energy stores would be expected to have increased survival during breeding compared to the two *Pseudacris* species that have fewer energy stores and longer breeding seasons.

Larval stage

Successful recruitment at the larval stage depends upon sufficient growth within the ephemeral pond. The rapid growth rate of tadpoles and early reproduction of *P. triseriata* permitted successful recruitment of young each year despite the decreasing hydroperiod of the pond. The other species present at the site were not as adaptable to the dry conditions, as evidenced by their poor rate of replacement in relation to *P. triseriata* (Table 8) and lower production of young (Figure 30). Rapid development and ability to shorten the larval period during pond drying (Bridges 2002; Durnin and Smith 2001) may allow *P. triseriata* to avoid pond desiccation and larval predators at the cost of smaller size at emergence, however reducing their ability to withstand desiccation and starvation (Alvarez and Nicieza 2002). In addition to avoiding pond drying, rapid development permits *P. triseriata* young to benefit from the abundance of terrestrial prey available, which may outweigh the costs of being small at emergence.

Recruitment for all species was less in 2003, and was surely due to the reduced hydroperiod. Literature values for average time to metamorphosis for the three abundant species are: 55-83 days for *P. triseriata* (Smith 1983); 73-113 days for *R. sylvatica* (Berven 1990); and 61-103 days for *P. crucifer* (Morin and Johnson 1988). From the range of times to metamorphosis and the hydroperiods of 98 and 85 days, in 2002 and 2003 respectively, it is reasonable to expect that *P. triseriata* would be more successful than the other two species. Using the estimated breeding dates of April 14 2002 and April 22 2003 for *P. triseriata*, only 93 and 74 days were available for growth and metamorphosis of *P. triseriata* tadpoles. From these estimates it is apparent why fewer tadpoles were able to transform in 2003 (n = 2862) when compared to 2002 (n = 9086). Excluding *R. sylvatica* and *P. crucifer*, other amphibians breeding at the pond had nearly no recruitment (Table 8), as they tended to breed later, preventing larvae from transforming before the pond dried.

High densities of larval species with overlapping diets may result in competition, within temporary ponds (Alford 1989). Alternatively, interspecific competition may not occur, as spatial segregation of larvae may prevent interaction between species (Skelly 1995a). Though competition effects were not measured during the study, *R. sylvatica* and *P. crucifer* have been implied as potential competitors to *P. triseriata* (see Maunder 1983; Skelly 1995a, 1996, 1997; Smith 1983; Smith and Van Buskirk 1995). The rapid drying of this pond may preclude competitive advantage, at the larval stage, for *P. triseriata* over both *R. sylvatica* and *P. crucifer*, or the absence of competition altogether.

Results from the larval sampling suggest that *Pseudacris* species abundances are correlated and the potential for interspecific competition exists. Though tadpole abundances of *P. triseriata* and *R. sylvatica* were not significantly correlated, they showed a trend that the abundances are correlated within the sampled plots. The observed abundance patterns may point to similar resources for the species or an artifact due to the timing of the survey. The timing of larval sampling may have affected the observed distribution of the amphibian species, most notably that of *P. triseriata* as several tadpoles were in late stages of development and some at metamorphic climax. Prior to metamorphosis, the abundance of tadpoles may have changed, affecting the observed distribution of tadpoles during the sampling. Similarly, the abundance and presence of insect predators was under-represented as adult dragonfly and damselflies had already emerged, and backswimmers were omitted from the predator counts during sampling. The other precaution in drawing conclusions from the sampling is that this was a single survey, and may not be representative of the system. Further sampling throughout the larval period might reveal what, if any, interactions occur between the species and all their predators and how they affect spatial segregation of tadpoles.

Experiments on larval communities have shown that predation and perturbations can mitigate competition and allow coexistence of competing species (Morin 1981; Morin and Johnson 1988; Relyea and Werner 1999; Smith 1983). The presence of aquatic invertebrate predators has also shown to be capable of eliminating recruitment from larval populations and determining amphibian species distributions within their range (Skelly 1995a). The predators reduce the abundance of the strongest competitor, reducing the density of larvae in the pond thus increasing the ability of competitors to acquire resources (Relyea and Werner 1999). The presence of odonate predators, which tend to select *P. triseriata* over *P. crucifer* as prey (Skelly 1995a), would favour the success of *P. crucifer*, but had no impact, as the abundance of emerging *P. triseriata* young of the year was clearly greater than that of *P. crucifer* (9086 and 2862 *P. triseriata* versus 1463 and 926 *P. crucifer* young in 2002 and 2003 respectively - Figure 30). The variation and heterogeneity of vegetation within the pond may have prevented the invertebrate predators from decimating *P. triseriata* tadpoles by means of creating refuges from predation (Smith 1983; Van Buskirk 1988), despite lack of evidence of tadpole segregation among pond microhabitats. Repeated sampling of tadpole abundances over the duration of the larval period may have uncovered some segregation of tadpoles earlier in the season when the odonate larvae were more abundant.

Growth

Both Smith (1987) and Christian (1982) show that *P. triseriata* can reach sexual maturity by the end of their first summer post-metamorphosis. The shape of the growth curve (Figure 20) suggests that maturity is reached by the end of the summer as the growth rate decreases and flattens out at near average adult size, indicating attainment of sexual maturity (Morrison and Hero 2003); otherwise growth would have remained linear throughout the summer. The growth rate decreases as energy resources are directed away from growth toward reproductive potential (Shirose and Brooks 1995). Using only the last two weeks of measured frogs, 40% of young of the year were of adult size. This likely underestimates the percent of mature frogs by the end of the summer as Smith (1987) found that 63% of young mature the first year. Smith's estimate may be more representative of *P. triseriata*, as it was not possible to follow individuals throughout the season. Young that emerged late may not have reached sexual maturity by the end of the summer. The clear advantage to reaching maturity by the end of summer is an increased possibility of contributing to breeding the following spring, given that survival is low and longevity in this population is likely only 2-3 years.

The advantage of rapid growth during the first summer not only increases the probability that they will contribute to breeding, but the likelihood of surviving the first winter. Over-winter survival for marked young of the year in 2002 was low (1.1% returned of 1808 marked young of the year). Jenkins and Swanson (2000) show that glycogen stores of *P. triseriata* are related to body size, and that survival over winter is related to the extent of these glycogen stores. The likelihood that young of the year will survive the winter increases as the young grow faster and attain larger sizes (Christian 1982; Lyapkov et al. 2000).

Further investigation into the effects of date of emergence, growth rate and the relationship between body size and glycogen stores on the survival and breeding investment of individuals will show the importance of attaining large size and sexual maturity early in life among amphibians in temperate climates due to low over-winter survival.

Hibernation

Hibernation success is difficult to estimate, as hibernacula were not discovered during the study and only 29 marked individuals returned in 2003 (20 young adults, 8 adult from 2002, and 1 adult from 2001). Evidence of areas in which hibernation occurred was inferred from adult immigration patterns to the outer fence, assuming that breeding migration occurs in a straight line from the hibernacula to the outer fence and then to the pond. Success of hibernation in the *Phalaris* humid prairies was demonstrated with ten adults captured in the hibernation fences, while successful hibernation also occurred in the shrubby and arid prairie vegetations with five frogs captured in each. There was no direct evidence that *P. triseriata* used the woody areas to hibernate. Only one individual was found near the hibernation fences located just outside of a wooded area. In 2002, as all adults entering the pond were marked, the presence of unmarked individuals emerging from the pond suggests either that there were individuals that escaped capture or that hibernation occurred within the pond area. Hibernation was found to occur at least 110 m from the pond and it is very likely that hibernation occurs even further away. Outer fence entry patterns reveal that 70% of the adults emerge and migrate from the southwestern corner of *Phalaris* reeds and the shrubby mixed with woody vegetation, while only 13% emerge from the arid prairies of the outer fence facing the road. The preferred vegetation type or location for hibernation is thus likely the humid prairie and shrubby with woody vegetation found in the southwestern corner of the study site.

Distribution of immigrants (Figure 9) suggests that hibernation occurs in all the vegetation types present at the study pond. The difference in the distribution of adults coming to the outer fence to that of the young exiting the outer fence suggest that survival is different among the vegetations, with lower survival in the shrubby sections compared to both humid and arid prairie sections. If the emigration pattern of the young indicates over-winter habitat selection, the choice of habitats does not reflect the perceived survival over winter in those vegetations. The difference in proportions of emigrants and immigrants does not account for potential dispersal of young from the shrubby sections to another breeding pond to the east or south of the study site. Despite the perceived non-random over-winter survival with respect to vegetation more *P. triseriata* emigrated to shrubby and humid prairie vegetations than to the arid prairies next to the road.

Three hypotheses may explain the low numbers of emerging adults from northern arid sections, A J K and L that back onto the road, in the absence of significant losses to road mortality. Firstly, an alternative breeding pond may divert breeding *P. triseriata* away from the study pond. There is a temporary shallower pool across the road, but no *P. triseriata* calling was heard in 2002 and only a few calls were heard from the pond late in the breeding season of 2003. The absence of calling and larvae both years suggest the pond is not used by *P. triseriata*. The second hypothesis is that the arid prairie sections across the road are not suitable for hibernation. Emergence of adults from similar arid prairies was observed from the southeast of the study site, suggesting that the vegetation should permit successful hibernation. In addition, immigrating individuals during breeding migrations from the roadside of the outer fence likewise suggest that hibernation occurs in these arid vegetations. The last hypothesis for the low abundance of individuals from the sections near the road is that dispersal to areas across the road is low. Only 11.0% of 2297 young of the year and 5.6% of 285 of adults exiting the outer fence exited near the road in sections A J K and L. Young of the year were more likely to disperse towards the road than adults (Yates corrected $p = 0.0067$ pooled over both years).

Comparisons of the number of young of the year emigrating from the pond to the outer fence show that the proportion exiting toward the road decreases from the pond to the outer fence (Yates corrected $p < 0.0001$), suggesting that they may be avoiding the road. The road may act as a barrier reducing or suppressing dispersal in that direction (Demaynadier and Hunter 1998; Haddad 1999; Vos and Chardon 1998).

Habitat preferences

Habitat preference has been inferred from dispersal experiments and from disproportionate use of habitats (Demaynadier and Hunter 1999). Heatwole (1961) suggests that amphibian behavioural responses to various components of the environment and habitat types are likely to influence if they stay within a certain habitat. Semlitsch's (1981) proposal of frog movement being mediated in search of suitable habitat when wet and remaining within them when found is partially supported, as few marked individuals were found in different vegetations from their first capture. Species have an affinity to certain characteristic habitats, and should be reflected by predictable differences in densities of a species within different local habitats (Hecnar and M'Closkey 1998). Similarly, Kleeberger and Werner (1983) suggest that preference is reflected by the distribution of directional orientation of migration. Rothermel and Semlitsch (2002) suggest that certain factors within a vegetation type may hinder dispersal and can reduce the rate of dispersal within those vegetations. Though reduction in dispersal rates may be possible, the small size and the ability to climb vegetation should permit *P. triseriata* easy movement through even dense vegetation. As in Haddad's (1999) study, evidence (Figures 15b and 17) suggests that dispersal rates are reduced in preferred habitats and so residence time is longer, whereas residence time is lower in unsuitable habitats and suggests that dispersal is promoted in unfavourable habitats.

Overall, animals disperse for two main non-exclusive reasons. They may be dispersing away from a current sub-optimal predicament, on the probability that elsewhere may be better. Or they may be simply moving at random neither away from or towards any place in particular. Rothermel and Semlitsch (2002) suggests that even juvenile frogs are capable of detecting and avoiding unfavourable habitat. The costs of remaining within unsuitable habitat are likely to be increased risk of mortality due to desiccation or predation, or reduced growth rate. The increased costs in unfavourable habitats should elicit a response in young of the year to move away from their current location or remain where they are if in a suitable habitat. Movement is unlikely to occur if predation is likely, but movement was generally from dusk to dawn when most visual predators are not active. Habitat preferences within anurans are likely based upon maximizing growth and reducing mortality sources in addition to maintain hydration and preferable temperature. The absence of differences in the apparent rates of growth across the different vegetations suggests that food was not limiting across the study area (as per Christian 1982). If food is not limiting, then the reason for dispersal is not in search of food, but is either random movement or related to the suitability of the vegetation or habitat with respect to the frog's physiological requirements.

Young of the year habitat preferences were variable between and within years as the monthly emigration from the pond and outer fences varied. Emigration from the pond was non-random with respect to directional orientation both years, suggesting some active choice of habitats, given that larval abundance was evenly distributed within the pond. Habitat enclosure experiments demonstrated that young of the year move rapidly over altered terrain, and similarly quickly in forest, arid prairie and shrubby enclosures, while remaining longer in the humid prairie enclosures. Despite few captures in the arid enclosure, those individuals caught moved faster than those in the humid enclosure and similarly as fast as those in the other enclosures. The inferences from the enclosures suggest that like adults, young prefer the reedy humid prairie vegetation to all others as fewer were caught and those caught had longer residence times. The between fence migration rates of marked and unmarked cohorts in 2003 reiterate the observation that young of the year move quickly in shrubby habitats and slower in the humid prairies. Despite the differences in rates of movement in the vegetation types, the number of young caught within both the humid prairie and shrubby vegetations were similar and suggests that target-oriented dispersal (Sjogren-Gulve 1998) may explain why young of the year use the shrubby vegetation despite the apparent dislike for that vegetation.

The lingering of young of the year in arid prairies near the road but not the enclosures may suggest that they are capable of foraging within the vegetation, but the road acts like a barrier, suppressing young of the year from exiting the outer fence near and thus increasing residence time within the arid prairies near the road (Demaynadier and Hunter 1998; Haddad 1999; Vos and Chardon 1998). The relative proportion of young returning from the different vegetation zones after exiting the pond fence reveal that more individuals return from sections near the road, sections A J K and L, than from all other sections combined (16.2% returned of 358 in sections facing the road versus 3.9% of 2504 for all other sections, Yates corrected $p < 0.0001$). The return of individuals to the pond suggests that survival is possible between the two fences in the arid prairies, but movement towards the road is not favoured. The road may have a large negative influence (Vos and Chardon 1998), acting as a barrier to movement, which affected the distribution patterns, driving *P. triseriata* towards the southern areas at this study site.

Results from the between fence captures reveal that, in 2002, humid sections had greater captures (Figures 16a and 16d), while the other two were poor in comparison due to very dry conditions throughout the summer of 2002. The humid prairie reed grass maintained some moisture even during the hottest days of 2002, allowing for movement to continue in those sections, as movement occurs more often when it is wet (Mazerole 2001; Semlitsch 1981), while movement in drier sections would have been greatly reduced resulting in few captures at the outer fence in those sections. The perceived difference in the moisture of the three vegetations likely best explain why the rates of capture were higher and therefore residence time was lower than the other vegetations in humid prairies which is contradictory to the other findings.

Adult habitat preferences remained constant over both years with emigrating adults preferring both the humid *Phalaris* prairie sections in the southwest and the shrubby southeastern sections, as the number of captures within each vegetation remained similar during migrations. Few adults emigrated north towards the arid prairies near the road. The sole enclosure experiment involving adults supports these conclusions about preferences. The greater rates of dispersal within forest and arid prairies suggest those habitats are usually avoided and reduced rates of movement observed in shrubby and humid prairie sections imply that those vegetation types are preferred.

Residence time in enclosures, migration rates, orientation of migrants, and number of captures per metre of vegetation experiments suggest that despite slight differences in direction of orientation that adults and young of the year have similar preferences for humid prairie vegetation, with some variation within young of the year preferences. Despite the perceived preference for the humid prairie vegetation in the enclosure experiments and migration rates between fences, the numbers of captures per metre in each vegetation and directional orientation of migrants suggest the shrubby vegetation is also used to a similar degree as the humid prairie vegetation. The use of the shrubby vegetation despite its apparent unsuitability may suggest target-oriented dispersal (Sjogren-Gulve 1998) within the shrubby vegetation, as individuals must pass through the shrubby vegetation towards some target outside of the studied area.

Future studies looking at the mechanisms influencing dispersal and whether target oriented dispersal occurs within *P. triseriata* will need to monitor dispersal over distances greater than 50 m from the breeding pond, and like Spencer (1964) monitor dispersal between ponds and surrounding areas. Further experiments including several study sites will be able to verify if the findings from this study site are applicable to other breeding ponds or whether the observations and conclusions drawn are specific to this breeding pond.

Survivorship

Low survival at each stage, rapid growth and the ability to reach sexual maturity by the end of the first summer suggest that *P. triseriata* are short-lived. The low estimate of adult over-winter survival of 2.6% and only one individual returning from the 2001-marked cohort confirms not only are they short lived but also population turnover is likely annual. Similarly, young of the year survival to breeding adult, which includes over-winter survival estimated from only one year of observation, is 1.1% of 1808 marked young of the year. The marked individuals were mostly late emerging individuals. Smith (1987) found that young of the year that emerge late might be smaller and less likely to return the following year. Smith (1987) estimated that 19% of male young of the year survived to maturity, whereas Tucker (1995) estimated that *Pseudacris streckeri illinoensis* juvenile survival to adult was 2.8%. The absence of data on the number of young of the year that will return in 2004 and exclusion of early emerging young of the year (as they were not marked) likely underestimates the juvenile survival, making it unclear whether survival is similar to Smith's estimate, or if this population of *P. triseriata* survival is similar to *P. streckeri illinoensis* in Tucker's study.

The survival analysis of marking in adults and young of the year produces two pictures. There was no significant difference in mortality of marked adults during the breeding season, whereas mortality of young of the year appears to increase when marked. The significant results suggest that it is highly likely a difference in mortality is present, but the test does not account for differences in survival between early and late young of the year. Smith (1987) found that there was a positive relationship between survival and early emergence. The difference in mortality between emergence dates may account for the difference in mortality of marking in 2002 (2.65% versus 8.97%), but does not explain the large disparity between marked and unmarked observed survival of young of the year in 2003 (10.9% versus 92.5%). One possible explanation for the large disparity may be that survival of unmarked young of the year is overestimated as many exited the outer fence within the first few weeks after emergence, and it is unknown if they survived much longer. Alternatively, young of the year may have escaped capture at the pond fence and exited the outer fence, thus artificially increasing the survival estimate of unmarked young of the year in 2003. Differences between early and late emerging cohorts and missed captures may account for some of the variation between marked and unmarked survival estimates, making conclusions on the effects of marking young of the year unclear.

The benefit of investing so much effort into monitoring one population permitted the accumulation of survival data which combined with long term monitoring could produce more reliable estimates of survivorship at each stage and perhaps clarification of the effect of marking on survival in *P. triseriata.*

Sensitivity analysis

The sensitivity analysis revealed that population growth of *P. triseriata* is most sensitive to changes in the survival of the eggs and tadpoles. The construction of the matrix included data from one to two years from this study and should be used with caution. The other parameters have been estimated from other studies and the estimate of tadpole survival relies upon estimates of adult fertility and egg survival to determine the initial abundance of tadpoles. Further parameterization would require a longer-term project with the goal of obtaining those parameters, which was not the goal at the outset of this project.

The yearly turnover of the population makes *P. triseriata* inherently more vulnerable to chance recruitment failure. A bad recruitment year could lead to complete collapse of the adult breeding population the following year. Given the limitations of the current model, conservation efforts aimed at preservation of the species should aim to lengthen or preserve the hydroperiod to greater than 80 days to ensure that at least a proportion of the larvae can metamorphose before the pond dries.

The apparent replacement or competition that has been observed between *R. sylvatica* and *P. triseriata*, in other studies may be a result of the fragility of Western Chorus Frog populations (ie. Maunder 1983) and not a result of competition. Both populations are likely to be stressed, but *R. sylvatica* are longer lived and are more likely to be able to be capable of recovering from a bad year of recruitment. The longevity of adult wood frogs allows them to appear to replace *P. triseriata* populations.

A more reliable model of the population dynamics of *P. triseriata* should include survivorship estimates from longer monitoring programs from several studies, and might incorporate hydroperiod variability and its effects on the demography of *P. triseriata.*

Summary

Pseudacris triseriata breeding occurs soon after snow melts in early April and may continue into mid May, in a temporary pond in southern Quebec. Migration to the breeding pond appears to be triggered by air temperatures above 5°C for several consecutive days. Breeding migration to and from the pond occurs in the same pattern each year, with migrants generally exiting where they entered. Sex ratios in the breeding pond were biased in favour of males, which is common among pond breeding frogs. Breeding mortality is high, more so in males than females. Female breeding mortality increased when freezing interrupted the breeding period in 2002. Emigration from the breeding pond occurs in a straight line away from the pond.

Pseudacris triseriata tadpoles begin to emerge at the end of June, with metamorphosis occurring 66 to 88 days after the peak breeding migration. *Pseudacris triseriata* tadpole abundance is evenly distributed within the different vegetations within the pond. Though tadpole abundances within sampled plots were correlated for comparisons between *Pseudacris* species and larval predators were present, the recruitment success of *P. triseriata* was greater than all other amphibian species present. The abundance of emerging *P. triseriata* young appears to have greater dependence upon the hydroperiod of the pond, with more emerging with longer hydroperiod, than interspecific competition with other anuran larvae. Following metamorphosis, most of the froglets emigrate away from the pond into the moist vegetation surrounding the pond. Young of the year emigration pattern is non-random as they begin making habitat choices after exiting the water. Many froglets continue to emerge even after the pond has dried, suggesting that there are suitable microhabitats within the pond vicinity.

Growth in young is linear during the summer, and diminishes as they become sexually mature by the end of August. Some young that reached sexual maturity in the first summer returned the following year to breed at the same pond. Turnover of breeding adults occurs annually with very few individuals returning to breed. The absence of differences in growth rates between vegetation types suggest that food is not limiting and that dispersal is mediated by habitat suitability.

Hibernacula were not found, but hibernation appears to be equally likely within each vegetation type, with adults emerging from the pond, between the two fences, but more than two-thirds of adults immigrated from more than 50 m, with some emerging more than 110 m from the pond. The apparent preference for shrubby and humid prairies as over-wintering habitat did not reflect over-winter survival, as fewer adults emerged from shrubby vegetations than expected.

The preferred habitat of *P. triseriata* appears to be the humid reed prairies to the southwest of the breeding pond. Despite the perceived preferences, similar numbers of frogs were caught in the humid prairie and the shrubby vegetations to the south and east, possibly due to target-oriented dispersal to areas outside of the study area. Though adult and young of the year emigration patterns are different, their habitat preferences are similar. The road to the north of the pond may affect dispersal by inhibiting dispersal across the road. Young of the year frequently disperse at least 50 m from their natal pond, and have been captured 275 m from this pond. It is unknown if individuals from this population migrate to a nearby pond, but other studies have observed migration distances of 750 m, suggesting that dispersal between breeding populations is likely.

The sensitivity analysis, though based on only two years of data, suggests that populations are most sensitive to the recruitment of juveniles from the larval stage and upon the fertility of those juveniles returning the following season to breed. The hydroperiod of the breeding pool may determine the success of a population.

The observed declines of *P. triseriata* within their global range may be a result of the sensitivity of this species to changes to the hydorperiod and to the areas surrounding their breeding ponds. Decreases in hydroperiod and loss of breeding habitat would result in diminishing populations, and if *P. triseriata* depends upon closely linked populations for recovery, the alteration of habitat may prevent dispersal. Similarly, if target-oriented dispersal occurs within *P. triseriata* removal or alteration of vegetation surrounding breeding ponds could prevent successful dispersal to over-wintering habitat and thereby reduce the number of mature individuals returning to breed. This frog is more vulnerable to habitat loss and fragmentation than perceived, as their dispersal ability has been underestimated. The habitats critical to the survival of *P. triseriata* are first and foremost a temporary breeding pond of sufficient hydroperiod to allow successful recruitment of juveniles and a matrix of suitable foraging and over-wintering habitats of which humid prairie vegetation appears to be the preferred at this location.

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Table 1: Timing of breeding migrations to and from pond.

Species	Year	Immigration		Emigration	
		Start	Peak	Start	Last exit
P. triseriata	2002	April 8	April 12	April 17	May 16
	2003	April 19	April 20	May 1	May 27
P. crucifer	2002	April 9	April 12	April 18	May 31
	2003	April 15	April 20	May 1	May 23
R. sylvatica	2002	April 9	April 12	April 15	May 16
	2003	April 14	April 20	April 21	May 26
B. americanus	2002	April 12	April 15	May 6	June 11
	2003	April 28	May 8	May 1	May 25
H. versicolor	2002	May 28	May 31	May 31	June 19
	2003	May 12	May 27	May 27	May 31

Table 2: Comparisons of the monthly distributions of *Pseudacris triseriata* young of the year. Testing for change in direction as the season progresses.

		Test Statistic	*p*	n*
	POND EXIT			
2002	All months	-13.6019	**< 0.0001**	2255
	June vs. July	-21.0199	**< 0.0001**	2000
	July vs. August	-2.8603	**0.029**	1104
	August vs. September	-4.0993	**0.006**	255
2003	All months	-9.1100	**< 0.0001**	2857
	June vs. July	-5.3938	**0.002**	2764
	July vs. August	-6.5946	**< 0.001**	2499
	OUTER EXIT			
2002	All months	-14.7608	**< 0.0001**	678
	July vs. August	-11.6856	**< 0.0001**	575
	August vs. September	-8.2100	**< 0.0001**	158
2003	All months	-3.9345	**0.005**	1603
	July vs. August	-4.4446	**0.005**	1572
	August vs. September	-2.1728	**0.042**	202

* n is the number of individuals in the comparison

Table 3: Comparisons of directional orientation of both immigrating and emigrating *Pseudacris triseriata* within and between years at both the outer and pond fences. YOY = Young of the year.

	Test Statistic	*p*	n*
Outer Fence Entry			
Adult 2002 vs. 2003	-23.5630	**< 0.0001**	1332
YOY 2002 vs. 2003	-0.2414	0.334	82
YOY vs. adult 2002	1.4773	0.997	884
YOY vs. adult 2003	-33.4160	**< 0.0001**	530
Pond Fence Entry			
Adult 2002 vs. 2003	-0.4186	0.245	1468
YOY 2002 vs. 2003	-3.4805	**< 0.01**	160
YOY vs. adult 2002	-7.3240	**< 0.0001**	844
YOY vs. adult 2003	-51.3790	**< 0.0001**	784
Pond Fence Exit			
Adult 2002 vs. 2003	-0.9815	0.135	469
YOY 2002 vs. 2003	-35.1938	**< 0.0001**	2000
YOY vs. Adult 2002	-42.4649	**< 0.0001**	1317
YOY vs. Adult 2003	-8.1575	**< 0.001**	3014
Outer Fence Exit			
Adult 2002 vs. 2003	-1.0011	0.127	284
YOY 2002 vs. 2003	-2.7487	**0.024**	2289
YOY vs. Adult 2002	-2.7487	**0.024**	785
YOY vs. Adult 2003	-13.4930	**< 0.0001**	1788

* n is the number of individuals in the comparison
YOY = young of the year

Table 4: Comparisons of the distributions of migrating *Pseudacris triseriata* between fences within years.

	Test Statistic	*p*	n[*]
ADULTS			
Pond entry vs. Outer entry 2002	-21.4250	**< 0.0001**	1720
Pond entry vs. Outer entry 2003	-9.1792	**< 0.0001**	1080
Pond entry vs. Pond exit 2002	-11.7940	**< 0.0001**	1156
Pond entry vs. Pond exit 2003	-2.1430	**0.043**	781
Pond exit vs. Outer exit 2002	-0.5793	0.204	408
Pond exit vs. Outer exit 2003	-3.4501	**0.014**	345
Outer entry vs. Outer exit 2002	-10.6680	**< 0.0001**	972
Outer entry vs. Outer exit 2003	-6.0903	**< 0.001**	644
MARKED ADULTS			
Pond entry vs. Pond exit	-0.8800	0.153	278
Pond exit vs. Outer exit	-4.2469	**< 0.01**	185
ADULTS VS METAMORPHS			
Outer entry ’03 vs. YOY Outer exit ’02	-2.3019	**0.037**	1145
Outer entry ’03 vs. YOY Outer exit Aug/Sep ’02	-7.8396	**< 0.001**	609
YOY 2003			
Pond exit vs. Outer exit marked individuals only	0.9426	0.946	208
All Pond exit vs. Marked Outer exit	-5.6521	**< 0.01**	1225
All Pond exit vs. All Outer exit	-19.7981	**< 0.0001**	4457

[*] n is the number of individuals in the comparison

YOY = young of the year

Table 5: Comparisons of the distributions of migrating *Pseudacris triseriata* within and between the sexes.

		Test Statistic	*p*	n*
INTERSEX WITHIN YEAR				
Pond exit	2002	0.1457	0.423	317
	2003	0.4503	0.561	152
Pond entry	2002	-8.5322	**< 0.0001**	840
	2003	0.3877	0.547	630
Outer exit	2002	0.9085	1	91
	2003	0.8719	1	195
Outer entry	2002	-4.1942	**0.006**	881
	2003	-3.1892	**0.015**	454
INTRASEX BETWEEN YEARS				
Pond exit	Male	0.4339	0.562	256
	Female	-0.8854	0.148	213
Pond entry	Male	0.1997	0.454	905
	Female	-3.2186	**0.014**	565
Outer exit	Male	-0.0281	0.335	116
	Female	-0.1336	0.295	170
Outer entry	Male	-22.3393	**< 0.0001**	711
	Female	-5.5249	**0.001**	624
INTRASEX BETWEEN FENCE				
Male Pond entry vs. exit	2002	-7.0677	**< 0.001**	694
	2003	-0.9741	0.140	467
Female Pond entry vs. exit	2002	-4.8914	**0.003**	463
	2003	-0.5608	0.213	315

*** n is the number of individuals in the comparison**

Table 6: Survivorship estimates of *Pseudacris triseriata* for different life stages and seasons. The number of individuals surviving is in brackets. Comparisons of survival were done using a 2x2 contingency table.

		% Survival		
		Male	Female	χ^2 - p value
Breeding Adult	2002	22.4 (163)	29.6 (141)	< 0.01
	2003	18.2 (72)	34.0 (80)	< 0.0001
Between years	χ^2 - p value	0.0029	0.657	0.64*
	Total	20.9%	31.0%	< 0.0001
Over-wintering adults	’02-’03	2.5 (4)	2.8 (4)	0.88
		Marked	Not Marked	χ^2 - p value
Toe clipped breeding adults 2003		21.2 (50)	27.4 (102)	0.10
		2002	2003	χ^2 - p value
Tadpole to Metamorph		6.2 (9086)	3.2 (2862)	<< 0.0001
Young of the Year	until recapture	7.7 (699)	59.7 (1708)	<< 0.0001

* represents the comparison of survival for the breeding population of 2002 to that of 2003.

Table 7: Demographic vital rates and transition probabilities for *Pseudacris triseriata* used in the transition matrix.

Vital Rate *	Mean	SD	Range
Embryo survival [a]	0.734	0.153	0.377 to 0.9
Larval survival [b]	0.0469	0.021	0.0319 to 0.0618
Remain juvenile [c]	0.0798	0.0399	0 to 0.1597
Juvenile to adult ** [c]	0.0951	0.0475	0.011 to 0.19
Adult survival [d]	0.0284	-	
Clutch Size [e]	260		
Age at maturity	1-2	-	

* Vital rates and transition probabilities are for females only

** Probability of juvenile becoming an adult

[a] average embryo survival from Howard et al. 2002; Kramer 1978; McCallum and Trauth 2001; Pettus and Angleton 1967; Starnes et al. 2000.

[b] average larval survival estimated from number of young exiting the pond in the current study given the estimated number of embryo that survived from the egg stage.

[c] calculated using the upper survival range of 0.19 for juvenile to adult from Smith 1987 and low of 0.011 from current study.

[d] estimated from current study

[e] estimated from regression of number of eggs per SVL of female in Pettus and Angleton 1967, using the value of 25.48 mm for an average female in the current population

Table 8: Production of young of the year in relation to adult population estimates during the study.

	2002			2003		
Species	Pop	Meta.	Replace	Pop	Meta.	Replace
P. triseriata	1171	9086	7.76	630	2862	4.54
P. crucifer	1338	1463	1.09	1146	926	0.80
R. sylvatica	677	1775	2.62	754	227	0.30
B. americanus	37	0	0	20	6	0.30
H. versicolor	32	1	0.03	72	0*	0
R. pipiens	12	0	0	7	0	0
R. clamitans	18	0	0	2	0	0

pop. = population within the breeding pond;
meta. = number of young of the year that exited the pond;
replace = replacement rate, number young of the year produced per adult.
* does not include the 27 young that were reared off site and re-introduced.

Table 9: Breeding population sizes and sex ratios (expressed as percent males in the population) for all anurans breeding within the study pond. Comparisons using χ^2 analysis with 1 degree of freedom reveal that sex ratios differed from 1:1 for most species. * = $p < 0.05$; ** = $p < 0.001$

	2002	2003
	Breeding population (% males)	Breeding population (% males)
P. triseriata	1171 (58.4)**	630 (61.6)**
P. crucifer	1338	1146 (70.9)**
R. sylvatica	677	754 (63.0)**
B. americanus	37 (59.4)*	20 (85.0)**
H. versicolor	32 (50.0)	72 (66.2)*
R. pipiens	12 (83.3)*	7 (71.4)
R. clamitans	18 (77.8)*	2 (50.0)

Table 10: Number of adult anurans caught at fences migrating to or from breeding pond.

	2002				2003			
	Immigration		Emigration		Immigration		Emigration	
	Outer	Pond	Pond	Outer	Outer	Pond	Pond	Outer
P. triseriata	1246	1068	317	91	453	630	152	194
P. crucifer	1031	1338	361	195	700	1150	308	284
R. sylvatica	523	677	287*	352	444	761	415	486
B. americanus	26	34	31	30	19	20	12	16
H. versicolor	19	32	10	2	17	77	6	8
R. pipiens	12	10	8	3	2	5	7	6
R. clamitans	3	7	18	0	1	1	1	0

*= unknown number of females were released prior to data collection and not reflected in total

Table 11: Comparions of the outer and pond fence directional orientation of immigrating *Pseudacris triseriata* (PSTR), *Pseudacris crucifer* (PCR), and *Rana sylvatica* (RSY), for both adult and young of the year (YOY) life stages. Only those comparisons with more than 15 individuals per species are shown.

	Test Statistic	*p*	n*
Outer Fence			
Adult PSTR vs. RSY 2003	-11.5540	**< 0.0001**	895
Adult PSTR vs. PCR 2002	-20.9220	**< 0.0001**	940
Adult PSTR vs. PCR 2003	-15.9730	**< 0.0001**	1149
Adult RSY vs. PCR 2003	-40.8830	**< 0.0001**	1142
Adult all species 2003	-32.8870	**< 0.0001**	1593
YOY PSTR vs. PCR 2003	-2.9797	**0.018**	118
Pond Fence			
Adult PSTR vs. RSY 2002	-6.0121	**< 0.001**	1026
Adult PSTR vs. RSY 2003	-25.5070	**< 0.0001**	1390
Adult PSTR vs. PCR 2002	-2.7950	**0.022**	927
Adult PSTR vs. PCR 2003	-2.3230	**0.036**	1778
Adult RSY vs. PCR 2002	-0.6581	0.183	275
Adult RSY vs. PCR 2003	-21.2210	**< 0.0001**	1910
Adult all species 2002	-5.7512	**< 0.001**	1114
Adult all species 2003	-22.7340	**< 0.0001**	2539
YOY PSTR vs. PCR 2003	0.2374	0.468	215

* where n is the number of individuals in the comparison

Table 12: Comparisons of the pond and outer fences directional orientation of emigrating *Pseudacris triseriata* (PSTR), *Pseudacris crucifer* (PCR), and *Rana sylvatica* (RSY). Only those comparisons with more than 15 individuals per species are shown.

	Test Statistic	*p*	n*
Pond Fence			
Adult PSTR vs. RSY 2002	0.2672	0.484	341
Adult PSTR vs. RSY 2003	-3.1855	**0.015**	567
Adult PSTR vs. PCR 2002	0.3104	0.505	340
Adult PSTR vs. PCR 2003	-1.9830	0.051	460
Adult RSY vs. PCR 2002	-0.3830	0.260	47
Adult RSY vs. PCR 2003	-2.8817	**0.020**	723
Adult all species 2002	0.3462	0.557	364
Adult all species 2003	-3.9045	**< 0.01**	875
YOY PSTR vs. RSY 2002	-202.0160	**< 0.0001**	2000
YOY PSTR vs. RSY 2003	-23.1350	**< 0.0001**	3089
YOY PSTR vs. PCR 2002	-12.7001	**< 0.0001**	2000
YOY PSTR vs. PCR 2003	-47.4780	**< 0.0001**	3785
YOY RSY vs. PCR 2002	-426.1700	**< 0.0001**	3238
YOY RSY vs. PCR 2003	-13.0490	**< 0.0001**	1150
Outer Fence			
Adult PSTR vs. RSY 2002	-2.4927	**0.031**	139
Adult PSTR vs. RSY 2003	-24.6390	**< 0.0001**	678
Adult PSTR vs. PCR 2003	-1.3148	0.095	475
Adult RSY vs. PCR 2003	-21.5210	**< 0.0001**	767
Adult all species 2003	-23.6650	**< 0.0001**	960
YOY PSTR vs. RSY 2002	-9.4260	**< 0.0001**	1137
YOY PSTR vs. RSY 2003	0.7009	0.751	1629
YOY PSTR vs. PCR 2002	-6.9172	0.181	1007
YOY PSTR vs. PCR 2003	-34.5520	**< 0.0001**	2059
YOY RSY vs. PCR 2002	-11.7470	**< 0.0001**	756
YOY RSY vs. PCR 2003	-1.9451	0.053	498
YOY all species 2002	-9.7067	**< 0.0001**	1450
YOY all species 2003	-23.7820	**< 0.0001**	2093

* where n is the number of individuals in the comparison

Table 13: Tadpole survey of abundance of larvae and larval predators within four different habitats found in the pond per m^2 sampled. Survey took place June 23 2003, several days prior to first emergence of *Pseudacris triseriata* young of the year.

Habitat	Area m^2	Depth (cm)	Predators		Amphibian Larvae					
			Total	Dragonfly larvae	Total	PSTR	RSY	PCR	HVR	AMB
Submerged vegetation	75	13.0	4	3	23	7	1	14	1	0
		11.5	4	3	6	2	1	3	0	0
Emergent vegetation	825	7.7	4	4	0	0	0	0	0	0
		9.9	4	0	22	11	4	7	0	0
		18.7	0	0	4	2	2	0	0	0
		7.9	10	3	7	3	1	3	0	0
		11.7	8	4	7	5	4	2	2	0
		15.8	4	2	8	2	6	0	0	0
Open water	109	21.5	1	0	8	1	3	3	1	1
		20.2	5	0	20	8	7	4	1	0
		23.0	1	1	1	0	1	0	0	0
Woody emergent vegetation	582	8.0	0	0	0	0	0	0	0	0
		16.0	5	0	17	10	5	0	2	0
		17.0	0	0	0	0	0	0	0	0
		10.8	0	0	1	1	0	0	0	0
		16.8	0	0	14	2	9	3	0	0

PSTR = *Pseudacris triseriata;* RSY = *Rana sylvatica*; PCR = *Pseudacris crucifer*; HVR = *Hyla versicolor*; AMB = *Ambystoma laterale.*

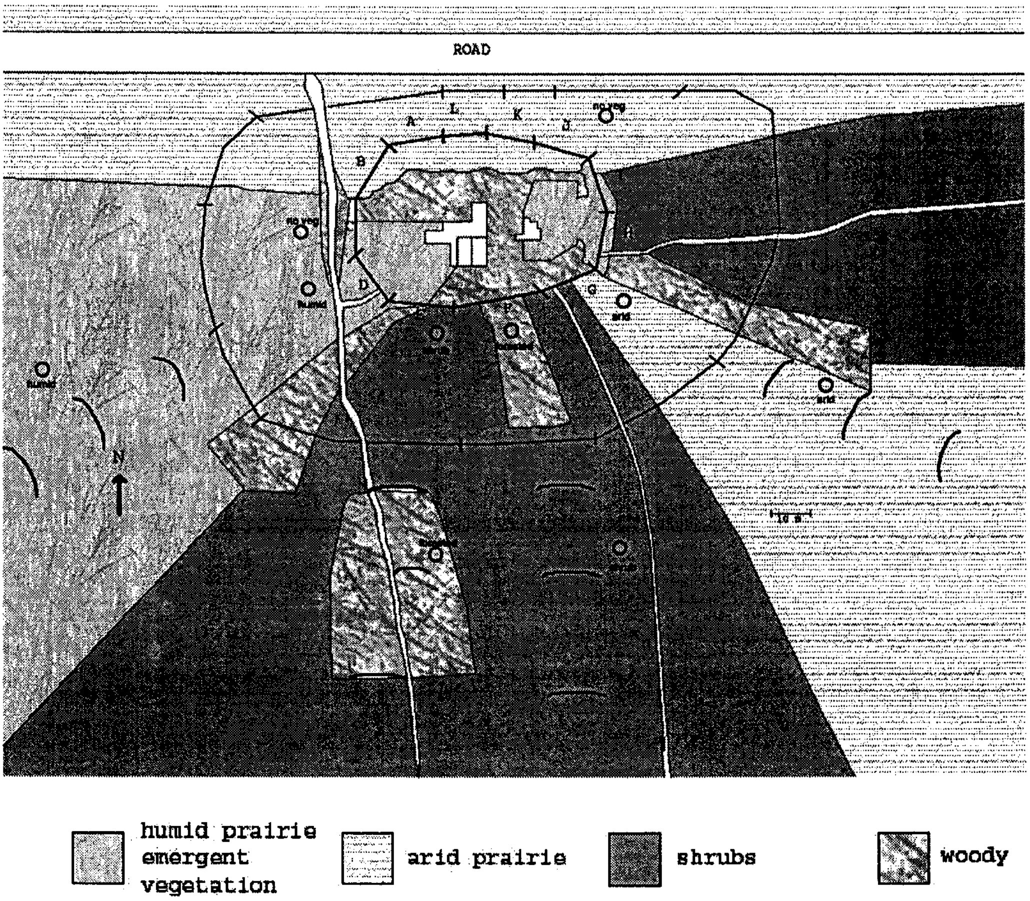


Figure 1: Idealized view of study site. The pond and outer fence are divided into sections labelled counter-clockwise A through L. The four major vegetation types are shown: humid prairie, arid prairie, shrubby and woody/forested. Lines dividing the vegetations are representative, only fences and irrigation canals exist as physical dividers. The approximate locations of habitat enclosures are shown as black circles with enclosure type labelled (no veg = de-vegetated). The locations of the hibernation fences in each vegetation types are shown radiating outwards from the outer fence.

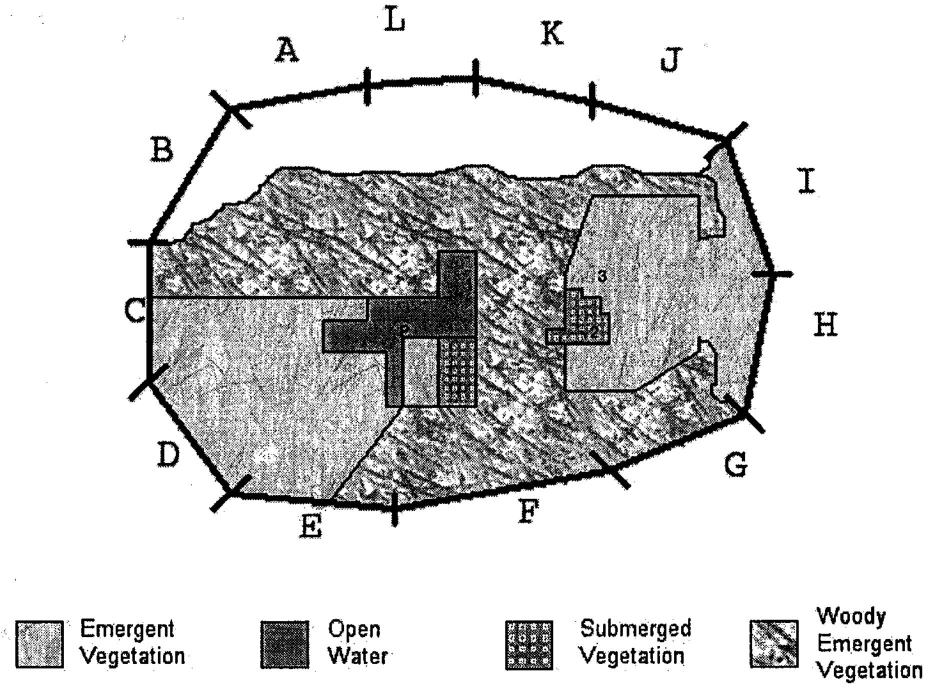


Figure 2: Diagram of the pond and the four categories of vegetation identified for tadpole sampling. The locations of pond depth measuring sticks are shown (P = Pole; 1, 2, 3 see Figure 8).

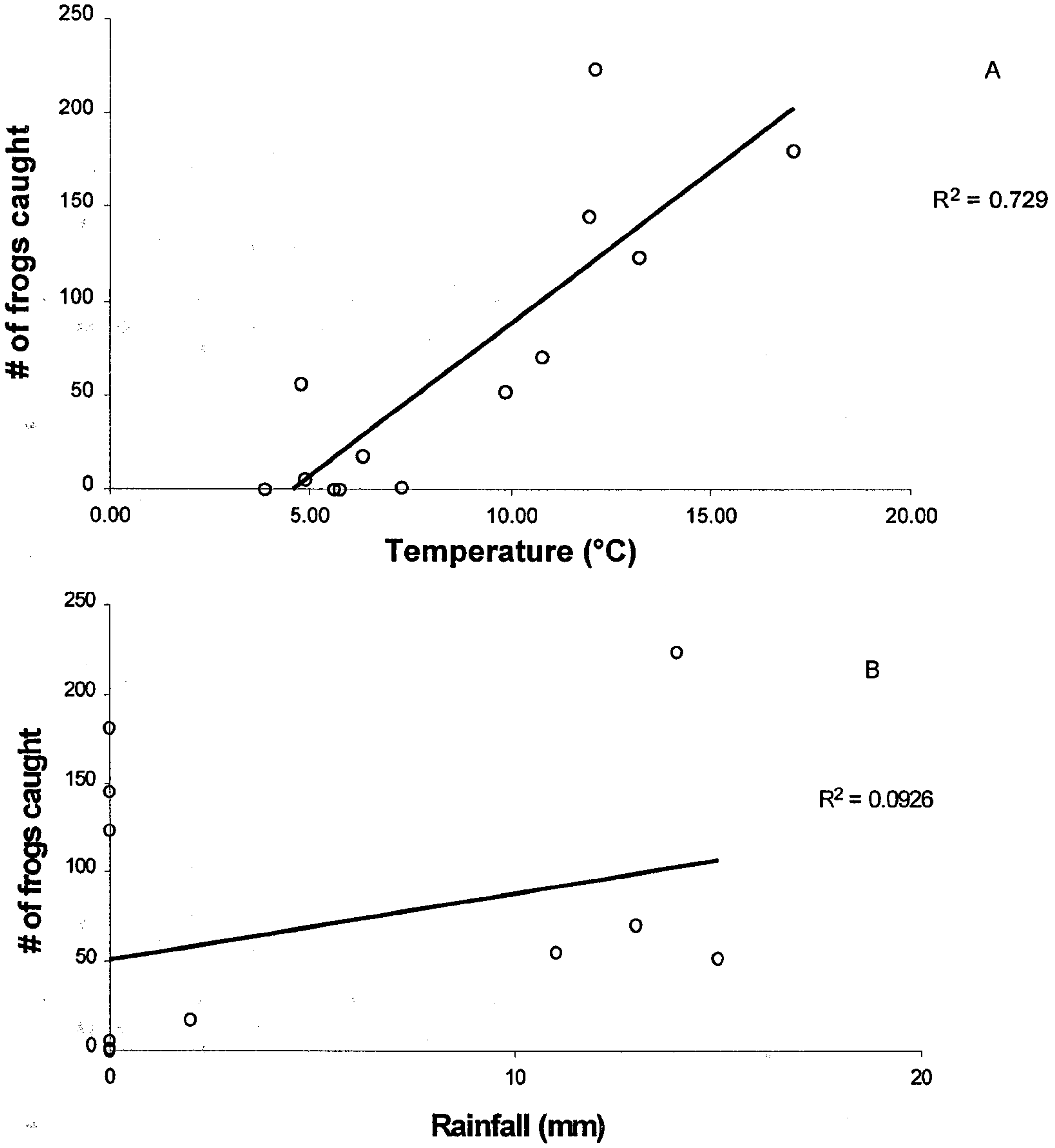


Figure 3: Plot of the number of *Pseudacris triseriata* adults caught immigrating at both the pond and outer fences between April 15-27th 2003. The regression line of migrants versus daily average temperature (A) is estimated by = 16.2 × average temperature - 74.2 ($F_{1,11}$ = 29.7, p = 0.0002; β = 16.2, t_{11} = 5.4, p = 0.0002). The regression line of migrants versus daily rainfall (B) is estimated by # of frogs = 3.7 × rainfall + 51.7 ($F_{1,11}$ = 1.1, p = 0.312; β = 3.7, t_{11} = 1.1, p = 0.312).

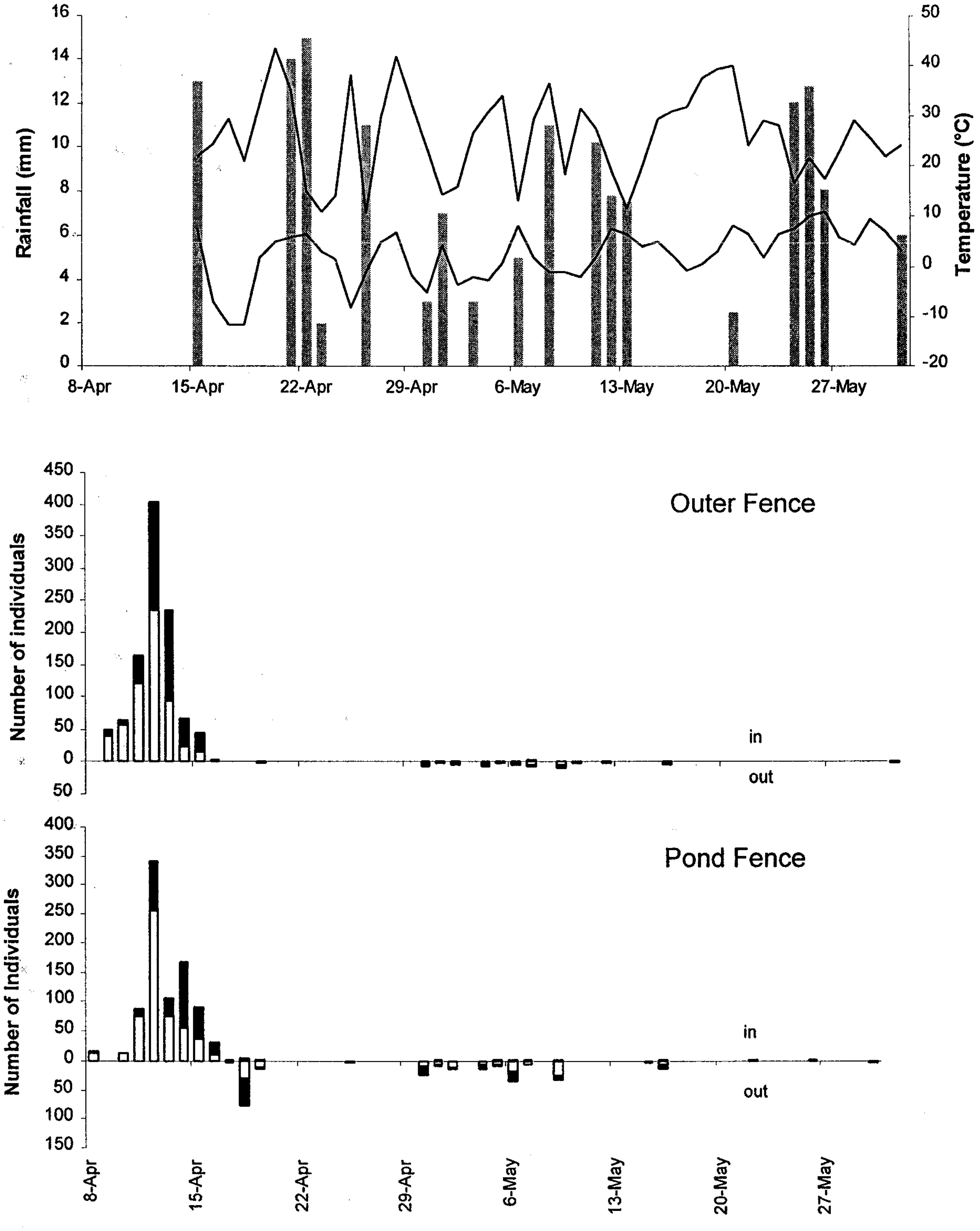


Figure 4: Daily immigration and emigration of adult *Pseudacris triseriata* relative to air temperature and rainfall during the period of April 8 to May 30 2003. The upper graph shows daily maximum and minimum temperatures (lines) and daily rainfall (bars) and the lower graphs show the migration at the pond and outer fences during 2003. The total number of migrants during a day is shown with both the number of males (open bars) and females (closed bars), with the direction of movement either towards the pond (in) or away from the pond (out).

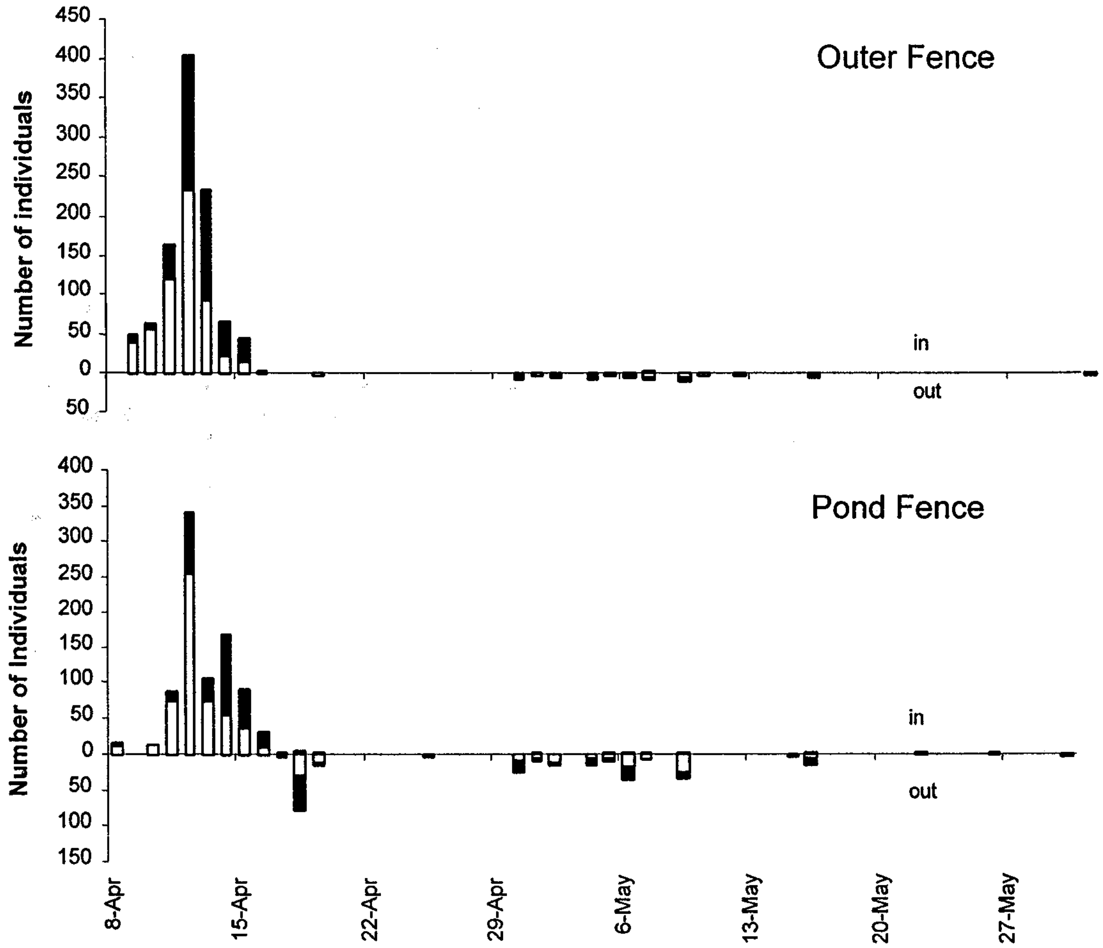


Figure 5: Daily immigration and emigration of adult *Pseudacris triseriata* in 2002 at both the outer and pond fences. The total number of migrants during a day is shown with both the number of males (open bars) and females (closed bars), with the direction of movement either towards the pond (in) or away from the pond (out).

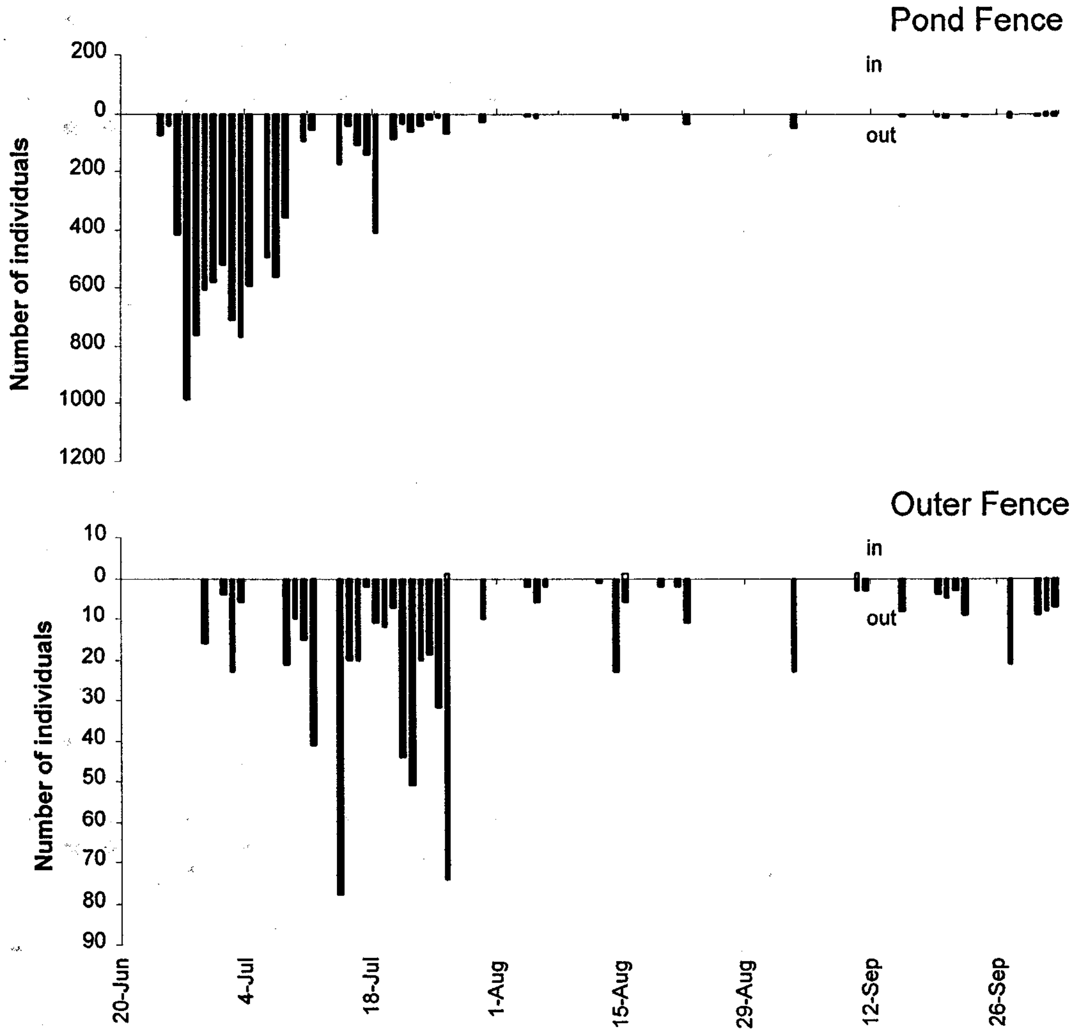


Figure 6: *Pseudacris triseriata* young of the year daily migration at both the pond fence and outer fence in 2002, with the direction of movement either towards the pond (in) or away from the pond (out).

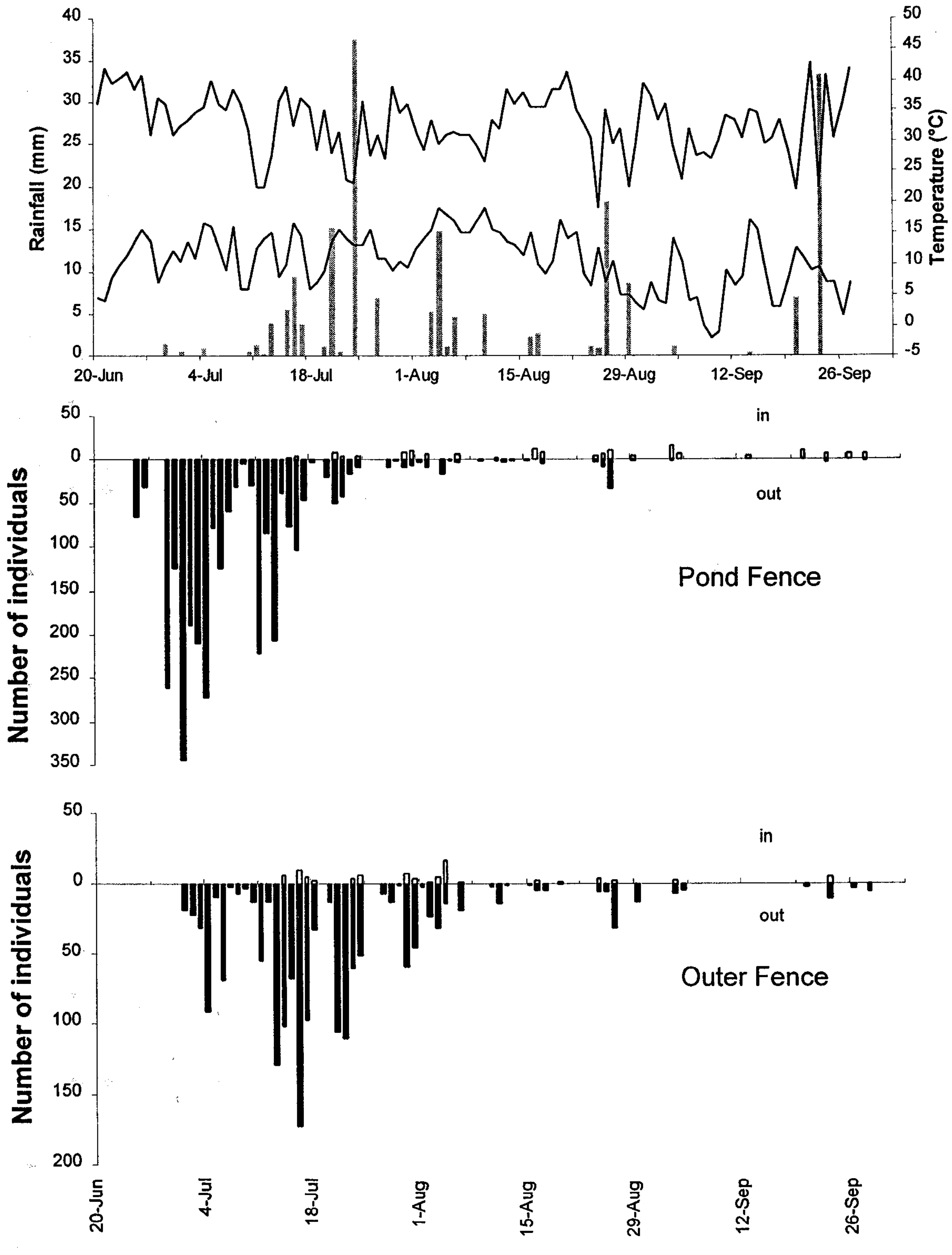


Figure 7: Young of the year migration relative to air temperature and rainfall in 2003. The upper graph shows the daily rainfall (bars) and the daily maximum and minimum temperatures (lines), while the lower two graphs show the migration of young of the year at both fences with the direction of movement either towards the pond (in) or away from the pond (out).

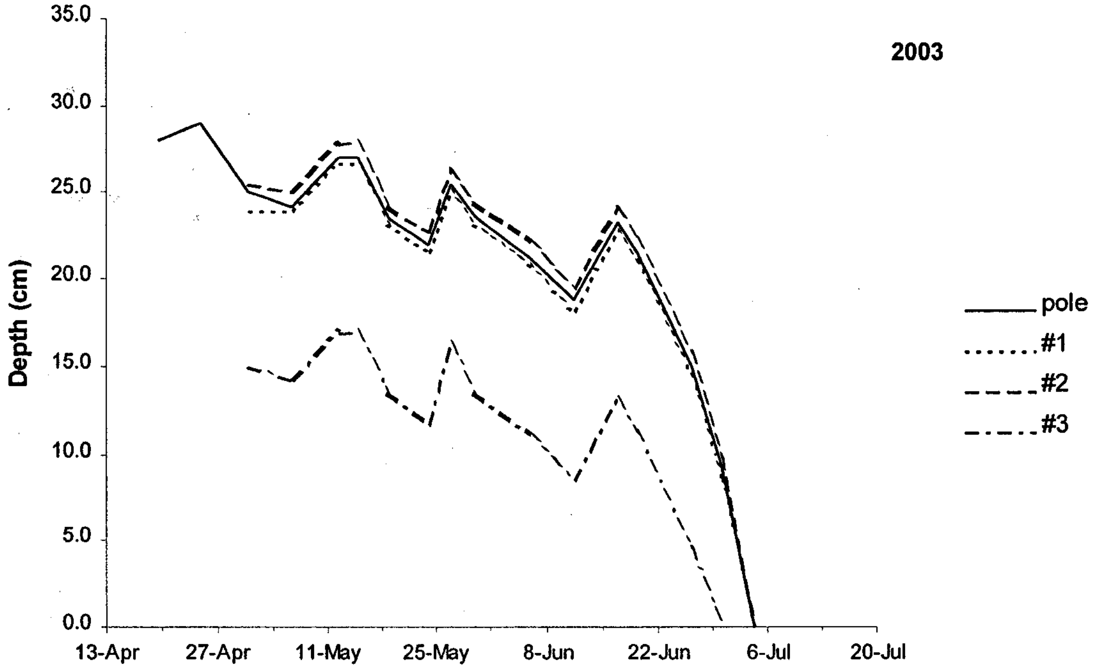


Figure 8: Depth of the pond at four locations during the 2003 season (see Figure 2 for the locations of measuring sticks)

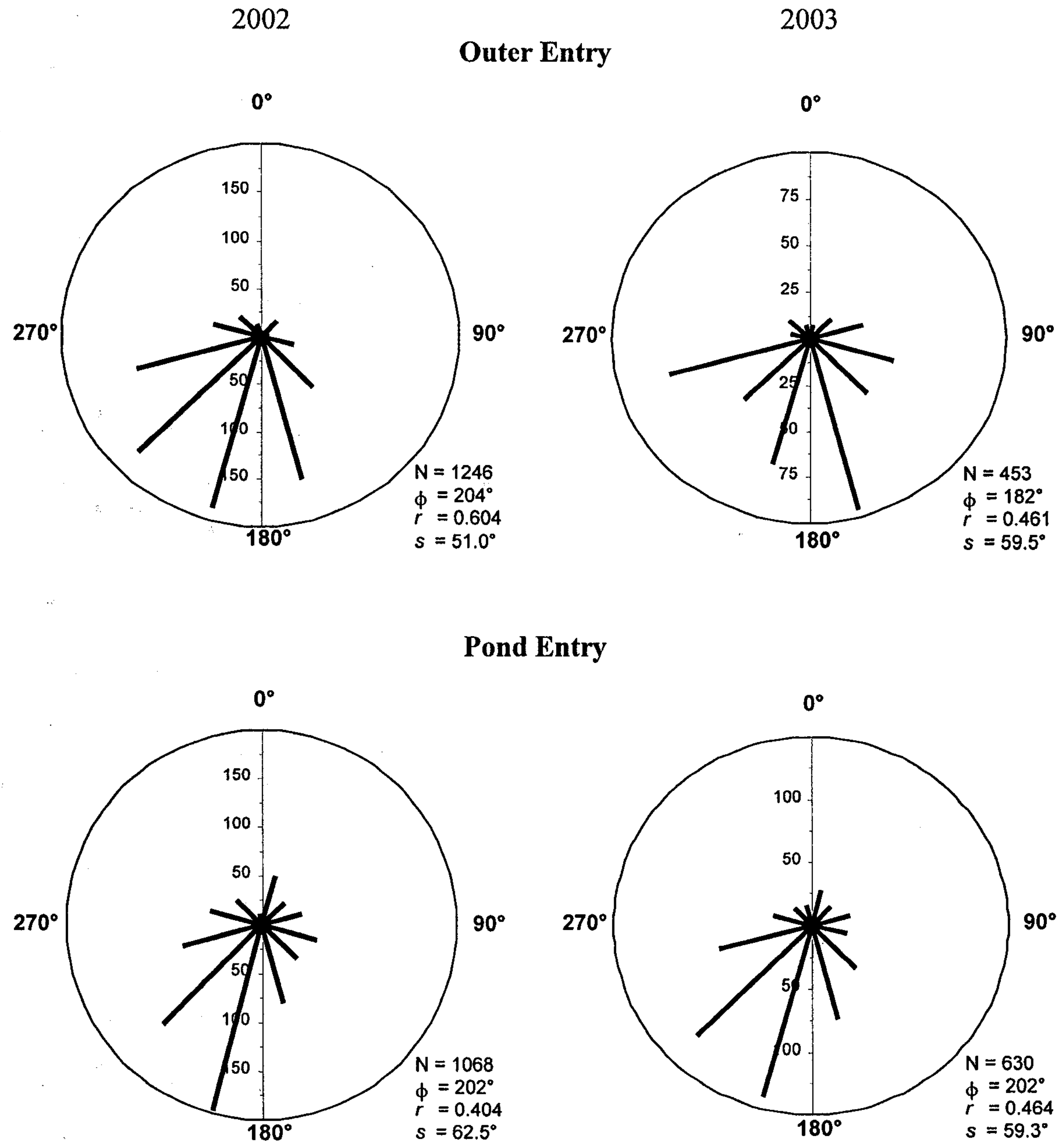


Figure 9: Adult *Pseudacris triseriata* immigration patterns at both the pond and outer fences. The immigration patterns from 2002 are on the left and those from 2003 on the right. 0° corresponds to the division of sections L and K, the North of the study site. The average angle (ϕ), vector length (*r*), and angular deviation (*s*) are given for the mean direction of each distribution. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction.

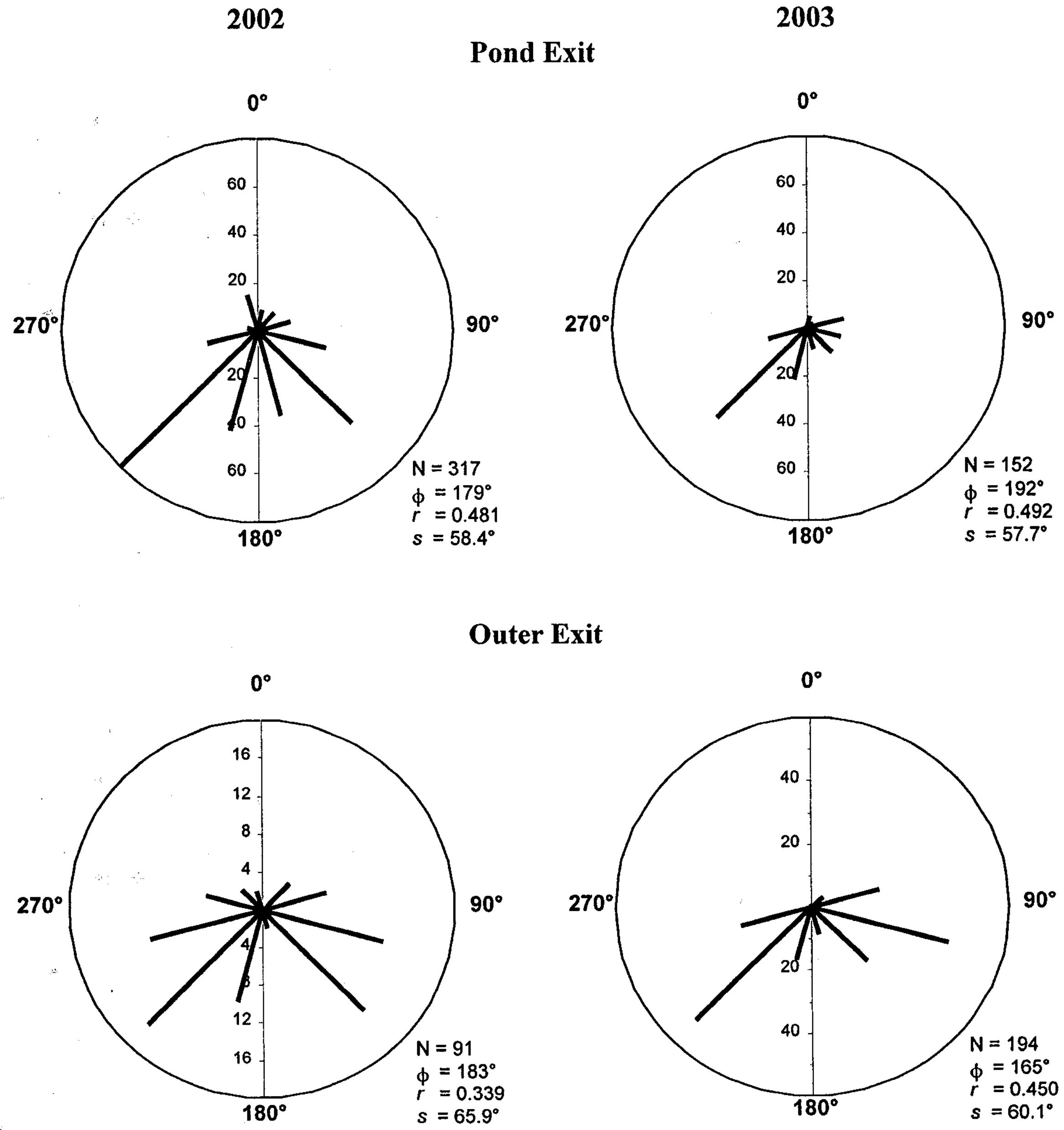


Figure 10: Emigration of *Pseudacris triseriata* adults from both the pond and outer fences. Emigration patterns for 2002 are on the left and those of 2003 are on the right. 0° corresponds to the division of sections L and K, the North of the study site. The average angle (ϕ), vector length (*r*), and angular deviation (*s*) are given for the mean direction of each distribution. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction.

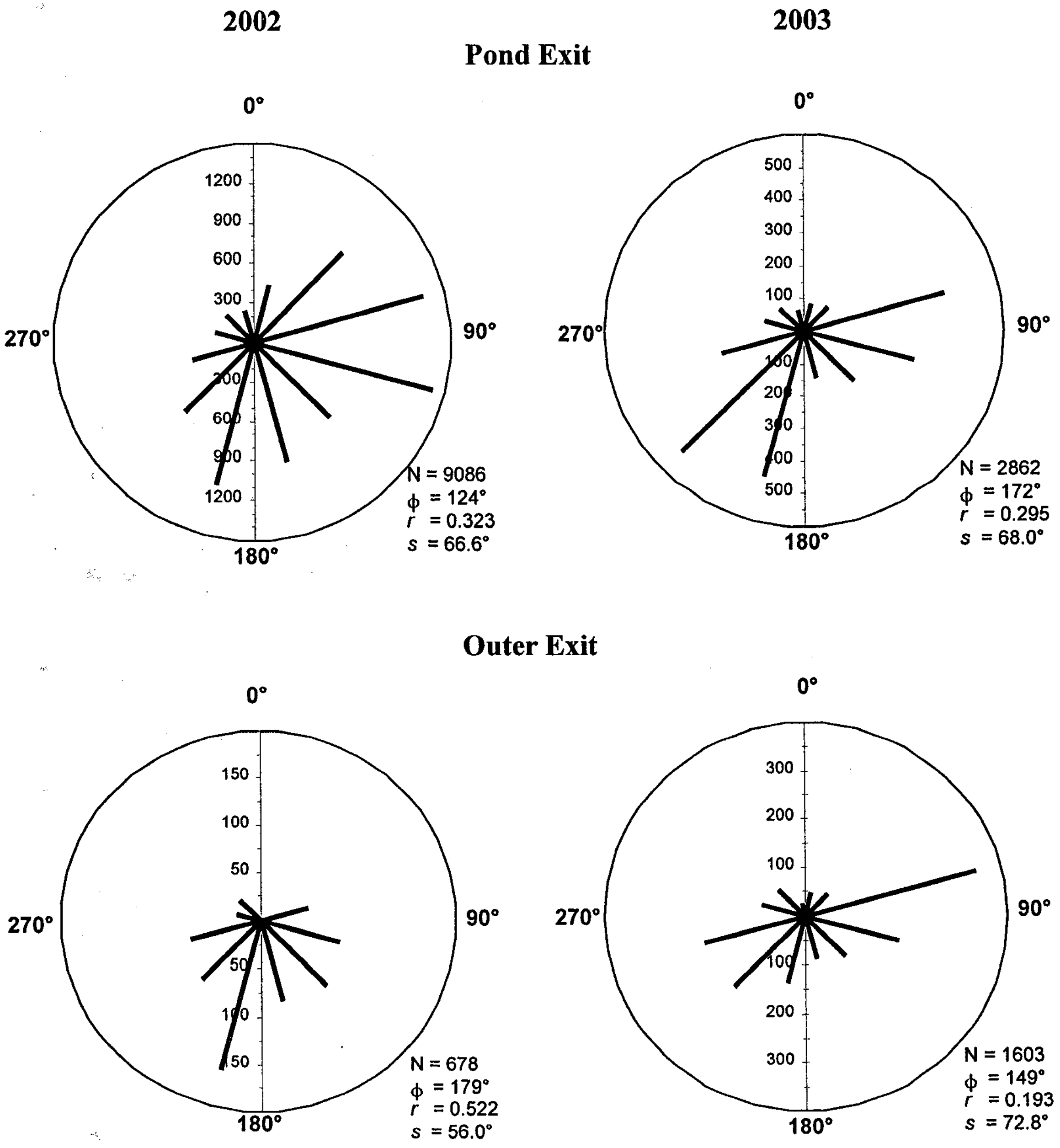


Figure 11: Young of the year emigration patterns at both pond and outer fences with emigration patterns from 2002 on the left and those of 2003 on the right. 0° corresponds to the division of sections L and K, the North of the study site. The average angle (ϕ), vector length (*r*), and angular deviation (*s*) are given for the mean direction of each distribution. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction.

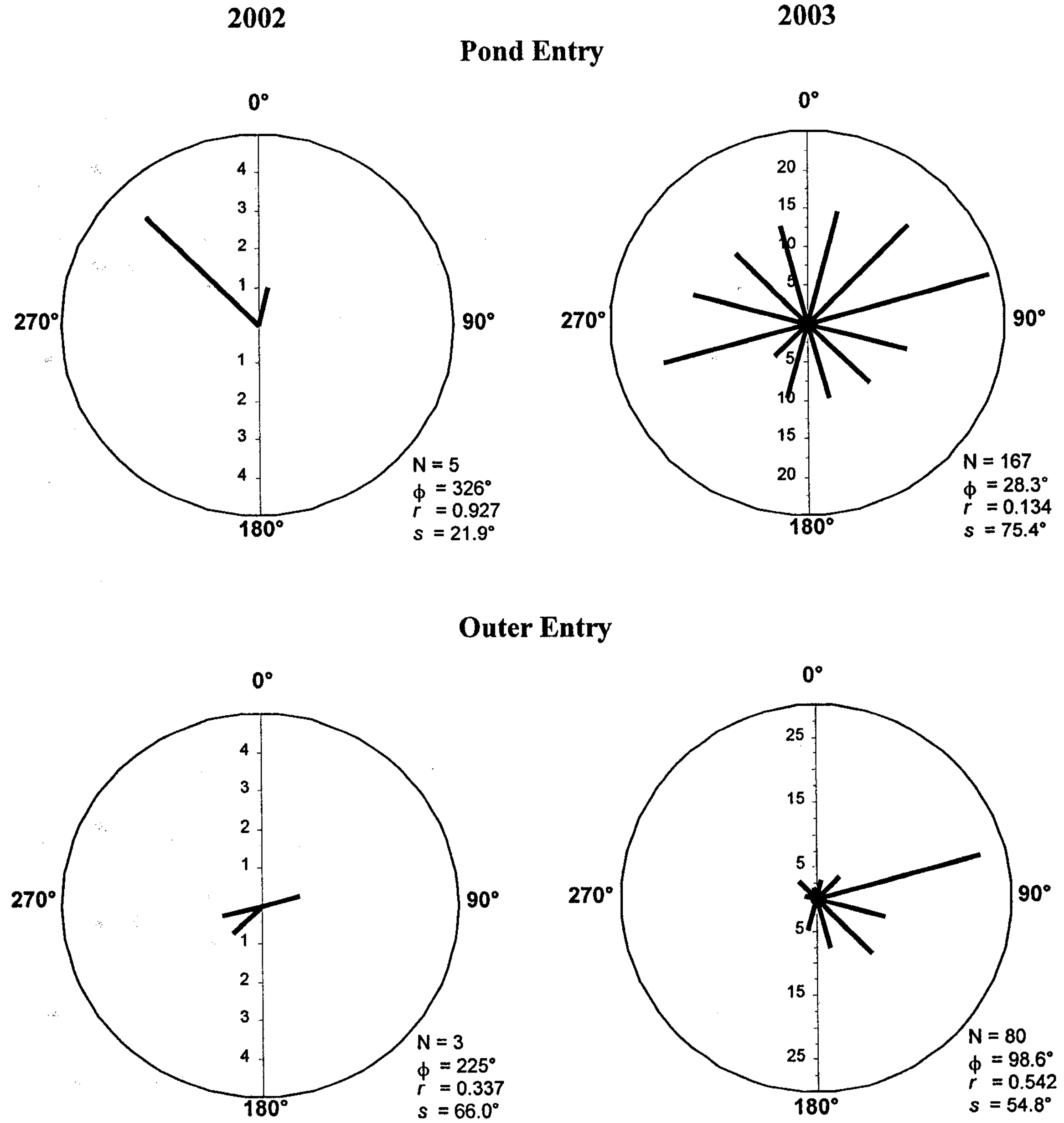
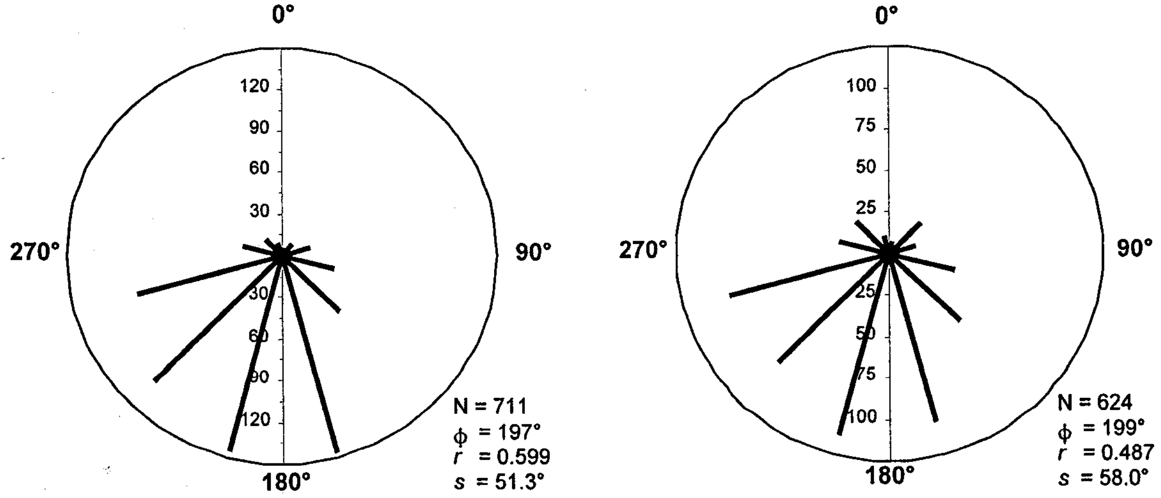


Figure 12: Young of the year immigration patterns at both pond and outer fence with immigration patterns from 2002 on the left and those of 2003 on the right. 0° corresponds to the division of sections L and K, the North of the study site. The average angle (ϕ), vector length (*r*), and angular deviation (*s*) are given for the mean direction of each distribution. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction.

Males **Females**

Outer Entry



Pond Entry

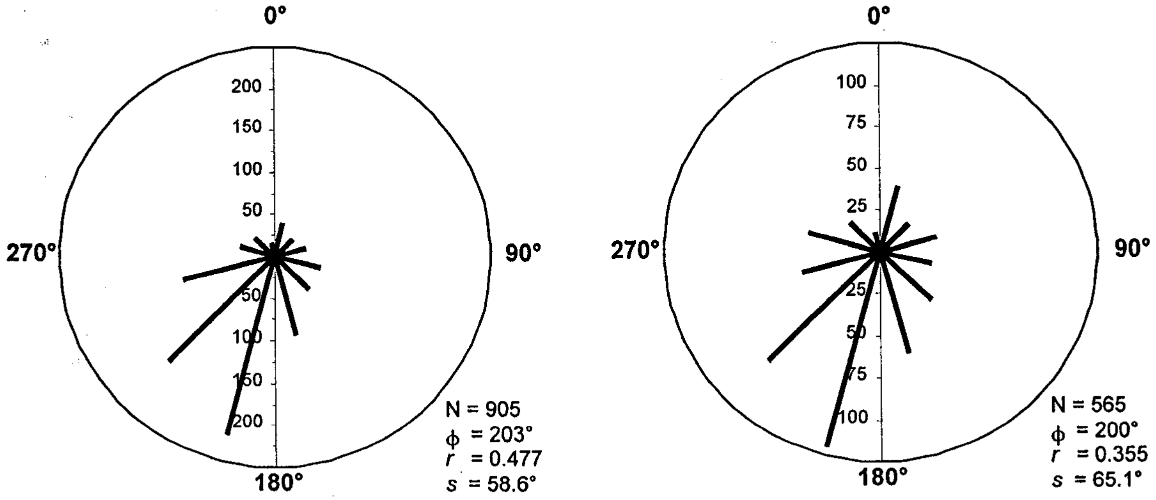


Figure 13: Immigration patterns of *Pseudacris triseriata* males (left) and females (right). Plotted values represent the sum of individuals from 2002 and 2003. 0° corresponds to the division of sections L and K, the North of the study site. The average angle (ϕ), vector length (*r*), and angular deviation (*s*) are given for the mean direction of each distribution. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction.

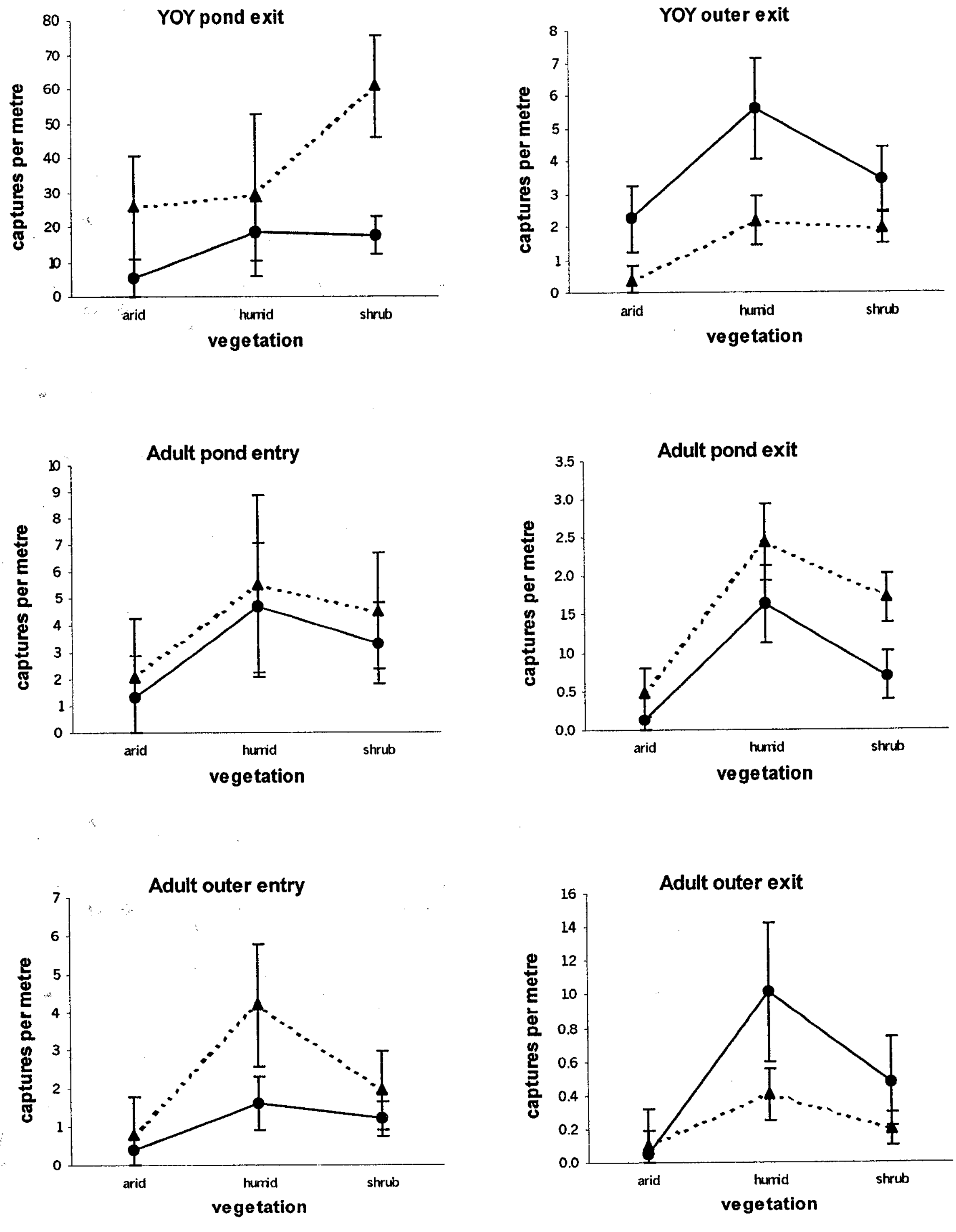


Figure 14: Least square mean number of captured *Pseudacris triseriata* per metre of fence in each vegetation. The mean number of captures per metre and 1.96 × SE (error bars) for each vegetation is given for 2002 (▲, dashed line) and for 2003 (●, whole line). Significant differences ($p < 0.05$) existed among vegetations for all comparisons except during adult pond entry in 2002 and 2003. See results section for statistics and multiple comparison results.

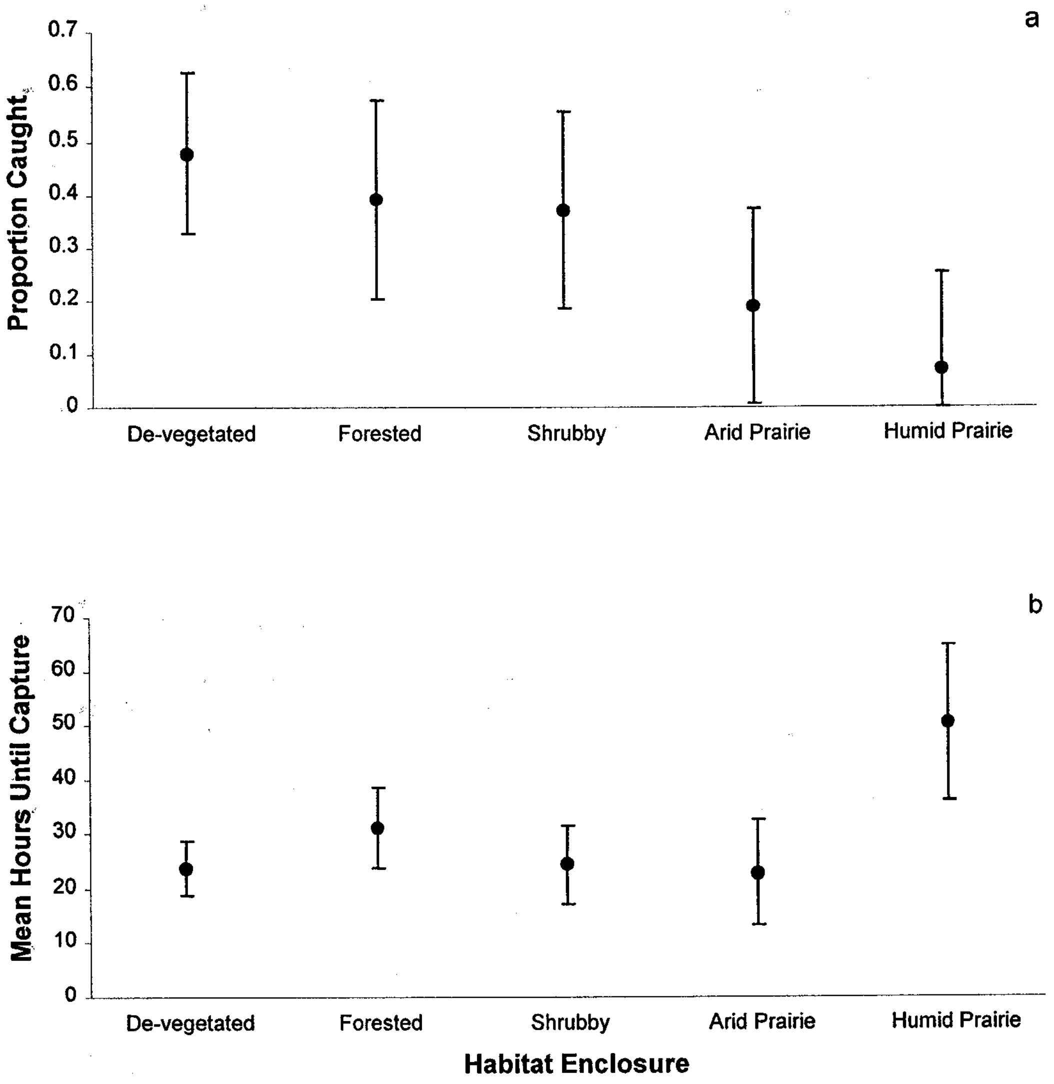


Figure 15: Plot of the least square mean proportions caught (A) and the least square mean hours until capture (B) of *Pseudacris triseriata* young of the year in enclosures. Four to five trials were used to calculate the mean and standard error. Error bars represent $1.96\times SE$ for each treatment. The proportion of individuals caught was significantly different among habitat enclosures ($F_{4,23} = 3.6$; $p = 0.021$). The mean hours until capture was significantly different among habitat type ($F_{4,92} = 3.5$; $p = 0.011$) with individuals in the humid prairies taking the longest to reach the enclosure fence.

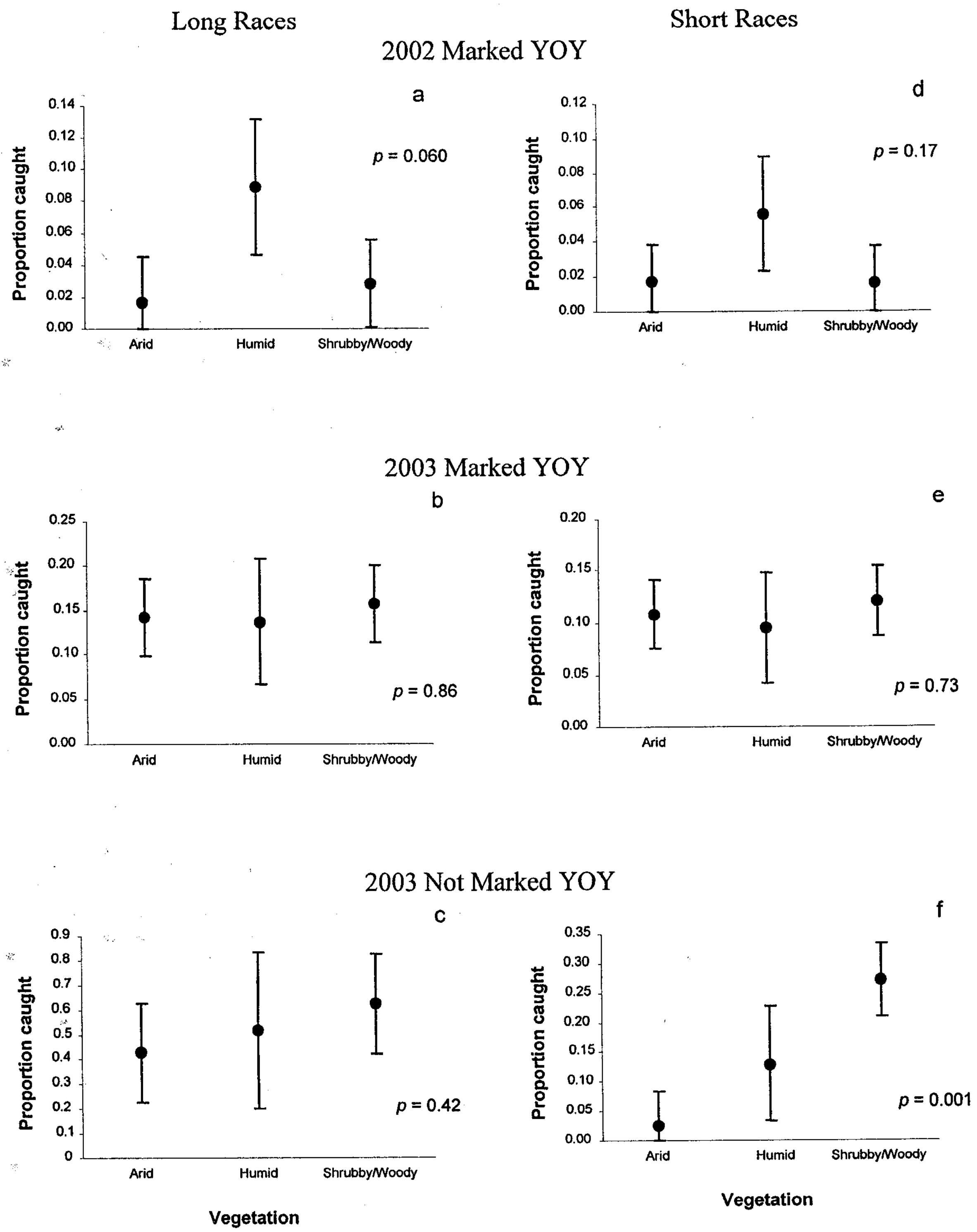


Figure 16: Proportion of *Pseudacris triseriata* young of the year caught at the outer fence from those released at the pond fence. The twelve sections are grouped by similar vegetation composition. The *p* values for the comparison among vegetations are shown for each figure. Error bars represent 1.96 × SE for each treatment.

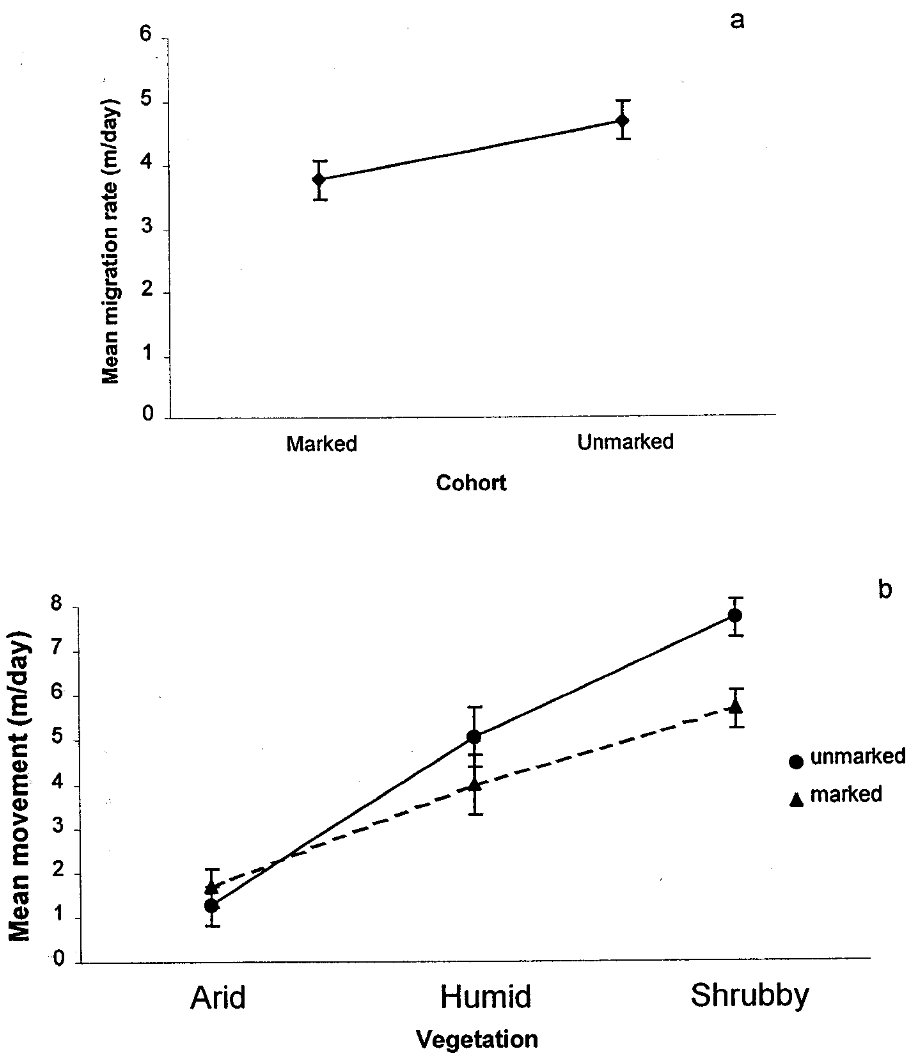


Figure 17: Comparison of least square mean migration rates for both marked and unmarked cohorts, in 2003, using the first five individuals to reach the outer fence. Error bars represent 1.96×SE for each treatment. (a) Marked individuals moved slower than unmarked individuals in comparison between the two cohorts in 2003 (t_{118} = -1.74, p = 0.085). (b) Least square mean migration rates of marked (▲) and unmarked (•) young of the year were significantly different across vegetation types (marked $F_{2,57} = 71.9, p < 0.0001$; and unmarked $F_{2,57} = 278.9, p < 0.0001$).

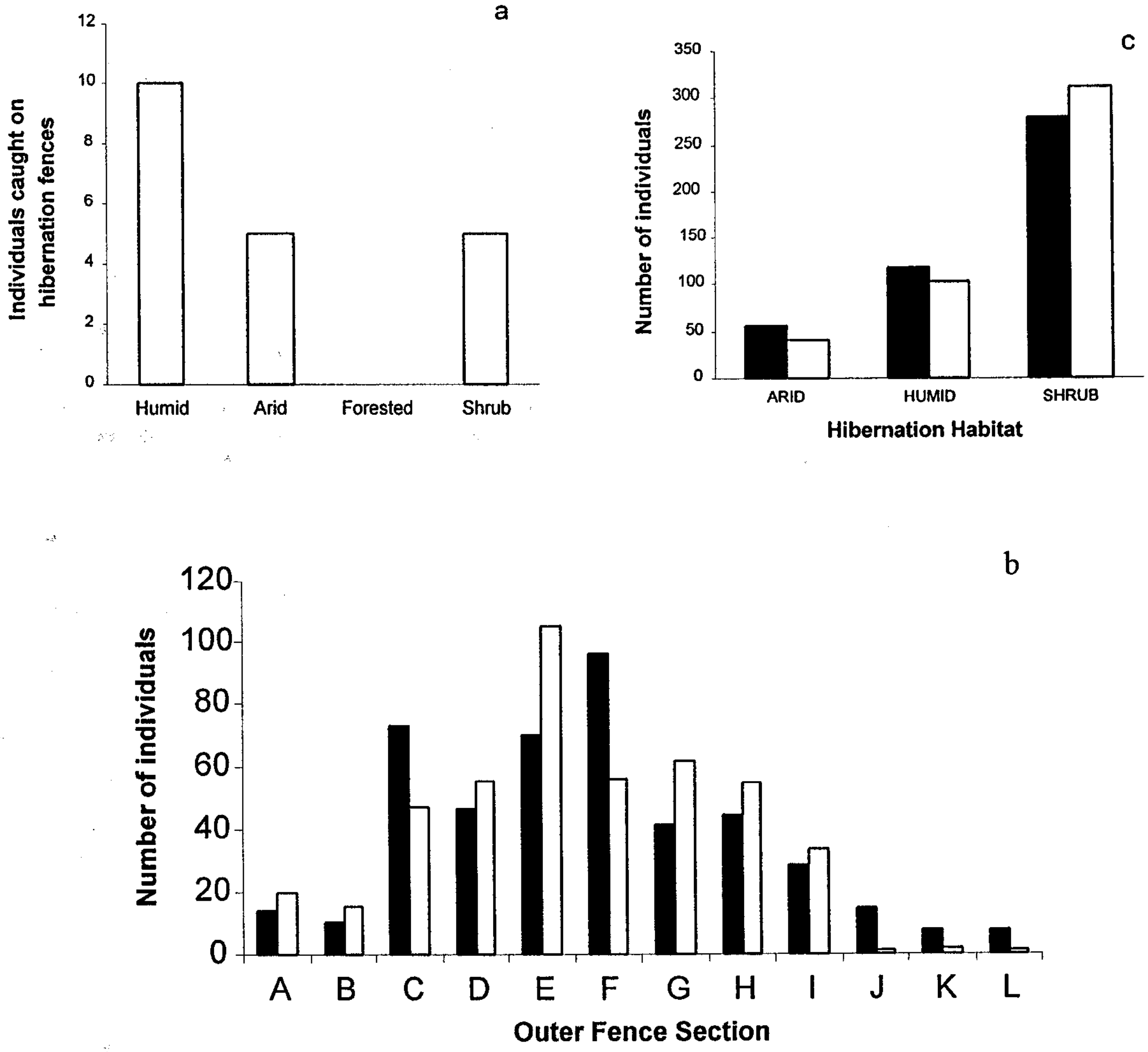


Figure 18: Evidence of over-wintering habitat success for *Pseudacris triseriata*. (a) The number of individual adults caught in hibernation fence arrays was significantly non-random (χ^2 = 10.0, 3 df, p = 0.018). (b) The observed directional orientation of adults migrating to the outer fence emerging after hibernation in 2003 (closed bars) was significantly different than orientation of migrants expected (open bars) based on the proportion of young of the year exiting the outer fence in 2002 (MRPP Test statistic = -1.80, p < 0.0001). (c) Grouping sections by vegetation type shows that the observed number (closed bars) of adults emerging after hibernation from within each vegetation is significantly different than the expected (open bars) number of migrants (χ^2 = 11.1, 1 df, p < 0.001).

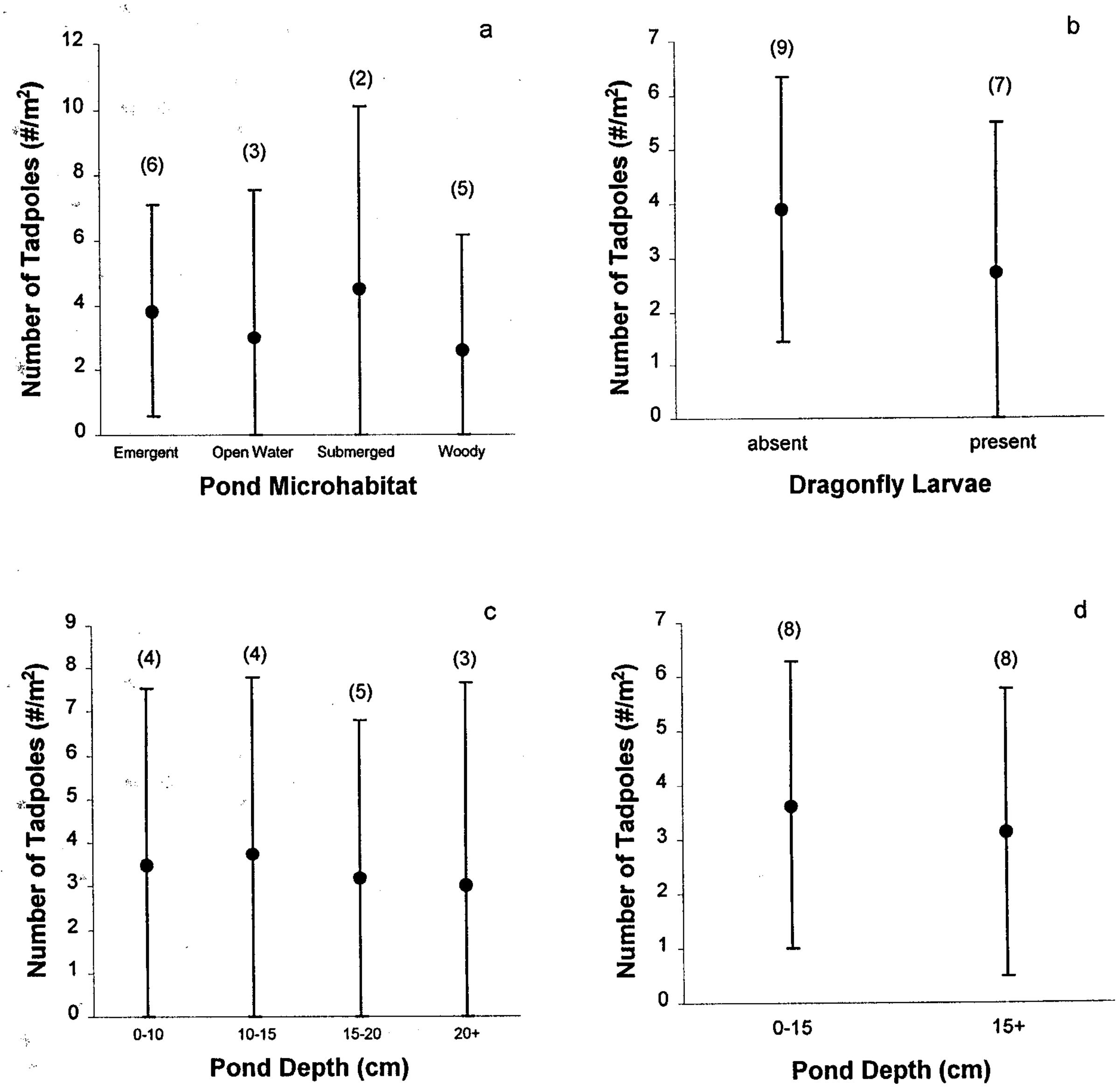


Figure 19: Comparison of the least square mean abundance of *Pseudacris triseriata* tadpoles to different pond characters with 1.96×SE bars shown for each treatment. The area in m^2 represented by each mean is shown in brackets. (a) Mean abundance of chorus frog tadpoles across the four microhabitats found within the pond. The mean abundance of tadpoles does not differ among the habitats ($F_{3,12} = 0.15$, $p = 0.930$). (b) Mean abundance of *P. triseriata* tadpoles compared to presence of Dragonfly larvae. The abundance of tadpoles did not differ between presence and absence of the larval predators ($F_{1,14} = 0.38$, $p = 0.546$). (c-d) Abundance of *P. triseriata* tadpoles compared to pond depth did not differ among levels ($F_{3,12} = 0.024$, $p = 0.995$).

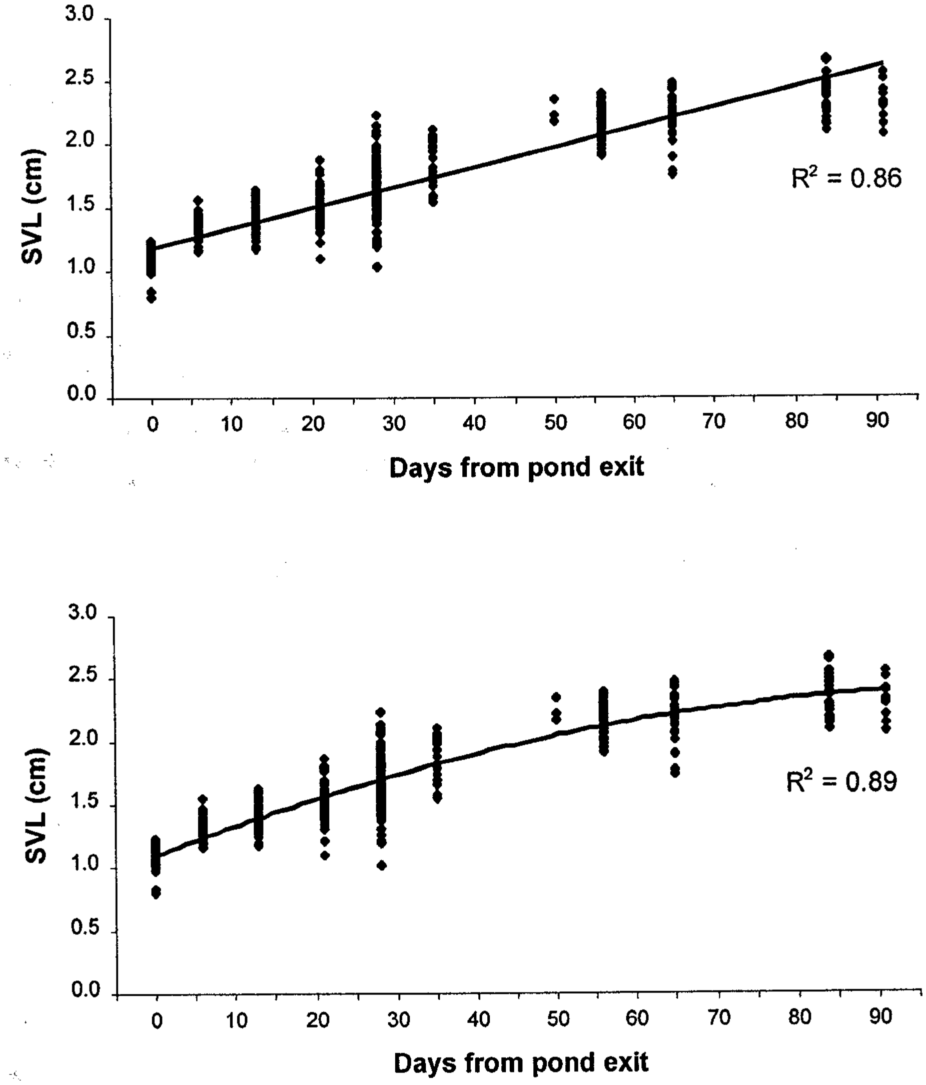


Figure 20: Regression plots for the growth of *Pseudacris triseriata* young of the year from June 30 until September 28 2003. The upper plot shows the linear regression where $\beta = 0.0158$ (± 0.0003 SE, $t = 59.6$, $p < 0.0001$), and the constant = 1.174 (± 0.0103 SE, $t = 114.3$, $p < 0.0001$). The lower plot shows the quadratic polynomial regression where SVL = $1.095 + 0.0247 \times \text{days} - 0.0001 \times \text{days}^2$ (± 0.0112 SE, $t = 97.9$ for the constant; ± 0.0003 SE, $t = 32.4$ for the days term and ± 0.0000 SE, $t = -12.2$ for the days^2 term, all $p < 0.0001$). Both of the regressions were significant ($F_{1,585} = 3558.5$ for the linear and $F_{2,584} = 2306.7$ for the quadratic where $p < 0.0001$ for both).

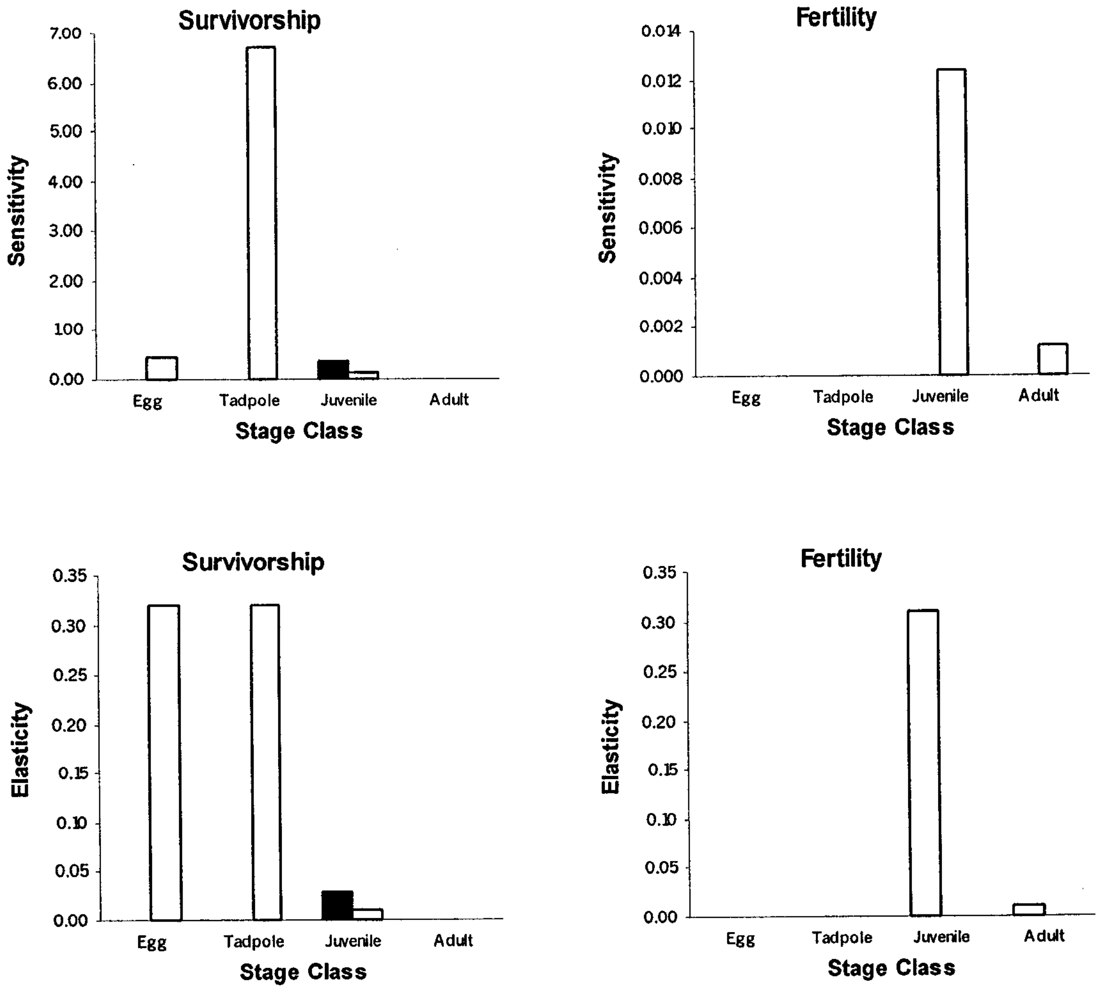


Figure 21: Sensitivity and elasticity plots for the life stages of *Pseudacris triseriata*. The sensitivity values (upper plots) and elasticity values (lower plots) for each life stage affect on the growth rate, λ, are shown for graduating from one class to the other (open bars) and for remaining in the same class (black bars).

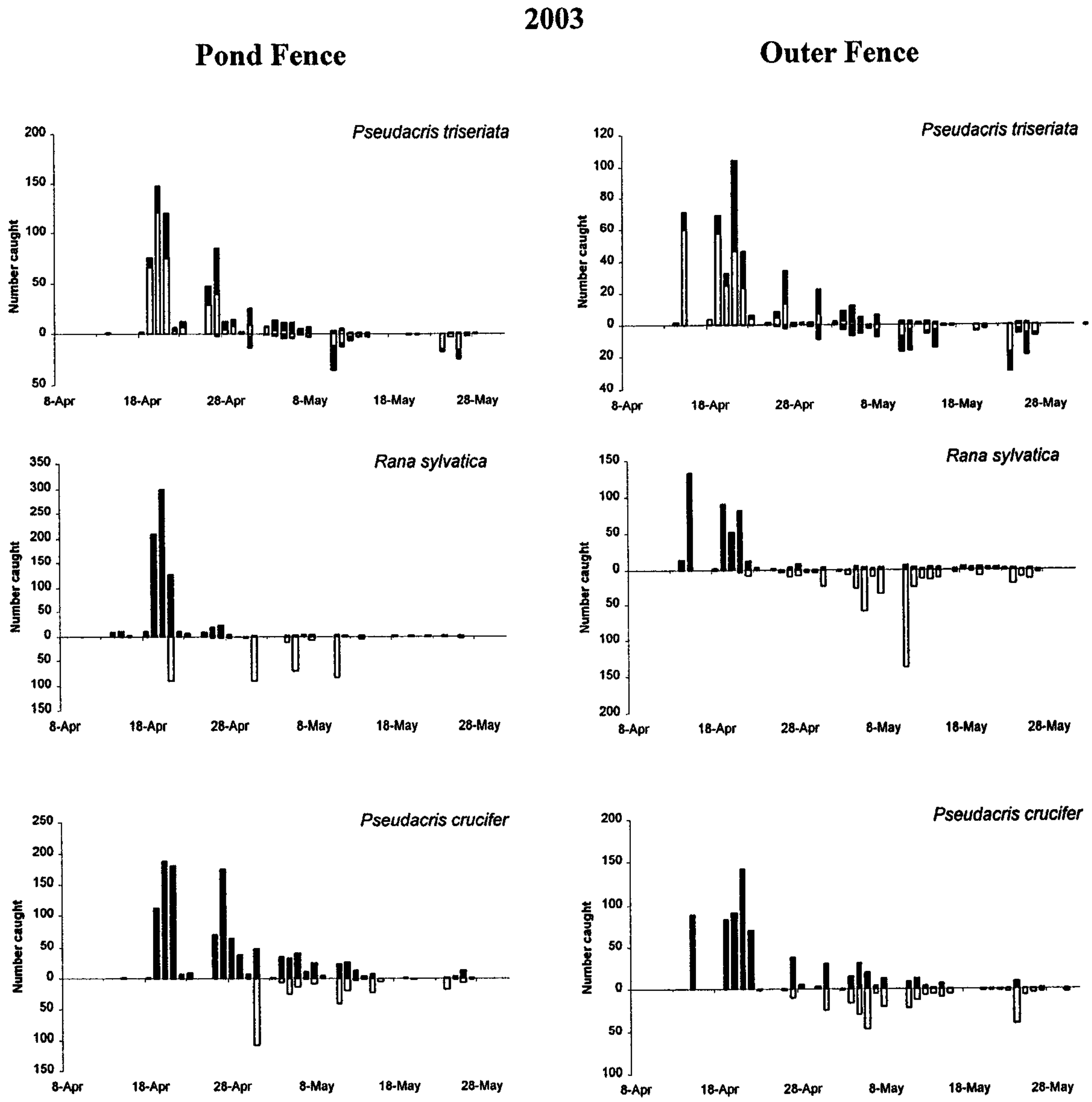


Figure 22: Migration of *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* adults during the period of April 8 to May 30 2003. Adult migration at the pond fence is on the left, while migration at the outer fence is on the right. Values above the x-axis correspond to adult migration towards the pond while values below the x-axis refer to emigration away from the pond. In *P. triseriata* graphs, both the number of males (white bars) and females (black bars) are shown as a function of the total number of individuals moving.

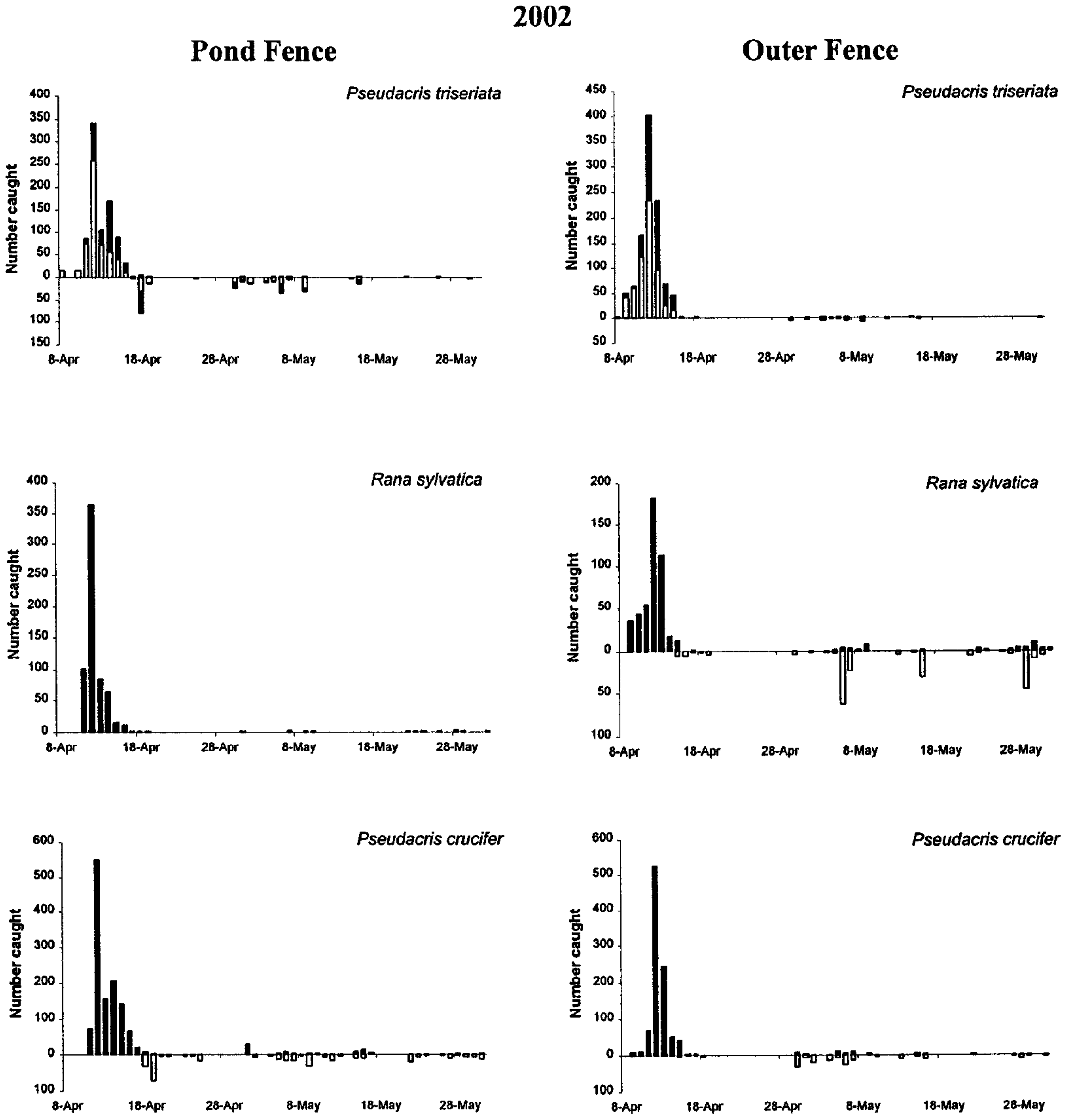


Figure 23: Migration of *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* adults during the period of April 8 to May 30 2002. Adult migration at the pond fence is on the left, while migration at the outer fence is on the right. Values above the x-axis correspond to adult migration towards the pond while values below the x-axis refer to emigration away from the pond. For *R. sylvatica* pond migration, only immigration is shown, as emigration was not recorded. In *P. triseriata* graphs both the number of males (white bars) and females (black bars) are shown as a function of the total number of individuals moving.

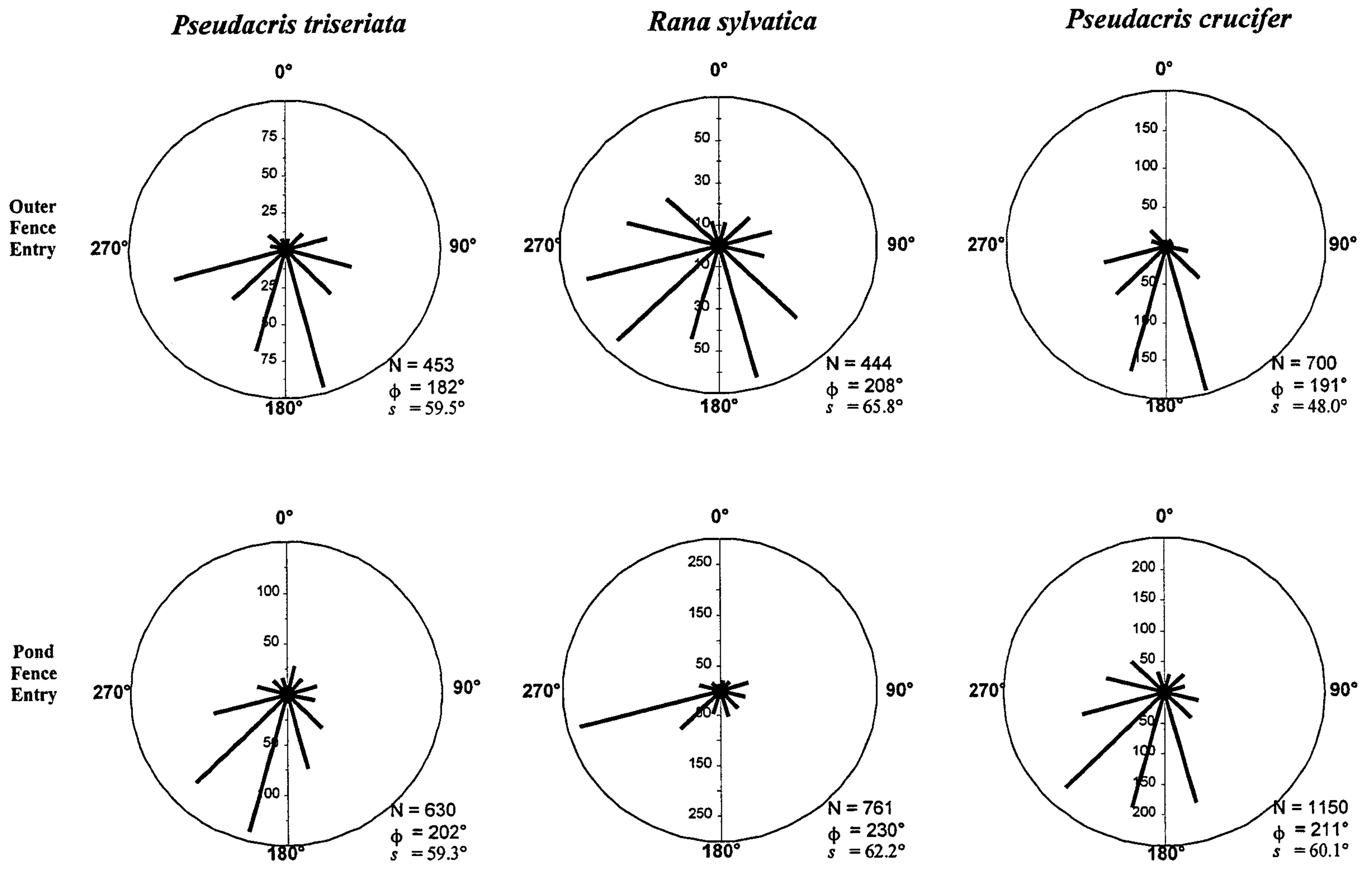


Figure 24: Immigration patterns to both the outer and pond fences for *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* in 2003. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction. ϕ = average angle, *s* = angular deviation.

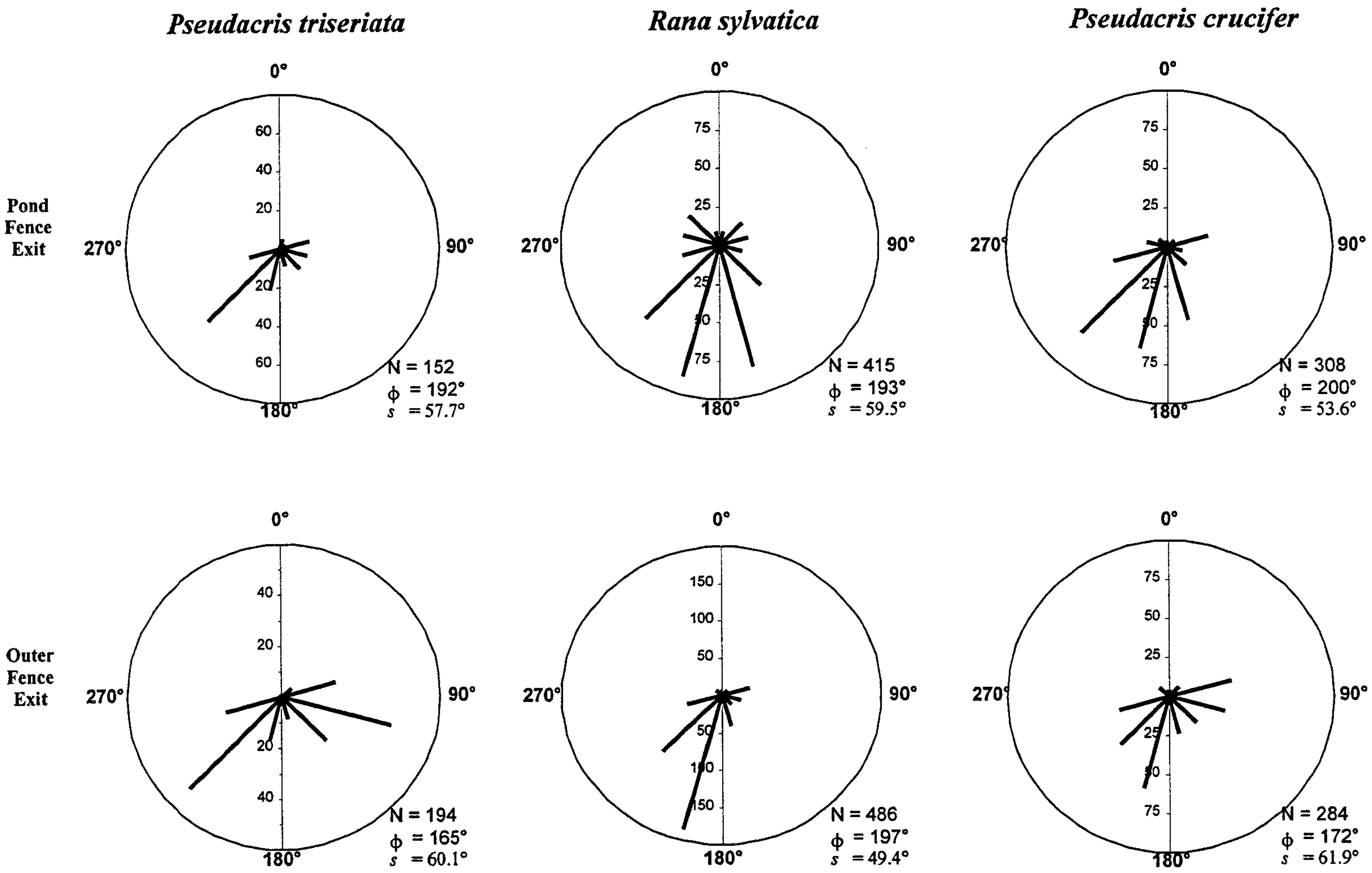


Figure 25: Emigration patterns from both the outer and pond fences for *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* in 2003. The length of the line based on the scale in each circle indicates the number of animals moving to or from that direction. ϕ = average angle, *s* = angular deviation.

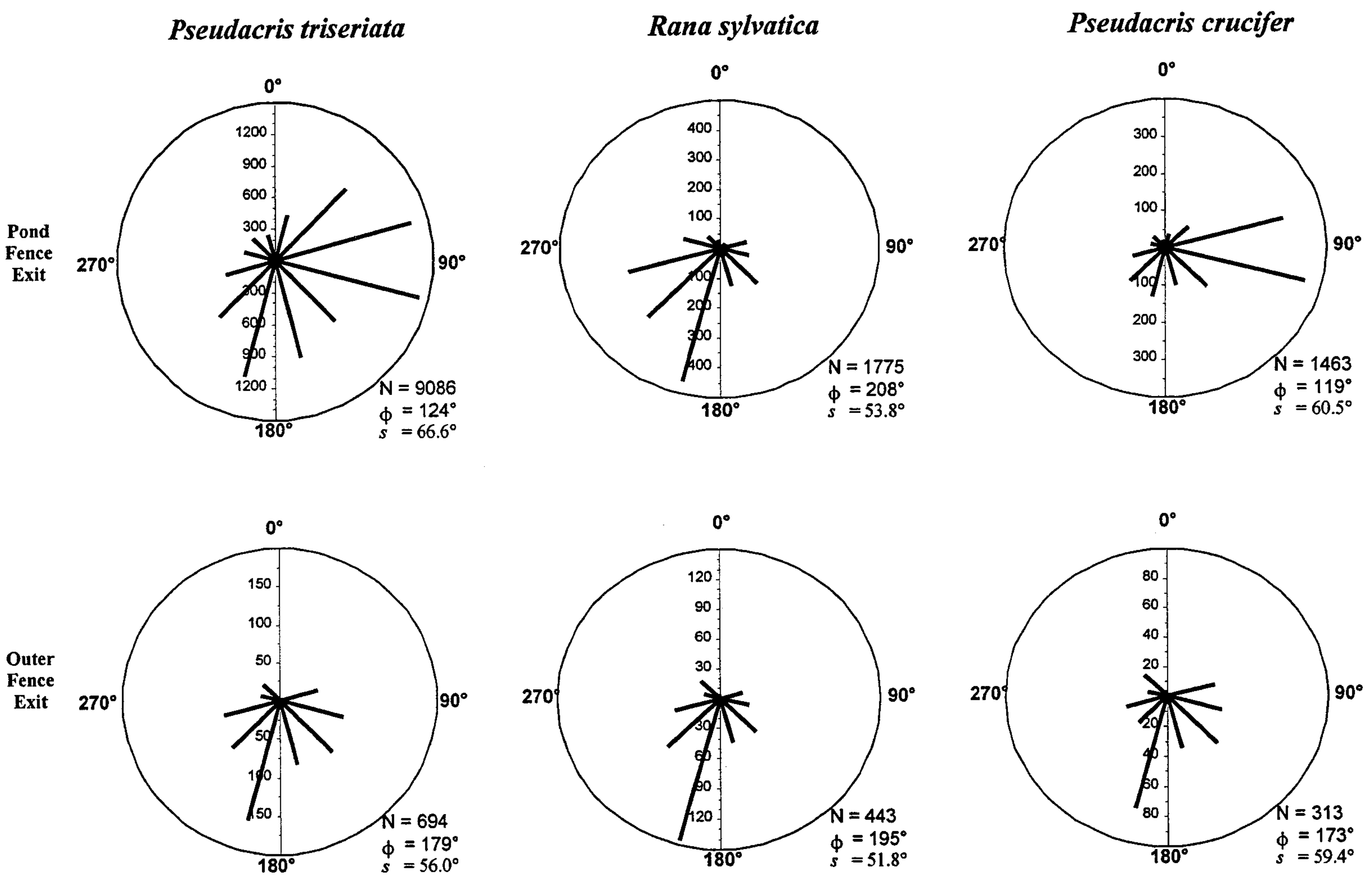


Figure 26: Emigration patterns for juvenile from both the outer and pond fences for *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* in 2002. The scale in each circle indicates the number of animals moving to or from the indicated direction. ϕ = average angle, *s* = angular deviation.

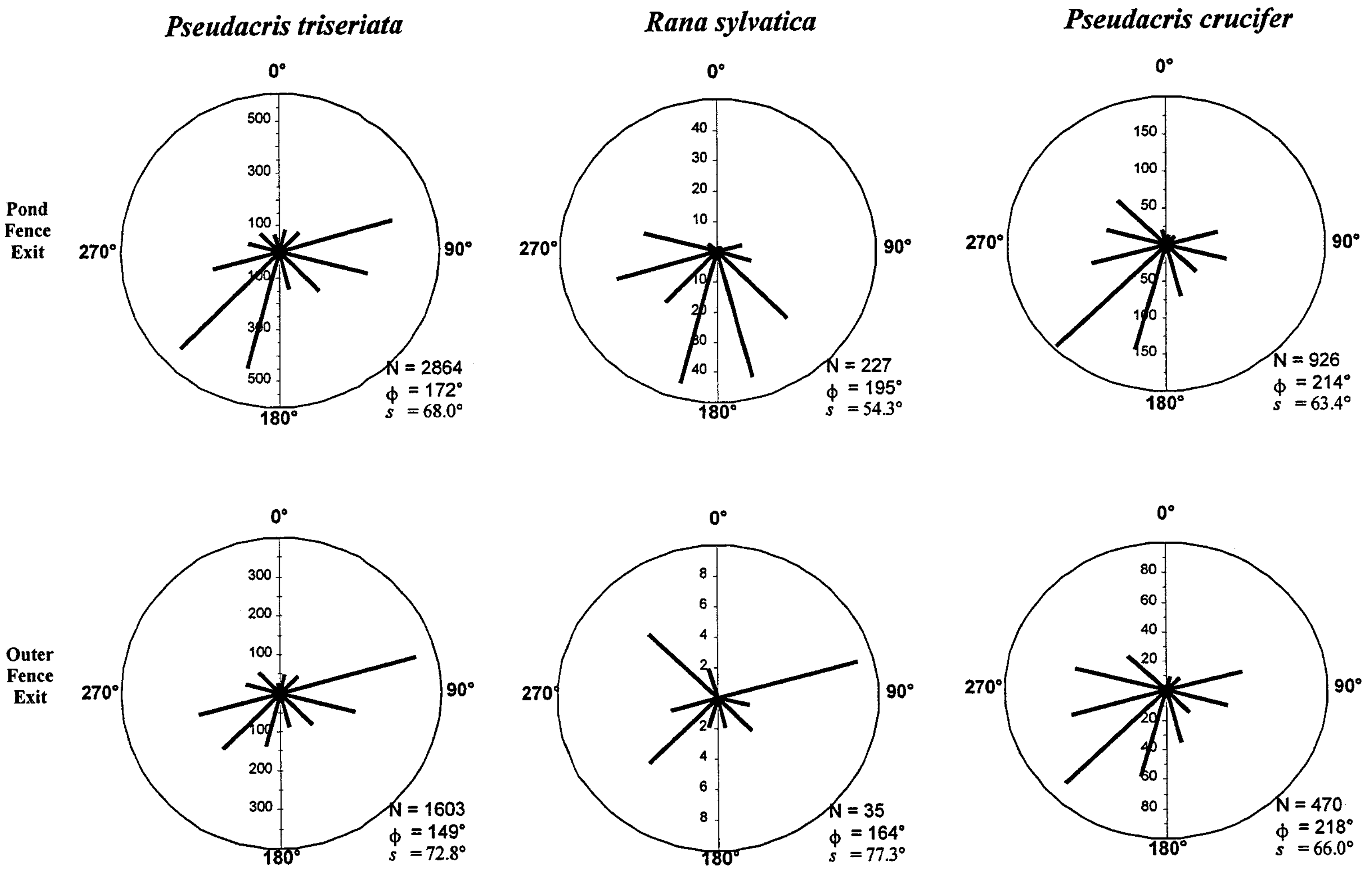


Figure 27: Emigration of young of the year from both the outer and pond fences for *Pseudacris triseriata*, *Rana sylvatica*, and *P. crucifer* in 2003. The scale in each circle indicates the number of animals moving to or from the indicated direction. ϕ = average angle, *s* = angular deviation.

Rana sylvatica

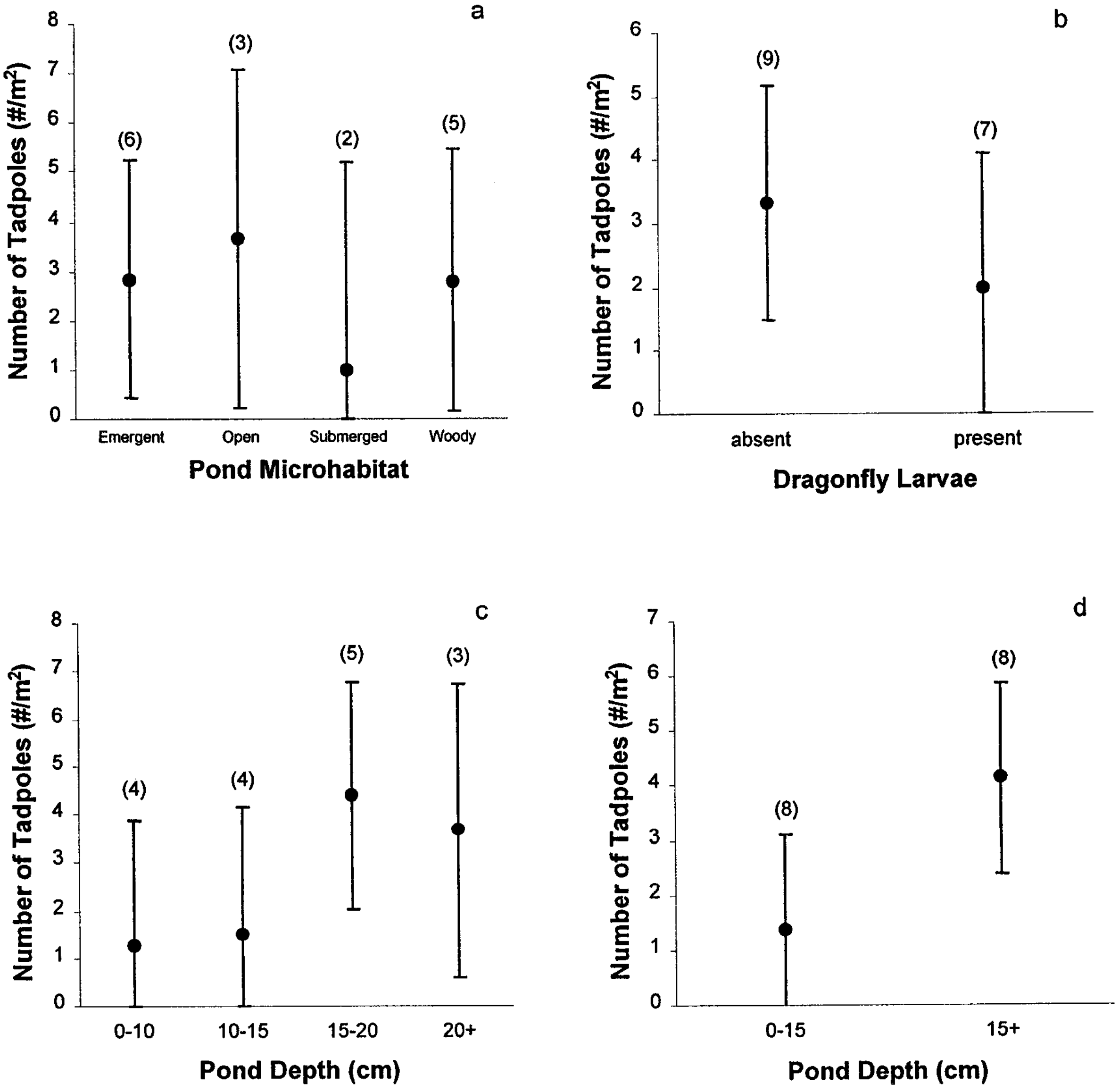


Figure 28: Comparison of the least square mean abundance of *Rana sylvatica* tadpoles to different pond characters with 1.96×SE bars shown for each treatment. The area in m^2 represented by each mean is shown in brackets. (a) Mean abundance of wood frog tadpoles across the four microhabitats found within the pond. The mean abundance of tadpoles does not segregate among the habitats ($F_{3,12} = 0.33$, $p = 0.814$). (b) Mean abundance of *R. sylvatica* tadpoles compared to presence of Dragonfly larvae. The abundance of tadpoles did not differ between presence and absence of the larval predators ($F_{1,14} = 0.88$, $p = 0.365$). (c) Abundance of *R. sylvatica* tadpoles compared to pond depth did not differ among levels ($F_{3,12} = 1.4$, $p = 0.282$) but did when only (d) two depth classes were considered ($F_{1,14} = 4.8$, $p = 0.046$).

Pseudacris crucifer

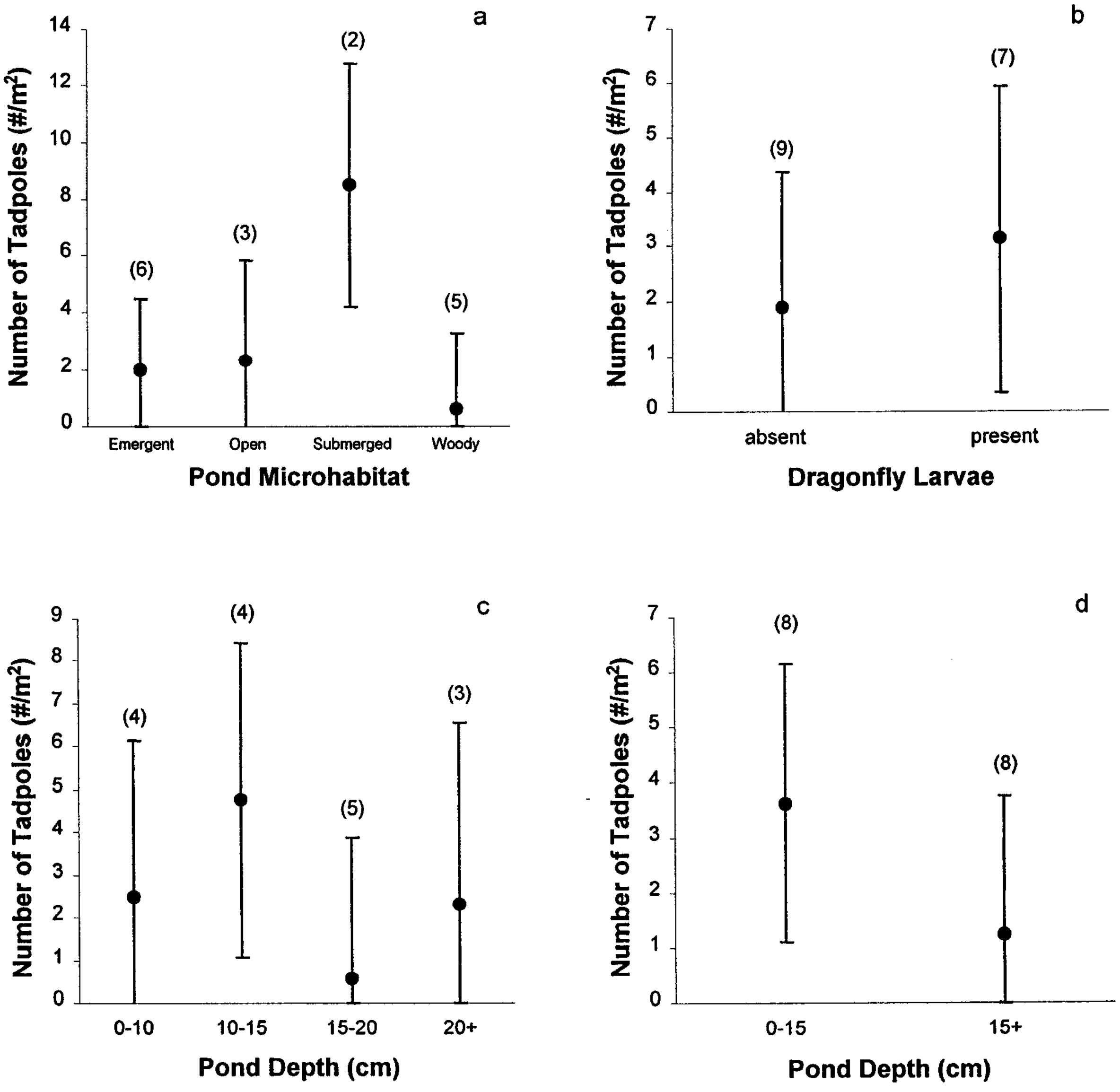


Figure 29: Comparison of the least square mean abundance of *Pseudacris crucifer* tadpoles to different pond characters with 1.96 × SE bars shown for each treatment. The area in m^2 represented by each mean is shown in brackets. (a) Mean abundance of Spring Peeper tadpoles across the four microhabitats found within the pond. The mean abundance of tadpoles may segregate among the habitats ($F_{3,12} = 3.2, p = 0.062$). (b) Mean abundance of *P. crucifer* tadpoles compared to presence of Dragonfly larvae. The abundance of tadpoles did not differ between presence and absence of the larval predators ($F_{1,14} = 0.43$, $p = 0.521$). (c) The abundance of tadpoles did not significantly segregate with pond depth ($F_{3,12} = 0.91$, $p = 0.463$), or (d) when only two depth classes were considered ($F_{1,14} = 1.7, p = 0.210$).

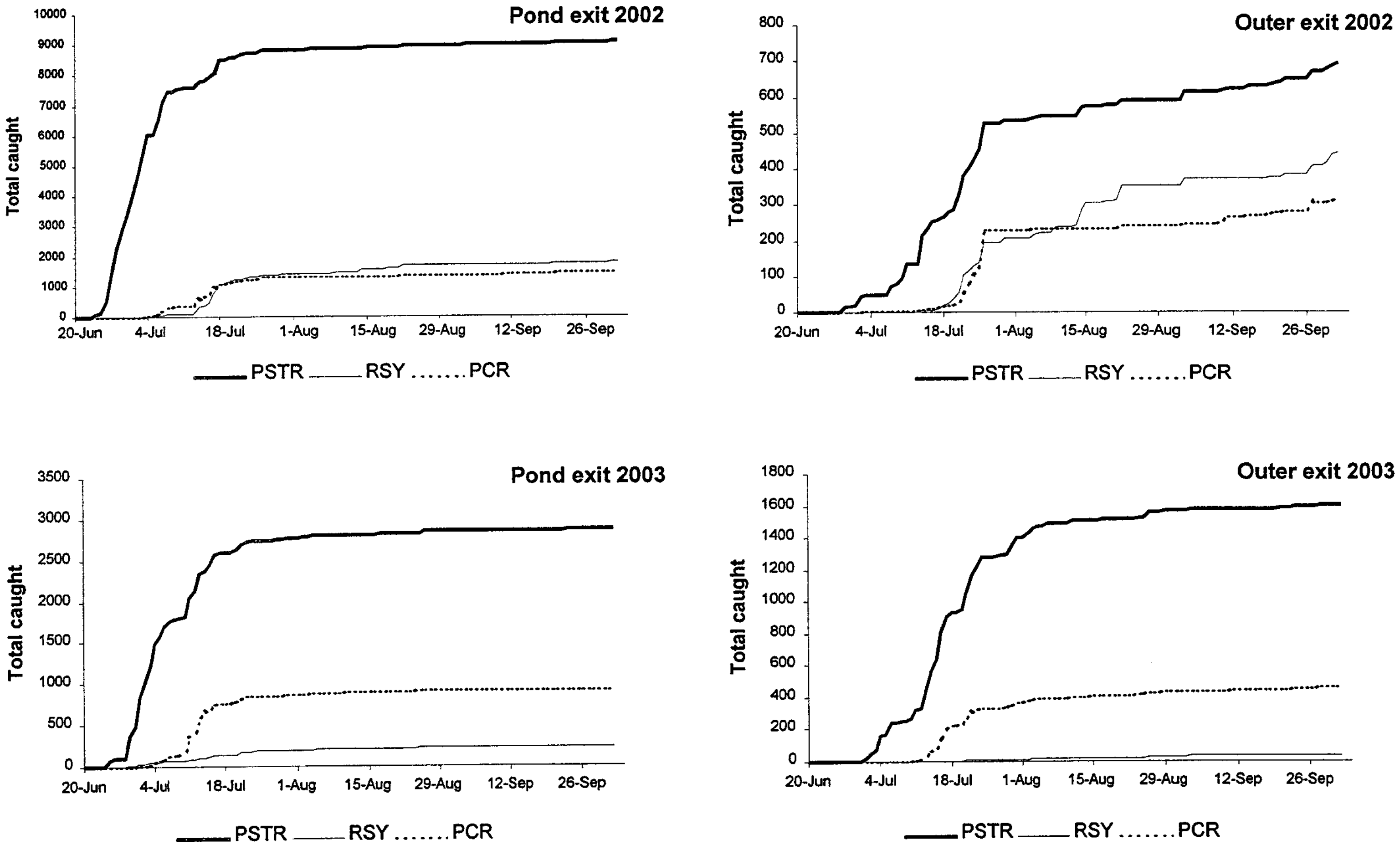


Figure 30: Total captures for young of the year for *Pseudacris triseriata, Rana sylvatica* and *Pseudacris crucifer*. Graphs on the left show the total number of young of the year produced during a given year, and graphs on the right show the number of young of the year that reached the outer fence.

Appendices

Appendix 1: McGill University Animal Use Protocol 2002

Appendix 2: McGill University Animal Use Protocol 2003

Appendix 3: Provincial Permit 2002

Appendix 4: Provincial Permit 2003