INTRODUCED BULLFROGS (*RANA CATESBEIANA*) IN BRITISH COLUMBIA: IMPACTS ON NATIVE PACIFIC TREEFROGS (*HYLA REGILLA*) AND RED-LEGGED FROGS (*RANA AURORA*)

by

Purnima Govindarajulu
B. Sc., McGill University, 1991
M.Sc., McGill University, 1994

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Abstract

Supervisor: Dr. B. R. Anholt

Introduced species are considered one of the greatest threats to biodiversity, next only to habitat destruction. I studied the ecology, distribution, and impacts of one such introduced species: the American bullfrog (*Rana catesbeiana*). Bullfrogs were introduced to British Columbia in the 1930's for the farming of frog legs. The frog farms were not economically successful and the bullfrogs were introduced to the wild. Call surveys and information from naturalists and the public was collated to map the current distribution of bullfrogs in British Columbia. Populations of bullfrogs are found in southern British Columbia, on Vancouver Island, on the Lower Mainland, in the Gulf Islands and in the Okanagan.

Natural history data and observations on marked populations in the Greater Victoria area were used to study the ecology of bullfrogs. The population ecology of bullfrogs was very similar to that in their native range in eastern North America and was governed by seasonal rhythms of air and water temperature. Bullfrog populations are expanding their range due to introduction by humans into new habitats and through migration.

Bullfrogs are considered a key species in structuring the anuran community composition in their native habitat. I examined the impact of bullfrogs on native Pacific treefrogs (*Hyla regilla*) and red-legged frogs (*Rana aurora*), focusing mainly on larval competitive interactions. Using Capture-Mark-Recapture techniques, I estimated survival of treefrog tadpoles in ponds with and without bullfrogs. I was unable to detect a difference caused by bullfrogs over the natural variation in treefrog tadpole survival rates among ponds. In artificial pond experiments I was able to show that bullfrog tadpoles had a negative effect on the development rate of the two native tadpoles and on the growth rate of red-legged frog tadpoles. Bullfrogs did not affect the survival rate of the native tadpoles in these experiments.

The demography of bullfrog populations was studied using four marked populations in the Greater Victoria area. The life-cycle of the bullfrog consisted of two alternate larval development trajectories. Tadpoles could either metamorphose after a year in the larval stage (fast-track) or spend two years in the larval stage (slow-track). Bullfrogs attained sexual maturity two years following metamorphic transformation. Linear, stage-based matrix models were used to assess the factors controlling bullfrog population growth rate. Population growth rates were most sensitive to the proportion of tadpoles entering the fast-track option of the larval life-cycle and to early post-metamorphic survival rates.

This study adds to previous published studies that have documented negative effects of bullfrogs on native species. I assessed the most effective methods of bullfrog population control. Based on logistics and on perturbation analysis of population matrix models, the most effective stages to cull are the early post-metamorphic stages: metamorphs and juveniles. However, all bullfrog control efforts are bound to be expensive and labour intensive. Habitat modification to favour native species and permit coexistence with bullfrogs may be the more effective long-term management option.

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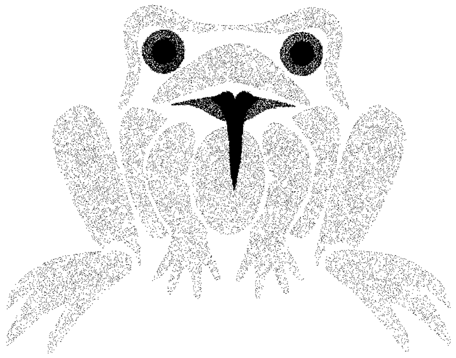
DEDICATION

To my parents, for permitting me to wander

and

To Neuman, for showing me how.

CHAPTER 1



INTRODUCED BULLFROGS IN BRITISH COLUMBIA: A FRAMEWORK FOR STUDY

General Introduction

Organisms have been moved by the vagaries of wind, ocean currents, and continental drift ever since life originated on this planet. Such movements and subsequent colonizations are considered part of the natural evolution of the ecosystems of the world (Vermeij 1991). This is distinguished from the human mediated transport of organisms beyond their natural range and the associated ecological changes wrought by these introduced species. Even though only a very small fraction of these introduced species cause extensive economic and ecological damage (Williamson and Fitter 1996, Kolar and Lodge 2001), it is the enormity of this damage that has attracted attention and given rise to a new sub-discipline of ecology: Invasion Biology. While Darwin (1860) discussed the rapid establishment of introduced species within island ecosystems, it was Charles Elton who pioneered research into the ecological impacts of introduced species with his book *The Ecology of Invasions by Animals and Plants* in 1958. Research is now focused on identifying characteristics of successful invaders (Oka 1983, Reichard and Hamilton 1997, Ricciardi and Rasmussen 1998, Goodwin 1999), recognizing characteristics of communities that are prone to invasions (Vermeij 1996, Tilman 1997), and assessing the impacts of species introductions on the ecological community (Vitousek 1990, Lodge 1993).

The American bullfrog (*Rana catesbeiana*) was widely introduced in Western North America in the early 20th century in an effort to farm frogs for human consumption (Jennings and Hayes 1985, Bury and Whelan 1986). Since then the range of the bullfrog has expanded through natural migration and repeated introductions. In **Chapter 2**, I describe the history of bullfrog introductions in British Columbia, Canada, and document their range expansion in the past decade. This chapter also summarizes the natural history of bullfrogs, comparing characteristics of populations in the native and introduced ranges.

The expansion of the range and population size of bullfrogs has been associated with declines in native amphibian species (Moyle 1973, Green 1978, Hammerson 1982, Fisher and Shaffer 1995, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001a), although the extent to which bullfrogs are responsible for these declines has been debated (Hayes and Jennings 1986, Adams et al. 1998, Adams 2000). The successful establishment of an introduced species can be modeled as an addition of a link within the food web of the native community (Abrams 1996). Each successful invader takes resources and prey from the lower trophic levels, competes within its trophic level and, in turn, becomes food for higher trophic levels (Figure 1). In so doing, introduced species can change the population size and traits such as the behaviour, morphology, and physiology of organisms that interact with it. Such interactions are termed direct effects. Other members of the food web can also be affected because they interact with species directly affected by the introduced species (Figure 1). Such effects are termed indirect effects because they arise due to changes in intermediate species. When the indirect effect is caused by a change in the population size of the intermediate species, it is called a *density mediated indirect effect*, while a *trait mediated indirect effect* is due to a change in some trait (e.g., behaviour) of the intermediate species (Abrams et al. 1996).

Introduced animals have caused the most drastic ecological effects through direct predation; for example, brown tree snakes on endemic birds in Guam (Fritts and Rodda 1998), Nile perch on the diverse cichlids in Lake Victoria, (Baskin 1992), predatory snail *Euglandia rosea* on the Partulid treesnails of Society Islands (Cowie 1992). In contrast, introduced plants and some invertebrates are capable of equally large effects through direct competition, mainly through swamping and habitat pre-emption; for example, invasive reeds in salt marshes (Daehler and Strong 1996, Angradi et al. 2001, Alvarez and Cushman 2002), ivy (Alvarez and Cushman 2002), zebra and quagga mussels (Schloesser et al. 1998), all of which form dense mono-specific stands that smother native species. While it is theoretically possible that organisms in higher trophic levels benefit from the additional resources provided by the introduced species, there is little information on this (Saurez et al. 2000). It is possible that the presence of such strong consumptive effects by native predators/herbivores precludes the establishment of the introduced species (Maron and Montserrat 2001). The introduced cane toad in Australia serves as a counterpoint to the expectation of positive effects on higher trophic levels. This introduced amphibian is highly toxic in all its life-history stages, and has caused declines of naïve native predators (Crossland 2000, Phillips et al. 2003). While early research focused primarily on direct effects, it is now clear that indirect effects are widespread and can range from positive or negative effects on single species to radical changes of ecosystem functions (Kiesecker et al. 2001b, Crooks 2002, Schreiber et al. 2002, Vazquez 2002, Townsend 2003).

Due to their complex life-histories, bullfrogs are expected to have different effects as adults than as tadpoles (Janssen and Jude 2001, Taniguchi et al. 2002). As adults, the major impact of bullfrogs on the native community is assumed to be due to direct predation (Moyle 1973, Hayes and Jennings 1986). Bullfrogs are voracious carnivores whose diet includes insects, tadpoles, frogs, fish, small mammals, and even reptiles and small birds (Bury and Whelan 1986, Werner et al. 1995). Consequently, we would expect declines in a number of native species. Although there are anecdotal reports of predation and decline in numbers (Jennings and Cook 1998, Marunouchi et al. 2003), the effect of this additional mortality on population dynamics of native species has not been quantified.

Bullfrog tadpoles on the other hand are mainly herbivorous. They filter feed on phytoplankton (Seale 1980) and scrape algae and detritus with their keratinized mouthparts (Bury and Whelan 1986, Werner 1994). At this life-history stage their effects within the native food web are complex (Figure 2), but they are expected to have the strongest competitive effect on native tadpoles due to higher resource overlap and shared predators. Previous experimental studies have demonstrated both direct and indirect competitive effects of bullfrog tadpoles on native tadpoles (Figure 2, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001a). In **Chapter 3**, using Capture-Mark-Recapture (CMR) methods, I examine whether the competitive effects detected under experimental settings translated into decreased survival rates for native Pacific treefrog tadpoles under field conditions.

Chapter 4 and **5** cover experimental studies conducted in artificial ponds. I examined the mechanism and strength of larval competition and assessed how differential vulnerability to predators influenced these competitive interactions. Pacific treefrog tadpoles that hatch in spring face competition from much larger bullfrog tadpoles that have over-wintered in the pond. Larger tadpoles are not only expected to have higher per-capita competitive effects (Werner 1994) but are also immune from predation by gape-limited native predators such as the roughskin newt. This differential vulnerability favours bullfrog tadpoles through both *density mediated* and *trait mediated indirect effects*. Predation decreases population size of native tadpoles thereby decreasing the competition experienced by bullfrog tadpoles from native tadpoles (*density mediated indirect effect*). In addition, tadpoles decrease activity in the presence of a predator to minimize predation risk (Skelly and Werner 1990, Skelly 1994); this leads to reduced foraging effort and lower competitive effects on the species immune to predation (*trait mediated indirect effect*) (Werner 1992, Werner and Anholt 1993, Relyea and Werner 1999). Thus, the presence of a predator has been shown to shift competitive effects in favour of the less vulnerable species and can lead to coexistence or competitive exclusion, as the case may be (Werner 1991, Werner and McPeek 1994, Skelly 1996, Werner and Anholt 1996, Relyea 2000, Peacor and Werner 2001). In **Chapter 4**, I compare the *intra-specific* and *inter-specific* competitive effects between native treefrog tadpoles and introduced bullfrog tadpoles and, assess whether *trait mediated indirect effects* caused by the presence of a native predator affect these competitive interactions.

Surveys of the distribution of these native frogs indicated that Pacific treefrogs persist in areas where bullfrogs have been introduced but red-legged frog populations are extirpated (Hayes and Jennings 1986, Fisher and Shaffer 1995). In **Chapter 5**, I compare the competitive interactions between bullfrog tadpoles and these two native species. These comparisons are useful because the difference between coexistence and competitive exclusion among species is often determined by the relative strengths of *intra* and *inter-specific* competition in the various life-history stages.

Recently, attention has been focused on the phenomenon of 'invasional meltdown' (Simberloff and Von Holle 1999) where the successful establishment of one introduced species is thought to facilitate further invasions through positive interactions among introduced species. In western North America, sunfish have been widely introduced and have been shown to facilitate bullfrog invasions through a *density mediated indirect effect* (Adams et al. 2003). The sunfish dramatically decrease dragonfly larvae populations. Dragonfly larvae are very efficient predators of bullfrog tadpoles and their presence has been shown to deter persistence of bullfrog tadpoles in a community, both in their native and introduced habitats (Werner and McPeek 1994, Adams et al. 2003). Native tadpoles are very vulnerable to predation by sunfish, but bullfrog tadpoles are immune because they are both large and noxious to fish (Kruse and Francis 1977). In **Chapter 5**, I assess whether these introduced sunfish biased competitive interactions in favour of bullfrog tadpoles through *trait mediated indirect effects* similar to those studied in Chapter 4 with native predators.

As data accumulate on the negative impacts of bullfrogs, efforts are being initiated to control their spread (Banks et al. 2003). To be most effective, control efforts should target the life-history stage that most contributes to population growth rate. However, little is known about the demography of bullfrogs in their introduced range. In **Chapter 6**, I present Capture-Mark-Recapture estimates of post-metamorphic survival rates as these have been shown to be important in determining population growth rate in other anurans (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002). Then, to help target control efforts, I use prospective demographic perturbation analysis to identify the vital rates that contribute the most to population growth rate (Shea and Kelly 1998, Caswell 2000, Heppell et al. 2000).

In **Chapter 7**, I summarize the results of the preceding chapters and suggest reasons for the recent range expansion of bullfrogs in British Columbia. I conclude with a proposal for the control of bullfrog populations and a mitigation plan for affected native frog species.

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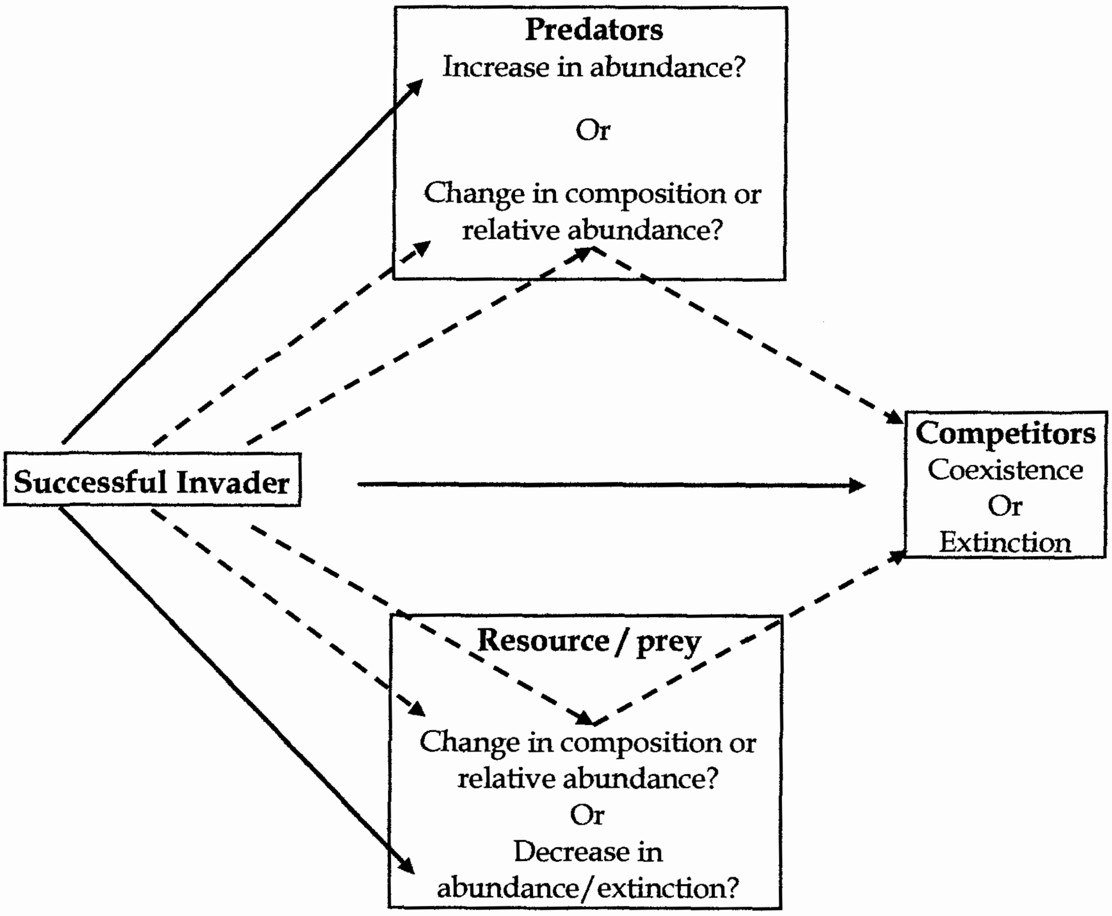


Figure 1.1: Interactions of a successfully established introduced species within the native food web, focusing on the changes effected by the introduced species. Arrows point from the effector to the affected. A direct effect (solid arrows) involves only two species. An indirect effect (dashed arrows) can involve three or more species.

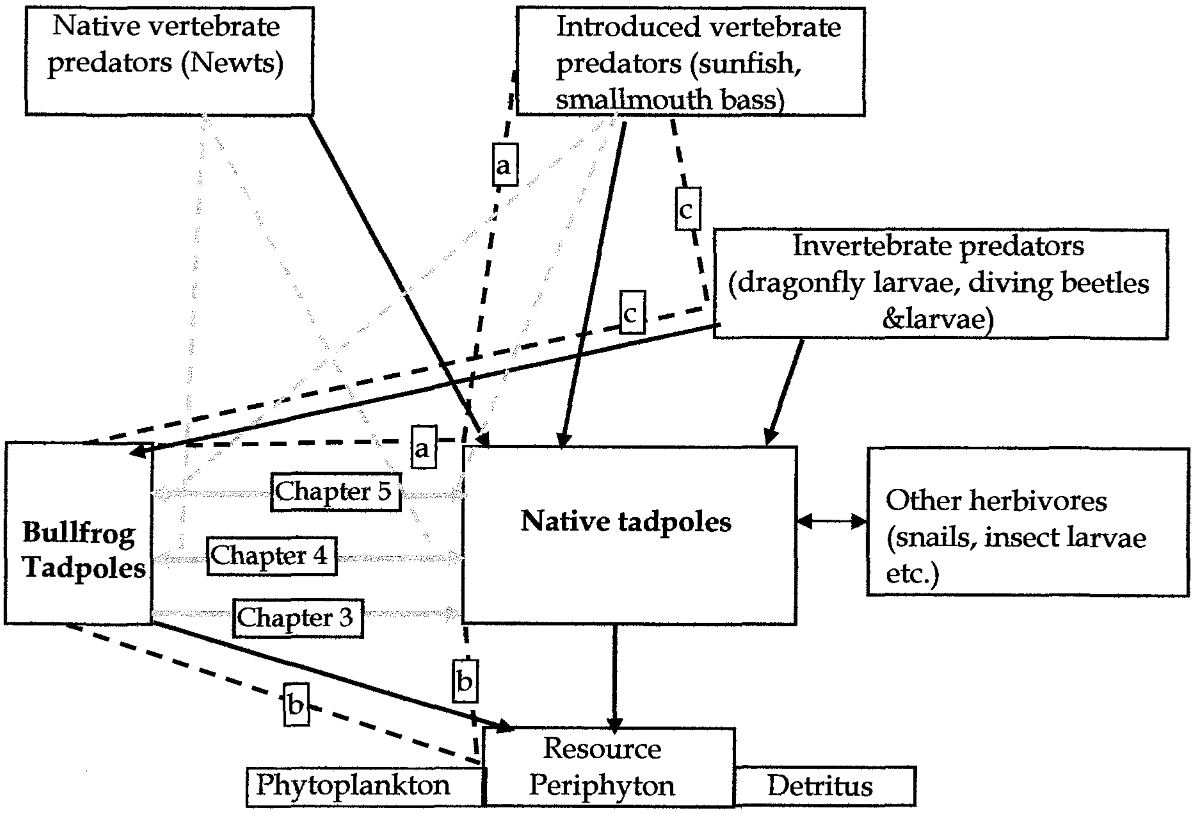
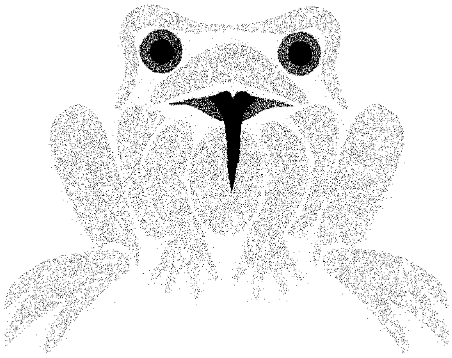


Figure 1.2: A partial interaction web of the introduced bullfrog tadpoles and the native community within which they have integrated. Solid lines indicate known or hypothesized direct effects. Arrows point to the organisms that are negatively impacted by the interaction. Labelled dashed lines indicate known indirect effects. (**a**) Competition from bullfrog tadpoles causes native red-legged tadpoles to shift habitat use to deeper water where they are more vulnerable to predation from introduced smallmouth bass (Kiesecker and Blaustein, 1998). This effect is magnified in human modified habitats where resources are clumped (Kiesecker et al. 2001). (**b**) Grazing pressure from introduced bullfrogs changes the species composition of the periphyton algae. This decreases food quality for the native tadpoles, decreasing their growth rates (Kupferberg, 1997). (**c**) Invertebrate predators, in particular dragonfly larvae, strongly limit the abundance of bullfrog tadpoles. Introduced sunfish decrease the number of dragonfly larvae and so indirectly facilitate the expansion of bullfrog tadpole numbers (Adams et al. 2003). The lines in grey graphically represent the three thesis chapters that examine interactions between bullfrog tadpoles and native tadpoles.

CHAPTER 2



HISTORY, DISTRIBUTION, AND NATURAL HISTORY OF BULLFROG POPULATIONS (*RANA CATESBEIANA*) IN BRITISH COLUMBIA

Abstract

The American bullfrog (*Rana catesbeiana)* was introduced to British Columbia (BC) in the 1930's to stock frog farms which eventually failed and the stocks were released into the wild. Current populations are restricted to southwestern British Columbia, close to putative centres of introduction, except for an isolated population in a town in the southern interior, Osoyoos. The ecology of bullfrog populations in British Columbia is structured by seasonal temperature patterns, as it is in their native range in eastern North America. Bullfrogs emerged from hibernation in late April or early May when water temperatures were around 10° C. Breeding choruses were fully developed in June when water temperatures reached 15° C and air temperatures peaked over 20° C. Eggs were laid from mid-June to mid July when the mean water temperature was approximately 20° C. Mean egg mass size was 13,014 ± 7,296 eggs (mean ± SD). Tadpoles hatched in 3 to 5 days and over-wintered the first year as tadpoles. Approximately 68% of the tadpoles metamorphosed at the end of the following summer but the remaining spent a second winter in the pond. Males reached sexual maturity two years after metamorphosis. Bullfrog population density in British Columbia varied from 9.9×10^{-4} frogs/m^2 to 5.3×10^{-2}, which is similar to that in their native range. Terrestrial insects formed the largest prey group of bullfrogs <150 grams, while frogs were the major food item of larger bullfrogs. Unlike many species that exhibit marked divergence in ecology and population structure when introduced to new habitats, bullfrog populations in British Columbia were similar to those in the northern parts of their native range.

Introduction

The American bullfrog (*Rana catesbeiana*) is a common and widely distributed species in eastern North America, ranging from Nova Scotia south to central Florida and westward across the Great Plains (Stebbins 1985, Bury and Whelan 1986). As the largest frog on the continent, it has been hunted for its meaty legs throughout its native range (Bury and Whelan 1986, Berril et al. 1991). Over the past century, bullfrog farming has also been attempted around the world to meet the increasing demand for frog legs. Escaped and released bullfrogs from these farms have now established feral populations in western North America, South America, Europe, Japan and the Caribbean (Mahon and Aiken 1977, Green and Campbell 1992, Stumpel 1992, Banks et al. 2003, Marunouchi et al. 2003). Throughout their introduced range, bullfrogs are thought to have a negative effect on native fauna (Moyle 1973, Hecnar and M'Closkey 1996), and recently there have been studies quantifying these impacts (Hayes and Jennings 1986, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001).

Awareness of the enormous economic and ecological costs of introduced species has increased in the past decades (Bartley and Subasinghe 1996, Williamson 1996, Pimentel et al. 2000), but ecological information necessary to formulate mitigation efforts is often lacking. Although bullfrogs have been recorded in British Columbia (BC) since the 1930's, there has not been a systematic study of their distribution and ecology here. In this study I document the history of bullfrog introductions in BC, and map their current distribution. I also present a description of their natural history using mark-recapture studies and field observations in southern Vancouver Island. Genetic drift due to small founder populations and adaptation to local conditions can cause introduced species to diverge in appearance, behaviour, life history characteristics and population structure. Therefore, I compare the ecology of bullfrogs in BC to that in their native range in order to assess significant differences between the two regions.

Methods

The history of bullfrog introductions was deduced from published reports, press releases about early frog farming enterprises, and interviews with local naturalists. To map the current distribution of bullfrogs, I requested information from naturalists, provincial biologists, and natural history groups through mail-in-surveys and through requests in the print, radio and television media. I also carried out breeding call surveys on southern Vancouver Island and the Gulf Islands. The yearly rate of bullfrog range expansion was estimated from field surveys in the Greater Victoria area.

Data on breeding phenology, tadpole and frog size, growth and population structure was gathered from populations in the Greater Victoria area. Water temperatures were recorded using data loggers (HOBO-TEMP, Onset Computer Corporation) in three ponds. Mean air temperature was that recorded by Environment Canada at the Victoria International Airport. Number of eggs in an egg mass was estimated by counting eggs within randomly placed 2.5 cm^2 quadrats and extrapolating over the area of the egg mass. Tadpoles were sampled using minnow traps and hand nets from three ponds to estimate size and development (Gosner 1960).

Growth rate and population size was estimated from Capture-Mark-Recapture (CMR) studies conducted in four ponds at increasing distance from the putative centre of introduction. Beaver and Copley Ponds were at the centre of the range and Trevlac Pond and Prior Lake were 4 km and 6.5 km away respectively. The four ponds differed in size (Beaver Pond- 3340 m^2, Copley Pond- 255 m^2, Trevlac Pond- 29,600 m^2, Prior Lake - 59,200m^2). I captured frogs from 1998 to 2003 in Copley Pond, 1999 to 2003 in Beaver and Trevlac Ponds, and 1999 to 2002 in Prior Lake. A total of 387 frogs in Beaver Pond, 59 in Copley Pond, 226 in Trevlac Pond, and 549 in Prior Lake were marked. There was a minimum of three capture occasions each year, except for 2003, when there was only one recapture occasion.

Sex of the frogs was determined based on the presence of secondary sexual characteristics, such as enlarged tympanum, yellow throat colouration and swollen nuptial pads in males. In the absence of these, frogs were classified as female. This method of sex determination is thought to be reliable only for larger frogs and so frogs under 150 grams were divided into metamorphs (<30 g) and juveniles (30 to 150 g). To enable comparisons with published studies, growth rate was estimated as both increase in weight per day and increase in length per day. Population size was estimated using Jolly-Seber models implemented within the program MARK (White and Burnham 1999). Metamorphs were separated from other frogs for this analysis because during the peak metamorphic season in fall, metamorphs increase rapidly in number. They also emigrate from the natal ponds at a high rate resulting in very low recapture rates. With the exception of a few years, the sparseness of data made it unreliable to estimate population size of metamorphs.

Diet composition was summarised using stomach contents of 150 bullfrogs (metamorphs = 42, juveniles = 40, females = 26 and males = 42) culled during control efforts in southern Vancouver Island. Food items were identified mainly to Order, and percentage diet composition was calculated as the number of frogs with diet item in stomach divided by the total number of frogs in the sample.

Results and Discussion

History of bullfrog introductions in BC

Bullfrog farms were set up in the south west of British Columbia in the 1930's and 1940's (Table 1). Entrepreneurs expected the frogs to reach market size (450 to 650 g) within three years and the frog legs to sell for $1.00 to $1.75/lb (current value = $13.70 to $24.00/lb, Statistics Canada). This made frog farming a potentially lucrative venture, but there are no records of profitable frog farms (Culley 1981, Jennings and Hayes 1985, Bury and Whelan 1986, Lambert 1998). It is assumed that the frogs either escaped or were released into the wild, where they established feral populations (Carl 1945, Green 1978, Mason 1991). A secondary avenue of bullfrog introductions was through aquatic garden supply companies. These primarily imported green frogs (*Rana clamitans*) and leopard frogs (*Rana pipiens*), but on occasion also imported bullfrogs (personal communication, J. Alston-Stewart, 1999). Since I was unable to find records of frog farms after the 1940's, I assume that the extant bullfrog populations in the province are descended from source populations established more than sixty years ago.

Bullfrog Distribution

In British Columbia bullfrogs are found in the Lower Mainland (Vancouver, Langley, Richmond, Surrey, White Rock, Port Moody, and Powell River); on southeast Vancouver Island in towns from Victoria to Campbell River, in Port Alberni; and on some of the Gulf Islands (Salt Spring, Lasqueti, Texada and Pender) (Figure 1). Bullfrogs are found mainly in the southwest, an area classified as the Georgia

Depression Ecoprovince (Demarchi 1988). Only one bullfrog population has been found in the Southern Interior Ecoprovince, in Osoyoos (personal communication, S. L. Ashpole). Both these Ecoprovinces are on the leeward side of mountain ranges and are characterized by warm, dry climates (Demarchi 1988, Campbell et al. 1990). In their native range, bullfrogs are found across a broad range of climates from the continental climate of southern Ontario (cold winters, hot summers) to the semi-tropical climate of Florida. In general, they are found in lower elevations, although some populations have adapted to elevation as high as 1,900 metres above sea level (Moyle 1973, Bury and Luckenbach 1976, Bury and Whelan 1986). Thus, the restricted distribution of bullfrogs in British Columbia may be the result of the history of introductions rather than limitations imposed by climatic factors.

Although human mediated transport is the primary avenue of long distance dispersal, bullfrogs are capable of localized range expansion through migration. Newly metamorphosed bullfrogs emigrate from natal ponds only in the fall but bullfrog adults move throughout the active season (Currie and Bellis 1969, Ryan 1980). In the Greater Victoria area, bullfrogs expanded their range by an average of 2 km/year (range 1 to 5 km/year) from 1997 to 2003 (Figure 2), and solitary migrating bullfrogs were found > 3 km from previously known range limits. Of the 1675 bullfrogs marked over five years, I found only three frogs that had moved from one study site to another. Two of these were metamorphs that had dispersed over two kilometres, and one was an adult male that had moved 250 metres. Introduced bullfrogs in England dispersed no more than 600 metres in a year (Banks et al. 2003). This is similar to dispersal distances recorded in their native range (Raney 1940, Ingram and Raney 1943, Willis et al. 1956).

Under natural conditions ranid frogs move 2 to 6.5 km during dispersal (Seburn et al. 1997, Pilliod et al. 2002), but under unusual circumstances larger frogs can move up to 15 km (Marsh and Trenham 2001). Introduced cane toads (*Bufo marinus*), which are similar in size to bullfrogs, have been expanding their range in Australia at the rate of 15.1 km/year (Easteal and Floyd 1986). The rate of range expansion in this study was not uniform in all directions. It was most rapid towards the southwest where there are many small lakes and streams (Figure 2). Mature bullfrogs are restricted to permanent ponds and lakes but metamorphs and migrating bullfrogs can be found along streams and ditches (Kupferberg 1997). Bullfrogs have been shown to be capable of moving over 250 meters in a day (Raney 1940); consequently, their slower range expansion is most likely constrained by habitat requirements rather than their ability to move long distances.

Natural History

In their native habitat, bullfrogs span a wide latitudinal range and vary widely in their ecology and population structure (Willis et al. 1956). Bullfrog populations in Victoria, (48°39′ N) are at the northern limit of their distribution range in North America and, as with most amphibians, air and water temperatures determine the seasonal rhythms of emergence, breeding, and hibernation of the bullfrogs (Figure 3).

Hibernation, Emergence, and Breeding

At similar latitudes, bullfrog populations in the native range enter hibernation by late September to early October (Raney and Ingram 1941, Willis et al. 1956). In BC, due to milder weather conditions, some bullfrogs do not enter hibernation until November. In their native range bullfrogs emerge in late April or May (Ryan 1953) when water temperatures are between 13°C-17°C (Willis et al. 1956), but I recorded bullfrog emergence when water temperature was just over 10°C (Figure 3).

Although males call intermittently from early May, full breeding choruses do not develop until June, when temperatures consistently remain over 15°C (Figure 3, Willis et al. 1956, Bruneau and Magnin 1980, Ryan 1980). Breeding choruses seem to diminish in intensity when nighttime temperatures drop below 10°C even during the height of the breeding season. Males continue to call until early August. All calling males were observed in shallow water (< 1 m deep), close to shore, usually under overhanging vegetation. In their native habitat, males aggressively defend breeding territories (Emlen 1968, Howard 1978, Ryan 1980) and, although non-calling males were often found within a few metres of calling males, I rarely observed male-male aggression.

As in their native range, most egg masses were laid between mid-June and mid-July, when water temperatures were around 20°C (Viparina and Just 1975, Bruneau and Magnin 1980, Ryan 1980). However, egg masses were observed as early as the end of May and as late as the end of July. Mean egg mass size was 13,014 ± 7,296 eggs (N= 15, mean ± SD) and ranged from as small as 2,190 eggs to as large as 25,500 eggs, which is similar to egg mass sizes in the native habitat (Willis et al. 1956, Currie and Bellis 1969, Bruneau and Magnin 1980, Ryan 1980). Egg mass size is known to be related to female body size in bullfrogs (Bruneau and Magnin 1980, Howard 1981).

Tadpoles

Bullfrog eggs hatched within 3 to 5 days. By early September these tadpoles were 4.6 ± 0.9 cm long (mean ± SD,) and at Gosner Development stage 25.4 ± 0.7 (Gosner 1960). Tadpoles in BC do not attain metamorphosis within the first season. The duration of the larval period in bullfrogs varies from less than a year in the lower latitudes (Cohen and Howard 1958, Viparina and Just 1975) to over two years in the higher latitudes (Willis et al. 1956, Collins 1979). In BC, 60 to 75% of the tadpoles sampled the following May were under Gosner Developmental Stage 30 and were inferred to be the tadpoles that hatched the previous summer. The tadpoles in more advanced developmental stages (> Gosner stage 30) probably represent those that had over-wintered for a second time. At similar latitudes in the native range, bullfrog tadpoles are known to spend at least two years as tadpoles (Ryan 1953).

In general, the timing of metamorphosis depends on the size of tadpoles, growth rate, the risk of predation, and desiccation from pond drying (Collins 1979, Werner 1986, Newman 1992). Because of the need to over-winter, bullfrogs are restricted to permanent ponds with no risk of desiccation and, being both large and distasteful, predation rate on second year bullfrog tadpoles is low (Cecil and Just 1979). Therefore, timing of metamorphosis is thought to be governed by growth rate and size in this species. The size of tadpoles in BC populations (Figure 4) is similar to that observed in their native range (Viparina and Just 1975, Collins 1979). Both size and growth rate have experimentally been shown to be strongly negatively correlated to tadpole density in a number of amphibian species (Travis 1984, Werner 1994) but there are no field estimates of the relationship between population size, growth rate, and size of bullfrog tadpoles in either their native or introduced habitats.

Metamorphosis and growth

A few newly metamorphosed bullfrogs were observed throughout the summer, but hundreds emerged from the ponds between the end of July and early September. Mean metamorph size (Table 2) is similar to that recorded for bullfrogs in the native range (Raney and Ingram 1941, Ryan 1953, Collins 1979). Metamorph size in amphibians is again dependent on density during the larval period (Berven 1990, Goater 1994, Morey and Reznick 2001, Alvarez and Nicieza 2002, Altwegg 2003). Bullfrog growth rate was highest for smaller size classes and declined once sexual maturity was reached (Table 2). Both male and female bullfrogs declined in body weight during the breeding season (Figure 5) due to investment in reproductive effort (Shirose et al. 1993). The patterns of growth and estimated growth rates are within the range of growth rates observed for bullfrogs in their native habitats (Raney and Ingram 1941, Ryan 1953, Schroeder and Baskett 1968, Bruneau and Magnin 1980, Howard 1981, Shirose et al. 1993, Werner et al. 1995).

Although some males exhibited secondary sexual characteristics when they weighed as little as 70 g, the method of sex determination using external characters alone is reliable only at larger sizes. This study agrees with studies in the native range which show that bullfrogs attain sexual maturity between 10 cm and 12.5 cm snout vent length and 150 g (Figure 5, Ryan 1953, Willis et al. 1956, Schroeder and Baskett 1968, Shirose et al. 1993). In their native range, some bullfrog populations are sexually dimorphic while others are not (Durham and Bennett 1963, Schroeder and Baskett 1968, Howard 1981, Shirose et al. 1993). Overall, male and female bullfrogs in our populations were similar in size and growth rate (Figure 5, Table 2), but the age structure of the populations is unknown.

Estimates of time to sexual maturity range from as long as 4 to 5 years post-transformation for females in central Ontario and Quebec (Bruneau and Magnin 1980, Shirose et al. 1993) to two years post-transformation in more southerly populations (Raney and Ingram 1941, Ryan 1953, Schroeder and Baskett 1968). From individuals that were marked as metamorphs and later recaptured and from estimated growth rates, I estimate that male bullfrogs reach sexual maturity approximately two years post-metamorphic transformation. Sexual maturity in females cannot be determined by external features and so the time to female sexual maturity in BC populations is unknown. Female bullfrogs are thought to delay sexual maturity for one to two years longer than males because of the high costs involved in egg maturation and increased risks of predation when gravid (Howard 1981, Shirose et al. 1993).

Population Size

It has been suggested that organisms reach much higher densities in their introduced range compared to their native range (Lampo and De Leo 1998). Bullfrog tadpole density in Copley Pond was estimated to be as high as 106 ± 52 tadpoles/m^3 (mean ± SE), using Capture-Mark-Recapture methods (tadpoles marked=2344). The density of tadpoles is extremely variable between ponds and even within a pond (Turnipseed and Altig 1975, Caldwell et al. 1980). Therefore, making meaningful comparison between the introduced and native habitats is not possible.

In the terrestrial phase, bullfrogs can attain densities close to 100/m^2 in some areas of California where they have been introduced (Cohen and Howard 1958). Post--metamorphic population densities in our study areas were much lower, even during July and August when large numbers of metamorphs are added to the population (Table 3). Within each pond population density varied among years and this variation was not synchronized among the four study ponds (Table 3). Prior Lake, which is furthest away from the centre of introduction, had a lower bullfrog population density than the other three ponds but it is unclear whether this is due to distance from the centre of introduction, time since colonization, or some other unknown habitat feature. Estimated bullfrog population densities in the native range varied from 0.14 frogs/m^2 (Currie and Bellis 1969) to as low as 4.2×10^{-4} frogs/m^2 (Shirose et al. 1993). The estimates from the four locations in Victoria fall within this natural range of population densities (Table 3).

Diet

Bullfrogs are generalist sit-and-wait predators with a diet that includes a variety of invertebrate and vertebrate taxa (Bury and Whelan 1986). Of the 150 frogs collected only 6 recently metamorphosed frogs and 7 breeding males had empty stomachs. As expected, size had a strong influence on the diets of bullfrogs (Bruneau and Magnin 1980). The diet of metamorphs was dominated by small terrestrial insects (43% wasps, 28% beetles, 23% aphids). Juveniles consumed larger invertebrates but again the diet was dominated by terrestrial insects (63% wasps, 40% beetles, 25% odonates, 13% aphids). Some of the larger juveniles (10%) consumed vertebrates including two frogs, one newt, and a small rodent. Bullfrog adults eat large prey such as crayfish, frogs, snakes, and birds. Forty six percent of the adult females and 43% of the adult male bullfrogs had frog remains in their stomach. In their native range, adult bullfrogs consume mainly green frogs (*Rana clamitans*) (Werner et al. 1995), but, in our sample, almost all the frogs consumed were bullfrogs. This probably reflects the very low number of native frogs in areas where bullfrogs are well established (Moyle 1973). Given that bullfrogs are generalist predators, it is not surprising that the diet of BC bullfrogs is similar to that observed in the native range (Raney and Ingram 1941, Stewart and Sandison 1972, Bruneau and Magnin 1980, Bury and Whelan 1986, Werner et al. 1995).

In summary, bullfrog populations in British Colombia are found in the southwestern part of the province, not far from putative centres of introduction. Populations on southern Vancouver Island have been expanding their range rapidly over the past decade, almost 60 years after they were first introduced into this area. Either because initial introduced populations were large minimizing effects of genetic drift and/or because of similarity in habitat, the population ecology of bullfrogs on southern Vancouver Island is similar to that of populations in the northern parts of their native range in eastern North America.

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Table 1: Dates and locations of documented bullfrog introductions to British Columbia, Canada.

Date	**Location**	**Population Source**	**Information Source**
1930	Victoria, Vancouver Island	Aquatic garden supply company	Personal communication, J. Alston-Stewart.
1937	White Rock	Frog farm	Newspaper article: Victoria Daily Times, June 4, 1937
Late 1930's	Powell River	Frog farm	Lambert (1998)
Late 1930's	Lasqueti Island	Frog farm	Mason (1991)
1945	Burnaby Lake, Deer Lake	Naturalized population (from frog farms in the area in 1930's)	Carl (1945)
1945	Vancouver	Frog farm	Newspaper article: Vancouver Sun, October 23, 1945
1949	Aldergrove	Frog farm	Newspaper article: Vancouver Sun, August 17, 1949 The Daily Colonist, August 21, 1949
1976	Errington, Vancouver Island	Naturalized population (from frog farms in the area in 1930's)	Green (1978)

Table 2: Size and growth rate of bullfrogs in the Greater Victoria area.

Size/Sex	**N (Size)**	**Weight (g)** Mean ±SD	**Length (cm)** Mean ±SD	**N (Growth rate)**	**Growth (g/day)** Mean ±SE	**Growth (mm/day)** Mean ±SE
Metamorphs (< 30g)	1218	16.8 ± 5.1	5.9 ± 2.2	31	0.23 ± 0.03	0.18 ± 0.02
Small Juveniles (30 g to 100 g)	368	53.9 ± 18.1	9.1 ± 3.4	62	0.46 ± 0.05	0.18 ± 0.01
Large Juveniles (100 g to 150 g)	190	126.9 ± 15.9	11.9 ± 0.7	22	0.76 ± 0.15	0.18 ± 0.03
Females (> 150 g)	113	253.2 ± 85.9	14.7 ± 1.7	23	0.09 ± 0.11	0.06 ± 0.02
Males (> 150 g)	182	261.0 ± 82.3	14.8 ± 1.4	41	0.10 ± 0.12	0.01 ± 0.02

Table 3: Population density of bullfrogs in four ponds in Victoria, from 1999 to 2002. A total of 387 frogs in Beaver Pond, 59 in Copley Pond, 226 in Trevlac Pond, and 549 in Prior Lake were marked. Population density in Trevlac Pond in 2002 could not be estimated due to low recapture rates.

Year	**Population Density** (frogs/m^2 (SE))			
	Beaver Pond	**Copley Pond**	**Trevlac Pond**	**Prior Lake**
1999	3.4×10^{-2} (1.7×10^{-2})	3.9×10^{-2} (6.8×10^{-3})	2.8×10^{-3} (1.3×10^{-3})	1.4×10^{-3} (2.8×10^{-4})
2000	1.7×10^{-2} (4.1×10^{-3})	5.3×10^{-2} (3.9×10^{-3})	2.9×10^{-3} (1.5×10^{-3})	6.7×10^{-4} (1.5×10^{-4})
2001	2.8×10^{-2} (9.7×10^{-3})	3.0×10^{-2} (8.9×10^{-3})	3.0×10^{-3} (1.4×10^{-3})	4.1×10^{-4} (1.1×10^{-4})
2002	1.3×10^{-2} (4.2×10^{-3})	3.6×10^{-2} (6.1×10^{-3})		9.9×10^{-4} (6.1×10^{-4})
Mean (SD)	2.3×10^{-2} (1.0×10^{-2})	3.9×10^{-2} (9.8×10^{-3})	2.9×10^{-3} (1.1×10^{-4})	8.8×10^{-4} (4.4×10^{-4})
Metamorph	7.1×10^{-2} (3.7×10^{-3})		1.6×10^{-2} (1.8×10^{-3})	7.1×10^{-3} (5.6×10^{-3})

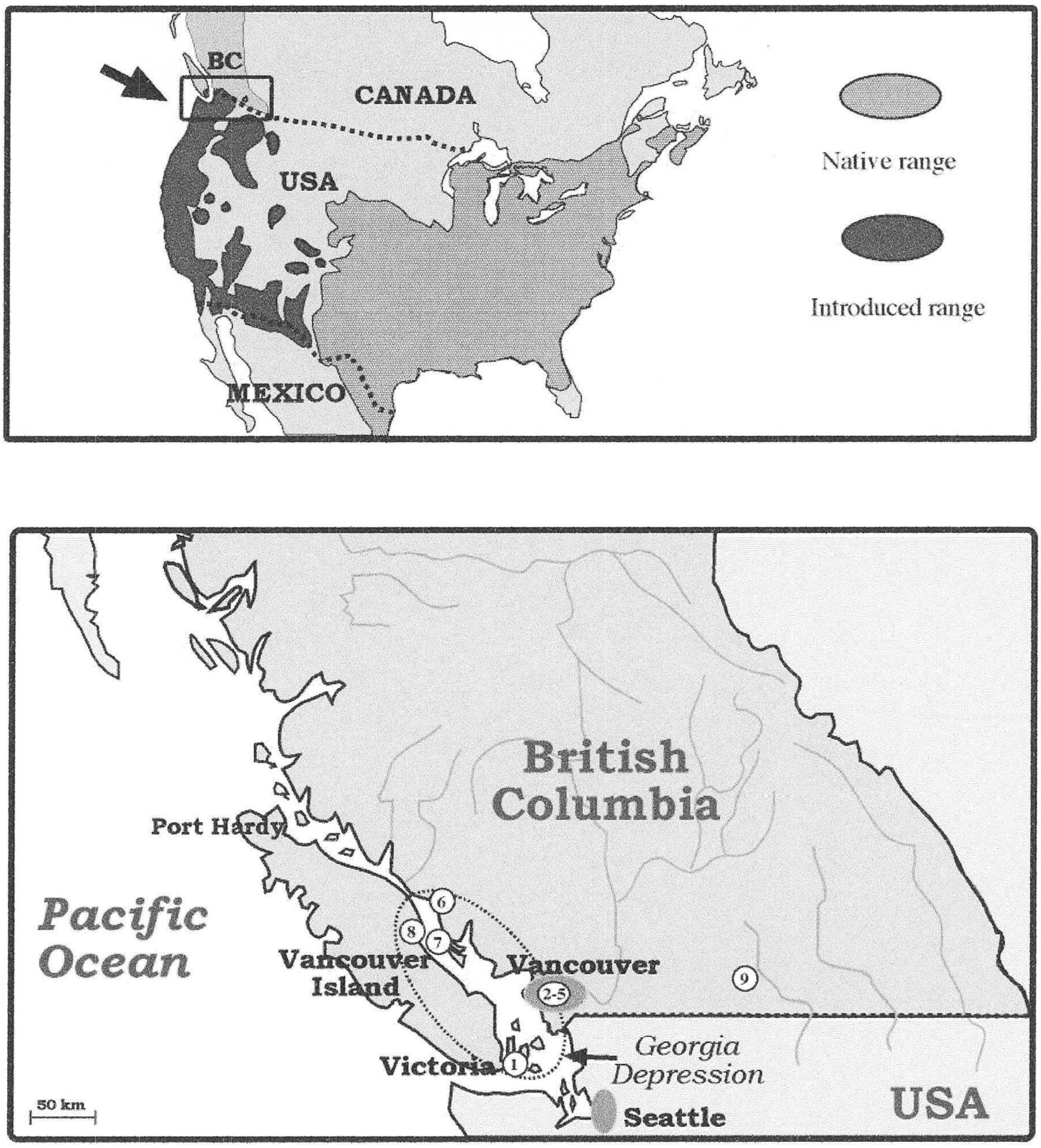


Figure 1: Native and introduced range of bullfrogs in North America, with detailed distribution in British Columbia. The numbers indicate bullfrog populations 1. Victoria 2. Vancouver 3. Surrey 4. Port Moody 5. Richmond 6. Powell River 7. Lasqueti and Texada Island 8. Campbell River 9. Osoyoos.

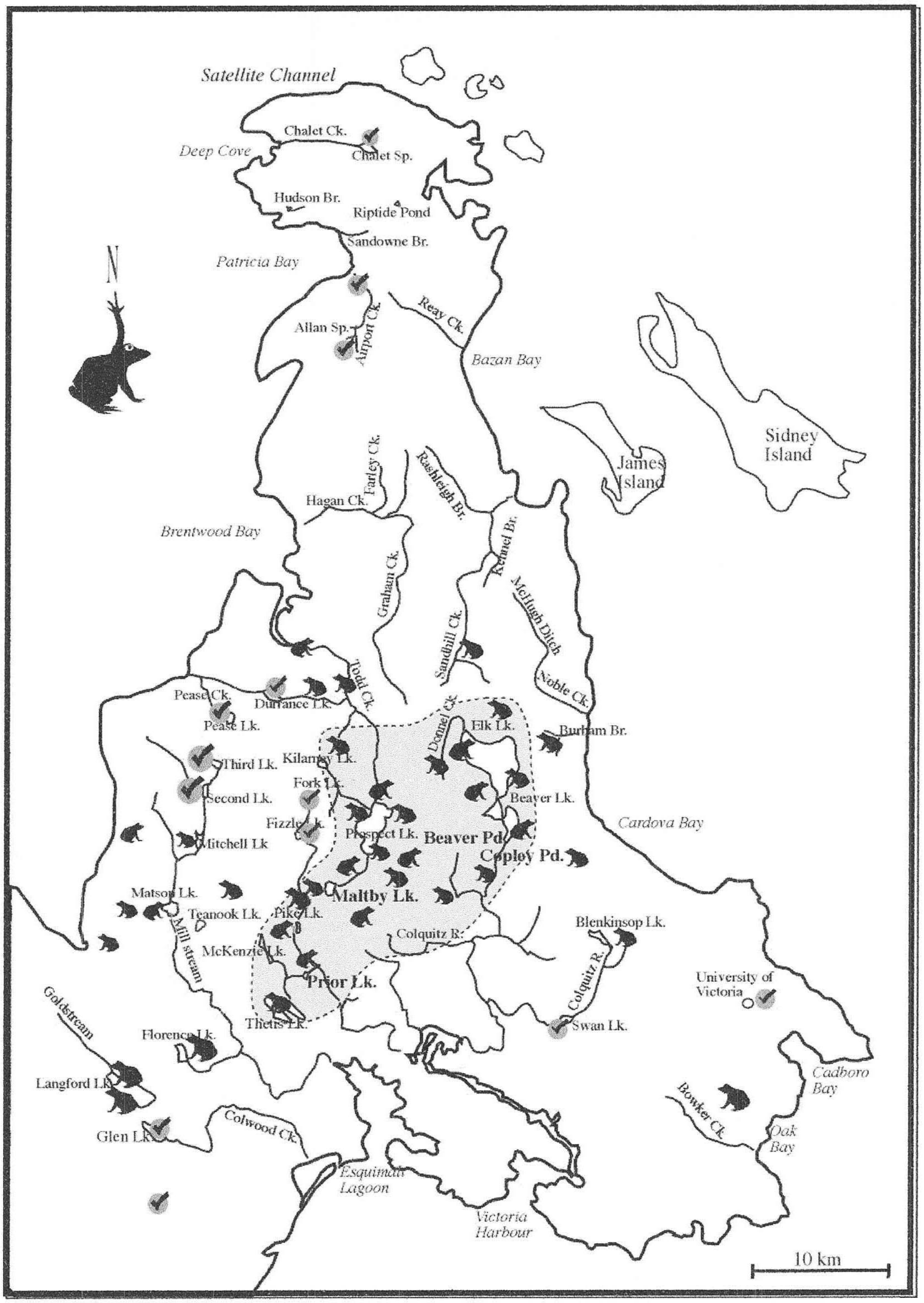


Figure 2: Distribution of bullfrogs in the Greater Victoria area. The grey area indicates bullfrog range in 1997. The frog icons indicate colonization by bullfrogs since 1997. Check marks indicate lakes not colonized by bullfrogs or where bullfrogs have been successfully eradicated.

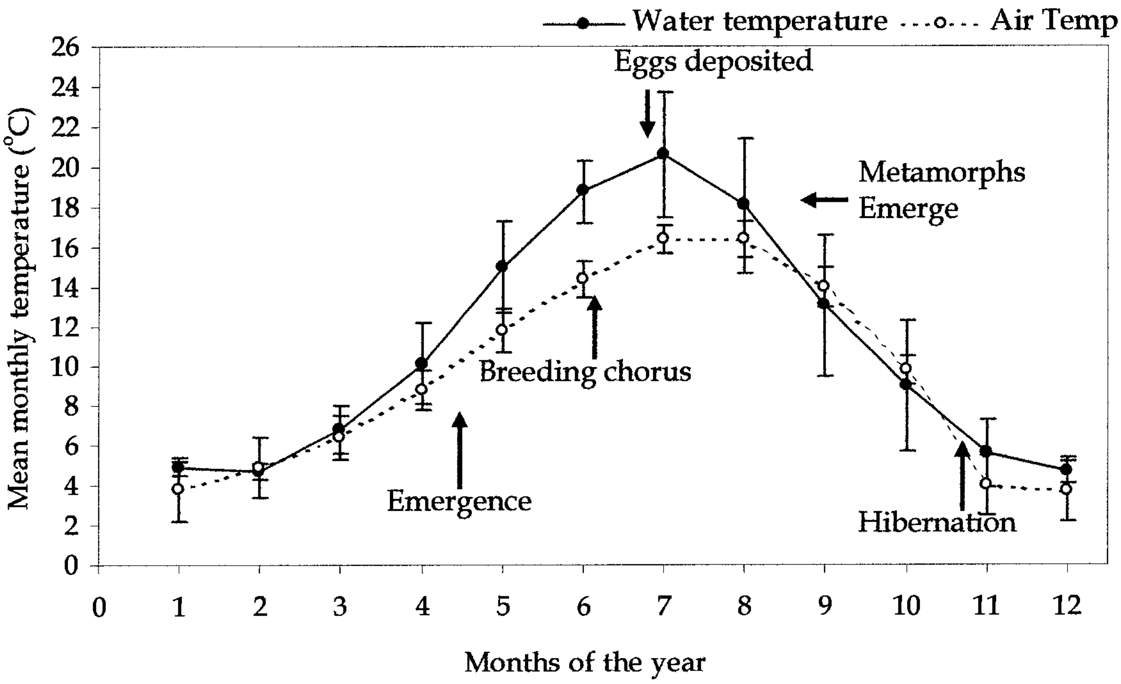


Figure 3: Phenology of bullfrog populations in relation to mean water and air temperature on southern Vancouver Island.

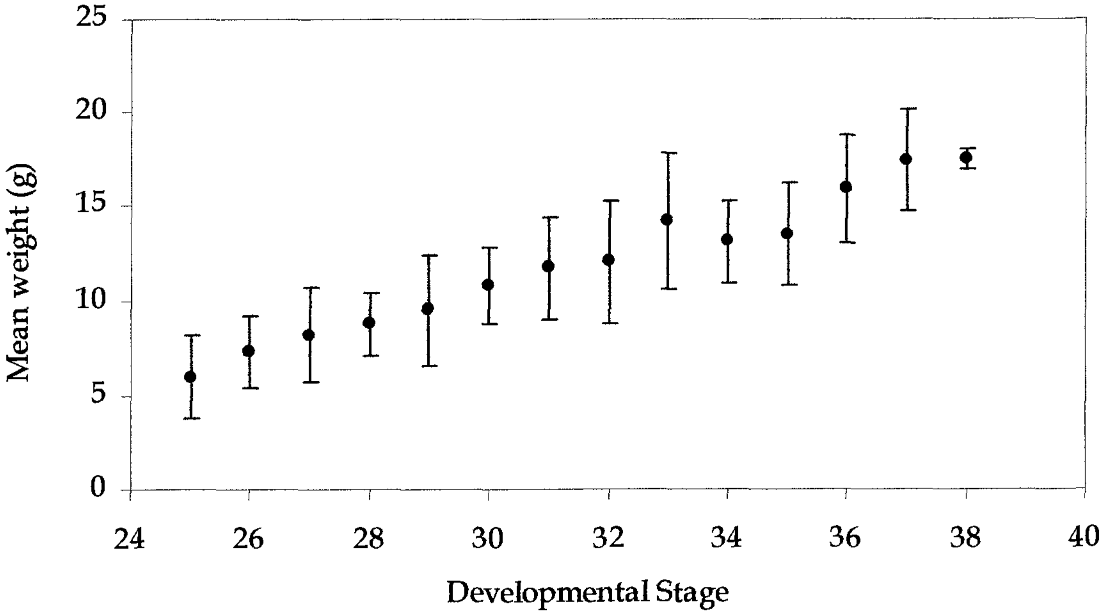


Figure 4: Mean weight of bullfrog tadpoles against Gosner Development stage (N=299). Samples were collected from southern Vancouver Island.

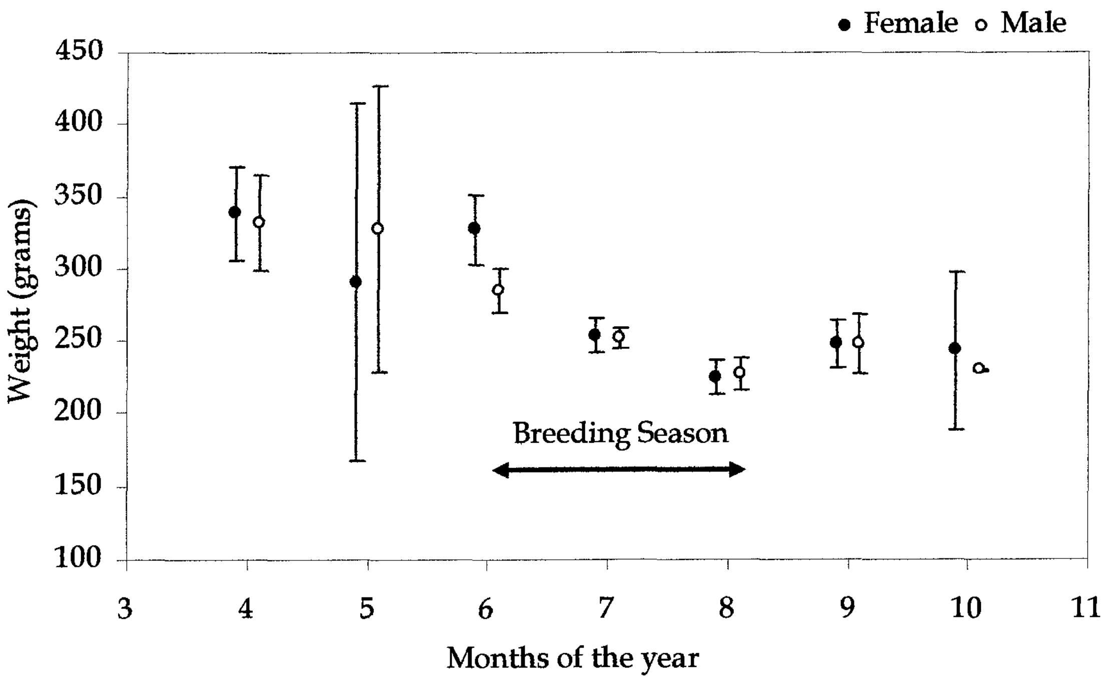


Figure 5: Mean weight (± SD) of female (N=113) and male (N=182) bullfrogs over the active season. The sexes do not differ in mean body weight. Both sexes decreased in body weight through the breeding season.

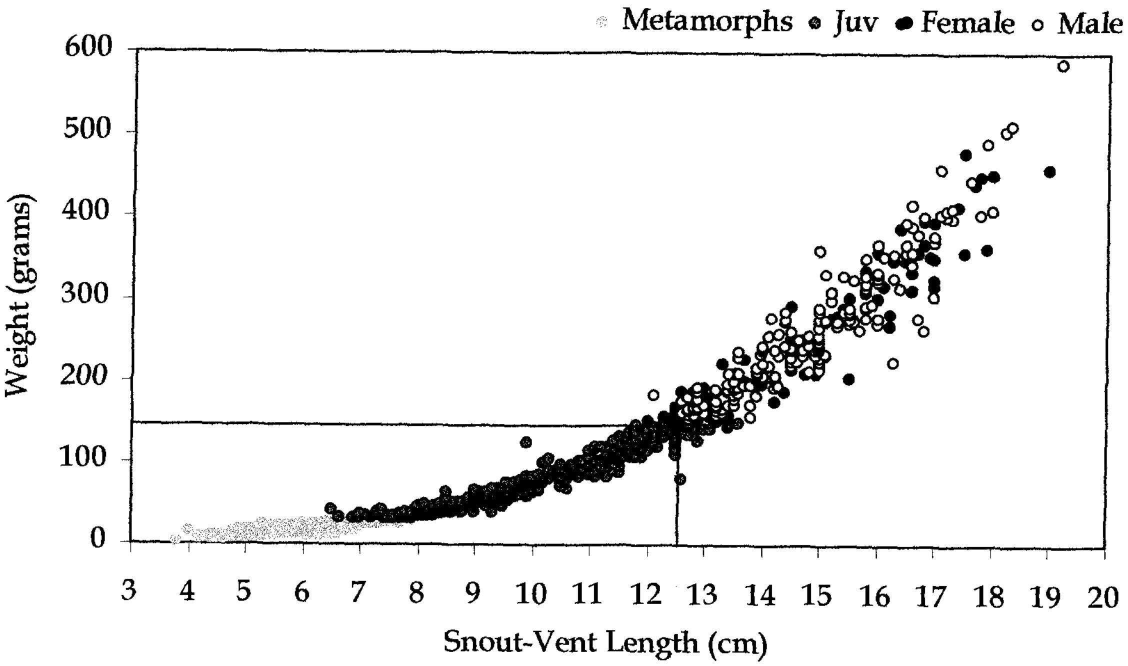
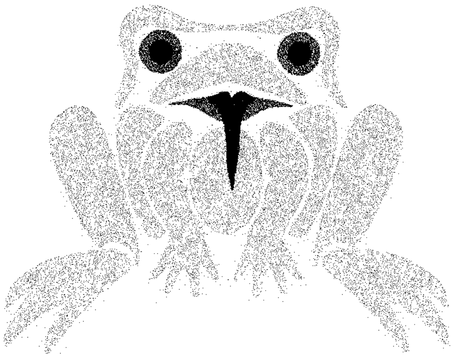


Figure 6: Weight of bullfrogs against snout-vent length. Frogs over 150 grams were classified as adults based on the reliable presence of secondary sexual characters.

CHAPTER 3



FACTORS INFLUENCING THE DAILY SURVIVAL RATES OF PACIFIC TREEFROG TADPOLES (*HYLA REGILLA*) UNDER NATURAL CONDITIONS

Abstract

Numerous theories and experimental studies have identified factors influencing the survival of tadpoles but few have been assessed under field conditions. In this study, I obtained the first estimates of daily survival rates of tadpoles under field conditions using Capture-Mark-Recapture (CMR) methods and quantified the effects of abiotic and biotic factors on this survival rate. Specifically, I assessed the effect of temperature, intra-specific density, and the presence of introduced bullfrogs (*Rana catesbeiana*) on the survival rate of Pacific treefrog (*Hyla regilla*) tadpoles in Victoria, British Columbia, Canada. Daily survival rates of tadpoles were relatively constant within a season and between years. Among ponds, daily survival rates varied from a high of 95.4% to a low of 87.9%. Temperature and intra-specific density interacted strongly to affect survival rates. At low densities, survival rates increased with temperature, but at high densities, survival decreased with increasing temperature. It was not possible to detect the effect of introduced bullfrogs over the variation accounted for by differences in temperature and intra-specific density in the ponds.

Introduction

Evidence of worldwide amphibian declines (Houlahan et al. 2000) has made it essential to develop a comprehensive understanding of the factors governing their population dynamics. Numerous factors have been implicated in amphibian declines (Alford and Richards 1999), and many of these factors affect only one or two of the life-history stages. A major impediment to assessing the effects of these factors is the difficulty in estimating growth and survival rates of each life-history stage in the field. So it has become increasingly urgent to obtain stage-specific survival and growth estimates, assess how these are affected by environmental change and ultimately to assess how these changes affect population growth rate (λ) (Biek et al. 2002).

Among the amphibian life stages examined, tadpoles have been extensively studied and have been shown to suffer reduced survival and growth due to habitat modification (Adams 2000, Davidson et al. 2001, Kiesecker et al. 2001), chemical contaminants (Russel et al. 1995, Davidson et al. 2002, Hayes et al. 2002), UV-B radiation (Anzalone et al. 1998, Blaustein et al. 1998), introduced predators (Fisher and Shaffer 1995, Knapp and Matthews 2000b), and introduced competitors (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999). Generally, the effects of these factors are studied in the laboratory, in field enclosures, or in artificial ponds. This is due to the logistical difficulty of quantifying the effects under free ranging field conditions. Recently concerns have been raised that the venue of the experiment may influence the outcome (Skelly and Kiesecker 2001), particularly in experiments with larval amphibians.

In this study, I obtained the first estimates of daily survival rate of tadpoles under field conditions and examined the temporal and spatial variation in these rates caused by biotic and abiotic factors. This was possible due to the development of new safe techniques for marking tadpoles (Anholt et al. 1998) and sophisticated statistical methods for reliable survival rate estimation from Capture-Mark-Recapture (CMR) data (Lebreton et al., 1992). While the main focus of this paper is on survival estimation, I also present data on tadpole size and development rate in these ponds because theoretical models and experimental studies suggest the three variables are correlated (Werner 1986, Ludwig and Rowe 1990, Werner and Anholt 1993, Abrams and Rowe 1996).

Survival rate of Pacific treefrog (*Hyla regilla*) tadpoles was estimated in natural ponds in Victoria, British Columbia in the spring of 1998, 1999, and 2001. I examined the temporal variability in tadpole survival rate within a season and also among years. It is known that mortality of tadpoles decreases with increasing size as they become less vulnerable to gape-limited predators (Travis et al. 1985, Semlitsch and Gibbons 1988, Semlitsch 1993, Puttlitz et al. 1999). One would expect survival rates of tadpoles to increase as the season progresses and tadpoles get larger. However, there is very little data on the changes in the identity and abundance of predators as the season progresses and how this might affect tadpole survival.

First, I examined whether daily survival rates of tadpoles vary within the season. The number of metamorphs leaving a pond has been shown to vary by over an order of magnitude from year to year (Berven 1990, Pechmann et al. 1991). This may be due to either recruitment or tadpole survival. By comparing data over the years for each pond, I was able to assess whether differences in the size of the metamorphic cohort was caused by variable tadpole survival rates between years.

Second, I examined spatial variation in survival rate in five ponds in 2001 and assessed the effect of temperature and intra-specific density on tadpole survival and growth. Although temperature has been shown to have strong effects on growth rate and size at metamorphosis (Harkey and Semlitsch 1988, Newman 1998, Blouin and Brown 2000, Alvarez and Nicieza 2002), its effect on survival rate is not well understood (but see Harkey and Semlitsch 1988). In experimental studies, tadpoles have been shown to decrease performance in response to intra-specific competition (Gurevitch et al. 1992, Werner 1994, Alford 1999, Skelly and Kiesecker 2001). However, more recent studies have questioned the relevance of these density effects under natural conditions (Loman 2001).

Finally, the presence of American bullfrogs (*Rana catesbeiana*) has been associated with population declines in native amphibians in western North America (Moyle 1973, Fisher and Shaffer 1995). Direct negative effects on the growth and survival of native amphibians have also been documented in experimental studies (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001). I examined whether impacts of the introduced bullfrog can be detected over the natural variation in tadpole survival and growth among ponds.

Methods

The Study Species

Pacific treefrogs are common and widely distributed throughout the Pacific Northwest of North America. In British Columbia, their breeding season extends from early March to the end of June, and tadpoles are most abundant from May to June. They start to metamorphose and leave the ponds by mid June.

Bullfrogs were introduced into British Columbia in the 1930's but did not increase in abundance or range until the 1990's. They do not breed until June and tadpoles spend at least one winter in the pond prior to metamorphosis. Consequently, when the Pacific treefrog tadpoles hatch in spring they face competition from second-year bullfrog tadpoles that have over-wintered in the ponds.

Field Sites

Trevlac Pond: It is a permanent pond, approximately 150 x 200 m with many small islands that divide it into channels. Except for a few deep channels, it is less than a metre deep in most areas. The shoreline of the pond is densely vegetated with cattails (*Typha latifolia*), hardhack (*Spiraea douglasii*), and willow (*Salix* spp.). Treefrog tadpoles are found mostly in the shallow water amongst the cattails. I sampled an area of approximately 44 m^2 in 1998 and 1999 and 22 m^2 in 2001. Records indicate that bullfrogs invaded this pond in 1995.

Kerfoot Pond: It is also a permanent pond, approximately 50 x 100 m, and 5 metres deep on average. However, treefrog tadpoles are only found on a shallow (< 1 m deep) ledge, densely vegetated with yellow iris (*Iris pseudoacorus*) and cattails. I sampled an area of approximately 56 m^2 in 1999 and 49 m^2 in 2001. Bullfrogs have not yet invaded this pond.

Alpaca Pond: This is an irrigation pond set in the midst of a grazing meadow. It is also a permanent pond, approximately 40 x 10 m, and 0.75 metres deep on average. The pond edge is a gentle grassy slope extending into the shallows. This is where the tadpoles congregate. I sampled an area of approximately 57 m^2. Bullfrogs have been breeding in this pond since 1997.

Willow Pond: It is also a permanent irrigation pond. It is approximately 10 x 5 m, and 0.75 metres deep. The shoreline vegetation is a mix of willow, cattails and rushes (*Juncus* sp.). I sampled an area of approximately 19 m^2. Bullfrogs arrived here at the same time as at Alpaca Pond.

Cindy Pond: It is a shallow, temporary pond set in the midst a meadow. It is approximately 10 x 5 m, and < 0.5 metres deep. Large clumps of rushes were distributed all through the pond. I sampled an area of approximately 24 m^2. Being a temporary pond, it had no over-wintering bullfrog tadpoles.

Temperatures in the ponds were recorded using temperature loggers (HOBO-TEMP, Onset Computer Corporation). The relative density of tadpoles in each pond was assessed using capture-per-unit-effort as total number of tadpoles captured divided by area of capture and capture time (Table 1). Population size was also estimated from Capture-Mark-Recapture data using Jolly-Seber models implemented within the program MARK (Seber 1986, White and Burnham 1999). This was used to calculate absolute density (Table 1). The predator complex in the four permanent ponds was similar and consisted of predaceous diving beetle larvae and adults (Dytiscidae), dragonfly larvae (Aeshnidae), roughskin newt (*Taricha granulosa)* larvae and adults, and introduced pumpkinseed sunfish (*Lepomis gibbosus*). The only temporary pond, Cindy Pond, did not have newts or sunfish, but was otherwise similar.

Capture-Mark-Recapture (CMR) methods

The pilot study of 1998 had only four capture occasions and was conducted to assess the capture effort necessary for adequate levels of precision in survival rate estimation. There were seven capture occasions in 1999 and 2001, with much higher numbers of marked tadpoles (Table 1). In 1998 and the first two intervals of 1999 there was only one day between consecutive days of capture. In the four later intervals of 1999 there were two days between consecutive days of capture and in 2001 there were three days between capture sessions. The total number of tadpoles captured varied between years and between ponds (Table 1). By the last day of capture, approximately 50% of all the tadpoles caught were marked, except in Alpaca Pond where percent recaptured remained at 20%.

In each pond I selected a discrete, shallow patch of habitat and captured tadpoles using dip-nets. Migration to and from these patches was found to be negligible (*unpublished data*). Tadpoles were brought into the laboratory for marking and were returned to the same area the following morning. The tadpoles were anaesthetized using a 0.02% solution of tricaine methanesulfonate (MS-222) and were injected with a biologically inert fluorescent elastomere paint (Northwest Marine Technologies Inc., Washington, USA) under the skin, at the point where the tail fin attaches dorsally to the body of the tadpole (Anholt et al. 1998). Tadpoles were measured, weighed, and staged immediately after the marking procedure (Gosner 1960). Only tadpoles that were at least 8 mm in snout-vent length and Gosner development Stage $\geq$ 26 were marked. Tadpoles captured on a given day were batch marked with the same colour of elastomere. Individual marks are not possible for this many tadpoles. Tadpole mortality and mark loss were less than 1% following the procedure (*personal observation*). Animals damaged during capture or marking (<<1%) were euthanized with an overdose of MS-222. Marked tadpoles do not suffer increased risk of predation compared to unmarked tadpoles (Anholt et al. 1998). Multiple marking of tadpoles did not affect their chances of surviving the procedure or their growth rate in captivity (*unpublished data*).

Field Enclosures

Field enclosures were used to estimate development rate of tadpoles, as the CMR tadpoles could not be individually marked. The enclosures were constructed of a metal frame with fibreglass mesh sides and top. The metal frame was hammered into the substrate to prevent migration into and out of the enclosure. In 1999, there were three enclosures (0.2 m^2) in each pond, stocked with 10 tadpoles in Kerfoot Pond and 20 tadpoles in Trevlac Pond. In 2001, there were two enclosures (0.5 m^2) in each pond, and each enclosure was stocked with 10 tadpoles. Initial densities were similar to that observed in the field as well as to those used in other tadpole enclosure experiments in the Pacific Northwest (Kupferberg 1997, Adams 2000). Differential mortality in the enclosures changed the density as the experiment progressed. Prior to stocking, the enclosures were cleared of all other tadpoles, insect predators, fish, and salamanders.

Every week to ten days the tadpoles were measured, weighed, and their development stage recorded.

Data analysis

Survival: Survival and recapture probabilities were estimated from the CMR data using maximum likelihood methods implemented in the software program MARK (White and Burnham 1999). Lebreton et al. (1992) provide a comprehensive introduction to CMR statistics. The data from each year were analyzed separately because the recapture intervals differed between years. The starting point for model selection was the Cormack-Jolly-Seber (CJS) model which included time dependence for both survival and recapture probabilities (Lebreton et al. 1992). Simpler alternative models such as constant survival and recapture models, and those based on biological information (covariates: density, temperature and presence of bullfrogs) were also constructed. Selection among these models was based on sample-size adjusted Akaike's Information Criterion (AIC_c) and relative model fit was assessed using AIC weights (Burnham and Anderson 2002). I used Analysis of Deviance (ANODEV) to partition differences in models' log-likelihoods (Skalski et al. 1993) and to estimate the amount of deviance explained by the various reduced and covariate models (Frederiksen and Bregnballe 2000).

The assumptions of CMR analysis are those of equal probability of survival and recapture among individuals in a group within a recapture interval (t). These assumptions were tested for the starting CJS model of each data set using bootstrap Goodness-of-fit analysis with 500 replicates. This analysis showed that data from Alpaca, Cindy and Trevlac Ponds in 2001 showed slight deviation from the expected binomial error distribution. The lack of a regular pattern of violations in Test 2 and 3 in program RELEASE indicates that these deviations are not due to systematic bias, either biological or sampling (Burnham et al. 1987). The over-dispersion could have been due to slight variation in survival and recapture probabilities of tadpoles of different sizes and development stages. It is not possible to model this variation using my data because the tadpoles are not individually marked. Consequently, in these cases I used the over-dispersion quasi-likelihood parameter ($\hat{c}$) to adjust the AIC_c values to $QAIC_c$. The $\hat{c}$ for

Trevlac Pond was 1.29, Alpaca Pond was 1.50, and Cindy Pond 1.28. Adjusting with $\hat{c}$ did not change the rank of the models relative to each other in any case.

Development Rate: The mean development stage (Gosner 1960) of the tadpoles in each enclosure was used as the dependent variable and this was plotted against time as the independent variable to estimate tadpole development rate in each pond. I used an Analysis of Covariance (ANCOVA) to examine differences in development rate among ponds.

Size of tadpoles and metamorphs: In 1999, I recorded the snout-vent length and in 2001 the mass of the tadpoles captured for marking in each pond. Tadpoles increase in length and mass until the initiation of metamorphosis at Gosner stage 40, at which point they cease to feed and can lose up to 50% of their mass (Werner 1986). Unfortunately, only tadpoles in Alpaca, Cindy and Kerfoot ponds had reached metamorphosis at the end of the study in 2001. I compared the size of tadpoles just prior to initiation of metamorphosis (Gosner stage 39) and also at the end of metamorphosis (Gosner stage 46), using univariate Analysis of Variance (ANOVA), followed by Student-Neuman-Keuls test for differences between means (Underwood 1997).

Results

Recapture rate

Recapture rates are affected by sampling and logistical factors. Models with time dependent recapture rates fit better than models with constant recapture rates (Table 2, 3 and 4) in all cases except Alpaca Pond. In general, recapture rates increased as the season progressed (Figure 1) and may have been due to an unconscious bias towards capturing marked tadpoles.

Survival rate

Variation within a season

In 1999, the time dependent survival model had overwhelming support in both ponds (Table 2). However, the pattern of variation of the estimated survival rates (Figure 2) showed that daily survival rate decreased dramatically during interval 4 (June 10th to 13th) in Trevlac Pond, and interval 3 (June 8th to 13th) in Kerfoot Pond. Post-hoc model fitting to accommodate this decrease suggests that the survival rate during these intervals is markedly lower than the mean survival rate of the other intervals (Table 2, Post-hoc comparisons, Trevlac Pond: Model 2 versus Model 3, Kerfoot Pond: Model 1 versus Model 3). This decrease could have been correlated with aerial spraying of insecticide in the vicinity of the ponds or caused by aberrant tadpole handling or marking procedures. The anomalous survival rates during these intervals explain 69% of the time variation in Trevlac Pond and 79% of the variation in Kerfoot Pond (ANODEV). In Kerfoot Pond, the model with constant survival except for interval 3 has three times the support of the time dependent model (Table 2, Post-hoc comparison, Model 1 versus Model 2). However, in Trevlac Pond the time dependence in survival rates was not solely due to the low probability of survival in interval 4 (Table 2, Post-hoc comparison, Model 1 versus Model 2).

In 2001, the constant survival (*Model* Φ_c) model was the best-fit model in Alpaca, Kerfoot and Willow Ponds (Table 3). The time dependent (*Model* Φ_t) and constant survival models fit the data equally well in Trevlac and Cindy Ponds (Table 3). Because *Model* Φ_c fits as well or better than *Model* Φ_t in all cases except Trevlac Pond in 1999, there seems to be more support for the hypothesis of constant survival rather than variable survival of tadpoles through the season. The estimated survival rates do not show a monotonic pattern of increase or decrease that would be expected if survival were size-dependent (Figure 2). The survival rates also vary asynchronously between the ponds making it unlikely that this variation is weather related.

Variation in survival rates between years

The mean survival rates were similar between years in both ponds, if the one exceptionally low survival rate in 1999 is ignored - Trevlac Pond 0.913 ± 0.02 in 1999 compared to 0.909 ± 0.005 in 2001 and Kerfoot Pond 0.954 ± 0.02 in 1999 compared to 0.937 ± 0.004 in 2001 (mean ± SE). In the pilot study in 1998 at Trevlac Pond, the estimated mean daily survival rate was 0.861 ± 0.12.

Variation in survival rates among ponds

As survival rate varied among ponds, I examined whether density and temperature could account for these variations. This analysis is confined to the data set from 2001. I used capture-per-unit-effort (CPUE) as the surrogate variable for density of tadpoles (*see Discussion*). Both density and temperature and the interaction term between the two factors had significant effects on survival (Table 4), and this model had two and a half times the support of the more general model $\Phi_{pond}\ P_{pond\ x\ time}$. The $\Phi_{density\ x\ temperature}P_{ponds\ x\ time}$ model accounted for 99.6% of the deviance of the global model $\Phi_{ponds}\ P_{ponds\ x\ time}$. There was no support for the additive model or the models with only one of the factors.

Kerfoot Pond, with low density of tadpoles and a mean water temperature of 18.0° C, had the highest mean survival rate (Figure 3). The lowest mean daily survival rate was in Cindy and Willow Ponds due to high density in the former and low mean water temperatures in the latter. To better understand the model $\Phi_{density\ x\ temperature}P_{ponds\ xtime}$, I used density and temperature values in the observed range and the model logistic regression equation to predict survival rates (Figure 4). This simulation shows that at low tadpole densities, the mean daily survival rate increases as the mean temperature of the pond increases. This is the expected pattern based on previous experimental studies (Newman 1998). Surprisingly, the model also predicts that at high tadpole densities the daily survival rate decreases with increasing pond temperatures.

To test the accuracy of the model $\Phi_{density\ x\ temperature}P_{ponds\ xtime}$, I used the logistic regression equation derived from the data in 2001 to predict the mean daily survival rate in Trevlac and Kerfoot Ponds 1999. The model predicted survival rates that were within 2% of the observed survival rates in both ponds (Trevlac Pond: Predicted $\Phi = 0.932$ compared to Observed $\Phi = 0.913 \pm 0.02$; Kerfoot Pond: Predicted $\Phi = 0.965$ compared to Observed $\Phi = 0.954 \pm 0.02$).

Impact of bullfrogs on daily survival rate

Models that included the presence/absence of bullfrogs did not fit the data any better than the $\Phi_{density\ x\ temperature}P_{ponds\ xtime}$ model (Table 5). Given that there were only five replicate ponds, there was very limited power to detect effects of bullfrog after accounting for the variation in survival due to density, temperature, and the interaction between these two factors.

Development Rate

In 1999, development rate was marginally faster in Kerfoot Pond compared to Trevlac Pond (Figure 5, ANCOVA pond x time, $F_{1,32}$=3.43, P=0.07). In 2001, development rate again varied between ponds (ANCOVA pond x time, $F_{4,37}$ =9.71, P<0.001). The ranking of development rates was similar to that of estimated survival rates in the five ponds. Kerfoot Pond had the fastest development rate, followed by Alpaca and Trevlac ponds. Willow and Cindy Ponds that had the lowest survival rates also had slow development rates (Figure 5).

Size of tadpoles and metamorphs

In 1999, there was no difference between the ponds in the size of tadpoles prior to initiation of metamorphosis (< Gosner Stage 39) (Figure 6) and not enough of a sample size to make comparisons after initiation of metamorphosis. In 2001, at the initiation of metamorphosis (Gosner Stage 39), tadpoles in Cindy Pond were significantly smaller than the other ponds (Figure 6, ANOVA $F_{4,303}$ = 25.01, P <0.001). Only tadpoles in the three high temperature ponds (Alpaca, Cindy and Kerfoot Ponds) had completed metamorphosis by the end of the study. Metamorphs in Kerfoot Pond were significantly larger than those in Alpaca Pond, which were larger than those in Cindy Pond (Figure 6, ANOVA $F_{2,125}$=10.42, P< 0.001).

Discussion

The daily survival rate of Pacific treefrog tadpoles under field conditions was estimated with less than 1% standard error using CMR techniques. In most ponds, the daily survival rate remained relatively constant over the season and was similar between years. Comparing among ponds, the average daily survival rate of Pacific treefrog tadpoles ranged from a high of 95.4% (Kerfoot, 1999) to a low of 87.9% (Willow Pond, 2001). This variation was best explained by differences in tadpole density and average water temperature in the ponds. The effect of introduced bullfrogs, if any, was not detectable with the sample size in my study. Theoretical models have suggested potential trade-offs between survival, growth, and development rate (Wilbur and

Collins, 1973; Werner 1986). In this study, ponds with high survival rates also had rapid development rates and initiated metamorphosis at larger sizes. However, when survival rates were low, tadpoles may have been constrained from accelerating development rates as predicted by the models due to low water temperature.

A number of laboratory studies have shown that tadpole predators are size-selective and also that larger tadpoles swim faster and evade predators better (Alford 1999). I expected that daily survival rates would increase, as tadpoles grew larger and became less vulnerable to gape-limited predators (Formanowicz 1886, Richards and Bull 1990, Semlitsch 1990, Tejedo 1993). However, in this study, as in some other field studies (Herreid and Kinney 1966, Calef 1972, Riis 1991), daily survival rates generally remained constant over the season (Figure 2). In ponds in the study area, Pacific treefrog tadpoles attain a size refuge from roughskin newt larvae by about stage 28 (9 mm SVL/0.250 g) and partial refuge from other predators by about stage 34 (12mm/0.450g) (*personal observation*). They remain vulnerable to sunfish throughout their larval life. One of the reasons for the lack of the expected pattern of increasing survival rates may be that the captured cohorts were mostly < Stage 35. It is also possible that the wide range of predator sizes from invertebrate predators to pumpkinseed sunfish meant that the tadpoles did not have a size refuge (Calef 1972). Pacific treefrog tadpoles can also adjust their anti-predator responses according to their level of vulnerability to predation (Puttlitz et al. 1999). This may tend to even out size-specific mortality rates.

Survival and development rates were surprisingly similar between years in the two ponds where there was multi-year data. The estimated survival rate in Trevlac Pond was the same in 1999 and 2001 (91%) and not statistically different from the 86% (SE ± 12%) estimated during the pilot study in 1998. In Kerfoot Pond, survival estimates varied by less than 2% between 1999 and 2001 (95.4% compared to 93.7%). Similarly, the development rate was only marginally lower in both ponds in 1999 (Figure 5). This may be due to higher initial densities in the enclosures in 1999 compared to 2001. Long-term studies on larval survival conducted mainly in temporary ponds have shown large year-to-year fluctuations in the number of metamorphs that recruit into the population (Berven 1990, Pechmann and Wilbur 1994, Loman 2002). However, this study suggests that survival, growth, and development rates may be more stable over time in some permanent ponds (Adams 2000).

Density, temperature, and the interaction between the two factors, accounted for almost all the variation observed in daily survival rates between ponds. It is important to point out that while density-dependent effects on tadpole life-history traits have been extensively studied (Alford 1999), there are no standard methods to assess densities of tadpoles under field conditions. Densities are estimated using fixed time dip-net sampling, line transects, visual counts, traps, and complete counts within drop-box samplers (pipe) and are reported using various units such as number/area, number/volume, number/trap and other capture-per-unit-effort (CPUE) measures (Wilbur 1984, Skelly 1995, Adams et al. 1998). I used CPUE in the CMR survival analysis as it provided an independent assessment of the relative density of tadpoles in the five ponds. I also estimated abundance of tadpoles using the CMR data (Seber 1986). The density estimates from this method were similar to that provided by the CPUE method (Table 1) and led to identical conclusions in the CMR model fitting process. The advantage of using CPUE is the ease of implementation. CPUE measures enable density estimation in a large number of sites. The disadvantage is that CPUE measures are very sensitive to the skill level of the experimenters and therefore are not comparable between studies. Abundance estimates derived from CMR data are unbiased in this sense and are therefore comparable between studies. However, CMR abundance estimation assumes equal probabilities of capture for marked and unmarked tadpoles. The increasing recapture probability as the experiment progressed suggests that there may have been an unconscious bias toward capturing marked tadpoles (Figure 1). Similar studies in the future will benefit from an independent assessment of density such as using a drop box sampler.

Increasing intra-specific densities can decrease survival, development rate, and size at metamorphosis by depleting food supply (exploitative competition) and also by decreasing the efficiency of food gathering through physical or chemical inhibition (interference competition). It is debatable whether food can become limiting for generalist herbivores such as treefrog tadpoles under natural conditions (Licht 1974) but experimental supplementation of food has resulted in increased survival and growth in some cases (Smith 1983, Newman 1987, Adams 2000). Not much is known about physical interference competition in treefrog tadpoles and chemical inhibition has never been recorded in this species.

The best-fit model for survival rates among the ponds in 2001 predicted that at high densities the survival rates of tadpoles decrease with increasing temperature but at low densities survival rates increase with increasing temperature (Figure 4). The strong interaction between density and temperature in the determination of survival rates is probably mediated through food limitation and metabolic needs of tadpoles at various temperatures. At high densities food limitation initially causes decreased growth and progressively leads to death due to starvation. At high temperatures the basic metabolic energy requirements of tadpoles are higher (Harkey and Semlitsch 1988) and tadpoles succumb to starvation more readily than at lower temperatures. Why survival rates should increase with increasing temperatures at low tadpole densities is unclear. Perhaps, tadpoles could reach a size refuge from predation earlier because higher temperatures lead to faster development.

The Model $\Phi_{density \times \mathrm{temperature}}$ for survival rates derived from the 2001 data was able to predict survival rates that were within 2% of actual observed survival rates in Kerfoot and Trevlac Ponds in 1999. This accuracy increases the level of confidence in the validity of the model. However, these results have to be interpreted with caution as neither food availability nor predator densities, which have been shown to have strong effects, were measured directly. Also the sample did not include a pond with low temperatures and high density of tadpoles, making extrapolation of model results tentative.

The role of introduced species in the declines of amphibians in the Pacific Northwest has attracted much attention (Hayes and Jennings 1986, Kiesecker and Blaustein 1998, Knapp and Matthews 2000a, Adams et al. 2003). In mesocosms and field enclosures red-legged frog and yellow-legged frog tadpoles suffered significant decreases in survival in the presence of bullfrogs (Kiesecker and Blaustein 1997, Kupferberg 1997, Lawler et al. 1999), but Pacific treefrog tadpoles showed small or no reductions in survival (Chapter 4 and 5, Kupferberg 1997, Adams 2000). Under field conditions, I was unable to detect a decline, if any, in treefrog survival caused by bullfrogs because the effect is likely to be small, the variation due to intra-specific density and temperature large, and the sample size limited.

Models on life-history tradeoffs in tadpoles predict that, under favourable conditions, tadpoles should delay metamorphosis and grow to a maximal size (Wilbur and Collins 1973, Werner 1986). Tadpoles in Alpaca Pond and Kerfoot Pond, which had the highest survival rates, did indeed grow to almost 1 gram prior to metamorphosis (Figure 6). However, they also had the fastest development rates compared to the other ponds (Figure 5). In these ponds, development rate, survival rate and size at metamorphosis were positively correlated. These same models predict that under unfavourable conditions, tadpoles should increase development rate and initiate metamorphosis once a minimal size is reached. Tadpoles in Cindy Pond and Willow Pond, which have the lowest survival rates, also had low development rates (Figure 5). As predicted by the theories, tadpoles in Cindy Pond initiated metamorphosis at a much smaller size compared to other ponds (Figure 6). However, tadpoles in Willow Pond did not initiate metamorphosis at these small sizes.

Willow Pond had the lowest mean water temperature compared to the other ponds (Table 1). Low temperatures are known to retard tissue differentiation thereby decreasing development rates leading to larger stage specific size (Smith-Gill and Berven 1979, Alvarez and Nicieza 2002). Low temperatures are known to decrease levels of thyroid hormone and depress tissue response to this hormone, both of which delay initiation of metamorphosis (Viparina and Just 1975, Galton 1988, Harkey and Semlitsch 1988). It is possible that tadpoles are inhibited from initiating metamorphosis at the size predicted by the theoretical models because of the low water temperature of this pond.

Conclusions

The Capture-Mark-Recapture method is well suited for precisely estimating survival rates of tadpoles under field conditions and provides a convenient technique for testing life-history theories under natural conditions. As expected from numerous experimental studies, survival rates were strongly influenced by intra-specific density, but were also affected by water temperature. Correlations predicted by theoretical models between survival, growth, and development rates were partially met, but I suggest that patterns observed in the field may be influenced by water temperature. Theoretical models often assume uniform temperature among ponds but my data suggest that differences in water temperature may play a pivotal role in explaining patterns of tadpole life-history traits observed under natural conditions.

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Table1: Details of capture effort, cohort size, developmental stage, and population density in the ponds over the three years of the study.

Pond	Capture period	Mean no. captured (tads/day)	Mean dev. stage	Mean temp. (°C)	Density (CPUE) (tads/min.m^2)	Density (CMR) (tads/m^3)
1998						
Trevlac	28/5-3/6	125±48	28±4	-	-	-
1999						
Trevlac	3/6-19/6	652±162	30±3	17.7±1.9	0.06±0.02	59.5±2.8
Kerfoot	4/6-20/6	301±135	33±4	19.4±3.3	0.03±0.01	31.1±5.5
2001						
Trevlac	4/6-28/6	247±55	31±3	15.5±2.0	0.09±0.04	85.9±4.16
Kerfoot	30/5-23/6	394±71	35±4	18.4±3.1	0.06±0.02	76.6±1.6
Alpaca	29/5-22/6	526±104	34±6	18.9±3.0	0.10±0.02	114.6±8.7
Cindy	29/5-22/6	272±27	34±6	18.6±3.5	0.13±0.01	162.1±10.4
Willow	29/5-22/6	103±40	31±3	14.6±2.3	0.06±0.02	56.7±1.2

Table 2: Model selection for estimating survival (Φ) and recapture (P) probabilities in 1999. The post-hoc model fitting is to accommodate the one unusually low period of survival.

Model	**AIC$_c$**	**Δ AIC$_c$**	**AIC$_c$weight**	**N**	**Dev.**
Trevlac Pond					
1.$\Phi_t P_t$	7426.19	0.00	1.0	11	118.14
Kerfoot Pond					
1.$\Phi_t P_t$	3517.46	0.00	1.0	11	96.04
	Post-hoc Model fitting				
Trevlac Pond					
1.$\Phi_t P_t$	7426.19	0.00	0.83	11	118.14
2.$\Phi_{cexcept4th} P_t$	7429.32	3.13	0.17	8	127.30
3.$\Phi_c P_t$	7448.00	21.81	0.00	7	147.99
Kerfoot Pond					
1.$\Phi_{cexcept3rd} P_t$	3515.22	0.00	0.75	8	99.87
2.$\Phi_t P_t$	3517.46	2.24	0.25	11	96.04
3.$\Phi_c P_t$	3528.17	12.95	0.00	7	114.83

Notes: Subscripts of Φ and P indicate whether the probabilities were held constant (c) or allowed to vary with time (t). Models are arranged in descending level of support from top to bottom. AIC$_c$ is the sample size adjusted Akaike's Information Critereon, ΔAIC$_c$ is the difference between the best fit model and a particular model. AIC$_c$ weight can be interpreted as % support for a given model over the set of candidate models. N is the number of parameters in the model and 'Dev.' is model deviance.

Table 3: Model selection for estimating survival (Φ) and recapture (P) probabilities in 2001.

Model	**AIC$_c$/QAIC$_c$**	**ΔAIC$_c$/QAIC$_c$**	**AIC$_c$/QAIC$_c$ weight**	**N**	**Dev.**
Trevlac Pond ($\hat{c}$=1.29)					
$\Phi_t P_t$	2775.20	0.00	0.54	11	151.02
$\Phi_c P_t$	2779.20	0.39	0.44	7	161.97
$\Phi_c P_c$	2784.90	7.38	0.01	2	183.96
$\Phi_t P_c$	2789.70	12.17	0.00	7	177.16
Kerfoot Pond					
$\Phi_c P_t$	5607.34	0.00	0.83	7	125.53
$\Phi_t P_t$	5610.55	3.20	0.17	11	120.67
$\Phi_t P_c$	5670.43	63.09	0.00	7	188.62
$\Phi_c P_c$	5699.72	92.38	0.00	2	227.95
Alpaca Pond ($\hat{c}$=1.50)					
$\Phi_c P_c$	2659.47	0.00	0.89	2	143.58
$\Phi_c P_t$	2664.47	5.00	0.07	7	136.03
$\Phi_t P_c$	2666.58	7.11	0.03	7	139.19
$\Phi_t P_t$	2667.80	8.33	0.01	11	128.96
Cindy Pond ($\hat{c}$=1.28)					
$\Phi_c P_t$	2484.53	0.00	0.48	7	156.75
$\Phi_t P_c$	2484.72	0.19	0.44	7	157.00
$\Phi_t P_t$	2488.18	3.65	0.08	11	151.07
$\Phi_c P_c$	2504.38	19.85	0.00	2	195.04
Willow Pond					
$\Phi_c P_t$	1379.36	0.00	0.94	7	130.34
$\Phi_t P_t$	1384.86	5.50	0.06	11	127.61
$\Phi_t P_c$	1389.84	10.48	0.00	7	140.82
$\Phi_c P_c$	1402.10	22.74	0.00	2	163.24

Table 4: Model selection assessing the effect of density and temperature on daily survival rates, 2001 data.

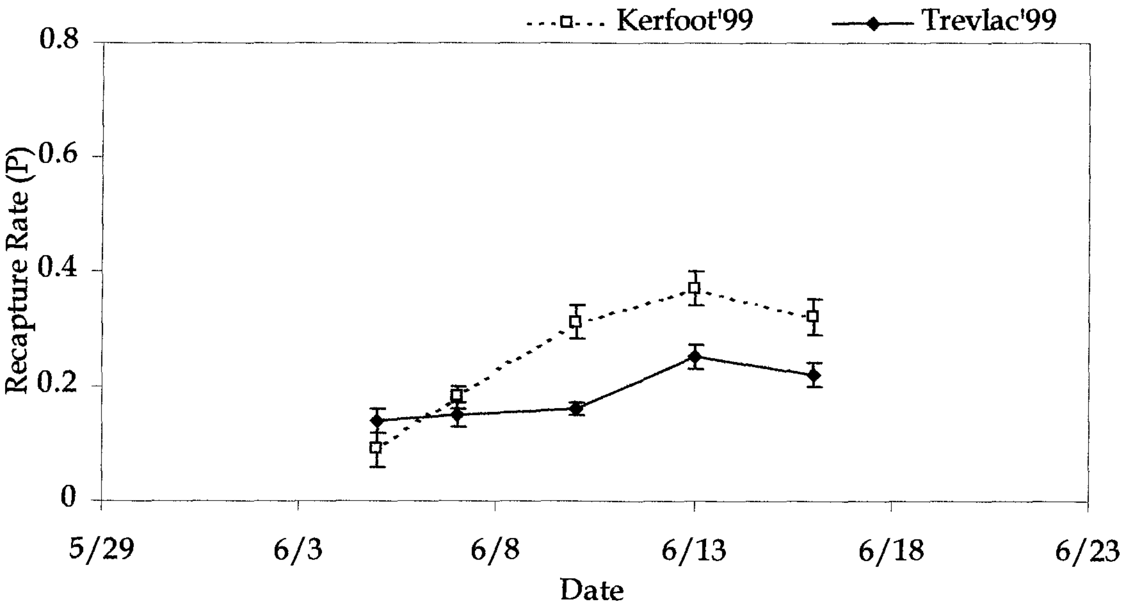
Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	N	Deviance
$\Phi_{density \times temperature}P_{pond \times t}$	14545.21	0.00	0.72	34	710.83
$\Phi_{pond}P_{pond \times t}$	14547.06	1.85	0.28	35	710.62
$\Phi_{pondxt}P_{pond \times t}$	14561.79	16.58	0.00	55	679.32
$\Phi_{density + temperature}P_{pond \times t}$	14565.76	20.55	0.00	33	738.36
$\Phi_{density}P_{pond \times t}$	14569.59	24.37	0.00	32	745.48
$\Phi_{temperature}P_{pond \times t}$	14580.74	35.53	0.00	32	759.09

Notes: Subscripts indicate factors included in the model. 'x' indicates the inclusion of an interaction term. '+' indicates that the factors are additive.

Table 5: Model selection to assess the effect presence of bullfrog tadpoles has on daily survival rate of treefrog tadpoles. Φ_{DT} denotes the best-fit model from previous analysis, which included density, temperature, and the interaction between the terms.

Model	**QAIC$_c$**	**ΔQAIC$_c$**	**QAIC$_c$ weight**	**N**	**Deviance**
$\Phi_{DT}P_{pond\ x\ t}$	14545.21	0.00	0.64	34	710.83
$\Phi_{pond}P_{pond\ x\ t}$	14547.06	1.85	0.26	35	710.62
$\Phi_{DT+BF}P_{pond\ x\ t}$	14550.79	4.97	0.05	35	714.43
$\Phi_{DT+BF+D*BF}P_{pond\ x\ t}$	14552.20	6.99	0.02	36	714.43
$\Phi_{DT+BF+T*BF}P_{pond\ x\ t}$	14552.20	6.99	0.02	36	714.43
$\Phi_{DT+BF+D*BF+T*BF}P_{pond\ x\ t}$	14554.21	9.00	0.01	37	714.43

Notes: Subscript D indicates density, T indicates temperature, and BF indicates the presence/absence of bullfrogs.



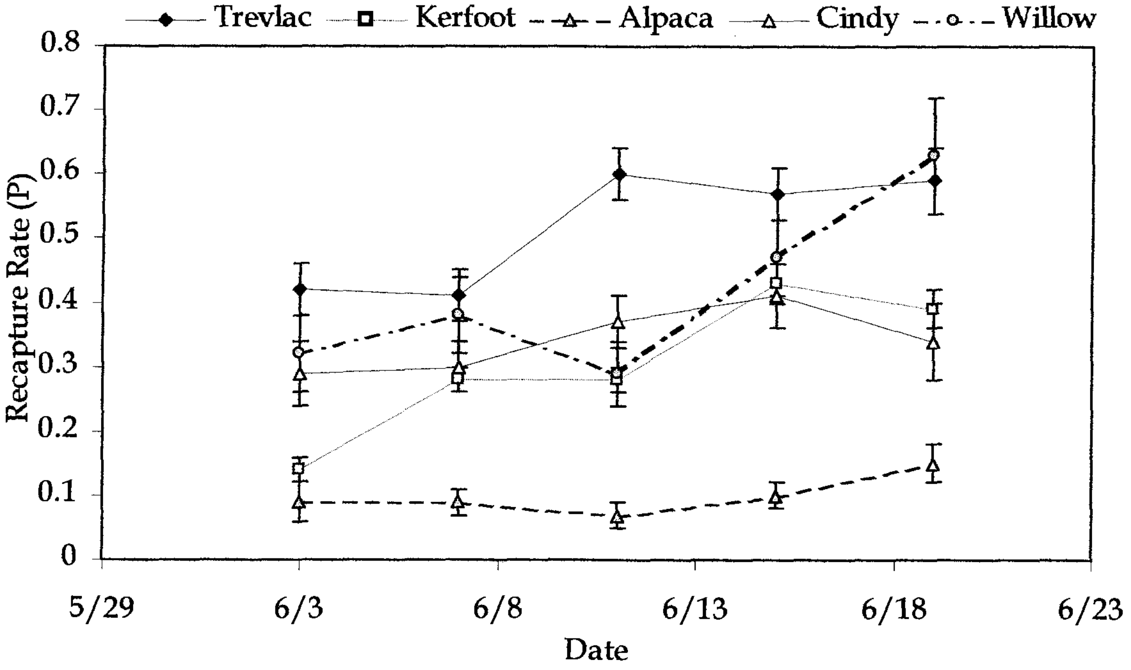


Figure 1: Estimated recapture rates of marked tadpoles in 1999 (top panel) and 2001 (bottom panel).

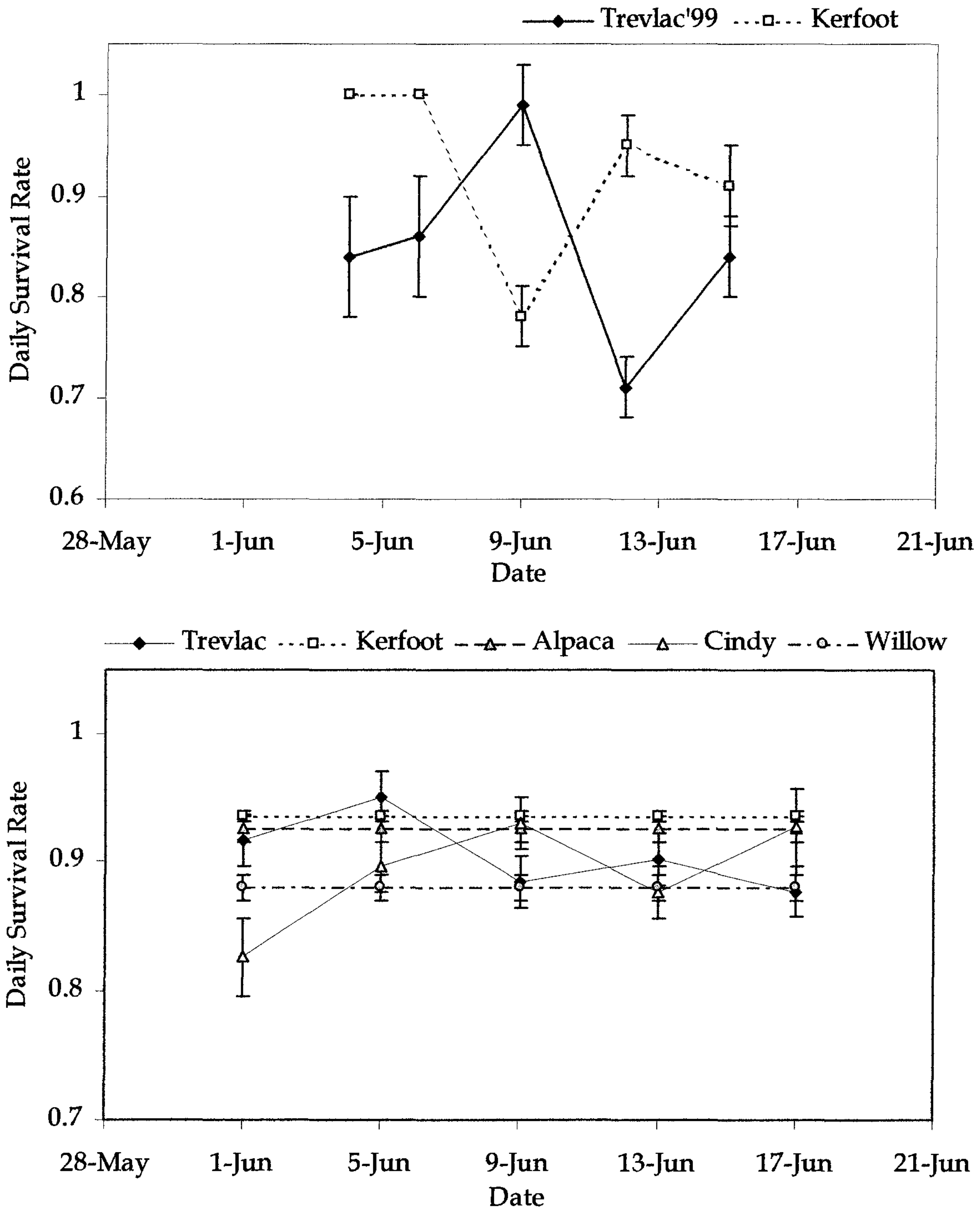


Figure 2: Estimated daily survival rates of treefrog tadpoles in 1999 (top panel) and 2001 bottom panel. In 1999, there was a sharp decline in survival during interval 3 in Kerfoot Pond and interval 4 in Trevlac Pond.

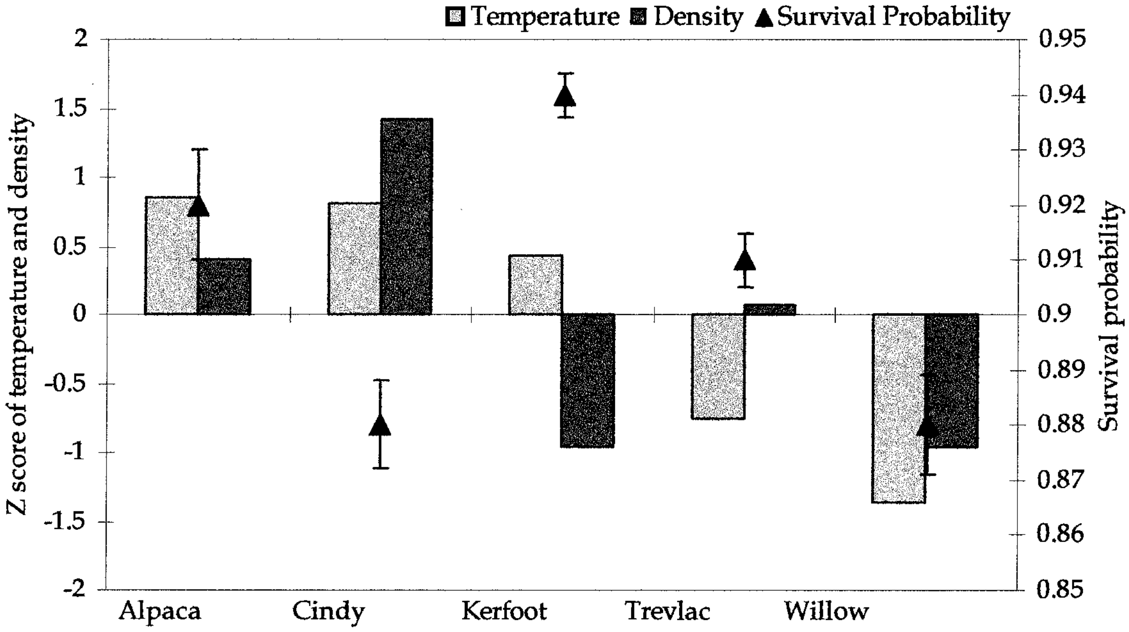


Figure 3: Mean survival rate of tadpoles in each pond plotted along with the relative density of tadpoles and mean temperature of each pond. Actual pond density and temperature values (Table 1) were converted to Z-scores (Z = (x - mean)/standard deviation) to facilitate graphing on a common axis.

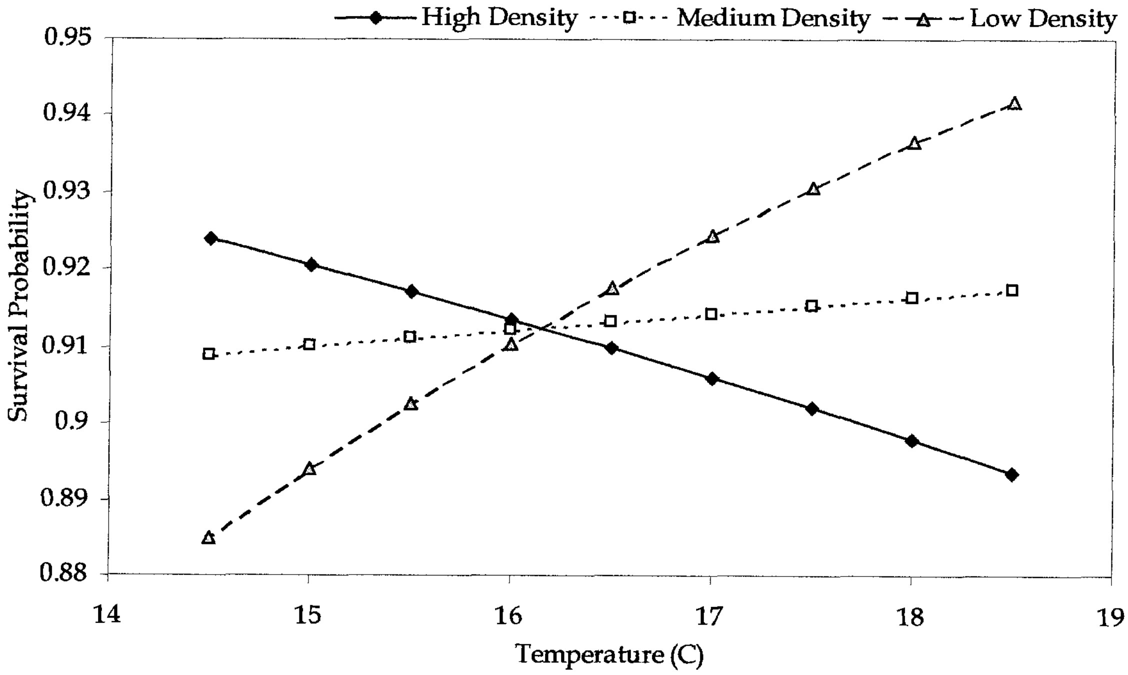
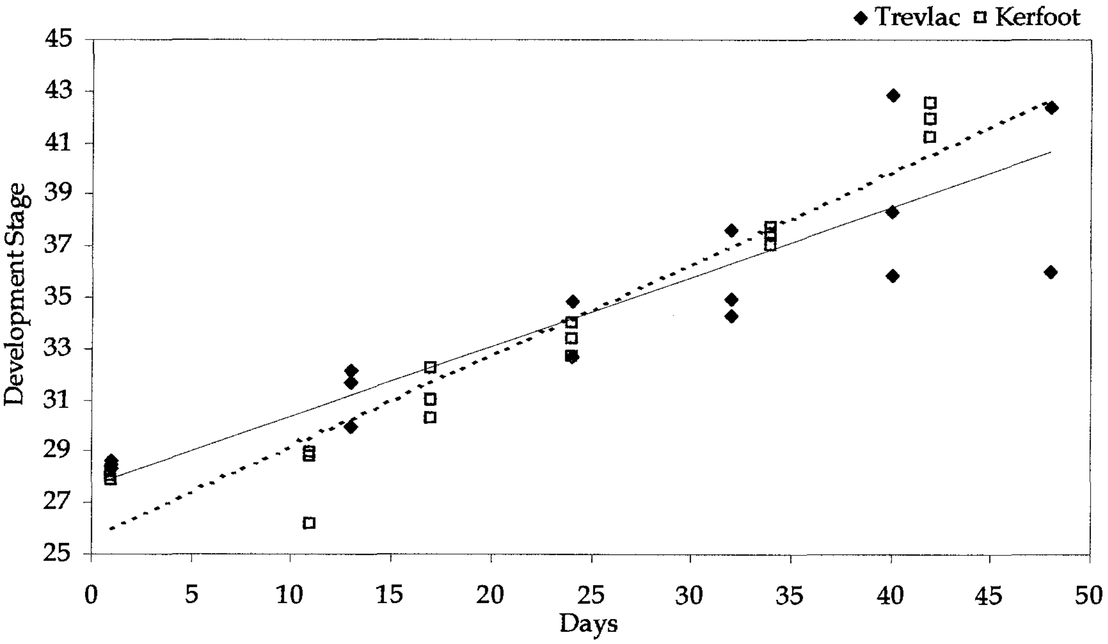


Figure 4: Survival rates predicted by logistic regression of Model $\Phi_{\text{density x temperature}}$ $Logit(\Phi)= -4.35+60.44(density)+0.426(temperature)-3.99(density*temperature)$.
At low densities the predicted survival rates increased with increasing temperature but at high densities daily survival rates decreased with increasing temperatures.



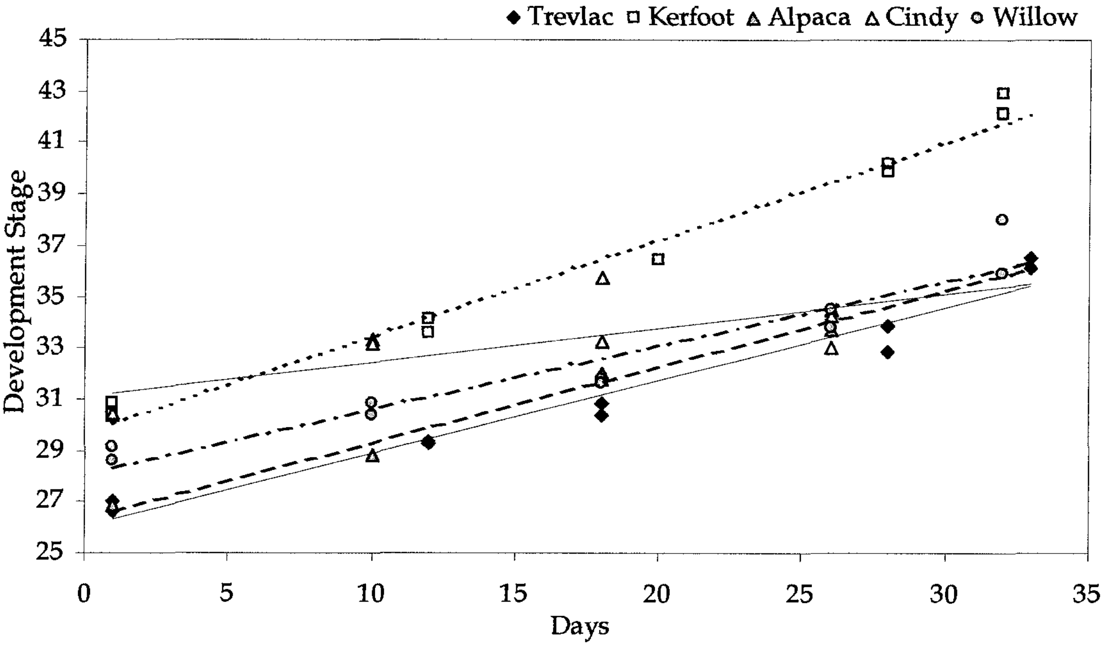
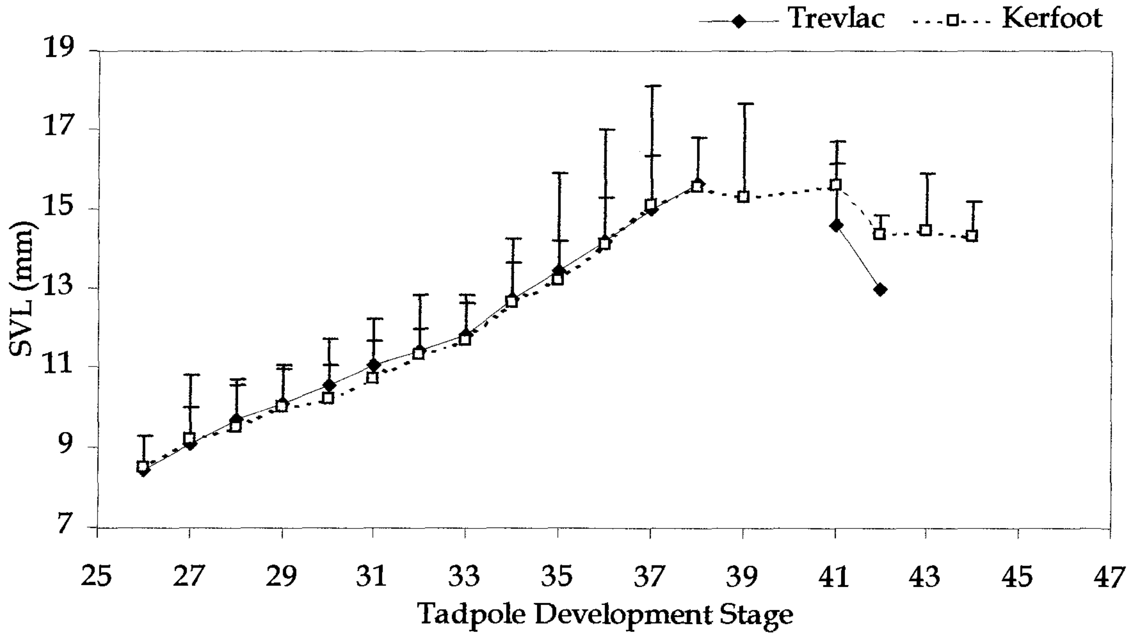


Figure 5: The development rate of tadpoles estimated using field enclosures. Regression equations and r^2 were, 1999: Trevlac Pond $y=27.7+0.27x$, $r^2=0.79$; Kerfoot Pond $y=25.7+0.36x$, $r^2=0.92$; 2001:Trevlac Pond $y=26.2+0.29x$, $r^2=0.97$; Kerfoot Pond: $y=29.6+0.38x$, $r^2=0.98$; Alpaca Pond: $y=26.3+0.30x$, $r^2=0.98$; Cindy Pond: $y=31.1+0.13x$, $r^2=0.54$; and Willow Pond: $y=28.1+0.25x$, $r^2=0.92$.



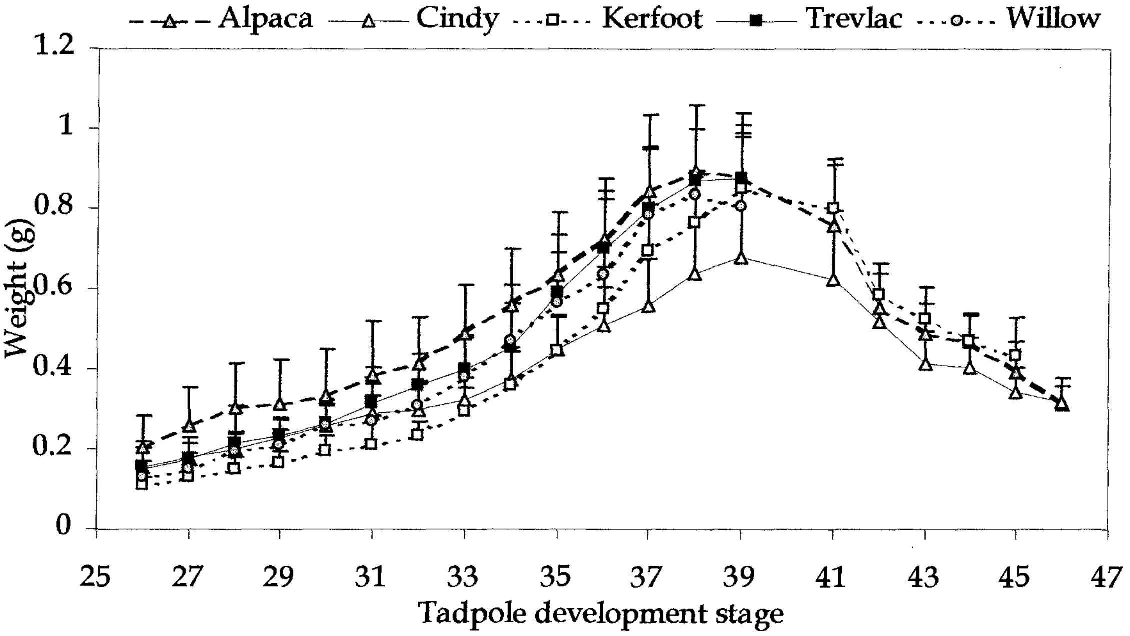
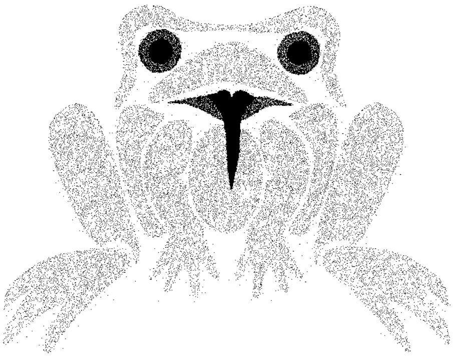


Figure 6: Mean size of tadpoles, snout-vent-length in 1999, and weight in 2001, against Gosner development stage. Metamorphosis is initiated at Stage 39.

CHAPTER 4



COMPETITIVE EFFECTS OF INTRODUCED BULLFROG TADPOLES ON NATIVE PACIFIC TREEFROG TADPOLES: EXPERIMENTAL MESOCOSM STUDY

Abstract

The introduction of bullfrogs (*Rana catesbeiana*) has been associated with the decline of native amphibian species in the Pacific Northwest, but the extent of their effect and the mechanisms of displacement are still unclear. In this study, I assessed direct *intra* and *inter-specific* competition between native treefrog tadpoles (*Hyla regilla*) and introduced bullfrog tadpoles. I also examined the strength of trait-mediated indirect competitive effects arising from the presence of a native predator: roughskin newts (*Taricha granulosa*). Bullfrog tadpoles are invulnerable to predation by newts but treefrog tadpoles are very vulnerable. Bullfrog tadpoles are expected to benefit in competitive interactions because treefrog tadpoles adaptively decrease foraging activity to minimize predation risk (trait-mediated indirect effect). Direct *intra-specific* competition decreased development and growth rate in both species. There was moderate evidence of direct *inter-specific* competitive effects. Bullfrog tadpoles decreased development rate of treefrog tadpoles and, in turn, treefrog tadpoles decreased growth rate of bullfrog tadpoles. There was little evidence for trait-mediated indirect competitive effects. The presence of newts did not bias competitive interactions in favour of bullfrog tadpoles. As expected from their larger size, the per-capita competitive effect of bullfrog tadpoles was an order of magnitude larger than that of treefrog tadpoles. The only exception to this pattern was in treefrog growth rate where per-capita competitive effect of bullfrog tadpoles was close to zero. In most cases, *intra-specific* competitive effects were stronger than *inter-specific* competitive effects for both species.

Introduction

Humans have deliberately introduced a number of species into freshwater habitats around the world. They have done this for several reasons: to increase commercial harvest e.g., Nile perch (Baskin 1992) and bullfrogs (Jennings and Hayes 1985); improve sport fishing e.g., trout (Ross 1991) and salmon (Spencer et al. 1991); control pests e.g., mosquitofish, tilapia, and guppies (Shireman 1984, Allan and Flecker 1993); and use as ornamentals e.g., purple loosestrife, water lilies, and other garden escapees (Pimentel et al. 2000). These introduced species have often caused dramatic declines in native species (Allan and Flecker 1993, Lodge 1993, Pimentel et al. 2000). These declines are primarily through predation (Ross 1991, Kaufman 1992, Knapp and Matthews 2000) but also through resource competition (Petren and Case 1996, Kiesecker et al. 2001), displacement from favourable habitats (Brown and Moyle 1991, Kiesecker and Blaustein 1998), and ecosystem change (Hurlbert et al. 1972, Vitousek 1990).

In North America, introduced bullfrogs (*Rana catesbieana*) have been implicated in the decline of many amphibian populations (Moyle 1973, Green 1978, Hammerson 1982, Fisher and Shaffer 1995, Kiesecker and Blaustein 1997, Kupferberg 1997b, Lawler et al. 1999). Adult bullfrogs prey on both the adult and larval stages of amphibians (Chapter 2, Bury and Whelan 1986, Werner et al. 1995, Kiesecker and Blaustein 1997). Currently, the extent of this predation and its impact on the population dynamics of native amphibians is not known. However, a number of experimental studies have documented competitive effects of larval bullfrogs on native tadpoles, involving a variety of direct and indirect mechanisms (Kupferberg 1997b, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001). In addition to direct exploitative competition, bullfrog tadpoles outcompete native yellow-legged frog (*Rana boylii*) tadpoles through a density-mediated indirect pathway by decreasing epiphytic diatoms, the preferred food source of yellow-legged frog tadpoles (Kupferberg 1997b). Interference competition has been documented between bullfrog tadpoles and native red-legged frog tadpoles when food resources are clumped (Kiesecker et al. 2001). This interference competition has then been shown to cause the red-legged frog tadpoles to shift microhabitat such that they become prone to predation by introduced smallmouth bass (Kiesecker and Blaustein 1998).

In this study, I examined the strength of competition between bullfrog tadpoles and Pacific treefrog tadpoles (*Hyla regilla*). Pacific treefrogs are widely distributed from Baja to southern British Columbia and remain common even in highly modified agricultural habitats where bullfrogs are abundant (Fisher and Shaffer 1995). Tadpoles of both species are often found at high densities (>100/m^3) and have similar diets (Kupferberg, 1997). If food is limited, there will be significant competition between these two species (Seale and Beckvar 1980). Pacific treefrog tadpoles, which hatch in spring, face competition from much larger, over-wintered bullfrog tadpoles. Large size is thought to increase per capita advantage in larval competition (Lawler and Morin 1993, Werner 1994) because large tadpoles have a higher ability to deplete resources. Consequently, the *inter-specific* competitive effect of bullfrog tadpoles on treefrog tadpoles is expected to be stronger than that of treefrog on bullfrog tadpoles. Smaller tadpoles, however, are more efficient in converting resources into growth and hence are usually better at maintaining growth even under resource-depleted conditions (Werner 1994).

Experimental studies assessing competition between the two species have had mixed results (Kupferberg, 1997; Adams, 2000). In the Kupferberg (1997) study, bullfrog tadpoles significantly decreased survival of treefrog tadpoles in small containers (12.7 litres) but not in 2 m^2 field enclosures. However, in the same field enclosures, bullfrog tadpoles decreased treefrog metamorph size by 16%. In the Adams (2000) study, carried out in field enclosures (1.66 m^2), bullfrog tadpoles did not significantly decrease survival, time to metamorphosis, or size at metamorphosis of treefrog tadpoles.

The outcome of inter-specific competition experiments is often influenced by venue and design (Skelly and Kiesecker, 2001) and multiple experiments increase our confidence that the results reflect real patterns of competition (Sarnelle 1997, Werner 1998, Skelly and Kiesecker 2001). I explored competition between the two species in a mesocosm experiment, using additive density manipulations (Underwood 1986) designed to measure the per capita competitive effect of bullfrog on bullfrog, bullfrog on treefrog, treefrog on bullfrog, and treefrog on treefrog tadpoles (Table 1). The relative strength of the per-capita *intra-specific* competitive effect can be compared to *inter-specific* competitive effect for both species using this experimental design.

Pairwise competitive interactions can be modified in complex aquatic communities by higher order interactions which arise due to the influence of a third intervening species (Vandermeer 1969, Neill 1974, Morin et al. 1988, Abrams 1991, Werner 1992). In particular, the risk of predation is an ever-present force that shapes larval community dynamics and has been shown to qualitatively alter competitive interactions between species (Werner 1991, Werner and McPeek 1994, Skelly 1995a, Werner and Anholt 1996, Relyea 2000, Peacor and Werner 2001). Tadpoles have been shown to decrease foraging effort in the presence of predators, thereby decreasing development and growth rates (Werner 1992, Werner and Anholt 1993, Skelly 1996, Lardner 1998). The extent of this anti-predator behaviour depends on resource availability, which is dependent on the extent of competition faced by the tadpoles (Werner and Anholt 1993). This is of particular importance in competitive interactions between bullfrog and treefrog tadpoles, because second year bullfrog tadpoles are not susceptible to native aquatic predators. Pacific treefrog tadpoles remain vulnerable to these predators for most of their larval life. This differential susceptibility to predators is expected to indirectly increase the competitive advantage of bullfrogs over Pacific treefrog tadpoles.

Roughskin newts are the dominant predators of treefrog tadpoles in British Columbia (Calef 1972). In this experiment, the density treatments were crossed with the presence and absence of a caged roughskin newt in a factorial design. A statistically significant interaction term between the two experimental factors (competitor density and predator presence) would indicate the presence of a trait-mediated indirect competitive effect due to anti-predator behaviour in this system(Wilson and Lefcort 1993, Van Buskirk 2001).

To summarize: I estimated the direct density dependent *intra-specific* and *inter-specific* competitive effects between introduced bullfrog and native Pacific treefrog tadpoles. I assessed whether the presence of a native predator decreased foraging by treefrog tadpoles and whether this biased competition in favour of bullfrog tadpoles through a trait-mediated indirect pathway.

Methods

Experimental set-up

The experimental design consisted of five density treatments crossed with the presence and absence of a caged roughskin newt as the predator (Table 1). These ten treatments constituted a block, which was replicated five times.

Cattle watering tanks were used as artificial ponds (Skelly and Kiesecker 2001). The tanks were set out in an open field within the Forestry Compound at the University of Victoria, British Columbia, Canada. These tanks were 1.6 meters in diameter and filled to a depth of 0.5 meters (1000 liters). The tanks were covered with 40% shade cloth to avoid excessive water temperatures (mean ± SD, 18.3^{0}C ± 2.7) and to prevent oviposition by dragonflies. Each tank was stocked with 300g of leaf litter (mainly *Quercus* and *Acer*) to provide cover for the tadpoles and to encourage the growth of periphyton (Werner and Anholt 1996, Peacor and Werner 1997). The tanks were fertilized with dissolved $NaNO_3$ and K_3PO_4 in the atomic ratio 40:1 N:P to discourage the growth of inedible cyanobacteria (Anholt 1994). To prevent bacterial blooms that reduce oxygen levels, all tanks were inoculated with *Daphnia* spp. To ensure adequate algal growth, the tanks were filled with water and set-up a month before initiation of the experiment. A few days before the tadpoles were introduced, 50 g of Purina Rabbit Chow was added to the tanks as supplemental tadpole food.

Roughskin newts were housed in fibreglass mesh bags (30 cm in diameter, 50 cm deep) attached to the side of the tank. The newts were fed two treefrog tadpoles every third day to ensure that the chemical scent of predation remained fresh in the tanks (Chivers et al. 2001). Pacific treefrog egg masses were collected from a local pond. They were hatched in children's wading pools and raised there until they were large enough to be handled (> 6mm SVL). The initial mean weight of treefrog tadpoles was 0.056 ± 0.017 grams (N=50, mean ± SD) and they were at Gosner development stage 25.8 ± 0.44. Second year bullfrog tadpoles were captured locally from McKenzie Lake and Trevlac Pond. The initial weight of bullfrog tadpoles was 9.11 ± 2.13 grams (N=10) and they were at Gosner development stage 29.2 ± 1.96.

The experiments were initiated during the week of 5th June 2000, by setting up one block on each day of the week. Tadpoles were randomly assigned to experimental blocks and treatments. The density of tadpoles is extremely variable between ponds and even within a pond (Turnipseed and Altig 1975, Caldwell et al. 1980). I chose experimental densities that represented the lower half of treefrog tadpole density range observed in the field (220 ± 170 tadpoles/m^3, *unpublished data*). Similarly, for bullfrogs I chose experimental densities lower than those observed in the field (106 ± 52 tadpoles/m^3, *unpublished data*). These densities were used because previous experiments using higher densities experienced high levels of mortality, requiring replacement of tadpoles (Kupferberg 1997b). This would not have been possible in this experimental set-up. Also, experiments in mesocosms are thought to overestimate competitive effects (Skelly 2002). Experimental densities in the lower range provide a conservative estimate of the degree of competition in natural ponds.

Treefrog tadpole behaviour was assessed using scan samples. Observations were carried out during weeks four and five of the experiment. Each tank was observed twice during the experiment. One block was observed per day, mainly on sunny days between 11 am and 3 pm to prevent the confounding effect of varying activity levels during the day. I waited ten minutes after opening the lids of the tanks to permit the tadpoles to return to normal activity. I then counted the number of tadpoles feeding and moving. It was not possible to separate feeding from moving because treefrog tadpoles switch between these two activities in a matter of seconds and it was not possible to distinguish between the two activities during a scan sample. I also counted the number of tadpoles within a 30 cm radius of the predator cage. This variable was used to assess if there was spatial avoidance of the predator. Pacific treefrogs have been shown to sense chemosensory gradients of predation cues (Chivers et al. 2001). I therefore expected them to avoid cages with predators (Relyea and Werner 1999).

The experiment was terminated during the week of July 17th when at least a few metamorphs were observed in most of the tanks. The tanks were drained and the leaf litter removed by hand to ensure that all the tadpoles were captured. Tadpoles were weighed and their developmental stage determined immediately following capture. To assess whether the treatments actually changed the food availability for the tadpoles, terracotta tiles (225 cm^2) were hung on the side and near the bottom of the tanks. The periphyton from the sampling tiles was scraped off with a razor blade and washed down with distilled water. The sample was then filtered through a glass fibre filter (GF/C or GF/F) and frozen for later analysis. The concentration of chlorophyll *a* was used to estimate the quantity of periphyton in each sample. Chlorophyll *a* concentration was estimated using standard spectrophotometric methods following ethanol extraction (Wintermans and DeMots 1965). To assess treatment effects on the way in which resources were converted to biomass of tadpoles, biomass production was simply calculated as the final total weight of tadpoles less the initial total weight of tadpoles.

Data Analysis

The three response variables used to assess competitive effects were percent survival, developmental rate, and logarithmic growth rate (Table 1). Tadpoles reach maximum weight at stage 37-38 after which they lose up to 50% of their body mass during metamorphosis (Pandian and Marian 1985, Werner 1986). In tanks with a high proportion of metamorphosing tadpoles, therefore, growth rate will be underestimated compared to tanks with few metamorphosing tadpoles. Because of this, for all metamorphosing tadpoles (Gosner Stage > 38) I used a mass-loss regression (Werner and Anholt, 1996), which plots weight against development stage, to back-estimate weight at Stage 38. It was these adjusted weights that I used in calculating final mean weight of tadpoles in each tank. Block 1 was excluded from survivorship analysis for treefrog tadpoles due to counting errors during set-up.

All statistical analyses were done on tank means. Percent survival was analyzed using logistic regression analysis. Development rate and growth rate of each species was analyzed separately using univariate ANCOVA models, with densities of bullfrog and treefrog tadpoles as continuous variables and newt presence as a fixed factor. Models within a pre-defined set were compared using the information theoretic approach to model selection (Table 2, Burnham and Anderson 2002). Model selection based on sample size adjusted Akaike's information criterion (AIC_c) enabled me to compare all models simultaneously, including models that were not nested in a statistical sense (Burnham and Anderson 2002). The model with the smallest AIC_c value is the most parsimonious model, given the data, and is considered the best-fit model. Akaike's weights, which sum to 1, express the relative support for a given model in a predetermined set of models (Burnham and Anderson 2002). Comparative support for two models can therefore be expressed as a ratio of their AIC weights (evidence ratio). When there was considerable uncertainty associated with model selection (AIC_c weight of best-fit model < 0.90), inference was based on multiple models in this set. The relative importance of experimental factors was calculated by summing the AIC_c weights (w_{cum}) of the models in which the factor was included. Per capita and per unit biomass competitive effects of the tadpoles were assessed using model averaged regression coefficients with unconditional standard errors. Model averaging adjusts for model uncertainty (Burnham and Anderson, 2002). The behaviour variables (proportions were arc-sine transformed), the estimate of the standing periphyton biomass (Chlorophyll *a* concentration), and the total biomass production of tadpoles were also analyzed using the information theoretic approach.

Percent survival data were overdispersed. This is common for grouped data (tanks) due to violations of assumptions of independence and parameter homogeneity within groups (Eberhardt 1978). The most severe overdispersion was caused due to low survival in two tanks in block 4 (variance inflation factor, $\hat{c} = 7.26$). Model selection with and without this block ($\hat{c} = 2.9$) gave similar results. The analysis is presented with this block included. In this case, quasi-likelihood methods for model fitting, calculating AIC_c values, and estimating standard errors of parameter estimates were used. For the other variables, inspection of the residuals showed that the data met assumptions of normality and equal variance. Statistical analyses were performed using the General Linear Models function in S-plus 6 for Windows (Insightful Corp., Seattle USA).

Results

Bullfrog tadpoles as recipients of competition

Survival: At the density levels used in this experiment bullfrog tadpoles experienced very low levels of mortality. Only two bullfrog tadpoles died through the entire experiment. Both were in the treatment with the highest density of bullfrog tadpoles (BF20/TF50).

Development rate: Mean development rate of bullfrog tadpoles during the experiment was 0.10 ± 0.03 stage/day (mean ± SD) and none of the tadpoles reached metamorphosis during the experiment. Competition decreased development rate of bullfrog tadpoles (Figure 1). The model with bullfrog competition alone had twice the support of the model with both bullfrog and treefrog competition (Table 3). When all models are considered together, *intra-specific* competition was far more important as a predictor of bullfrog development rate (w_{cum}=0.98) compared to *inter-specific* competition (w_{cum}=0.38). The per-capita competitive effect of bullfrog tadpoles was ($-2.4\text{x}10^{-3} \pm 7.6\text{x}10^{-4}$ stage/tadpole), two orders of magnitude stronger than that caused by each treefrog tadpole ($-8.6\text{x}10^{-5} \pm 8.5\text{x}10^{-5}$ stage/tadpole).

Growth rate: Bullfrog tadpoles grew little or lost weight during the experiment (Mean growth rate: $5.7\text{x}10^{-5} \pm 0.002$ percent/day). As with development rate, competition decreased growth rates of bullfrog tadpoles (Figure 1), but the model with both *intra* and *inter-specific* competition fit the data three times better than the model with *intra-specific* competitive effects alone (Table 3). However, the per-capita competitive effect of bullfrogs ($-1.2\text{x}10^{-4} \pm 4.3\text{x}10^{-5}$ percent/tadpole) was again two orders of magnitude stronger than the per-capita effect of treefrog tadpoles ($-9.0\text{x}10^{-6} \pm 4.3\text{x}10^{-6}$ percent/tadpole).

Treefrog tadpoles as recipients of competition

Survival: The overall mean percent survival of treefrog tadpoles in the experiment was 0.87 ± 0.12 (Mean ± SD). The presence of newts strongly decreased the survival rate of treefrog tadpoles (Table 4), from 0.90 ± 0.11 percent in the absence of newts to 0.83 ± 0.13 percent in the presence of newts (Figure 2). Competition had only a minor effect on the survival rate of treefrog tadpoles (Table 4).

Developmental Rate: The overall development rate of treefrog tadpoles was almost two and a half times that of bullfrog tadpoles (Mean ± SD: 0.24 ± 0.06 stage/day). Both *intra* and *inter-specific* competition and the presence of newts decreased the development rate of treefrog tadpoles (Figure 2, Table 4). There was also some evidence that the competitive effects of bullfrog tadpoles increased in the presence of newts (Model 2, Table 4), but this model had only two thirds the support of the model with main effects alone (Table 4). Using cumulative AIC weights, all three experimental factors were important in determining the development rate of treefrog tadpoles (treefrog tadpoles w_{cum}=1.0, newts w_{cum}=0.97, and bullfrog tadpoles w_{cum}=0.92). The per-capita *inter-specific* competitive effect of bullfrog tadpoles on treefrog tadpoles (Mean ± SE: $-1.8 \times 10^{-3} \pm 1.3 \times 10^{-4}$ stage/tadpole) was almost twice the per-capita *intra-specific* competitive effect of treefrog tadpoles on themselves ($-1.0 \times 10^{-3} \pm 1.3 \times 10^{-4}$ stage/tadpole).

Growth rate: Unlike bullfrog tadpoles, treefrog tadpoles in all treatment showed strong positive growth rate (Mean ± SD: 0.06 ± 0.01 percent/day), and tadpole body mass increased by an order of magnitude, from $5.6\text{x}10^{-2} \pm 1.7\text{x}10^{-2}$ g to $5.2\text{x}10^{-1} \pm 1.5\text{x}10^{-1}$ g. Growth rate of treefrog tadpoles was strongly affected by *intra-specific* competition (Figure 2, Table 4). Using cumulative AIC weights, treefrog tadpole density was the most important factor in determining growth rate of treefrog tadpoles (w_{cum}=1.0). The presence of newts was moderately important (w_{cum}=0.79). There was little evidence that predator presence increased competitive effects (Table 4). Increasing bullfrog density did not have a strong effect on treefrog growth rate (Table 4, w_{cum}=0.41) and the per-capita competitive effect of bullfrog tadpoles ($-3.5 \times 10^{-5} \pm 1.2 \times 10^{-4}$ percent/tadpole) was not different from zero. The per-capita *intra-specific* competitive effect of treefrog tadpoles was $-1.2 \times 10^{-4} \pm 1.1 \times 10^{-5}$ percent/tadpole.

Size of treefrog tadpoles: Both development rate and growth rate influence the size of tadpoles. Because tadpoles in each tank were at various stages of development at the termination of the experiment, it is not possible to statistically test treatment effect on tadpole size directly. However, mean tadpole size can be plotted against developmental stage to graphically assess treatment effects. *Inter-specific* competition from bullfrog tadpoles seemed to have little effect on size of tadpoles at any developmental stage (Figure 3). *Intra-specific* competition from treefrog tadpoles seemed to decrease size of tadpoles at developmental stages > 34, especially in the presence of newts (Figure 3).

Treefrog tadpole behaviour

Tadpole activity: Under the risk of predation, treefrog tadpoles are expected to spend more time hiding in the leaf litter. Fewer tadpoles are therefore expected to be observed feeding. As competition decreases per-capita resource availability, tadpoles have to spend more time foraging. A higher proportion of tadpoles are therefore expected be observed feeding. Contrary to these expectations, predator presence did not seem to affect the proportion of active tadpoles (Table 5, Newts w_{cum} = 0.28) and increasing competition decreased the proportion of active tadpoles (Table 5, treefrog tadpoles w_{cum} = 1.00). However, the effect size of increasing competition was small (regression coefficient = $-1.4\text{x}10^{-4} \pm 6.0\text{x}10^{-5}$).

Predator avoidance: There was a slight reduction in the number of tadpoles found in the vicinity of the cages (regression coefficient: -0.016 ± 0.018) but the model with newts fit the data only half as well as the null model (Table 5).

Resource Availability and Biomass Production

Chlorophyll a *concentration*: The standing crop of periphyton is expected to be higher in the presence of predators, because of lower tadpole foraging activity. Standing crop of periphyton is expected to decrease with increasing densities of tadpoles. Chlorophyll *a* concentrations was higher in the presence of newts (Figure 4). However, contrary to expectation, chlorophyll *a* concentrations increased with increasing densities of both species of tadpoles (Figure 4, regression coefficient: treefrog tadpoles = $7.6 \times 10^{-5} \pm 2.5 \times 10^{-5}$ µg/cm^2.tadpole, bullfrog tadpoles = $9.8 \times 10^{-4} \pm 2.3 \times 10^{-4}$ µg/cm^2.tadpole). The model with competitive factors alone had support equal to the model with the competitive factors plus the presence of newts as a factor (Table 6). Looking at the cumulative AIC weights, the density of tadpoles was more important (treefrog tadpoles w_{cum}=0.99, Bullfrog tadpoles w_{cum}=1.00) than the presence of newts (w_{cum}=0.57) in determining chlorophyll *a* concentrations.

Biomass Production: The two species differed strongly in the patterns of biomass production. Bullfrog biomass increased very slightly or decreased over the duration of the experiment (Figure 5) but treefrog biomass increased in all treatments. The greatest loss in bullfrog biomass was in the treatment with the highest number of bullfrog competitors (*intra-specific)*, particularly in the absence of predators (Figure 5). Support for the model with the two competitive effects was tied with that for the model with *intra-specific* competitive effects alone (Table 5). The presence of newts had only a moderate effect on bullfrog tadpole biomass production (bullfrog tadpoles w_{cum} = 1.00, treefrog tadpoles w_{cum} = 0.72, Newts w_{cum} = 0.41). Per-capita *intra-specific* competitive effect was an order of magnitude stronger than per-capita *inter-specific* competitive effect (regression coefficients: bullfrog tadpoles = -0.61 ± 0.14 g/tadpole, treefrog tadpoles = -0.02 ± 0.01 g/tadpole).

The best-fit model for treefrog tadpole biomass production was one that included all three main factors as well as the interaction term between treefrog density and predator presence (Table 6). This model fit four times better than the model with both interaction terms. Although growth rates decreased with increasing treefrog tadpole density, overall biomass production still increased (Figure 5). This increase was however inhibited in the presence of roughskin newts. Competition from bullfrog tadpoles marginally decreased biomass production of treefrog tadpoles (w_{cum}=0.96) especially in the presence of newts (Figure 5).

Discussion

Factors influencing competition between bullfrog and treefrog tadpoles

The idea that introduced bullfrogs have a negative effect on native amphibians has been discussed for almost two decades now (Moyle 1973, Green 1978, Hammerson 1982, Fisher and Shaffer 1995, Kupferberg 1997b, Kiesecker and Blaustein 1998, Lawler et al. 1999). In addition to bullfrogs being predators of native amphibians, bullfrog tadpoles are thought to have a competitive advantage over native tadpoles because of their larger size and invulnerability to native predators (Kupferberg 1997b, Lawler et al. 1999, Kiesecker et al. 2001). This expectation was only partially supported by this study. Pacific treefrog tadpoles experienced reduced development rate due to increasing competition from bullfrog tadpoles but percent survival and growth rate were not affected. In turn, bullfrog tadpoles experienced lowered growth rate due to increasing competition from Pacific treefrog tadpoles. Both bullfrog and treefrog tadpoles experienced more *intra-specific* competition than *inter-specific* competition. The per-capita competitive effect of bullfrog tadpoles was greater than that of treefrog tadpoles in most cases. While the presence of newts had a negative effect on survival, development, and growth of treefrog tadpoles, there was little evidence that the presence of this native predator biased competition in favour of bullfrog tadpoles.

An apparent paradox of invasive species is that they are able to establish in spite of "biotic resistance" from locally adapted native species (Sax and Brown 2000). It is widely accepted that this is possible because native species do not have a strong competitive effect on the introduced species. In support of this, I found that treefrog tadpoles had only a moderate negative effect on the growth rate (Table 3) and no effect on either survival or development rates of bullfrog tadpoles. Also, the per-capita competitive effect of treefrog tadpoles on bullfrog tadpoles was two orders of magnitude lower than the per-capita *intra-specific* competitive effect of bullfrog tadpoles. In their native habitat, bullfrog tadpoles experience significant competitive effects from green frog tadpoles (Werner 1994, Werner and Anholt 1996). Bullfrogs are also more vulnerable to predation by dragonfly nymphs compared to green frog tadpoles (Peacor and Werner 1997). In their introduced habitat, bullfrog tadpoles neither experience strong competitive effects from native treefrog tadpoles nor are they vulnerable to newts, which are dominant predators of native tadpoles (Calef 1972).

Biotic factors such as competition and predation were clearly not a barrier to the establishment and spread of bullfrogs, but abiotic factors can sometimes curb the spread of introduced species. Bullfrog tadpoles developed little (Gosner stage 29 to 33) and actually lost weight in some treatments (Figure 5). None of the bullfrog tadpoles reached metamorphosis during the experiment. Water temperature in the experimental tanks (18.3 ± 2.7^{0}C) was in the lower end of the preferred optimum (15 to 32^{0}C) for bullfrog tadpole development (Willis et al. 1956, Viparina and Just 1975, Bury and Whelan 1986). The temperature in the tanks was similar to that in natural ponds on southern Vancouver Island during this time (Chapter 3), and native tadpoles are capable of attaining metamorphosis within the growing season at these temperatures (Licht 1974). In eastern North America, forest canopy cover and its influence on water temperature and periphyton growth have been shown to have a profound effect on competitive relationships between tadpole species (Werner and Glennemeier 1999, Skelly et al. 2002, Halverson et al. 2003). In natural ponds on southern Vancouver Island, water temperature often stays below 20° C through the summer; this may prolong duration of the larval stages and slow down bullfrog population growth. In human modified landscapes water temperature in irrigation and garden ponds is much higher and this may enable bullfrog tadpoles to maintain maximal development rates. This may, in turn, indirectly favour the spread of bullfrogs in these areas (Fisher and Shaffer 1995).

Looking at treefrog tadpoles as recipients of competition, my study is similar to previous studies that have shown bullfrog tadpoles to have negligible direct mortality effects on Pacific treefrog tadpoles (Kupferberg, 1997, Adams, 2000). These previous studies did not examine development rate. The per-capita competitive effect of bullfrog tadpoles on development rate of treefrog tadpoles was an order of magnitude greater than the *intra-specific* competitive effect (Figure 2). Development rate and the ability to time the changes in life-history stages, are key adaptations in organisms with complex life-histories (Harris 1999). Slower development which leads to metamorphosis later in the season is associated with lower fitness in the terrestrial stages (Morin et al. 1990, Altwegg 2002a). A number of the native predators are gape-limited and slower development leaves the tadpoles vulnerable to these predators longer (Puttlitz et al. 1999). Given that daily survival rates in natural ponds can be as low as 88%, longer development periods will lead to fewer treefrog tadpoles reaching metamorphosis (Chapter 3). Optimal timing of metamorphosis in tadpole life-histories is based on the trade-off in growth and mortality risk between the aquatic and terrestrial stages (Werner 1986). Delayed treefrog tadpole development caused by bullfrog tadpoles will alter the timing of metamorphosis but the effect of this alteration on population dynamics cannot be predicted without data on the terrestrial life-history stage.

Theoretical models and experimental studies have shown that development rate is sensitive to changes in growth rate and that development rate can be adjusted adaptively to changes in growth rate (Wilbur 1980, Travis 1984, Hensley 1993). Under conditions of competitive resource limitation, tadpoles can either speed up development and metamorphose at a smaller size or slow down development but maintain optimal size (Wilbur 1980). In this study, Pacific treefrog tadpoles seemed to slow down development to maintain size at each stage when faced with *inter-specific* competition from bullfrog tadpoles (Figure 3). Previous studies have shown that treefrog metamorph size is decreased in the presence of competition from bullfrog tadpoles (Kupferberg 1997b, Adams 2000). Smaller size at metamorphosis has been associated with lower post-metamorphic survival rate (Berven 1990, Goater 1994, Scott 1994, Beck and

Congdon 1999, Morey and Reznick 2001, Altwegg 2003). This, in turn, has been shown to be a pivotal vital rate in population dynamics (Taylor and Scott 1997, Biek et al. 2002, Vonesh and De la Cruz 2002)

Effect of predators on inter-specific competition

The presence of caged newts decreased survival, development, and growth of treefrog tadpoles (Table 4). These declines are thought to be because tadpoles decrease foraging activity in response to an increase in perceived level of predation risk (Werner 1991, Lardner 1998, Altwegg 2002b). However, I was unable to detect such a change in the behavioural observations. The behavioural observations were carried out during weeks 4 and 5 of the experiment, and it is possible that most of the tadpoles had grown too large to be vulnerable to the gape-limited newts (Puttlitz et al. 1999). I also expected that, since bullfrog tadpoles were not vulnerable to predation from newts, the *inter-specific* competitive effects of these tadpoles would be stronger in the presence of these predators. There was weak support for this hypothesis in treefrog development rate (w_{cum}=0.37), where the presence of newts doubled the competitive effect of bullfrog tadpoles. In their native habitat, bullfrog tadpoles are able to out-compete green frog tadpoles in the presence of bluegill sunfish. Bluegill sunfish prey on dragonfly larvae which selectively prey on bullfrog tadpoles (Werner and McPeek 1994). This study indicates that native predators such as newts do not strongly influence the competitive interactions between native treefrog tadpoles and bullfrog tadpoles. On the other hand, bluegill sunfish, which have also been introduced to western North America, favour the establishment of bullfrogs through predator mediated indirect effects similar to those observed in the native habitat (Adams, 2000; Adams et al., 2003).

Effect of behaviour and food levels on *inter-specific* competition

There was no evidence of behavioural interference between bullfrog and treefrog tadpoles during foraging (but see Kiesecker et al. 2001). This is in keeping with the accepted view that anuran competitive interactions are mainly exploitative (Werner 1994, Kupferberg 1997b). Bullfrog tadpoles have been shown to decrease algal biomass in other studies (Seale 1980, Werner 1994, Kupferberg 1997b). In this study, periphyton biomass increased with increasing tadpole density (Figure 4), and, in particular, bullfrog tadpole density. It is possible that higher densities of tadpoles recycle nutrients from the detritus pool at a faster rate promoting greater algal growth (Werner 1994, Kupferberg 1997a). This indicates that food may not have been severely limited in this experimental set-up, and competitive effects of higher tadpole densities may have been inadvertently mitigated by higher resource availability. If resources were limited, total biomass production across all treatments would be relatively constant, and increasing production of one species would be compensated by decreasing production by another competing species (Werner and Anholt, 1996). However, such compensatory growth was not observed and total biomass production increased with increasing density of treefrog tadpoles (Figure 5), especially in the absence of predators. The lack of compensatory growth suggests that either resources were not limiting or that bullfrog and treefrog tadpoles exploit different resource pools. Bullfrog tadpoles can facultatively switch their mode of feeding from grazing on periphyton and detritus to filter feeding phytoplankton from the water column (Werner 1994), but, in general, hylid tadpoles are not efficient filter feeders (Seale and Beckvar 1980). It is possible that this difference in resource exploitation leads to weak inter-specific competition between ranid and hylid tadpoles observed in the field (Skelly 1995b).

Conclusion

This study confirmed previous studies, which have shown that bullfrog tadpoles do not directly affect the survival or growth rate of treefrog tadpoles (Kupferberg 1997b, Adams 2000). Contrary to previous studies, this study showed that bullfrog tadpoles do decrease development rate of treefrog tadpoles, especially in the presence of predators. Also, treefrog tadpoles can have a moderate *inter-specific* competitive effect on the growth of bullfrog tadpoles. There was little evidence that indirect effects mediated through the presence of a native predator biased competitive interactions in favour of the invulnerable bullfrog tadpoles. In general, *intra-specific* competitive effects were strong for both bullfrog and treefrog tadpoles but *inter-specific* competition between the two species was weak. Compared to other native species in the Pacific Northwest, Pacific treefrogs have shown the least decline in distribution and abundance (Fisher and Shaffer 1995). This could be attributed, in part, to their ability to tolerate competition from introduced bullfrogs, at least during the larval stages.

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Table 1: Density manipulation of bullfrog and treefrog tadpoles. These five density treatments were crossed in a fully factorial design with the presence and absence of roughskin newts as predators for a total of 10 treatment combinations.

Species	**Number of tadpoles per tank**				
	Treatment 1	Treatment 2	Treatment 3	Treatment 4	Treatment 5
Bullfrog	5	5	5	10	20
Treefrog	50	100	200	50	50

Comparisons to assess competition

	Comparison	Response variable *
Intra-specific competition		
Treefrog on Treefrog	Treatment 1, 2, 3	Of treefrog tadpoles
Bullfrog on Bullfrog	Treatment 1, 4, 5	Of bullfrog tadpoles
Inter-specific competition		
Bullfrog on Treefrog	Treatment 1, 4, 5	Of treefrog tadpoles
Treefrog on bullfrog	Treatment 1, 2, 3	Of bullfrog tadpoles

**Response variables were percent survival, development rate (stage/day), and growth rate (percent/day). Tank means were estimated as –*

$$\text{Percent survival} = \frac{\text{number of tadpoles at the end of the experiment}}{\text{number of tadpoles at the start of the experiment}}$$

$$\text{Development rate} = \frac{\text{(mean final development stage) – (mean initial development stage)}}{\text{experimental duration in days}}$$

$$\text{Growth rate} = \frac{\ln(\text{final mean tadpole wt}) - \ln(\text{initial mean tadpole wt})}{\text{experimental duration in days}}$$

Table 2: Candidate set of models and an explanation of the factors that they test for. BF=bullfrog tadpole density, TF=treefrog tadpole density, NEWT=caged presence of predatory roughskin newt; '*' denotes statistical interaction between terms. Because BF are not vulnerable to newts, the candidate set of models for bullfrogs does not include NEWT or BF*NEWT terms.

No	Model	Effects tested for
1	TF+BF+NEWT+TF*NEWT+BF*NEWT	Impact of direct competition and newt presence (Main effects). The statistical interaction terms test whether the slope of the regression between response variable and competitor density is different in the presence and absence of newts. A significant interaction term would indicate the presence of indirect competitive effects
2	TF+BF+NEWT+BF*NEWT	The statistical interaction term tests for indirect *inter-specific* competitive effect experienced by treefrogs in the presence of newts.
3	TF+BF+NEWT+TF*NEWT	The statistical interaction term tests for the indirect competitive effects of treefrog tadpoles in the presence of newts.
4	TF+BF+NEWT	Main effects alone. This model is not included in the candidate set of models examining the response of BF because BF are not vulnerable to newts.
5	BF+NEWT	Impact of direct competitive effect of BF and newt presence.
6	TF+NEWT	Impact of direct competitive effect of TF and newt presence.
7	NEWT	Impact of predator presence alone.
8	TF+BF	Impact of direct competitive effects alone.
9	BF	Impact of direct competition from BF.
10	TF	Impact of direct competition from TF.
11	NULL	Includes only blocking terms.

Table 3: Model selection for the effect of *intra* and *inter-specific* competition on the development and growth rates of bullfrog tadpoles. The table also includes the Log Likelihood of the model, the number of parameters (K), and the sample size adjusted Akaike's Information Criterion (AIC_c). The model with the smallest AIC_c is the most parsimonious model. ΔAIC_c gives the difference in AIC_c value between a given model and the most parsimonious model.

Model	**LogLik**	**K**	**AIC_c**	**Δ AIC_c**	**AIC_c weight w_i**
Bullfrog development Rate					
BF	107.87	4	-206.85	0.00	0.60
BF+TF	108.48	5	-205.60	1.25	0.32
NULL	103.88	3	-201.24	5.60	0.04
NEWT+BF+TF+NEWT*TF	108.90	7	-201.13	5.71	0.03
TF	103.96	4	-199.03	7.82	0.01
Bullfrog growth Rate					
BF+TF	254.18	5	-496.99	0.00	0.64
BF	251.78	4	-494.68	2.32	0.20
NULL	249.58	3	-492.65	4.35	0.07
NEWT+BF+TF+NEWT*TF	254.24	7	-491.81	5.18	0.05
TF	249.93	4	-490.97	6.02	0.03

Table 4: Response of treefrog tadpoles. For legend details see Table 2 and 3. Percent survival data were overdispersed and so quasi-likelihood methods were used for model fitting ($QAIC_c$) in this case.

Model	LogLik	K	$QAIC_c$/ AIC_c	Δ $QAIC_c$/ AIC_c	$QAIC_c$/ AIC_c weight w_i
Treefrog percent survival					
NEWT	-102.01	7	221.52	5.73	0.73
BF+NEWT	-101.77	8	224.18	8.39	0.19
TF+NEWT	-103.06	8	226.76	10.97	0.05
TF+BF+NEWT+TF*NEWT	-101.18	10	229.94	14.15	0.01
TF+BF+NEWT	-103.31	9	230.63	14.84	0.01
TF+BF+NEWT+BF*NEWT	-102.63	10	232.84	17.05	0.00
NULL	-109.66	6	233.86	18.07	0.00
TF+BF+NEWT+TF*NEWT+BF*NEWT	-101.27	11	233.97	18.18	0.00
BF	-109.19	7	235.88	20.09	0.00
TF	-111.37	7	240.24	24.45	0.00
TF+BF	-111.69	8	244.03	28.24	0.00
Treefrog development rate					
TF+BF+NEWT	100.57	6	-187.19	0.00	0.42
TF+BF+NEWT+BF*NEWT	101.51	7	-186.35	0.84	0.28
TF+BF+NEWT+TF*NEWT	100.57	7	-184.48	2.71	0.11
TF+BF+NEWT+TF*NEWT+BF*NEWT	101.80	8	-184.10	3.09	0.09
TF+NEWT	97.54	5	-183.71	3.48	0.07
TF+BF	96.45	5	-181.53	5.66	0.02
TF	93.85	4	-178.81	8.38	0.01
BF+NEWT	69.13	5	-126.89	60.30	0.00
BF	67.88	4	-126.88	60.31	0.00
NULL	66.61	3	-126.71	60.48	0.00
NEWT	67.79	4	-126.70	60.49	0.00
Treefrog growth rate					
TF+NEWT	208.59	5	-405.82	0.00	0.44
TF	206.32	4	-403.75	2.07	0.16
TF+BF+NEWT	208.74	6	-403.52	2.30	0.14
TF+BF+NEWT+TF*NEWT	209.92	7	-403.18	2.65	0.12
TF+BF+NEWT+TF*NEWT+BF*NEWT	210.66	8	-401.80	4.03	0.06
TF+BF	206.45	5	-401.54	4.29	0.05
TF+BF+NEWT+BF*NEWT	208.79	7	-400.91	4.91	0.04
BF	173.04	4	-337.18	68.64	0.00
BF+NEWT	173.62	5	-335.87	69.95	0.00
NULL	169.05	3	-331.57	74.25	0.00
NEWT	169.54	4	-330.19	75.63	0.00

Table 5: Model selection to assess the effect of predator presence and competition on the behaviour of tadpoles.

Model	LogLik	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ weight w_i
Proportion of treefrog tadpoles moving and feeding					
TF	69.55	8	-121.51	0.00	0.55
TF+BF	69.60	9	-119.20	2.31	0.17
TF+NEWT	69.58	9	-119.16	2.35	0.17
TF+BF+NEWT	69.63	10	-116.79	4.72	0.05
TF+BF+NEWT+NEWT*TF	70.18	11	-115.36	6.14	0.03
TF+BF+NEWT+NEWT*BF	69.70	11	-114.40	7.11	0.02
TF+BF+NEWT+NEWT*TF+NEWT*BF	70.66	12	-113.74	7.77	0.01
BF	57.82	8	-98.06	23.45	0.00
BF+NEWT	57.85	9	-95.70	25.81	0.00
NULL	54.12	7	-93.03	28.48	0.00
NEWT	54.15	8	-90.72	30.79	0.00
Newt Avoidance					
NULL	103.13	7	-191.05	0.00	0.38
NEWT	103.56	8	-189.53	1.52	0.18
TF	103.32	8	-189.06	1.99	0.14
BF	103.16	8	-188.73	2.32	0.12
TF+NEWT	103.75	9	-187.49	3.56	0.06
BF+NEWT	103.58	9	-187.16	3.89	0.05
TF+BF	103.32	9	-186.65	4.40	0.04
TF+BF+NEWT	103.75	10	-185.02	6.02	0.02
TF+BF+NEWT+NEWT*TF	103.75	11	-182.50	8.55	0.01
TF+BF+NEWT+NEWT*BF	103.75	11	-182.50	8.55	0.01
TF+BF+NEWT+NEWT*TF+NEWT*BF	103.75	12	-179.91	11.14	0.00

Table 6: Model selection for food availability (chlorophyll *a* concentration), bullfrog tadpole biomass production, and treefrog tadpole biomass production.

Model	**logLik**	**K**	**AIC_c**	**Δ AIC_c**	**AIC_c weight w_i**
Food availability					
TF+BF	305.37	9	-590.74	0.00	0.36
TF+BF+NEWT	306.60	10	-590.73	0.01	0.35
TF+BF+NEWT+NEWT*TF	306.84	11	-588.68	2.06	0.13
TF+BF+NEWT+NEWT*BF	306.73	11	-588.46	2.28	0.11
TF+BF+NEWT+NEWT*TF+NEWT*BF	306.86	12	-586.14	4.60	0.04
BF	300.13	8	-582.68	8.06	0.01
BF+NEWT	301.24	9	-582.47	8.27	0.00
TF+NEWT	297.50	9	-575.00	15.74	0.00
NULL	295.64	7	-576.07	14.67	0.00
NEWT	296.65	8	-575.73	15.02	0.00
TF	296.47	8	-575.37	15.37	0.00
Bullfrog biomass production					
BF+TF	-150.39	5	312.14	0.00	0.31
BF	-151.70	4	312.29	0.15	0.28
BF+TF+NEWT+NEWT*BF	-148.58	7	313.82	1.68	0.13
BF+TF+NEWT	-150.14	6	314.23	2.09	0.11
BF+NEWT	-151.45	5	314.26	2.12	0.11
BF+TF+NEWT+NEWT*TF	-149.91	7	316.49	4.35	0.03
BF+TF+NEWT+NEWT*TF+NEWT*BF	-148.56	8	316.64	4.50	0.03
NULL	-160.03	3	326.57	14.43	0.00
NEWT	-159.82	4	328.53	16.39	0.00
TF	-159.85	4	328.59	16.45	0.00
TF+NEWT	-159.64	5	330.65	18.51	0.00
Treefrog biomass production					
TF+BF+NEWT+NEWT*TF	-163.20	7	343.07	0.00	0.73
TF+BF+NEWT+NEWT*TF+NEWT*BF	-163.17	8	345.84	2.78	0.18
TF+NEWT	-168.83	5	349.03	5.96	0.04
TF+BF+NEWT	-167.66	6	349.27	6.21	0.03
TF+BF+NEWT+NEWT*BF	-167.01	7	350.68	7.61	0.02
TF	-173.55	4	355.98	12.91	0.00
TF+BF	-172.58	5	356.52	13.45	0.00
BF+NEWT	-177.94	5	367.25	24.19	0.00
NEWT	-183.76	4	376.42	33.35	0.00
BF	-181.31	4	371.51	28.44	0.00
NULL	-186.47	3	379.45	36.39	0.00

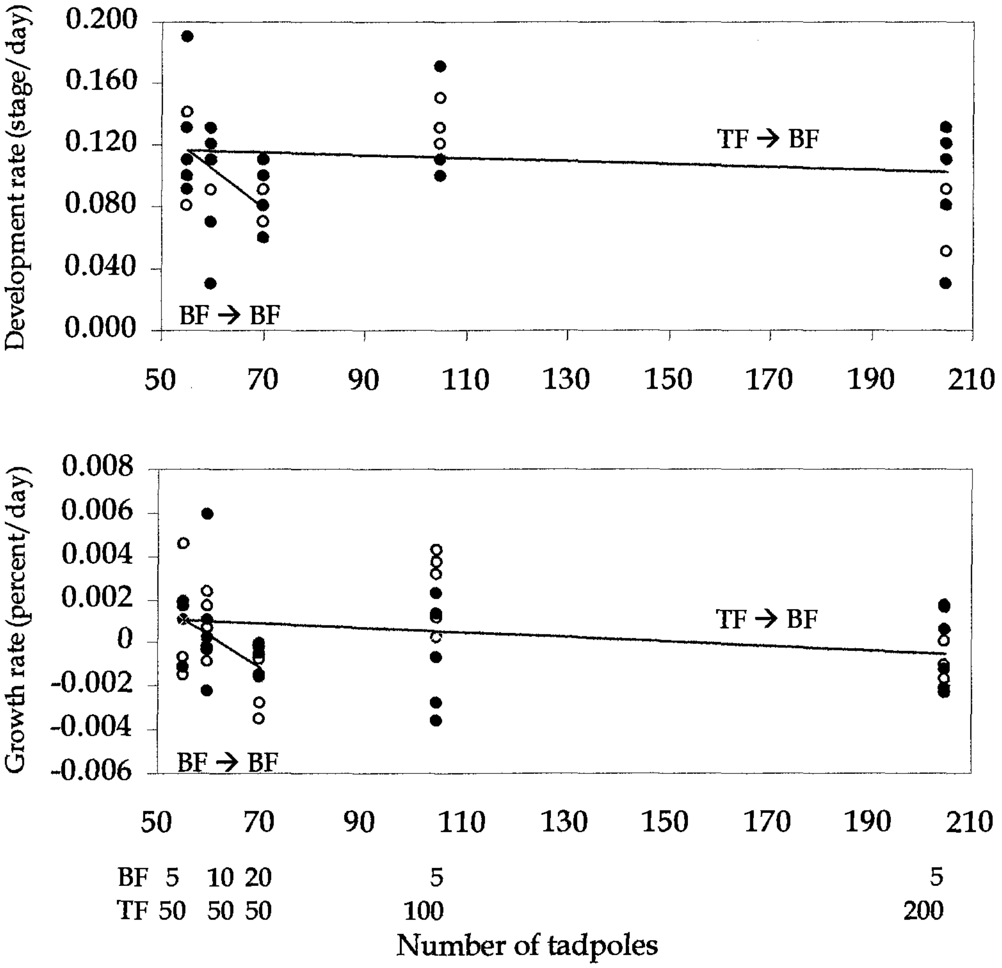


Figure 1: Development rate (top) and growth rate (bottom) of bullfrog tadpoles. The x-axis shows total number of tadpoles and the panel below indicates the number of bullfrog and treefrog tadpoles in that total. Closed symbols indicate treatments with newts present. *Intra-specific* competition is indicated by BF→BF and *inter-specific* competition by TF→BF.

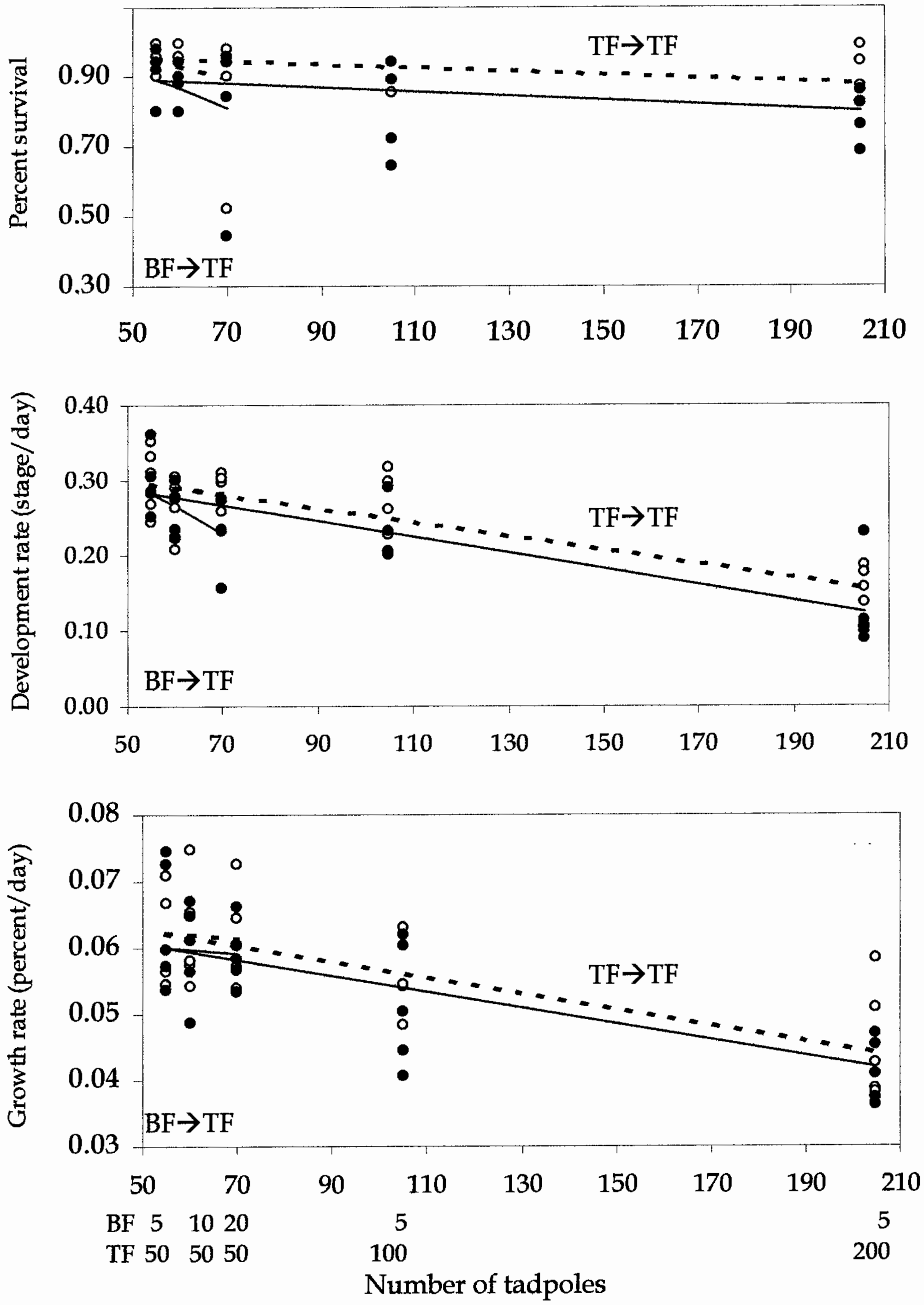


Figure 2: Percent survival (top), development rate (middle), and growth rate (bottom) of treefrog tadpoles. Closed symbols and solid lines indicate predator presence. In this case, *intra-specific* competition is TF→TF and *inter-specific* competition is BF→TF.

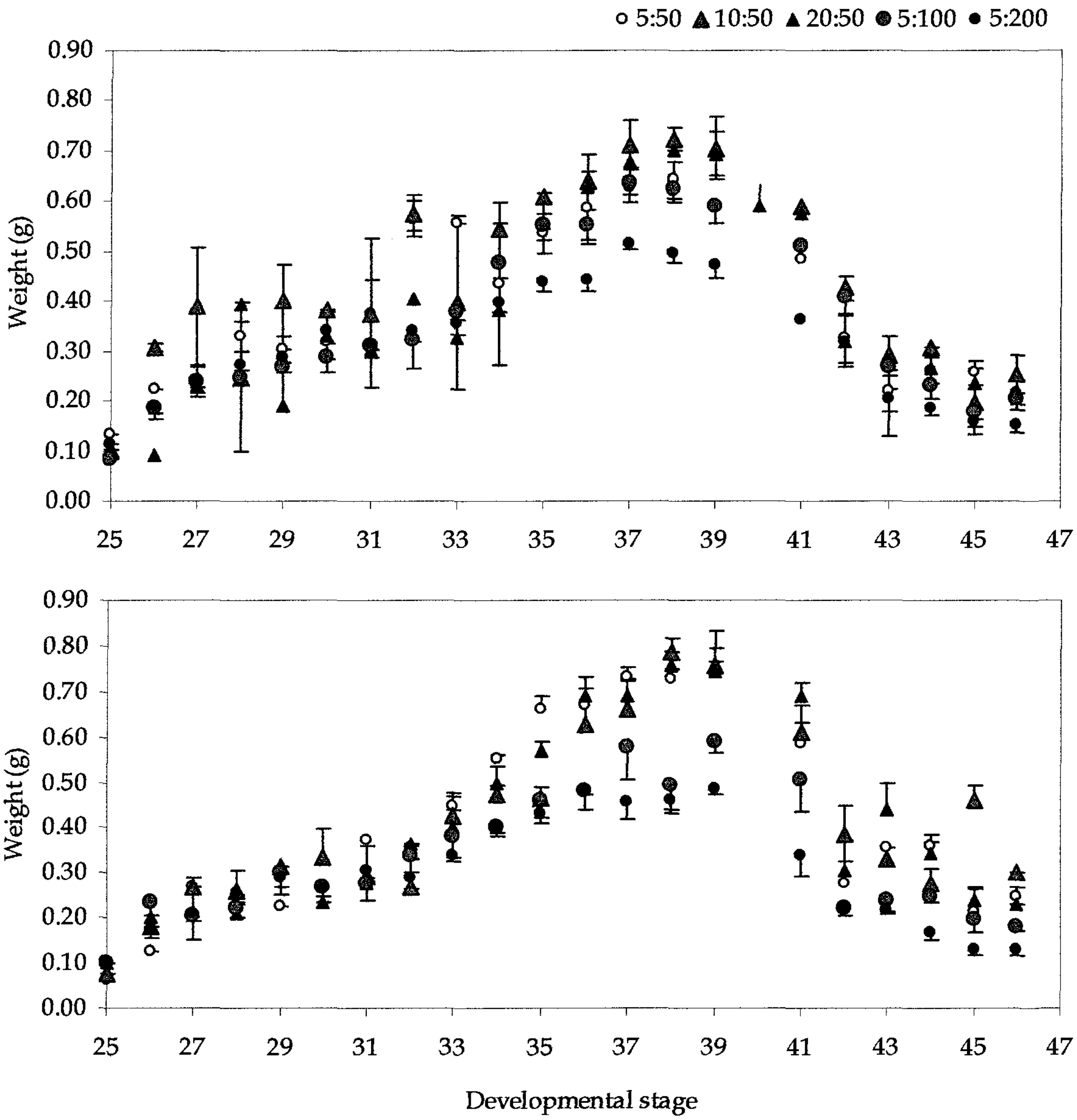


Figure 3: Size of treefrog tadpoles at each development stage in the absence of newts (top) and in the presence of newts (bottom). At higher *intra-specific* densities, particularly in the presence of newts, the size of treefrog tadpoles was smaller at developmental stages > 34.

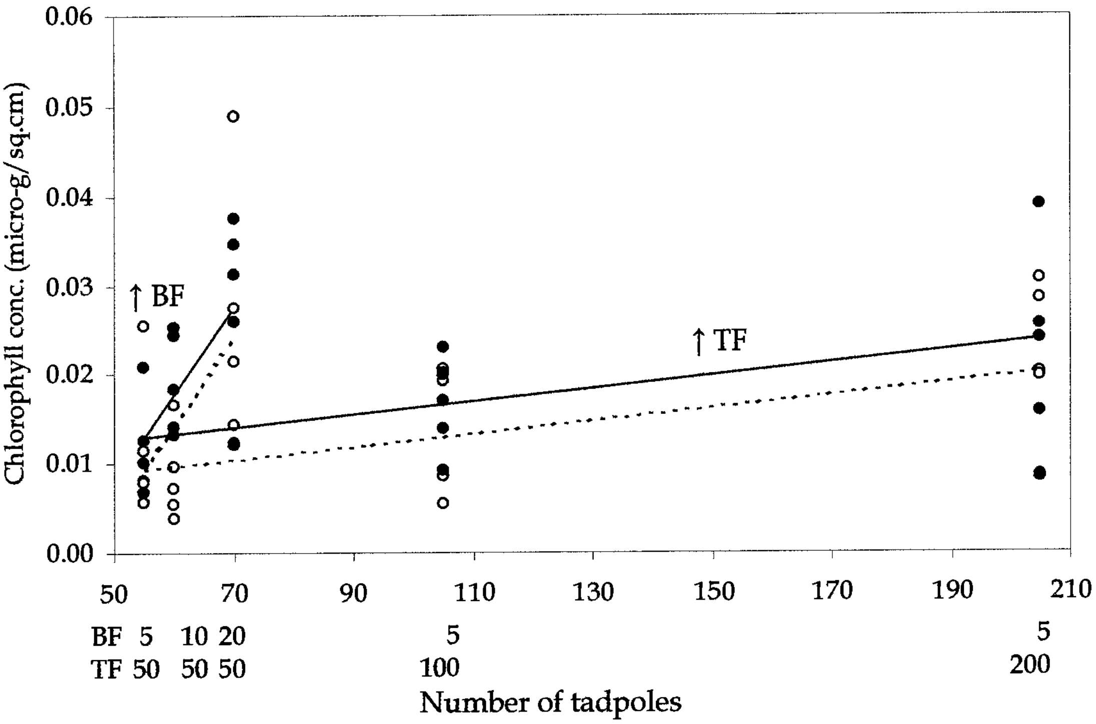


Figure 4: Chlorophyll *a* concentration (μg/cm²) was used to measure the quantity of periphyton in the tanks. Legend is as in Figure 1 and 2.

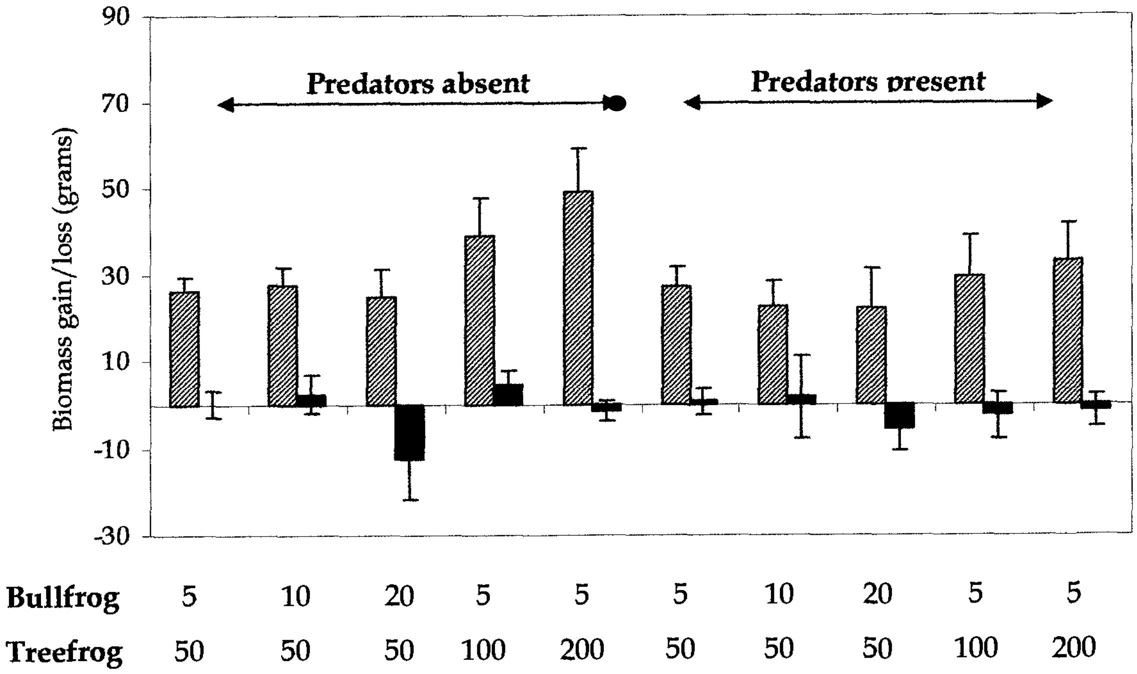
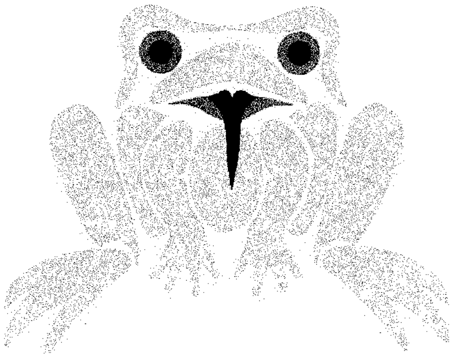


Figure 5: The total biomass (± SD) of the bullfrog tadpoles (black bars) and treefrog tadpole (hatched bars).

CHAPTER 5



COMPARISON OF COMPETITIVE EFFECTS OF INTRODUCED BULLFROG TADPOLES ON NATIVE RED-LEGGED FROG AND PACIFIC TREEFROG TADPOLES

Abstract

In this study, I compared the competitive effects of the introduced American bullfrog (*Rana catesbeiana*) on two native species: Pacific treefrog (*Hyla regilla*) and red-legged frog (*Rana aurora*). I assessed whether differences in larval life-history traits and behaviour of the two native tadpoles make them differentially susceptible to competition from bullfrog tadpoles. The competition between the introduced tadpole and the two native tadpoles can be exacerbated because of their differential vulnerability to predation by an introduced predator: pumpkinseed sunfish (*Leopomis gibbosus*). Bullfrog tadpoles are invulnerable to predation by these fish but both native tadpoles are susceptible. Predatory cues from the non-lethal presence of pumpkinseed sunfish are expected to elicit anti-predator behaviours, such as reduced foraging, in the native tadpoles. Such altered behaviour of the native tadpoles is expected to bias competitive interaction in favour of invulnerable bullfrog tadpoles (trait-mediated indirect effect). Introduced bullfrog tadpoles decreased both development and growth rate of red-legged frog tadpoles. Bullfrog tadpoles decreased the development rate of treefrog tadpoles but did not affect their growth rate. Bullfrog tadpoles were not affected by competition from native red-legged frog tadpoles. Both native tadpoles failed to express anti-predator behaviour in the presence of the introduced pumpkinseed sunfish. Pacific treefrog tadpoles seemed to be less affected by competition from bullfrog tadpoles because of their small size, higher activity levels, higher growth and development rates, and propensity to feed in the water column. Red-legged frog tadpoles seemed more vulnerable because of their larger size, slower development and growth rates, lower activity levels, and benthic habits.

Introduction

Declines in native species following the establishment of introduced species have been widely documented (Pimentel et al. 2000, Sax and Brown 2000). These declines are usually attributed to predation by (Ross 1991, Kaufman 1992, Knapp and Matthews 2000) and competition from (Brown and Moyle 1991, Petren and Case 1996, Kiesecker and Blaustein 1998, Kiesecker et al. 2001) the invading species . However, not all members of the invaded community are equally susceptible. Particularly in the case of competitive effects, two native species in similar niches can be affected in very different ways due to subtle variations in habitat specialization and indirect effects mediated through other members of the community.

The American bullfrog (*Rana catesbeiana*) has been widely introduced in the Pacific Northwest for almost a century now, but the extent of its impact is debated. While many studies have documented negative effects on native amphibians (Moyle 1973, Green 1978, Hammerson 1982, Fisher and Shaffer 1995, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001), other studies have questioned the actual magnitude and causality of these effects (Hayes and Jennings 1986, Adams et al. 1998, Adams 2000). Such opposing results could arise not only due to species-specific impacts of bullfrogs but also due to differences in indirect effects that depend on the community within which these impacts are measured.

In this study, I compared the competitive effects of the introduced bullfrog on two native frog species with widely overlapping distribution ranges in the Pacific Northwest (Stebbins 1985): the red-legged frog (*Rana aurora*) and the Pacific treefrog (*Hyla regilla*). I also examined whether the relative impact of these competitive effects is modified by indirect effects mediated through the non-lethal presence of pumpkinseed sunfish (*Leopomis gibbosus*), an introduced predator on the native tadpoles. Pumpkinseed sunfish have been introduced into lakes in British Columbia, probably as an unintentional consequence of sport-fish stocking.

In general, treefrog populations seem to persist where bullfrogs have been introduced while the red-legged frog and the closely related yellow-legged frog populations seem to decline (Hayes and Jennings 1986, Fisher and Shaffer 1995). Given the complex life histories of anurans, bullfrogs can cause declines in native species either through predation and/or competition in the adult or larval stage (Kiesecker and Blaustein 1997, Kupferberg 1997). In this study, I focus exclusively on competitive effects in the larval stages and examine whether the differential declines of Pacific treefrogs and red-legged frogs is due in part to different levels of competition that these species experience from the invading bullfrog tadpoles.

Strong competitive effects are expected at this stage because, in their native habitat, bullfrog tadpoles have been shown to have a negative impact on the growth rate of green frog tadpoles (*Rana clamitans*) (Werner 1991, Werner and Anholt 1996). The other reason to focus on the tadpole stage is because the three species overlap in habitat usage mainly during this stage. Pacific treefrogs are almost exclusively terrestrial in the post-metamorphic stages and only return to ponds to breed (Green and Campbell 1992). Post-metamorphic red-legged frogs are more aquatic but can forage in moist, forested, upland habitats far from water bodies (Green and Campbell 1992, Corkran and Thoms 1996, Pearl et al. 2004). Bullfrogs are almost exclusively aquatic, never straying far from standing water except during the spring and fall migrations (Bury and Whelan 1986).

Inter and *intra-specific* competitive interactions between anuran larvae depend on the relative size of the tadpoles and also on unique species traits such as behaviour (Werner 1994). Larger individuals are favoured in behaviourally mediated interference competition. The effect of size under exploitative competition depends on allometric size relationships of the resource gain and metabolic cost curves (Werner 1994). Larger tadpoles are better at resource acquisition and therefore have a higher per-capita negative effect on competitors. Smaller tadpoles usually have higher net gain curves and are able to sustain growth under lower resource levels, which enables them to be affected less by competitors (Werner 1994).

The three species of tadpoles in this study varied widely in size. Both red-legged frogs and Pacific treefrogs breed early in the year (Licht 1969), and their tadpoles face competition from second year bullfrog tadpoles that have over-wintered in the ponds. The size of these second year bullfrog tadpoles can range from 2 to 12 g (*unpublished* *data*). The native tadpoles are much smaller. At their maximum size, reached just prior to initiation of metamorphosis, red-legged frog tadpoles range in size from 1 to 2.5 grams, and Pacific treefrog tadpoles from 0.3 to 1 gram (*unpublished data*). Competition among tadpoles is thought to be mainly exploitative although behavioural interference competition has been observed between bullfrog and red-legged frog tadpoles under experimental conditions (Kiesecker et al. 2001). If competition between these tadpoles were mainly exploitative, treefrog tadpoles would fare better than red-legged frog tadpoles when faced with competition from introduced bullfrog tadpoles. However, if it were mainly behavioural interference competition, red-legged frog tadpoles would fare better than treefrog tadpoles.

In addition to relative size effects, species-specific traits such as activity levels affect competitive interactions between species. More active species gain more resources, maintain higher growth rates and hence are better competitors (Lawler 1989, Werner 1991, Werner 1992, Skelly 1995, Relyea and Werner 1999). However, the more active species are also more vulnerable to predation (Morin 1995). Tadpoles decrease activity levels in order to reduce predation risk (Skelly and Werner 1990, Relyea and Werner 1999, Van Buskirk 2000). The degree to which these anti-predator behaviours are performed affects the competitive relationship between species and can reverse competitive superiority (Werner and McPeek 1994, Skelly 1995, Werner and Anholt 1996, Relyea and Werner 1999, Relyea 2000). Additionally, activity levels increase when resources are low (Anholt and Werner 1995, Anholt et al. 1996, Anholt et al. 2000). This makes the expression of anti-predator behaviour sensitive to competitor induced resource depletion (Peacor and Werner 2000). Not much is known about the comparative activity levels of red-legged frog and treefrog tadpoles under the threat of predation from introduced pumpkinseed sunfish or under conditions of resource depletion due to competition from introduced bullfrogs.

Native fish in lentic habitats where treefrog and red-legged frogs breed are small and gape-limited, and do not pose a major predatory threat to the tadpoles (Hayes and Jennings 1986). The introduced sunfish, however, are capable of reducing native tadpole survival to zero in pond enclosures (Adams 2000, *unpublished data*). Bullfrog tadpoles are unpalatable to fish (Kruse and Francis 1977) and are rarely consumed even when the tadpoles are small. The large size of second year bullfrog tadpoles makes them invulnerable to predation by these fish. If native tadpoles decrease their activity in response to the threat of predation from the caged sunfish, resource competition would be further biased in favour of bullfrog tadpoles.

To summarize: I compared the *intra-specific* and *inter-specific* competitive interactions between introduced bullfrog and native red-legged frog tadpoles; I compared the *inter-specific* competitive effect of these two species on Pacific treefrog tadpoles; and I examined how the above competitive effects were modified by trait-mediated indirect effects arising due to anti-predator behaviour expressed by red-legged and treefrog tadpoles in the presence of introduced pumpkinseed sunfish.

Methods

Experimental set-up

The *intra* and *inter-specific* competitive effects between red-legged frog and bullfrog tadpoles were estimated using an additive density experimental design consisting of five treatments (Table 1, Underwood 1986). These treatments were crossed with the presence and absence of a caged pumpkinseed sunfish as predator to estimate the indirect effect of the predator on competitive interactions (Table 1). Fifty treefrog tadpoles were added to all the tanks and their response to the ten treatments was monitored. This enabled me to estimate the *inter-specific* competitive effect of bullfrog and red-legged tadpoles on treefrog tadpoles. However, this experimental design does not permit either the estimation of *intra-specific* competitive effects of treefrog tadpoles or the *inter-specific* competitive effect of treefrog tadpoles on the other two species. The ten treatments were replicated in four blocks.

Cattle watering tanks (diameter = 1.6 meters, depth = 0.5 meters) were used as artificial ponds as they have proven to be ideal mesocosms in other studies (Werner and Anholt 1996, Skelly and Kiesecker 2001). The tanks were set out in an open field at the University of Victoria, British Columbia, Canada. The tanks were covered with 40% shade cloth to avoid excessive water temperatures (mean ± SD, 17.1^{0}C ± 2.8) and to prevent oviposition by dragonflies. The tanks were stocked with 300g of leaf litter (mainly *Quercus* and *Acer*) to provide cover for the tadpoles and to encourage the growth of periphyton (Werner and Anholt 1996, Peacor and Werner 1997). The tanks were fertilized with dissolved $NaNO_3$ and K_3PO_4 in the atomic ratio 40:1 N:P to discourage the growth of inedible cyanobacteria (Anholt 1994). To prevent bacterial blooms that reduce oxygen levels, all tanks were inoculated with *Daphnia spp*. To ensure adequate algal growth, the tanks were filled with water and set-up more than a month before initiation of the experiment. A few days before the tadpoles were introduced into the tanks, the available food was supplemented by adding 50g of commercial rabbit food.

The density of tadpoles is extremely variable between ponds and even within a pond (Turnipseed and Altig 1975, Caldwell et al. 1980). Bullfrog tadpole density can be as high as 106 ± 52 tadpoles/m^3 (mean ± SD) (*unpublished data*). Pacific treefrog tadpole density varied from 31.1 ± 5.5 to 162.1 ± 10.4 tadpoles/m^3 (Chapter 3) and can be as high as 220 ± 170 tadpoles/m^3 (*unpublished data*). The field density of red-legged frog tadpoles has been estimated to range from 50 to 1800 tadpoles/m^3 (Kiesecker et al. 2001). Cattle tank studies are thought to overestimate the importance of competitive interactions (Skelly 2002). By setting experimental densities in the lower range of those observed in the field, the study provided a conservative estimate of the degree of competition.

Bullfrog tadpoles were captured locally from Prior Lake. Red-legged frog and Pacific treefrog egg masses were collected from local fishless ponds. They were hatched in children's wading pools and raised there until they were large enough to be handled (> 6mm SVL). The experiment was initiated on the 15th and 16th of May, 2002 by adding tadpoles to two blocks on each day. Tadpoles were randomly assigned to experimental blocks and treatments. Pumpkinseed sunfish were housed in fibreglass mesh bags (30 cm in diameter, 50 cm deep) attached to the side of the tank. Two treefrog tadpoles and one red-legged frog tadpole were fed to the fish every three days to ensure that the chemical scent of predation remained fresh in the tanks (Chivers and Smith 1998, Kats and Dill 1998).

The behaviour of tadpoles was videotaped during weeks four and five of the experiment. One block was videotaped per day, mainly on sunny days between 11 am and 3 pm to prevent the confounding effect of varying activity levels during the day. I waited ten minutes after opening the lids of the tanks to permit the tadpoles to return to normal activity. I videotaped four red-legged and four treefrog tadpoles for 30 seconds each. As it was not possible to truly randomly sub-sample the tadpoles in the tank, I chose one tadpole in each quarter of the tank for observation. Red-legged tadpoles were sometimes very difficult to see because they were under the leaf litter. In such cases I filmed all visible red-legged tadpoles to a maximum of four. From the videotapes the time each tadpole spent feeding, moving, and being inactive was recorded.

The experiment was terminated during the week of June 24th when at least a few treefrog metamorphs were observed in most of the tanks. The tanks were drained and the leaf litter removed by hand to ensure that all the tadpoles were captured. Tadpoles were weighed and their development stage determined immediately following capture. The standing crop of periphyton was estimated using unglazed tiles (225 cm^2) that hung on the side of the tanks, approximately 25 cm below the surface of the water (Kiffney and Richardson 2001). The concentration of chlorophyll *a* was used to estimate the quantity of periphyton in each sample (Nystrom et al. 2001). The periphyton was scraped off the sampling tiles using distilled water and filtered through a glass fibre filter (GF/C or GF/F). Chlorophyll *a* concentration was estimated using standard spectrophotometric methods following ethanol extraction (Wintermans and DeMots 1965).

Data Analysis

All statistical analyses were done on tank means. Three response variables were measured for each species: percent survival, developmental rate, and growth rate (Table 1). Tadpoles reach maximum weight at stage 37-38 after which they lose up to 50% of their body mass during metamorphic transformation (Pandian and Marian 1985, Werner 1986). In tanks with a high proportion of metamorphosing tadpoles, therefore, growth rate will be underestimated compared to tanks with few metamorphosing tadpoles. To avoid this bias, for all metamorphosing tadpoles (Gosner Stage > 38), I back-estimated their weight at Stage 38 using a mass-loss regression (Werner and Anholt, 1996). It was these adjusted weights that were used in calculating final mean weight of tadpoles in each tank. Such adjustment was only necessary for treefrog tadpoles, as the other tadpoles did not reach metamorphosis during the experiment.

The behaviour variables were estimated as proportions that together sum to 1. To maintain statistical independence in the analysis, I used only two of the three variables. I chose proportion of time spent feeding because this is most sensitive to changes in resource levels due to competition. I chose the proportion of time tadpoles spent moving because tadpoles are expected to decrease movement to minimize predation risk. The behaviour variables were arc-sine transformed prior to analysis to meet assumptions of normality and homoscedacity.

Percent survival was analyzed using logistic regression analysis. All other variables were analyzed using univariate ANCOVA models, with tadpole densities as a continuous variables and predator presence as a fixed factor (Table 2). Model selection was based on sample size adjusted Akaike's information criterion (AIC_c). Using this method, all models can be compared simultaneously, including models that are not nested in a statistical sense (Burnham and Anderson, 2002). The model with the smallest AIC_c value is the most parsimonious model, given the data, and is considered the best-fit model. Akaike's weights, which sum to 1, express the relative support for a given model in a pre-determined set of models (Burnham and Anderson, 2002). Comparative support for two models can therefore be expressed as a ratio of their AIC weights (evidence ratio). The relative importance of the experimental factors was calculated by summing the AIC_c weights (w_{cum}) of the models in which the factor was included. The per capita and per unit biomass competitive effect of tadpoles was assessed using model averaged regression coefficients with unconditional standard errors. These adjust for model uncertainty (Burnham and Anderson, 2002).

Treefrog tadpole survival data were overdispersed (overdispersion parameter $\hat{c}$ = 4.21). This is common with grouped data (tank means) due to violations of assumptions of independence and parameter homogeneity (Eberhardt 1978). I adjusted for this overdispersion in model selection by calculating quasi-likelihoods of the models (Crawley 2002). While percent survival in most tanks was high, there were two tanks (one red-legged frog and one treefrog tadpoles) where survival rate fell close to 50%. Analysis with and without these outliers gave similar results and they were retained in the final analysis. Statistical analyses were performed using the General Linear Models function in S-plus 6 for Windows (Insightful Corp., Seattle USA).

Results

Bullfrog tadpoles as recipients of competition

Survival: Bullfrog tadpoles in all treatments survived until the end of the experiment.

Development Rate: The development rate of bullfrog tadpoles was low (Table 3) compared to the two native species, and on average the tadpoles progressed from stage 26 ± 1.2 to stage 30 ± 2.0 (Mean ± SD). Increasing tadpole density decreased bullfrog tadpole development rate (Figure 1). The model with *intra-specific* competitive effects alone had three times the support as the model that included both bullfrog and red-legged frog tadpole density effects (Table 4).

Growth Rate: Bullfrog tadpole growth rate was close to zero during the experiment (Figure 1, Table 3). As expected from this, the null model was the best-fit model for growth rate (Table 4).

Red-legged frog tadpoles as recipients of competition

Survival: Mean survival was 0.93 ± 0.08 (mean ± SD). It varied little among experimental treatments (Figure 2) and the null model was the best-supported model (Table 5).

Development Rate: The development rate of red-legged frog tadpoles was only slightly faster than that of bullfrog tadpoles (Table 3). On average the tadpoles progressed from stage 25.6 ± 0.22 to stage 30.7 ± 2.4. Increasing tadpole density strongly decreased red-legged frog tadpole development rate (Figure 2). The best-supported model was the one that included both bullfrog and red-legged frog tadpole density effects (Table 5). The per-capita competitive effect of both species was very similar (Figure 2, Table 3). The presence of the predator did not decrease the development rate (Figure 2, Table 4) and therefore there was no evidence of trait-mediated indirect effects.

Growth Rate: Red-legged frog tadpoles maintained a positive growth rate (Table 3). They more than tripled their body mass over the experimental period (starting wt: 0.19±0.04 grams; end wt: 0.61±0.24 grams). As with development rate, the best-supported model was the one that included both bullfrog and red-legged frog tadpole density effects (Table 5). The per capita decrease in growth rate (Figure 2) effected by the two species was similar in magnitude (Table 3). The presence of the predator did not affect growth rate (Figure 2, Table 5).

Pacific treefrog tadpoles as recipients of competition

Survival: Mean survival was similar to that of red-legged frog tadpoles, 0.94 ± 0.08 (mean ± SD) and did not vary among experimental treatments (Figure 3). The null model was the best-supported model (Table 6).

Development Rate: The development rate of treefrog tadpoles was three times that of bullfrog tadpoles and more than twice that of red-legged frog tadpoles (Table 3). On average the tadpoles progressed from stage 26.2 ± 0.14 to stage 38.4 ± 1.5 and many of the tadpoles had reached metamorphosis by the end of the study. Overall, increasing tadpole density strongly decreased treefrog tadpole development rate (Figure 3). The best-supported model was the one that included both bullfrog and red-legged frog tadpole density effects (Table 6). The per-capita competitive effect of bullfrog tadpoles was slightly greater than that of red-legged frog tadpoles (Figure 3, Table 3). There was some evidence that the presence of fish decreased development rates (Figure 3), but the model that included this factor was only half as well supported as the model with competitor effects alone (Table 6). There was no evidence for trait-mediated indirect effects.

Growth Rate: As expected from their small size, treefrog tadpoles maintained the strongest positive growth rate (Table 3) and increased in body mass by an order of magnitude over the experimental period (starting wt: 0.06±0.007 grams to end wt: 0.60±0.10 grams). While increasing red-legged frog tadpole density decreased treefrog tadpole growth rate (Table 6), there was little evidence that bullfrog tadpole density had any effect (Figure 3). As with development rate above, there was some evidence that the presence of fish decreased treefrog tadpole growth rates (Figure 2), but the model that included this factor was only half as well supported as the model with red-legged frog density effects alone (Table 6).

Tadpole behaviour

Red-legged frog tadpoles used different microhabitats and were less active compared to Pacific treefrog tadpoles. Of all the red-legged frog tadpoles observed, 92% were found at the bottom of the tank close to leaf litter. Pacific treefrog tadpoles on the other hand were observed on the water surface (51%) or on the walls (41%). Red-legged frog tadpoles were also far less active compared to Pacific treefrog tadpoles (Figure 4).

Of the 298 tadpoles observed during the study, there were only six occasions when the tadpoles interacted. Five of these involved treefrog tadpoles bumping into each other during feeding bouts and could be interpreted as interference competition. The other instance was of a red-legged tadpole that was startled when a treefrog tadpole swam by. This did not appear to be a competitive interaction. I did not observe any behavioural interactions between bullfrog tadpoles and the native tadpoles.

In terms of individual tadpole behaviour, I predicted that predator presence would decrease the time tadpoles spent moving because it makes them more vulnerable to predatory attacks. However, neither tadpole species seemed to alter movement levels in response to predators (Table 7). I also predicted that increasing competitor densities would decrease resource levels and that tadpoles would have to spend more time feeding. Increasing competitor levels did not affect the time red-legged tadpoles spent feeding (Table 7). Both bullfrog density and fish presence affected the time treefrog tadpoles spent feeding (Table 7). Counter to my predictions, the time spent feeding decreased with increasing bullfrog tadpole density and increased in the presence of fish (regression coeff. ± SE: bullfrog density $-7.6\text{x}10^{-3} \pm 5.0\text{x}10^{-3}$, fish presence 0.25 ± 0.08).

Periphyton Biomass

The standing crop of periphyton was expected to decrease with increasing tadpole density due to higher grazing pressure. However, periphyton increased with increasing bullfrog tadpole density (Table 8, Figure 5, regression coefficient: $8.1\text{x}10^{-4} \pm 3.8\text{x}10^{-4}$ μg/cm^2). Red-legged frog tadpole density did not influence periphyton biomass (Table 8). I also expected that, as tadpoles decreased activity and grazing in the presence of fish, periphyton biomass would increase. Periphyton biomass did increase in the presence of fish (Table 8, Figure 5, regression coefficient: $2.2\text{x}10^{-2} \pm 7.9\text{x}10^{-3}$ μg/cm^2) even though observations did not detect any change in the behaviour of tadpoles.

Discussion

Comparison of competition among the three species

In all three species percent survival was not influenced by the experimental treatments, as is often the case in mesocosm studies (Blaustein and Margalit 1996, Van Buskirk 2000). Competition between bullfrog tadpoles and red-legged frog tadpoles was asymmetrical. Bullfrog tadpoles decreased both the development and growth rate of red-legged frog tadpoles (Table 5) but red-legged frog tadpoles did not affect either development or growth rate of bullfrog tadpoles (Table 4). The magnitude of the per-capita *inter-specific* competitive effect of bullfrog tadpoles on red-legged frog tadpoles was similar to the per-capita *intra-specific* competitive effect that red-legged frog tadpoles exerted on themselves (Table 3). In addition, the *intra-specific* competitive effect of bullfrogs on themselves was less than their *inter-specific* competitive effect on red-legged frog tadpoles (Table 3). Taken together, this indicates that second year bullfrog tadpoles are better larval competitors than red-legged frog tadpoles.

The competitive effect of bullfrogs on the two native tadpoles, the red-legged frog tadpole and the Pacific treefrog tadpole, was also asymmetrical. Bullfrog tadpoles decreased the development rates of the two native tadpoles (Table 5 and 6) and the magnitude of these effects was similar (Table 3). However, bullfrog tadpoles had a strong negative effect on the growth rate of red-legged tadpoles (Table 5) but no effect on the growth rate of treefrog tadpole (Table 6). This suggests that compared to red-legged frog tadpoles, treefrog tadpoles are less affected by competition from bullfrog tadpoles.

Consequence of competitive effects of bullfrog tadpoles

The decreased development rate of the two native tadpoles results in a longer time to metamorphosis. Given that daily mortality rate of tadpoles in natural ponds can be as high as 10% (Chapter 3), longer development time results in fewer tadpoles surviving to metamorphosis.

Both native species are under time constraints to metamorphose before the end of the summer because neither species can over-winter in the larval stage (Calef 1972, Green and Campbell 1992). The per-capita reduction in development rate caused by bullfrog tadpoles is similar between the two species. However, treefrog tadpoles have a much higher intrinsic development rate compared to red-legged frog tadpoles (Table 3). This higher rate allows treefrog tadpoles to attain metamorphosis before the end of the season. Red-legged frog tadpoles, on the other hand, because of their slower development rate and because this rate is further slowed in the presence of bullfrogs, may not be able to attain metamorphosis in time.

Bullfrog tadpoles decreased the growth rate of red-legged frog tadpoles but not treefrog tadpoles (Figure 2 and 3). A consequence of slower growth rate is that it prolongs the time tadpoles stay small, which results in them remaining susceptible to gape-limited predators for a longer time (Travis et al. 1985, Semlitsch 1990, Puttlitz et al. 1999).

Under conditions of high competition some tadpoles may be able to adaptively decrease development rate but maintain growth rates. However, if competitive conditions are severe, tadpoles may be unable to maintain such a trade-off (Wilbur 1980) When faced with competition from introduced bullfrog tadpoles, treefrog tadpoles seemed to be able to respond adaptively by decreasing their development rate while maintaining growth rate. Red-legged frog tadpoles seemed unable to sustain this trade-off and suffered both decreased development and growth rates (Lawler et al. 1999). In the case of red-legged frog tadpoles these decreased rates may eventually lead to smaller size at metamorphosis. Small size at metamorphosis has been shown to have negative fitness consequences in the terrestrial stages (Berven 1990, Goater 1994, Scott 1994, Morey and Reznick 2001, Altwegg and Reyer 2003).

Effect of size on competitive interaction

Competitive interactions among larval anurans are thought to be partly mediated through the relative size of the tadpoles (Werner 1994). The three species of tadpoles in this study varied in size by two orders of magnitude. The large size of bullfrog tadpoles is advantageous in behaviourally mediated interference competition (Kiesecker et al. 2001) but the few instances of behavioural interference that I observed were between treefrog tadpoles. *Inter-specific* competition between these three species is probably exploitative, although other forms of interference competition cannot be ruled out (Griffiths 1991, Kiesecker and Blaustein 1999).

In exploitative competition, organisms can be superior competitors by either being better at resource gathering and depletion (effect) or by being better able to convert these resources into growth and development (response) (Goldberg and Landa 1991, Werner 1994). The competitive response of tadpoles thus depends on the difference between the foraging gain and metabolic cost curves, both of which are modeled as power functions of body size (Werner 1994). It is not possible to simply predict the effect of size on the competitive relations between tadpoles because of the many factors that affect the shapes of these curves. In general, however, larger tadpoles are stronger at resource depletion and have stronger per-capita competitive effects (better effect competitors), while smaller tadpoles are able to maintain higher growth rates under lower resources (better response competitors) (Werner 1994).

In this experiment, larger size did not translate into higher per-capita competitive effects (Table 3). The larger bullfrog tadpoles had lower per-capita competitive effects on growth rate of treefrog tadpoles compared to the smaller red-legged frog tadpoles (Table 6). On the 'response' aspect of the interactions, the small treefrog tadpoles were able to maintain much higher development and growth rates compared to the larger red-legged frog and bullfrog tadpoles (Table 3). To a lesser extent, red-legged frog tadpoles were able to maintain higher development and growth rates compared to bullfrog tadpoles.

Effect of predators on competitive interactions

Tadpoles decrease their foraging activity to minimise predation risk (Werner and Anholt 1996, Lardner 1998, Altwegg 2002). Neither red-legged frog tadpoles nor treefrog tadpoles exhibited reduction in activity in response to caged pumpkinseed sunfish (Table 7). In a previous study, I was unable to detect anti-predator behaviour in treefrog tadpoles in response to roughskin newts, but noted reduction in development and growth rates of the tadpoles in the presence of predators (Chapter 4). In this study, neither red-legged frog nor treefrog tadpoles showed marked reduction in development and growth rates in response to caged pumpkinseed sunfish (Table 5 and 6). The lack of response is unlikely to be caused by insufficient predatory chemosensory cue in my cattle tanks as a previous study with a native predator demonstrated a significant response (Chapter 4). Both red-legged frog and treefrog tadpoles are very vulnerable to predation by fish (Goodsell and Kats 1999, Adams 2000, Matthews et al. 2001, Adams et al. 2003) and all tadpoles fed to the pumpkinseed sunfish in this experiment were consumed immediately. Tadpoles may react to a general predator cue or that of killed or injured conspecifics (Chivers and Smith 1998, Kiesecker et al. 1999). However, many tadpole species seem able to discriminate between cues and alter behaviours in response to specific native predators and the level of predation risk (Kiesecker et al. 1996, Eklov and Werner 2000, Relyea 2001b, a). The exact nature of the predator cue is unknown (Kats and Dill 1998). In other experimental studies both red-legged frog tadpoles and Pacific treefrog tadpoles have demonstrated anti-predator behaviours to native predators which resulted in changes to life-history response variables (Chapter x, Kupferberg 1998, Chivers et al. 2001a, Chivers et al. 2001b, Kiesecker et al. 2002). The red-legged frog and treefrog egg masses in this study were collected from fishless ponds. It is possible that they failed to react adaptively because they did not recognize the introduced pumpkinseed sunfish as a potential predator or assess their level of vulnerability to this new predator. Such an inability to recognise the potential threat of predation from introduced predators has been demonstrated before for red-legged frogs (Kiesecker and Blaustein 1997), Pacific treefrogs (Chivers et al. 2001b), and other amphibians (Gamradt and Kats 1996).

Effect of activity levels on competitive interactions

Activity levels are directly related to food gathering and therefore more active species are able to maintain higher growth and development rates than less active ones. All else being equal, more active tadpoles have been shown to be superior competitors (Lawler 1989, Werner 1991, Werner 1992, Skelly 1995, Relyea 2001b). In this study, treefrog tadpoles spent a greater proportion of the time feeding compared to red-legged frog tadpoles (Figure 4). This, in part, enabled treefrog tadpoles to maintain development and growth rates that were twice those of red-legged frog tadpoles (Table 3).

Higher activity levels also make the tadpoles more predation prone (Azevedo-Ramos et al. 1992, Werner and Anholt 1993, Skelly 1994). I expected that because second year bullfrog tadpoles are invulnerable to predation by pumpkinseed sunfish, competitive interactions would be biased in favour of bullfrogs tadpoles in the presence of this predator. Indirect effects that skew competitive interactions in favour of the less predation prone species have been demonstrated in a number of studies (Semlitsch 1993, Werner and McPeek 1994, Skelly 1995, Werner and Anholt 1996, Peacor and Werner 2000, Relyea 2000). However, because the naïve native tadpoles failed to react to the introduced sunfish, I was unable to detect predator mediated indirect effects in this study (Table 5 and 6).

Effect of resources on tadpole competition

Since both *intra* and *inter-specific* competition was observed in the experiment, I expected that the periphyton biomass would decrease with increasing density of tadpoles (Nystrom and Abjornsson 2000, Loman 2001). However, periphyton biomass was strongly positively correlated to bullfrog tadpole density and, to a lesser extent, to red-legged frog tadpole density. This could be because the tadpoles were not feeding predominantly on the periphyton and were recycling more nutrients from the detritus at higher densities (Seale 1980, Werner 1994).

The three species in this study are considered generalized tadpoles that use keratinised beaks and denticles for scraping periphyton and detritus (Stebbins and Cohen 1995). Treefrog tadpoles were clearly feeding on periphyton as they were observed scraping algae off the sidewalls of the cattle tanks. They also fed often on the film of pollen and algae on the surface of the water (Kupferberg et al. 1994). Red-legged frog tadpoles and bullfrog tadpoles were benthic, feeding in the detritus and leaf litter in the bottom of the cattle tanks. It is possible that the ranid tadpoles were filter feeding. Filter feeding by bullfrog tadpoles has been shown to reduce phytoplankton densities and increase nutrient cycling (Seale 1980, Seale and Beckvar 1980).

Based on these observations, it appears that microhabitat use and resource overlap were higher between bullfrog and red-legged frog tadpoles than between bullfrog and treefrog tadpoles. Because of this, competition is expected to be more severe between red-legged frog and bullfrog tadpoles. Bullfrog tadpoles can alter their feeding from benthic sources to feeding in the water column under conditions of resource depletion (Werner 1994). This may explain why bullfrog tadpoles depressed growth and development of red-legged tadpoles but were not affected in turn by competition from red-legged frog tadpoles.

Conclusion

Introduced bullfrog tadpoles negatively affected the two native species of tadpoles but the strength of these effects differed between the species. This difference is at least partially accounted for by differences in life-history traits and behaviour of the two native tadpoles. Pacific treefrog tadpoles, because of their small size, higher growth and development rates, higher activity levels, and propensity to feed in the water column seemed to be less affected by bullfrog tadpoles. Red-legged frog tadpoles were more vulnerable to competition from bullfrog tadpoles because of their larger size, slower development and growth rates, lower activity levels, and benthic habits. Differences in microhabitat use, resource utilization, and diet have been shown to be important in the relative performance of tadpoles and their distribution (Skelly and Golon 2003). These remain to be explored further with respect to the interactions between introduced bullfrog and the native red-legged frog and Pacific treefrog tadpoles.

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Table 1: Density manipulation of bullfrog, red-legged frog and treefrog tadpoles. These five density treatments were crossed in a fully factorial design with the presence and absence of pumpkinseed sunfish as predators for a total of 10 treatment combinations.

Species	**Number of tadpoles per tank**				
	Treatment 1	Treatment 2	Treatment 3	Treatment 4	Treatment 5
Bullfrog	5	5	5	10	30
Red-legged	10	30	60	10	10
Treefrog	50	50	50	50	50

Comparisons to assess competition:

	Comparison	Response variable *
Intra-specific competition		
Bullfrog on bullfrog	Treatment 1, 4, 5	Of bullfrog tadpoles
Red-legged on red-legged	Treatment 1, 2, 3	Of red-legged tadpoles
Inter-specific competition		
Bullfrog on red-legged	Treatment 1, 4, 5	Of red-legged tadpoles
Bullfrog on treefrog	Treatment 1, 4, 5	Of treefrog tadpoles
Red-legged on bullfrog	Treatment 1, 2, 3	Of bullfrog tadpoles
Red-legged on treefrog	Treatment 1, 2, 3	Of treefrog tadpoles

**Response variables were percent survival, development rate (stage/day), and growth rate (percent/day). Tank means were estimated as –*

$$\text{Percent survival} = \frac{\text{number of tadpoles at the end of the experiment}}{\text{number of tadpoles at the start of the experiment}}$$

$$\text{Development rate} = \frac{(\text{mean final development stage}) - (\text{mean initial development stage})}{\text{experimental duration in days}}$$

$$\text{Growth rate} = \frac{\ln(\text{final mean tadpole wt}) - \ln(\text{initial mean tadpole wt})}{\text{experimental duration in days}}$$

Table 2: Candidate set of models and an explanation of the factors that they test for. BF=bullfrog tadpole density, RL=red-legged frog tadpole density, TF=treefrog tadpole density, FISH=caged presence of predatory pumpkinseed sunfish; '*' denotes statistical interaction between terms. Because BF are not vulnerable to newts, the candidate set of models for bullfrogs does not include FISH or BF*FISH terms.

No.	Model	Effects tested for
1	RL+BF+FISH+RL*FISH+BF*FISH	The full model includes the main effect of RL tadpole and BF tadpole density and the presence/absence of fish as predator. The statistical interaction terms test for the presence of trait mediated indirect effects in the presence of the predator on competitive interactions.
2	RL+BF+FISH+BF*FISH	Same as above except for the absence of the interaction term between RL tadpole density and fish presence. The interaction term specifically tests whether the slope of the regression of response variable against BF tadpole density is different in the presence and absence of fish.
3	RL+BF+FISH+RL*FISH	As above.
4	RL+BF+FISH	Main effects alone. BF and RL tadpole densities are treated as co-variates and the presence/absence of fish as a fixed factor.
5	BF+FISH	Impact of direct competitive effect of BF tadpoles and fish presence.
6	RL+FISH	Impact of direct competitive effect of RL tadpoles and fish presence.
7	FISH	Impact of predator presence alone.
8	RL+BF	Impact of direct competitive effects alone.
9	BF	Impact of direct competition from BF alone.
10	RL	Impact of direct competition from RL alone.
11	NULL	Includes only blocking terms.

Table 3: Values in italics are the mean development rate and growth rate across all treatments and blocks, for each species. Just below the development and growth rates are the per capita competitive effects. Model averaged regression coefficients (multiplied by 10,000) with unconditional standard errors, which adjust for model uncertainty, were used to estimate these competitive effects. Asterisked values indicate statistically strong effects (Table 4, 5, 6).

		Recipient tadpole species		
Variable	**Competitor Species**	**Bullfrog**	**Red-legged frog**	**Treefrog**
Development rate				
Overall Mean (stage/day)		*0.10 ± 0.006*	*0.14 ± 0.008*	*0.30 ± 0.006*
Regression Coefficients	Bullfrog	-13.0 ± 5.9*	-18.6 ± 6.2*	-16.5 ± 6.0*
Regression Coefficients	Red-legged frog	-1.1 ± 3.3	-17.7 ± 3.1*	-12.1 ± 3.1*
Growth rate				
Overall Mean (percent/day)		*0.0006 ± 0.01*	*0.03 ± 0.008*	*0.06 ± 0.005*
Regression Coefficients	Bullfrog	-1.1 ± 0.78	-2.1 ± 0.86*	0.34 ± 0.91
Regression Coefficients	Red-legged frog	-0.57 ± 0.46	-2.9 ± 0.45*	-1.1 ± 0.40*

Table 4: Model selection for the effect of *intra* and *inter-specific* competition on the development and growth rates of bullfrog tadpoles. The table also includes the Log Likelihood of the model, the number of parameters (K), and the sample size adjusted Akaike's Information Criterion (AIC_c). The model with the smallest AIC_c is the most parsimonious model. ΔAIC_c gives the difference in AIC_c value between a given model and the most parsimonious model.

Model	**LogLik**	**K**	**AIC_c**	**Δ AIC_c**	**AIC_c weight w_i**
Bullfrog development Rate					
BF	80.55	6	-146.55	0.00	0.60
BF + RL	80.73	7	-143.97	2.58	0.17
NULL	77.85	5	-143.94	2.61	0.16
RL	77.97	6	-141.39	5.16	0.05
FISH + BF + RL + FISH*RL	81.96	9	-139.92	6.63	0.02
Bullfrog growth Rate					
NULL	162.90	5	-314.04	0.00	0.38
BF	163.72	6	-312.90	1.14	0.21
RL + BF	165.14	7	-312.78	1.26	0.20
RL	163.31	6	-312.07	1.97	0.14
RL + BF + FISH + RL*FISH	167.18	9	-310.35	3.69	0.06

Table 5: Model selection for the effect of *intra* and *inter-specific* competition on the percent survival, development and growth rates of red-legged frog tadpoles. Legend details as in Table 4.

Model	**LogLik**	**K**	**$QAIC_c$/ AIC_c**	**Δ $QAIC_c$/ AIC_c**	**$QAIC_c$/ AIC_c weight w_i**
Red-legged tadpole percent survival					
NULL	-62.38	5	136.53	0.00	0.57
RL	-62.04	6	138.63	2.10	0.20
BF	-62.81	6	140.16	3.63	0.09
FISH	-63.07	6	140.68	4.14	0.07
RL+BF	-62.54	7	142.57	6.04	0.03
FISH+RL	-62.70	7	142.91	6.37	0.02
FISH+BF	-63.50	7	144.51	7.98	0.01
FISH+RL+BF	-63.21	8	147.06	10.53	0.00
FISH+RL+BF+FISH*BF	-62.99	9	149.98	13.44	0.00
FISH+RL+BF+FISH*RL	-64.13	9	152.26	15.72	0.00
FISH+RL+BF+FISH*RL+FISH*BF	-64.19	10	155.97	19.44	0.00
Red-legged tadpole development rate					
RL + BF	82.31	7	-147.12	0.00	0.76
FISH + BF + RL	82.31	8	-143.98	3.14	0.16
FISH + BF + RL + FISH*BF	82.33	9	-140.67	6.45	0.03
FISH + BF + RL + FISH*RL	82.33	9	-140.66	6.45	0.03
RL	77.44	6	-140.33	6.79	0.03
FISH + RL	77.44	7	-137.38	9.74	0.01
FISH + BF + RL + FISH*BF + FISH*RL	82.34	10	-137.09	10.03	0.00
NULL	67.98	5	-124.19	22.93	0.00
BF	68.04	6	-121.54	25.57	0.00
FISH	67.98	6	-121.41	25.70	0.00
FISH + BF	68.05	7	-118.59	28.52	0.00
Red-legged tadpole growth rate					
RL + BF	161.71	7	-305.92	0.00	0.65
FISH + RL + BF	161.90	8	-303.16	2.76	0.16
RL	158.21	6	-301.88	4.05	0.09
FISH + BF + RL + FISH*RL	162.50	9	-300.99	4.93	0.06
FISH + RL	158.37	7	-299.24	6.68	0.02
FISH + BF + RL + FISH*RL + FISH*BF	162.69	10	-297.80	8.13	0.01
FISH + RL + BF + FISH*BF + FISH*RL	162.69	10	-297.80	8.13	0.01
NULL	143.34	5	-274.91	31.01	0.00
BF	143.44	6	-272.34	33.58	0.00
FISH	143.41	6	-272.28	33.64	0.00
FISH + BF	143.52	7	-269.54	36.38	0.00

Table 6: Model selection for the effect of *intra* and *inter-specific* competition on the percent survival, development and growth rates of treefrog tadpoles. Legend details as in Table 4.

Model	**LogLik**	**K**	**QAIC$_c$/ AIC$_c$**	**Δ QAIC$_c$/ AIC$_c$**	**QAIC$_c$/ AIC$_c$ weight w_i**
Treefrog tadpole percent survival					
NULL	-90.312	6	195.17	0.00	0.75
RL	-90.303	7	198.11	2.94	0.17
FISH	-91.490	7	200.48	5.31	0.05
BF	-92.888	7	203.28	8.11	0.01
FISH+RL	-91.472	8	203.59	8.42	0.01
RL+BF	-92.643	8	205.93	10.76	0.00
FISH+BF	-92.831	8	206.31	11.14	0.00
FISH+RL+BF	-92.967	9	209.93	14.76	0.00
FISH+RL+BF+FISH*BF	-92.716	10	213.02	17.85	0.00
FISH+RL+BF+FISH*RL	-92.928	10	213.44	18.27	0.00
FISH+RL+BF+FISH*RL+FISH*BF	-92.921	11	217.27	22.10	0.00
Treefrog development rate					
RL + BF	84.47	7	-151.43	0.00	0.59
FISH + BF + RL	85.20	8	-149.75	1.69	0.25
FISH + BF + RL + FISH*BF	85.37	9	-146.75	4.69	0.06
FISH + BF + RL + FISH*BF + FISH*RL	86.69	10	-145.79	5.64	0.03
RL	80.08	6	-145.62	5.81	0.03
FISH + RL	80.67	7	-145.62	5.81	0.03
FISH + BF + RL + FISH*RL	86.67	9	-143.83	7.60	0.01
NULL	75.50	5	-139.24	12.19	0.00
BF	75.99	6	-137.44	14.00	0.00
FISH	75.97	6	-137.39	14.05	0.00
FISH + BF	76.46	7	-135.43	16.01	0.00
Treefrog growth rate					
RL	162.67	6	-310.79	0.00	0.46
FISH + RL	163.59	7	-309.68	1.11	0.26
RL + BF	162.78	7	-308.06	2.73	0.12
FISH + RL + BF	163.71	8	-306.77	4.02	0.06
FISH + RL + BF + FISH*RL	164.83	9	-305.67	5.12	0.04
FISH + RL + BF + FISH*BF + FISH*RL	165.90	10	-304.22	6.57	0.02
FISH + RL + BF + FISH*BF	163.89	9	-303.78	7.01	0.01
BF	159.08	6	-303.60	7.18	0.01
NULL	157.58	5	-303.39	7.40	0.01
FISH + BF	159.84	7	-302.19	8.60	0.01
FISH	158.29	6	-302.03	8.76	0.01

Table 7: Model selection to assess the effect of predator presence and competition on the behaviour of tadpoles. Models with zero support are not shown in the table.

Model	LogLik	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ weight w_i
Red-legged tadpoles					
Mean proportion of time spent moving					
NULL	-7.83	5	27.42	0.00	0.47
RL	-7.63	6	29.80	2.38	0.14
BF	-7.68	6	29.91	2.49	0.14
FISH	-7.77	6	30.09	2.67	0.12
BF + RL	-7.23	7	31.96	4.54	0.05
FISH + RL	-7.56	7	32.62	5.20	0.03
FISH + BF	-7.65	7	32.79	5.37	0.03
FISH + BF + RL	-7.20	8	35.04	7.62	0.01
Mean proportion of time spent feeding					
NULL	-11.39	5	34.54	0.00	0.49
FISH	-11.22	6	36.99	2.45	0.14
RL	-11.32	6	37.19	2.65	0.13
BF	-11.37	6	37.29	2.75	0.12
FISH + RL	-11.15	7	39.79	5.25	0.04
FISH + BF	-11.19	7	39.89	5.35	0.03
RL + BF	-11.32	7	40.14	5.60	0.03
FISH + RL + BF	-11.14	8	42.93	8.39	0.01
Pacific treefrog tadpoles					
Mean proportion of time spent moving					
NULL	2.50	5	6.77	0.00	0.30
RL	3.66	6	7.23	0.46	0.24
FISH	3.11	6	8.33	1.56	0.14
FISH + RL	4.38	7	8.74	1.97	0.11
BF	2.65	6	9.25	2.48	0.09
RL + BF	3.68	7	10.14	3.37	0.06
FISH + BF	3.24	7	11.02	4.25	0.04
FISH + RL + BF	4.42	8	11.80	5.03	0.02
FISH + RL + BF + FISH*BF	4.81	9	14.38	7.61	0.01
FISH + RL + BF + FISH*RL	4.79	9	14.42	7.65	0.01
Mean proportion of time spent feeding					
FISH + BF	0.91	7	15.67	0.00	0.42
FISH	-0.91	6	16.37	0.70	0.30
FISH + RL	-0.63	7	18.76	3.09	0.09
FISH + RL + BF	0.93	8	18.79	3.12	0.09
FISH + RL + BF + FISH*BF	1.31	9	21.38	5.71	0.02
NULL	-5.01	5	21.79	6.12	0.02
BF	-3.73	6	22.00	6.33	0.02
FISH + RL + BF + FISH*RL	0.94	9	22.12	6.45	0.02

Table 8: Model selection to assess food availability using chlorophyll *a* concentrations of periphyton scraped from sampling tiles. Legend details as in Table 4.

Model	**logLik**	**K**	**AIC_c**	**Δ AIC_c**	**AIC_c weight w_i**
FISH + BF	175.74	7	-333.99	0.00	0.52
FISH	173.31	6	-332.07	1.92	0.20
FISH + BF + RL	175.79	8	-330.94	3.05	0.11
FISH + RL	173.52	7	-329.55	4.44	0.06
FISH + BF + RL + FISH*RL	176.34	9	-328.68	5.31	0.04
FISH + BF + RL + FISH*BF	176.08	9	-328.17	5.82	0.03
BF	170.76	6	-326.98	7.01	0.02
FISH + BF + RL + FISH*BF + FISH*RL	177.28	10	-326.97	7.02	0.02
NULL	169.15	5	-326.53	7.46	0.00
RL + BF	170.80	7	-324.09	9.90	0.00
RL	169.29	6	-324.03	9.96	0.00

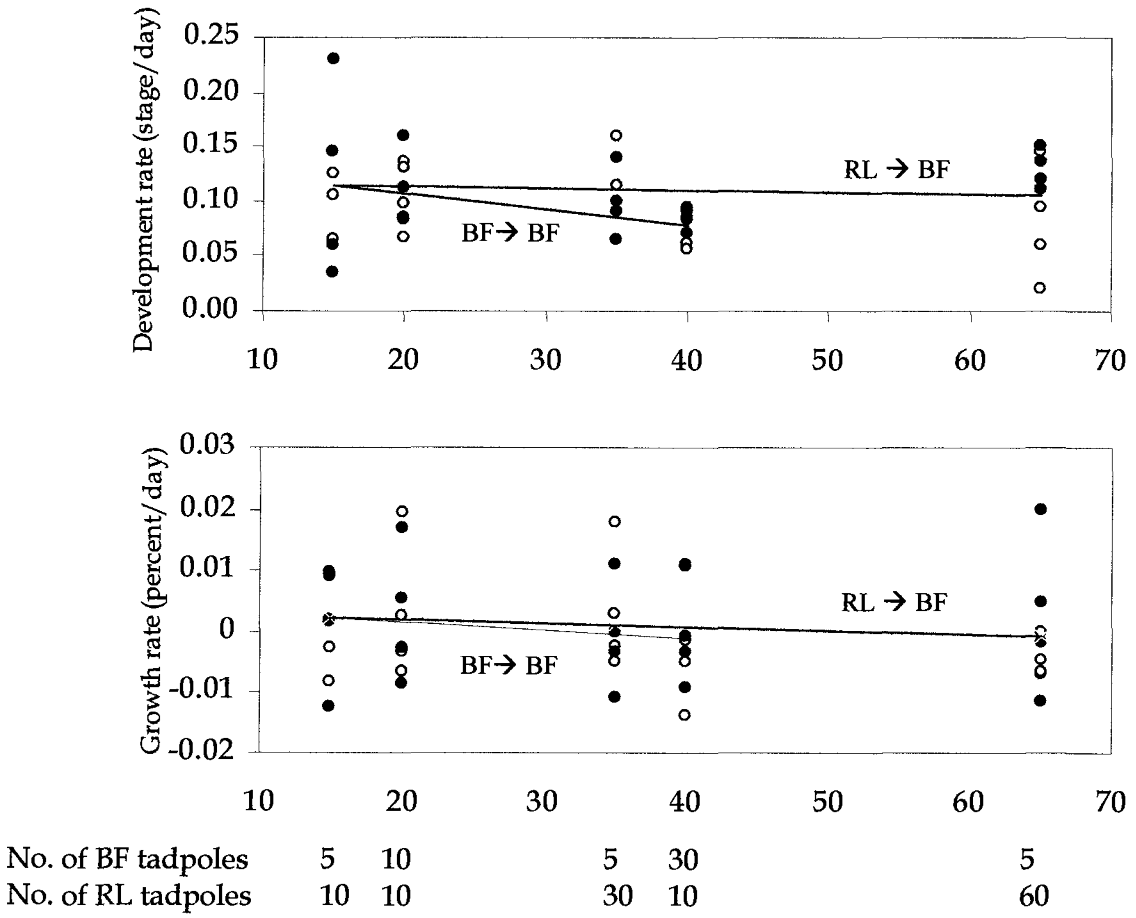


Figure 1: Development rate (top) and growth rate (bottom) of bullfrog tadpoles. The x-axis shows total number of tadpoles and the panel below indicates the number of bullfrog and red-legged frog tadpoles in that total. Closed symbols indicate treatments with fish present. *Intra-specific* competition is indicated by BF→BF and *inter-specific* competition by RL→BF.

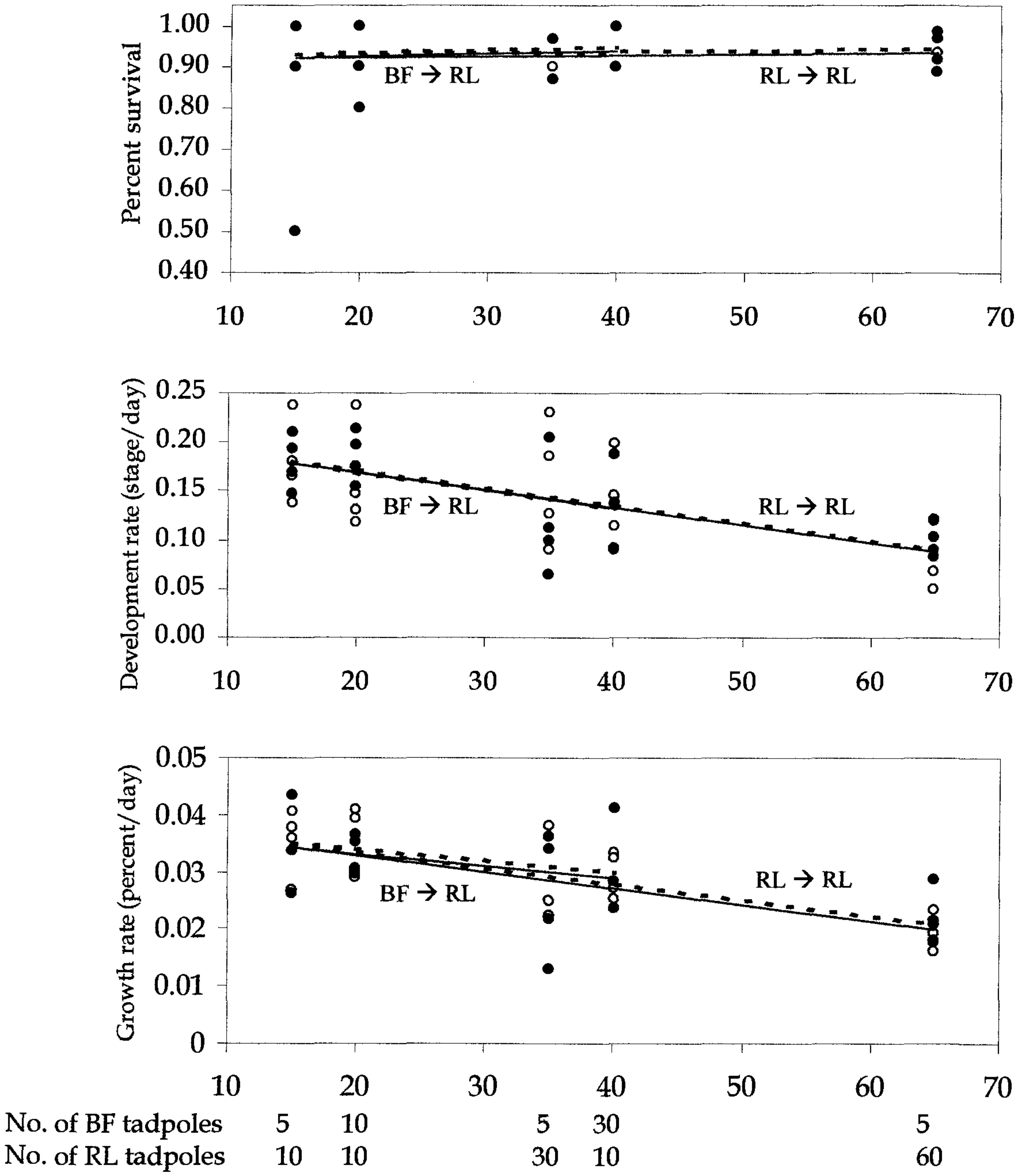


Figure 2: Percent survival (top), development rate (middle) and growth rate (bottom) of red-legged frog tadpoles. Legend as in Figure 1. *Intra-specific* competition is indicated by RL→RL and *inter-specific* competition by BF→RL.

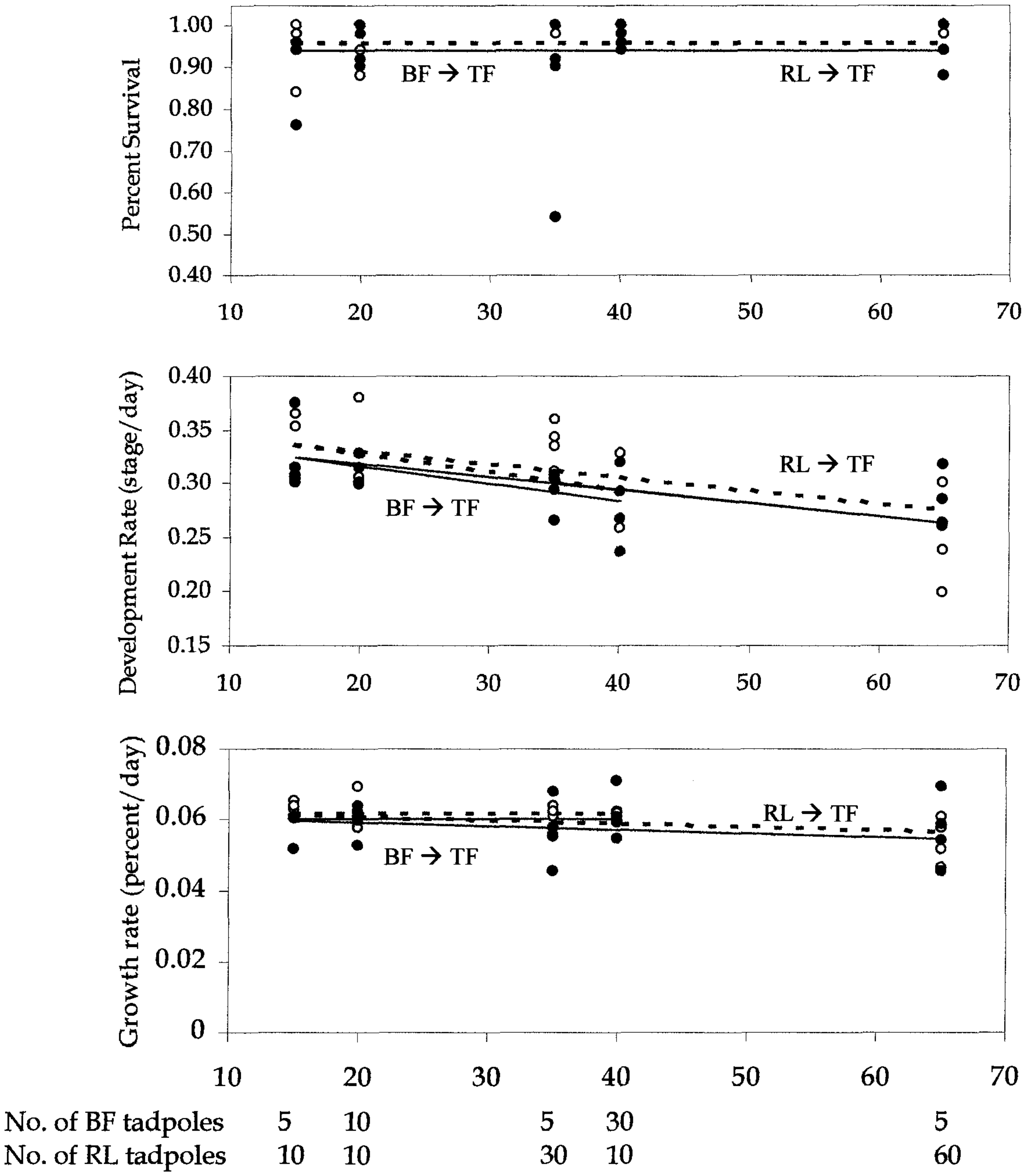


Figure 3: Percent survival (top), development rate (middle) and growth rate (bottom) of treefrog tadpoles. Legend as in Figure 1. *Inter-specific* competition from red-legged frog tadpoles is indicated as RL→TF and from bullfrog tadpoles as BF→TF.

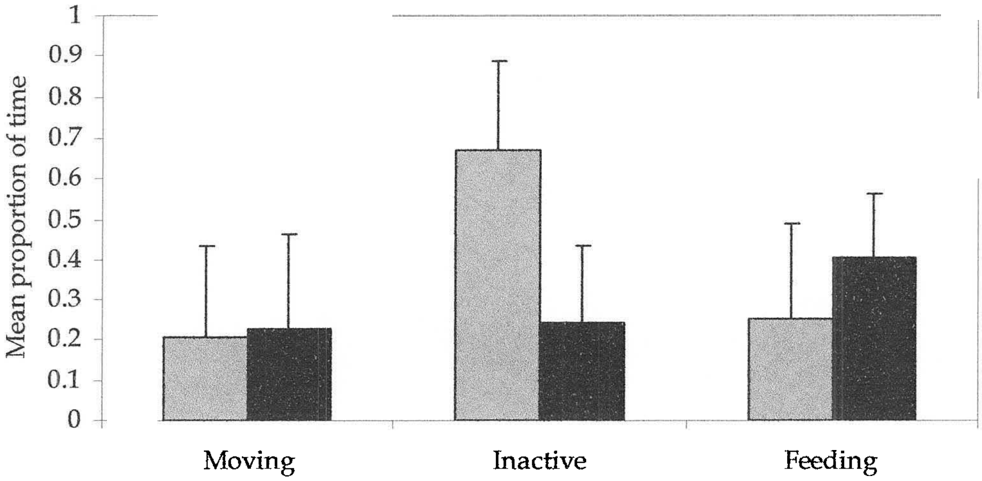
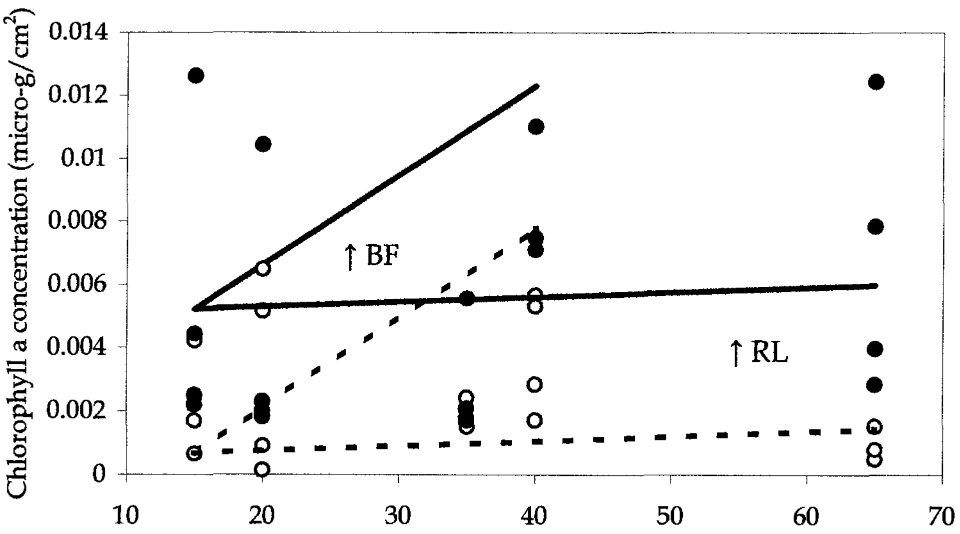


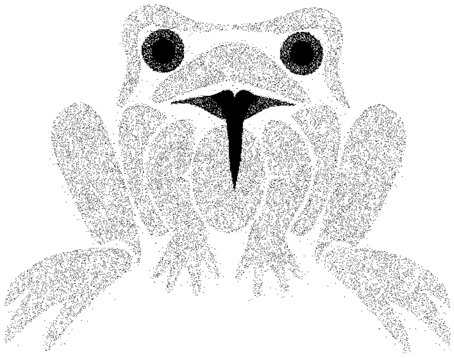
Figure 4: The proportion of time red-legged frog tadpoles (grey bars) and treefrog tadpoles (black bars) spent moving, being still and feeding. Red-legged frog tadpoles were more inactive compared to treefrog tadpoles.



No. of BF tadpoles	5	10	5	30	5
No. of RL tadpoles	10	10	30	10	60

Figure 5: Chlorophyll *a* concentrations used to estimate standing biomass of periphyton in the various competition treatments. The presence of fish (solid line) and increasing bullfrog tadpole density (↑BF) greatly increased chlorophyll *a* concentrations.

CHAPTER 6



SURVIVAL OF POST-METAMORPHIC BULLFROGS AND ITS INFLUENCE ON POPULATION GROWTH RATE: IMPLICATIONS FOR BULLFROG POPULATION CONTROL

Abstract

Introduced American bullfrogs (*Rana catesbeiana*) have negative effects on native fauna. However, there is a lack of adequate demographic information to design effective population control measures. I studied demography of four populations on southern Vancouver Island, Canada, using field observations and capture-mark-recapture methods to estimate growth, survival, and fecundity. Average egg mass size was 13,014 ± 7,296 eggs (N= 15, mean±SD), and eggs hatched within 3-5 days of being laid. Approximately 68% of the tadpoles metamorphosed the following year, while the reminder spent an additional year in the aquatic phase. Bullfrogs reached sexual maturity within two years of metamorphic transformation. Post-metamorphic survival ranged widely, from a low of 3% for some metamorphs to a high of 99% for some large bullfrogs, and was not correlated with habitat differences, population structure or weather conditions. Complementing these estimates with estimates from the literature, I parameterized a matrix population model. Prospective demographic perturbation analysis showed that bullfrog population growth rate (λ) was most influenced by the proportion of tadpoles metamorphosing early, and by early post-metamorphic survival rates. Projected population growth rate suggested declining populations at the individual study pond level, but this conflicted with the observation of a generally expanding population at the landscape level. I suggest that this can be reconciled by accounting for inter-pond migration. The effectiveness of control of different life-history stages both in relation to its effect on population growth rate and the logistical ease of implementing control was assessed. Culling of metamorphs soon after transformation in fall may be the most effective method of population control. However, all control efforts will be extremely labour intensive and costly, and the probability of eradication low.

Introduction

Population dynamics of amphibians are not well understood because it is difficult to concurrently estimate all the vital rates of their complex life-cycles that encompass both aquatic and terrestrial habitats (Chapter 2, Biek et al. 2002, Vonesh and De la Cruz 2002, Anholt et al. 2003). The introduced bullfrog (*Rana catesbeiana*) in western North America is no exception. While studies documenting their negative impacts accumulate (Moyle 1973, Hayes and Jennings 1986, Hecnar and M'Closkey 1996, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001), there is little demographic information on their populations. Analysis of transition matrix models can provide insight into population dynamics even when only minimal data on vital rates are available (Shea and Kelly 1998, Heppell et al. 2000a). Application of such analysis is not only useful in making projections about growth and expansion of bullfrog populations, but also in formulating techniques to control these expanding populations (Caswell 2000, Biek et al. 2002).

In this study, I estimated survival rates of post-metamorphic stages of bullfrogs, and then used this information in population matrix models to identify the vital rates that have the greatest influence on population growth rate. I focused on post-metamorphic survival rates because amphibian population growth rate has been shown to be more sensitive to changes in these survival rates, rather than larval transitions or fecundity (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002). Survival rate in four ponds was estimated over four to six years, and the patterns of variation examined in two different analyses. In the first analysis, spatial variation in *annual* survival among ponds was examined. In the second analysis, temporal variation in *daily* survival rate both within year (between season) and among years was examined in each pond.

Unlike many amphibians that move into upland habitats during the post-metamorphic phase, bullfrogs feed, mate and hibernate in permanent ponds (Bruneau and Magnin 1980a, Bury and Whelan 1986). This enabled me to treat bullfrogs at each pond site as a sub-population, as well as to use pond characteristics to examine factors affecting spatial variation in post-metamorphic survival rates (Marsh and Trenham 2001). If pond differences in basin structure, vegetational cover, food availability, predator density, and bullfrog population structure had a strong influence on the post-metamorphic survival rates, then these rates are expected to vary asynchronously among ponds (Skelly et al. 1999, Reaser 2000, Trenham et al. 2003). On the other hand, if weather variables such as precipitation and temperature had a strong influence on post-metamorphic survival rates of bullfrogs, then these rates are expected to vary synchronously among ponds (Anholt et al. 2003, Trenham et al. 2003). However, survival rates can be asynchronous despite the strong influence of weather variables, if the hydrology, basin structure, and vegetational cover around individual ponds modify the biotic impact of temperature and precipitation.

Year-to-year variation in population dynamics has been documented in a number of amphibians and it is often correlated to variation in weather conditions (Pechmann et al. 1991, Berven 1995, Shirose and Brooks 1995, Semlitsch et al. 1996, Green 2003). However, the differences in winter and summer survival have not been assessed before. During the active (summer) season biotic factors such as predation and food availability may be the main factors influencing survival rates (Berven 1995, Lampo and De Leo 1998). Winter survival may be more strongly influenced by abiotic factors such as temperature and rainfall (Shirose et al. 1993, Anholt et al. 2003). Therefore, for each pond, I examined whether survival rate of bullfrogs differed among years, and if yearly differences in temperature and precipitation in the two seasons accounted for these differences. Because recent studies have shown that weather affects survival of size/age classes differentially, the interaction between size and seasonal variables was also examined (Milner et al. 1999, Saether and Bakke 2000, Coulson et al. 2001).

Finally, using these estimates of post-metamorphic survival, field estimates of fecundity and tadpole transformation rates, and estimates of tadpole survival rates from the published literature, I constructed a stage-based population projection matrix. Using sensitivity and elasticity analyses I identified life stages and vital rates that strongly influenced population growth rate. Targeting these is considered the most effective way to control populations (Caswell 2000, De Kroon et al. 2000, but see Heppell et al, 2000b). The results are discussed in light of the logistical difficulties in managing these life-history stages.

To summarize: I examined the spatial and temporal variation in survival of the post-metamorphic stages of bullfrogs; I constructed a population matrix model and examined whether, as in other anuran populations, these stages strongly influence population growth rate; I assessed the effectiveness of culling post-metamorphic stages in efforts to manage and control the spread of these introduced bullfrog populations.

Methods

Field sites and marking

The four study ponds are in suburban Victoria, British Columbia, Canada (48°39′ N 123°25′ W). Beaver and Copley Pond are near the putative historic point of introduction of bullfrogs, while Trevlac Pond is 4 km away and Prior Lake is 6.5 km away from the first two ponds (Chapter 2). All four sites are permanent ponds with densely vegetated shorelines of cattails (*Typha latifolia*), hardhack (*Spiraea douglasii*), and willow (*Salix sp.)*. The ponds differed in area, bullfrog population density, number of frogs captured, duration of the marking effort, and mean size of adult frogs (Table 1). The four sites are treated as separate sub-populations because substantial migration between ponds was unlikely due to intervening distance. The closest intervening distance was 250 m between Copley Pond and Beaver Pond but over the study period only one migration event was observed. One adult male marked in Copley Pond was recaptured the following year in Beaver Pond.

Bullfrogs were captured by hand at night from a canoe between the months of May and October. The frogs were then taken to the laboratory where they were measured and individually marked using an inert elastomere paint injection (Northwest Marine Technologies Inc., Washington, USA) between the two layers of webbing membranes in their hind feet. The frogs were returned to the ponds the afternoon following capture. Mark loss was negligible (*personal observation*). There was a minimum of three capture occasions each year at each site, except for 2003 when there was only one recapture occasion.

Capture-Mark-Recapture (CMR) modelling

Survival and recapture rates were estimated using CMR methods (Lebreton et al. 1992). This method enabled me to generate models where estimates of survival and recapture rates are constrained to be dependent on categorical variables such as location, year, season; continuous variables such as population density, weight, temperature, precipitation and capture effort; and interactions between these variables. All these variables and their interactions can generate numerous complex models. However, sparseness of data on some occasions and in some locations required that the analyses be simplified by consolidating categorical variables. For example, size was consolidated to only two classes, metamorphs (< 30g) and other frogs (>30 g) in some analyses.

Models were fit using maximum-likelihood methods implemented in the program MARK (White and Burnham 1999) and model selection was based on sample size adjusted Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002). The model with the lowest AIC_c value is considered the model best supported by the data. Akaike weights indicate the relative support from the data for a particular model. When there was considerable uncertainty associated with model selection (AIC_c weight of best fit model < 0.90), inference was based on multiple models in this set (Burnham and Anderson 2002). The relative importance of a factor was calculated by summing the AIC_c weights (w_{cum}) of the models in which the factor was included. All data sets met the assumptions of CMR methods (Lebreton et al. 1992, White and Burnham 1999).

Spatial Variation among ponds: Metamorphs were excluded from this analysis due to low recapture rates in Copley Pond and Trevlac Pond. The analysis was also confined to the four years for which data from all ponds was available (1999-2002). Recapture probability was modeled as varying among ponds, among years, by pond area, and by capture effort. *Annual* survival probability was modelled as varying among ponds, among years and depending on the interaction between ponds and years. The interaction term examines whether the survival rates vary asynchronously among the ponds. I also tested whether variation among ponds could be explained by differences in the population density and/or mean size of frogs in each pond.

Seasonal and among year variation within ponds: For this analysis the year was divided into the active season (May to September) and the inactive winter season (October to April) and *daily* survival rates estimated within each season. Recapture probability was modelled as dependent on year, size class, and capture effort. Survival probability was modelled as varying among years, seasons, and size classes. In addition, I examined whether temporal variation among years and seasons was due to differences in mean seasonal temperature and precipitation. If temporal variation in survival rates was entirely weather related, the categorical variables, year and season, can be replaced by the covariates, mean temperature and precipitation. Retention of the 'season' variable indicates that seasonal differences in survival rate are not solely weather related. Interaction terms tested whether the weather variables had differential effects on survival during the two seasons and on the two size classes.

Matrix population modelling

Five stages were distinguished in the bullfrog life-cycle: egg and small tadpoles, 1st year tadpoles, 2nd year tadpoles, juveniles and adults (Figure 1). In British Columbia, bullfrog egg masses were laid from mid-June to mid-July. The eggs hatched within 3 to 5 days and, by early September, these tadpoles were 4.6 ± 0.9 cm long (mean ± SD) and at development stage 25.4 ± 0.7 (Gosner 1960). The tadpoles did not metamorphose within the first season and they spent the first winter hibernating as tadpoles. They became active again in April and 60% to 75% of these tadpoles (fast-track) metamorphosed by August of that year. The remainder hibernated for a second time (slow-track) and metamorphosed the following July. Metamorphs weighed 16.8 ± 5.1 grams on average and grew rapidly into juveniles (> 30 g) within two months after metamorphosis. Bullfrogs spent at least one year as juveniles and attained sexual maturity the following year. Egg masses contained an average of 13,014 ± 7,296 eggs (N= 15, mean ± SD) (Chapter 2). Survivorship of the post-metamorphic stages was estimated using combined data from the four ponds. Fecundity and tadpole transition probabilities were estimated from Beaver and Trevlac Ponds. Tadpole and embryo survival rates were obtained from the published literature (Cecil and Just 1979, Werner 1994, Biek et al. 2002).

The bullfrog life-cycle was translated into a stage-based, linear, time-invariant projection matrix (Figure 1). Because bullfrogs can pass through multiple stages within a year, each matrix element is composed of a number of lower level vital rates (Appendix 1). The goal of the population modelling was to explore how population growth rate is affected by changes to vital rates brought about by control efforts (Caswell 2000, 2001). The dominant eigenvalue of the projection matrix gives the asymptotic population growth rate λ (Caswell 2001). The sensitivity of λ to small additive changes in a matrix element a_{ij}, when all other matrix elements are held constant, is given by

$$S_{ij} = \delta\lambda / \delta a_{ij}$$

The larger the value of S_{ij}, the greater the change in λ produced by a small additive change in a_{ij}. These sensitivities are not directly interpretable in terms of vital rates because a number of these matrix elements are composed of more than one vital rate, and conversely some vital rates affect more than one transition element (Appendix 1). Therefore, the sensitivities of lower level vital rates were estimated (Caswell 2001). This enabled me to relate sensitivity of λ to actual vital rates that would be the targets of control efforts.

Sensitivity values of fecundity are not directly comparable to those of the survival and growth transitions because the two vital rates are measured on different scales. In this case, elasticity or proportional sensitivity is widely used and is estimated as

$$e_{ij} = \delta \log\lambda / \delta \log a_{ij}$$

This gives the proportional change in λ caused by a proportional change in a_{ij}. For example, the relative merits of decreasing fecundity to that of decreasing tadpole or adult survival can be evaluated using elasticity values.

Bullfrogs are unusual among anurans in having two alternative life-history pathways to metamorphosis, in addition to adults surviving multiple years to contribute to overall population growth. Loop analysis, which is an extension of elasticity analysis, makes it possible to compare the relative contribution of these alternative life-history paths to overall population growth rate (Van Groenendael et al. 1994, De Kroon et al. 2000, Heppell et al. 2000b). The life-cycle is first decomposed into un-branched loops in such a way that all transitions appear at least in one loop. The characteristic elasticity of the loop is the elasticity of the transition element unique to that loop. Loop elasticity is calculated as the characteristic elasticity of the loop multiplied by the number of transition elements in the loop. As for the elasticities of the individual elements, the sum of all loop elasticities is equal to 1 (Van Groenendael et al. 1994, Wardle 1998).

The confidence intervals for the asymptotic population growth rate and the sensitivities of the lower level vital rates were calculated empirically using bootstrap methods. First, I generated 10,000 transition matrices in which the elements were calculated by randomly drawing values from a normal distribution with mean and variance of the logit transformed estimate of the lower level vital rates. For each of these transition matrices sensitivity and elasticity analyses were performed as above, and population growth rate λ calculated. These values were then sorted by magnitude. The 250 and 9750 bootstrap replicates represent the lower and upper 95%confidence limit. All matrix analyses were performed using S-plus-2000 software package (Insightful Corp., Seattle USA).

Results

Post-metamorphic survival rates - Spatial variation among ponds

Post-metamorphic survival rates varied among ponds and this variation was asynchronous among ponds (Figure 2). The only models that had any support from the data retained the interaction term between year and pond (Model 1 and Model 2, Table 2). Among pond variation was not explained by the differences in mean adult frog size (Models 3 to 5, Table 2) or bullfrog population density differences among ponds and years (Models 7 and 10, Table 2).

Overall, Copley Pond had the highest survival rates in all years (Figure 2). Survival rates in the other three ponds were similar and much lower than that in Copley Pond. Mean recapture rate per year for all ponds was 0.84 ± 0.09 (SE).

Post-metamorphic survival rates - Temporal variation within ponds

As variation in survival rates was asynchronous among ponds, I examined the influence of season and weather in each pond separately. Recapture rate was dependent on capture effort in Beaver Pond and Copley Pond but not in Trevlac Pond and Prior Lake. Interestingly, a different model was selected as the best-fit model for survival rates in each pond. Seasonal differences and/or relationship to weather were important in all ponds except Copley Pond. However, the relationship of survival rate to the weather variables was very different among the ponds.

Beaver Pond: Overall daily summer survival was higher than daily winter survival (Table 3). In both seasons it was lower for metamorphs than other frogs (Table 3). The top three models were almost equally supported, and included seasonal variables, precipitation and temperature (Table 4). Precipitation seemed to have a stronger effect (w_{cum}= 0.72) on daily survival rates compared to temperature (w_{cum}= 0.37).

Copley Pond: The best-fit model here was the one with constant survival rate over the six years and between seasons (Table 4). This model had twice the support of the three seasonal, precipitation and temperature dependent models (Table 4, Models 2-4). These were all equally supported.

Trevlac Pond: Here daily winter survival was higher than summer survival (Table 3). Seasonal variation in survival was not completely explained by difference in weather variables alone (Season w_{cum}= 0.98), although both precipitation (w_{cum}= 0.85) and temperature (w_{cum}= 0.70) and the interaction between the two weather variables were retained in the top model (Table 4).

Prior Lake: As in Trevlac Pond, winter survival was higher than summer survival (Table 3). As in Beaver Pond, metamorph survival rate was lower than that for other frogs in both seasons (Table 3). Again, not all the seasonal variation was due to weather variables alone (Season w_{cum}= 0.99). Temperature (w_{cum}= 0.99) had a stronger influence on daily survival rates compared to precipitation (w_{cum}= 0.64).

To summarize: The four ponds could not have been more different in the patterns of temporal variation. Weather seemed to play an important role in determining survival rates, but the relationship appeared to be strongly influenced by habitat and/or population differences at the various pond sites. Overall, metamorphs had lower survival rates compared to other frogs in both seasons.

Population matrix modelling

Sensitivity analysis: Sensitivity analysis showed that population growth rate was most sensitive to changes in the fast-track tadpole transformation to juveniles (matrix element a_{42} Table 5). This transition element is a product of tadpole survival rate, probability of metamorphosis, metamorph survival, and juvenile survival (Appendix 1). Examining the sensitivities of the lower level vital rates it is clear that population growth rate is most sensitive to both metamorph and juvenile survival, and less sensitive to the probability of early versus late transformation (Table 6).

Elasticity and loop analysis: Elasticity analysis showed that relative contribution to population growth rate was more or less evenly distributed amongst most individual life-cycle transitions (Table 5). The exceptions to this pattern were the transition from 1st to 2nd year tadpoles, and from 2nd year tadpoles to juveniles. These transitions had low elasticity values. The elasticity patterns are better understood by linking individual transitions together into alternative pathways or loops, and by examining the relative contributions of these loops to λ. The bullfrog life-cycle can be divided into three un-branched loops – the slow-track where tadpoles metamorphose at the end of two years, the fast-track where tadpoles metamorphose at the end of one season, and the adult self-loop (Figure 1). Transitions a_{32} and a_{43} are unique to the slow-track loop, giving it a characteristic elasticity of 0.021 and a loop elasticity of 0.10 (bootstrap CI 0.04 to 0.21). Transition a_{42} is unique to the fast-track loop, giving it a characteristic elasticity of 0.192 and a loop elasticity of 0.77 (bootstrap CI 0.62 to 0.85). There is only one transition in the adult self-loop, giving it a loop elasticity of 0.13 (bootstrap CI 0.08 to 0.24).

In essence, loop analysis supports the inference from the sensitivity analysis that population growth rate is strongly affected by changes to the fast-track loop. This suggests that to be effective, control efforts should decrease the number of tadpoles that successfully transition this pathway either by decreasing the probability of early transformation or by decreasing early post-metamorphic survival. Strictly speaking, inference from sensitivity and elasticity analyses applies only to very small changes around the transition elements, because of potential non-linearity in the relationship between the transition elements and λ (De Kroon et al. 2000). To visualize potentially large changes that can result from control efforts, I ran a numerical simulation and plotted λ against various proportions of tadpoles entering the fast-track transition. I repeated the simulation assuming that metamorph survival was decreased to half and a quarter of its current value through control efforts (Figure 3). Numerical simulation showed that λ increases almost linearly with increasing proportions of fast-track tadpoles (Figure 3), although the best-fit line included second and third order terms.

Similarly, for a given proportion of fast-track tadpoles, λ declines almost linearly with decreasing metamorph survival rate.

Population growth rate: The asymptotic population growth rate estimated from the mean transition matrix indicated a stable or slightly declining bullfrog population (λ=0.86, bootstrap CI: 0.58 to 1.12).

Discussion

Post-metamorphic survival rates

Frog population dynamics have been shown to fluctuate dramatically due to uncertain reproductive conditions and recruitment into the post-metamorphic stages (Shirose and Brooks 1995, Semlitsch 2002, Green 2003). I found that post-metamorphic survival rates also vary considerably and can contribute to these observed fluctuations. I was unable to find clear patterns that related spatial variation in bullfrog survival rates to pond characteristics such as location in the introduced range, time since colonization, and population density or mean size of adult frogs in the population. As well, I was unable to explain temporal variation in these survival rates using weather fluctuations and seasonal variables alone. It is probable that data from four ponds over four to six years are insufficient to discern complex spatio-temporal patterns in survival rates.

Introduced species are expected to show high survival and growth rates during the early colonization phase due to low intra-specific densities and paucity of predators and parasites (Fagan 2002, Torchin et al. 2003). These rates are expected to decrease with time since colonization as intra-specific density, predators, and parasites accumulate (Lampo and De Leo 1998, Bohn et al. 2004). However, bullfrogs in Copley Pond at the centre of the introduced range had the highest survival rates (Figure 2) but these rates were almost six times that in Beaver Pond, which was also in the centre of the range. The two other ponds at the periphery of the introduced range showed lower survival rates.

The correlation between population density and survival rates can either be positive or negative, depending on population characteristics and environmental conditions (Berven 1990, Wilson and Osenberg 2002). High survival rates in high-quality environments can lead to high population density, and this results in a positive spatial correlation between population density and survival rates. However, within sites, survival rates can show a negative correlation temporally, as competition at high population densities leads to lower survival rates (Lampo and De Leo 1998). In this study, Copley Pond, with the highest population density, also had the highest mean survival rate (Figure 2). There was no indication that yearly variation in population density within each pond affected survival rates (Table 3, Model 7 and 10). Much larger data sets will be required to examine such correlations.

Previous studies of bullfrogs have shown that survival is lowest for small individuals and increases with size (Willis et al. 1956, Durham and Bennett 1963, Shirose and Brooks 1995). Metamorphs showed lower survival compared to juvenile and adult frogs in both Beaver Pond and Prior Lake during both seasons (Table 4). Winter survival was identical in the two ponds but summer survival was much lower in Prior Lake. Because bullfrogs are cannibalistic and smaller bullfrogs form the major portion of the diet of larger bullfrogs (Chapter 2, Bury and Whelan 1986, Pearl et al. 2004), I expected that ponds with higher densities of adult bullfrogs would have lower metamorph summer survival rates. Contrary to this expectation, Prior Lake, with the lowest density of large bullfrogs, also exhibited the lowest metamorph summer survival rates.

Extreme weather events such as harsh winters and drought are thought to be related to catastrophic mortality in frogs (Howard 1981, Shirose et al. 1993, Shirose and Brooks 1995, Anholt et al. 2003). These weather events tend to synchronize survival rates at the landscape level. In this study, although precipitation and temperature covariates were retained in many of the best-supported models, the relationship of these covariates to survival rates differed among ponds. In addition, the variation in survival rates was asynchronous among the pond sites. This supports the view that, in the absence of extreme weather events, habitat differences, pond structure, and population structure interact with weather variables resulting in temporally varying source and sink populations. This can lead to complex meta-population dynamics (Reaser 2000, Marsh and Trenham 2001, Trenham et al. 2003).

Population matrix modelling

Population matrix modelling highlighted two key features of bullfrog population dynamics. First, population growth rate was most sensitive to changes that affected the number of tadpoles entering the fast-track option of the life-cycle. In retrospect, this is not surprising because, in the absence of any trade-off to early metamorphosis, the fast-track tadpoles decrease the time to reproduction from four to three years. This results in an almost linear increase in population growth rate as the proportion of fast-track tadpoles increases in the population (Figure 3). Second, bullfrog population growth rate was very sensitive to changes in metamorph and juvenile survival rates. This agrees with previous studies that have used matrix modelling to study frog population dynamics (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002).

The projected asymptotic population growth rate from the matrix model suggested a stable or slightly declining population. This was contrary to my field observation that bullfrog populations were growing and expanding at the landscape level. This apparent contradiction can be reconciled if one assumes that there was permanent emigration of post-metamorphic stages from the study ponds. Using CMR techniques, permanent emigration cannot be distinguished from mortality, and immigrant frogs cannot be distinguished from unmarked resident frogs. This would result in an under-estimate of overall survival rates of post-metamorphic stages. The estimates of survival rate in this study are lower than those published for ranids elsewhere (Willis et al. 1956, Durham and Bennett 1963, Bruneau and Magnin 1980a, Shirose and Brooks 1995, Biek et al. 2002, Anholt et al. 2003).

Bullfrogs of all sizes move between ponds throughout the active season (Chapter 2, Ingram and Raney 1943, Willis et al. 1956). I observed large numbers of metamorphs dispersing from natal ponds in fall. Migration rates of 8% have been recorded for bullfrogs dispersing among ponds that are 150 to 1200 metres apart (Willis et al. 1956). Migration rates are also thought to be higher for recently metamorphosed bullfrogs (Shirose et al. 1993, Shirose and Brooks 1995). I, therefore, ran a numerical simulation to assess the effect of successful inter-pond migration would have on population growth rates.

As metamorphs were the most common stage observed migrating, the migration simulation is confined to this life-history stage. I assumed that a percentage of the frogs that emigrated from the study ponds survived at other ponds in the vicinity. I also assumed that an equal number of successful immigrants arrived at the study pond from these other ponds. Given these assumptions, metamorph survival rate will be increased by the percentage of successful inter-pond migration. I simulated inter-pond migration rates of 2% to 8% (Willis et al. 1956, Holenweg Peter 2001) and calculated population growth rates (Figure 3). As expected, increasing metamorph survival increased population growth rates, but the largest relative gains were when metamorph survival rate was low. For example, increasing metamorph survival rate from 4% to 6% caused a greater increase in population growth rate than increasing metamorph survival rate from 8% to 10%. The increase in population growth rate was also larger at higher proportions of fast-track tadpoles (Figure 3).

In general, factors that increase the proportion of tadpoles entering the fast-track option and those that increase metamorph and juvenile survival rates, lead to higher bullfrog population growth rates. The proportion of tadpoles that can fast-track depends on their development rate, which is strongly influenced by density and temperature (Harkey and Semlitsch 1988, Newman 1998). High tadpole density has clearly been shown to decrease development rates (Chapter 3, 4 and 5, Smith-Gill and Berven 1979, Bruneau and Magnin 1980b, Werner 1994, Kupferberg 1997). Temperature affects development rates both through physiological pathways and by influencing the growth of periphyton, the main food source of tadpoles (Willis et al. 1956, Viparina and Just 1975, Seale 1980, Harkey and Semlitsch 1988, Newman 1998, Blouin and Brown 2000, Alvarez and Nicieza 2002). One of the reasons why bullfrogs dominate in human modified habitats could be because in these habitats the natural vegetational canopy around ponds is removed thereby increasing water temperature (Halverson et al. 2003), and promoting higher development rate in bullfrog tadpoles.

Post-metamorphic vital rates can also be influenced by tadpole development and growth conditions, as both early metamorphosis and large size at metamorphosis have been shown to be advantageous (Berven and Gill 1983, Semlitsch et al. 1988, Berven 1990, Goater 1994, Beck and Congdon 1999, Morey and Reznick 2001, Alvarez and Nicieza 2002, Altwegg 2003). Metamorphic bullfrogs emigrate en mass from natal ponds in late fall. It is assumed that unless they find suitable ponds to overwinter they perish during this migration effort (Willis et al. 1956, Shirose and Brooks 1995). The proximity of suitable ponds for hibernation probably has a strong effect on metamorph survival rates and consequently on population dynamics (Cooke 1972, Sjogren-Gulve 1991, Gibbs 1993, Pilliod et al. 2002, Semlitsch 2002). Small bullfrogs also form a large part of the diet of large bullfrogs (Chapter 2, Werner et al. 1995) and therefore at high densities of adult bullfrogs one would expect low survival rates of metamorphs. However, I was unable to detect such an effect in the CMR post-metamorphic survival rate estimation studies.

The results of the matrix modelling should be interpreted with caution, as potentially important phenomena were not included due to lack of data. In particular, I did not explicitly account for (1) density-dependence in the tadpole stage, (2) trade-off if any between slow-track and fast-track development pathways, and (3) cannibalism by large bullfrogs of small bullfrogs, which may also be density dependent. First, density dependence in the tadpole stage can alter the proportion of fast-track and slow-track tadpoles but the actual effect on population dynamics depends on the shape of the density-dependent competition curve (Vonesh and De la Cruz 2002). Second, tadpoles that reach the minimum size first may metamorphose early and at a small size (fast-track) while slower growing tadpoles take advantage of the lower density created by the departure of the metamorphs. The slow growing tadpoles delay metamorphosis but attain a much larger size than the early cohort (slow-track) (Hensley 1993, Audo et al. 1995). As stated before, both early metamorphosis and large size at metamorphosis are beneficial in the post-metamorphic stages. Third, cannibalism can lead to interesting, non-linear, cyclical, and even chaotic dynamics, depending on the nature and strength of these inter-stage interactions (Caswell 2001).

Implications for the control of bullfrog populations

In light of the insights gained from the population matrix modelling I discuss the effectiveness and logistical difficulties in controlling each of the four major life-stages of bullfrogs.

Egg mass removal: Fecundity, which includes both survival and growth of adult females and egg mass size, had one of the highest elasticity values. Even though egg mass size alone had low sensitivity values, the complete removal of all egg masses from a pond will result in reproductive collapse. However, complete removal of all egg masses is difficult, if not impossible. First, bullfrog egg masses are very difficult to find because the jelly is virtually transparent, the eggs are black specks, and the whole mass is spread thinly near the surface of the water. Targeted searching within male calling territories can improve the probability of detecting these egg masses. Second, unlike most amphibian egg masses, bullfrog egg masses are fragile and break into pieces containing hundreds of eggs. Complete removal of the egg mass is difficult because some of these pieces remain hidden in the vegetation and sediment. A bilge pump to suck up the egg mass can reduce breakage. The use of chemical treatments, contained within the area where the egg mass was found, could reduce embryo survival to zero in the pieces that remain in the pond. It can take up to 4 hours to search for and remove one egg mass, not including the time required for marking male breeding territories. Searches and removal have to be carried out at least every other day because the egg masses hatch within 3 to 5 days after deposition. At this intense level of effort, egg mass removal can be successful. However, failure to notice and remove even one egg mass is sufficient to re-establish the population and reset control efforts to the beginning (Willis et al. 1956).

Culling of tadpoles: Tadpole survival rate had low sensitivity values. The transition from eggs to large tadpoles and the fast-track transition of large tadpoles to metamorphs both had high elasticity values. Reducing these transition values is expected to decrease population growth rate. Removing tadpoles and thereby decreasing tadpole densities could not only lead to higher survival rates but also faster development rates in the remaining tadpoles. Faster development rates will lead to an increase the proportion of tadpoles fast-tracking. Low tadpole densities could also lead to larger size at metamorphosis and therefore higher metamorph survival rates (Berven 1990, Goater 1994, Beck and Congdon 1999, Morey and Reznick 2001, Alvarez and Nicieza 2002). The actual effect culling of tadpoles has on bullfrog population growth rate will depend both on the proportion of total tadpoles removed and also on the shape of the density-dependent larval competition curve.

The capture-per-unit-effort of removing tadpoles is extremely variable, depending on both the habitat and on the size of tadpoles. In the first few months after hatching, tadpoles are very easy to catch, particularly in ponds with little vegetation and high tadpole density. Under these conditions, tadpole capture rates can be as high as 150 tadpoles/person-hour. However, in ponds with low visibility, dense vegetation, deep water, and low density of tadpoles, capture rates can be as low as 10 per person-hour.

Culling of post-metamorphic stages: Both metamorph and juvenile survival rates had high sensitivity values. Transition elements with these survival rates also had very high elasticity values making them excellent targets for control efforts. Adult survival had half the sensitivity value of metamorph and juvenile survival rates, although logistically it is more effective to target all post-metamorphic stages together. Unlike culling of tadpoles, decreasing density in the post-metamorphic stages is not expected to result in a compensatory increase in population growth rate because density dependent competition in these stages is not as strong and pervasive as in the larval stages (Berven 1990, Berven 1995, Altwegg 2003). However, removal of adults could decrease predation rates on smaller frogs, thereby increasing their survival rate.

Capture rate for metamorphs and juveniles ranged from 2 frogs/person-hour during most of the season to 30 frogs/person-hour during the peak metamorphic period in fall. Adult capture rates range from 2 males/person-hour to <0.5 females/person-hour. Male bullfrogs were very easy to capture during the breeding season but females are rarely captured before they have laid their eggs. Overall, metamorphs may be the most effective stage to target in control efforts because metamorphic survival has high sensitivity values, metamorphs are easy to capture soon after transformation in fall, and compensatory increase in survival and growth rate from decreasing metamorph density is unlikely.

Control of the post-metamorphic stages will be labour intensive, especially if there are a number of ponds within short distance of each other and inter-pond migration is high. In many parts of their range, bullfrog populations have been able to sustain high levels of harvesting (Willis et al. 1956, Bury and Whelan 1986). This suggests that large-scale elimination of introduced bullfrog populations through control efforts may not be very effective. However, in some isolated populations, it is possible that control efforts will decrease population sizes to levels low enough for stochastic demographic processes to cause extinction (Banks et al. 2003).

Conclusion

Post-metamorphic survival rates in bullfrogs varied asynchronously among ponds. There were no clear correlations between post-metamorphic survival rates and pond structure, bullfrog population characteristics or weather variables. Population growth rate was most strongly influenced by the number of tadpoles entering the fast-track development loop, which essentially decreased time from hatching to reproduction from four to three years. As in previous studies, both metamorph and juvenile survival rates have a strong influence on population growth rate. The population growth rate estimated from the population matrix indicated a slightly declining population, which was counter to my field observations. I suggest that this can be reconciled by taking into account migration rates among ponds at a landscape level. Culling of metamorphs may be the most effective way of controlling bullfrog population growth rate. However, elimination of bullfrog populations will be very costly, labour intensive, and will require long-term effort.

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Table 1: Characteristics of the four ponds used in the CMR study. Population density of juvenile and adult bullfrogs is expressed as per m^2 of pond area because bullfrogs remain close to the pond after metamorphosis. 'Recap' indicates the number of frogs that were recaptured at least once after the first marking occasion.

Pond	**Pond Size(m^2)**	**Pop. Density Mean(SD)/m^2**	**CMR duration**	**No. captured (recap)**	**Frog wt. Mean (SD) g**
Beaver Pond	3340	2.3×10^{-2} (1.0×10^{-2})	1998-2003	391 (77)	116.4(84.8)
Copley Pond	255	3.9×10^{-2} (9.8×10^{-3})	1998-2003	56 (25)	272.0(113.1)
Trevlac Pond	29,600	2.9×10^{-3} (1.1×10^{-4})	1999-2003	242 (35)	143.9(106.3)
Prior Lake	59,200	8.8×10^{-4} (4.4×10^{-4})	1999-2002	557 (54)	101.2(84.3)

Table 2: The ten best models for survival and recapture rates of bullfrogs in the four ponds. ϕ denotes survival rate and p denotes recapture rate. Size indicates mean size of adult bullfrogs in each pond. 'x' indicates the inclusion of an interaction term; '+' indicates that the terms are additive.

No.	**Model**	**AIC$_c$**	**Δ AIC$_c$**	**AIC$_c$ Weight**	**Model Likelihood**	**N**	**Dev**
1	Φ(pondxyear) p(.)	278.96	0.00	0.55	1.00	13	12.33
2	Φ(pondxyear) p(effort)	279.42	0.46	0.44	0.79	14	10.66
3	Φ(size+size^2) p(.)	289.67	10.71	0.00	0.00	4	41.77
4	Φ(pond+size+ size^2) p(.)	291.23	12.27	0.00	0.00	7	37.17
5	Φ(size+ size^2) p(effort)	291.60	12.64	0.00	0.00	5	41.66
6	Φ(pond) p(.)	291.61	12.65	0.00	0.00	5	41.67
7	Φ(pond+density) p(.)	292.82	13.86	0.00	0.00	6	40.83
8	Φ(pond) p(effort)	293.58	14.62	0.00	0.00	6	41.58
9	Φ(pond+year) p(.)	294.36	15.39	0.00	0.00	7	40.30
10	Φ(pond+density) p(effort)	294.73	15.77	0.00	0.00	7	40.67

Table 3: Recapture rate (per occasion) and daily summer and winter survival rates (mean ± SE) of bullfrogs in the four study ponds.

Pond	**Recapture Rate (per capture occasion)**	**Mean Winter ϕ rate (per day)**	**Mean Summer ϕ rate (per day)**
Beaver Pond			
Metamorphs	0.08 ± 0.02	0.989 ± 0.003	0.993 ± 0.002
Other frogs	0.18 ± 0.03	0.993 ± 0.001	0.996 ± 0.001
Copley Pond			
Other frogs	0.37 ± 0.05	0.999 ± 0.0003	Same as winter
Trevlac Pond			
Other frogs	0.16 ± 0.03	0.997 ± 0.001	0.987 ± 0.004
Prior Lake			
Metamorphs	0.12 ± 0.02	0.990 ± 0.002	0.975 ± 0.005
Other Frogs	0.12 ± 0.02	0.996 ± 0.001	0.989 ± 0.003

Table 4: Model selection looking at seasonal and weather related variation in survival rates within each pond. 'Size' indicates metamorph versus other frogs; 'sw' indicates summer versus winter; 'prp' indicates mean monthly precipitation; 'temp' indicates mean monthly temperature; '.' indicates constant for all group and times; and 'x' indicates the inclusion of an interaction term.

No.	Model	AIC_c	Δ AIC_c	AIC_c Weight	Model Likelihood	N	Dev
Beaver Pond							
1	Φ(size+prp)	658.53	0.00	0.16	1.00	6	261.75
2	Φ(size+temp+prp)	658.97	0.44	0.13	0.80	7	260.13
3	Φ(size+sw+prp)	659.09	0.56	0.12	0.76	7	260.25
4	Φ(size)	659.60	1.07	0.10	0.59	5	264.87
5	Φ(sizexprp)	660.39	1.86	0.06	0.39	7	261.55
Copley Pond							
1	Φ(.)	320.97	0.00	0.35	1.00	3	241.41
2	Φ(prp)	322.57	1.60	0.16	0.45	4	240.86
3	Φ(temp)	322.71	1.74	0.15	0.42	4	241.00
4	Φ(sw)	322.74	1.77	0.15	0.41	4	241.03
5	Φ(tempxprp)	324.52	3.55	0.06	0.17	6	238.37
Trevlac Pond							
1	Φ(sw+(tempxprp)	281.75	0.00	0.37	1.00	6	108.88
2	Φ(sw+(temp+prp)	283.65	1.90	0.14	0.39	5	112.91
3	Φ(years+sw)	283.69	1.94	0.14	0.38	7	108.65
4	Φ(swx(temp+prp))	283.75	2.00	0.13	0.37	7	108.71
5	Φ(sw+prp)	284.34	2.59	0.10	0.27	4	115.73
Prior Lake							
1	Φ(size+swx(temp))	595.75	0.00	0.36	1.00	6	237.04
2	Φ(size+swx(tempxprp))	597.45	1.70	0.15	0.43	9	232.57
3	Φ(size+swx(temp+prp))	597.76	2.01	0.13	0.37	8	234.95
4	Φ(sizexsw+(temp+prp))	598.10	2.35	0.11	0.31	7	237.34
5	Φ(size+sw+(temp+prp))	598.32	2.57	0.10	0.28	6	239.60

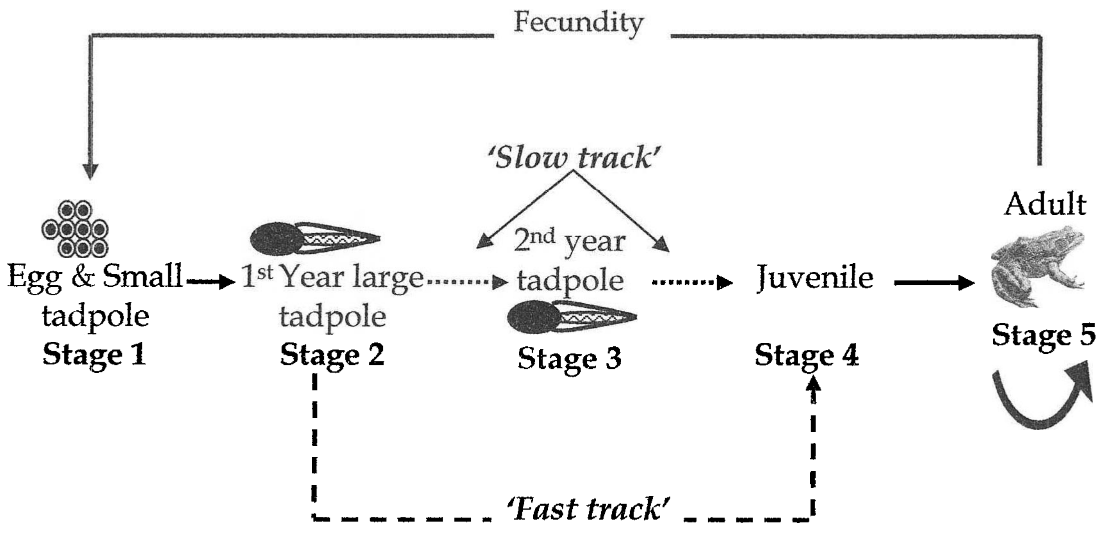
Table 5: Sensitivity and elasticity values of bullfrog population transition matrix.

Transition	a_{ij}	**Sensitivity (s_{ij})**	**Elasticity (e_{ij})**
Egg to tadpole survival	a_{21}	2.59	0.213
Slow track - tadpole to tadpole	a_{32}	0.23	0.021
Slow track - tadpole to juvenile	a_{43}	0.93	0.021
Fast track - tadpole to juvenile	a_{42}	10.25	0.192
Juvenile to adult	a_{54}	1.41	0.213
Adult survival	a_{55}	0.34	0.126
Fecundity	a_{15}	8.7×10^{-5}	0.213

Table 6: Sensitivity of lower level vital rates.

Lower level vital rate	**Sensitivity (95% CI)**
ϕ_{embryo}	0.20 (0.12 to 0.27)
$\phi_{\text{very small tadpole}}$	0.45 (0.28 to 0.62)
ϕ small tadpole summer	0.21 (0.13 to 0.28)
ϕ small tadpole winter	0.79 (0.44 to 1.29)
ϕ large tadpole summer	0.39 (0.24 to 0.51)
ϕ large tadpole winter	0.068 (0.046 to 0.095)
$\sigma_{\text{early}}/\sigma_{\text{late}}$ metamorphosis	0.19 (0.08 to 0.29)
ϕ metamorph summer	0.48 (0.28 to 0.78)
ϕ metamorph winter	1.88 (0.94 to 5.08)
ϕ juvenile	1.70 (0.82 to 2.15)
ϕ adult	0.91 (0.75 to 1.20)
Egg mass size	$1.4\text{x}10^{-5}$ ($8.4\text{x}10^{-6}$ to $2.0\text{x}10^{-5}$)

Bullfrog life cycle graph



Bullfrog population projection matrix

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & 2080 \\ 0.070 & 0 & 0 & 0 & 0 \\ 0 & 0.078 & 0 & 0 & 0 \\ 0 & 0.016 & 0.020 & 0 & 0 \\ 0 & 0 & 0 & 0.129 & 0.318 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{pmatrix}_{t}$$

Figure 1: Bullfrog life-cycle graph showing alternate pathways – Slow-track (dotted lines), where tadpoles attain metamorphosis after two years; Fast-track (dashed line), where tadpoles attain metamorphosis in one year, and adult self-loop (bold). The corresponding projection matrix is shown below. The sub-diagonal elements represent growth, the diagonal elements represent stasis and the top row indicates fecundity.

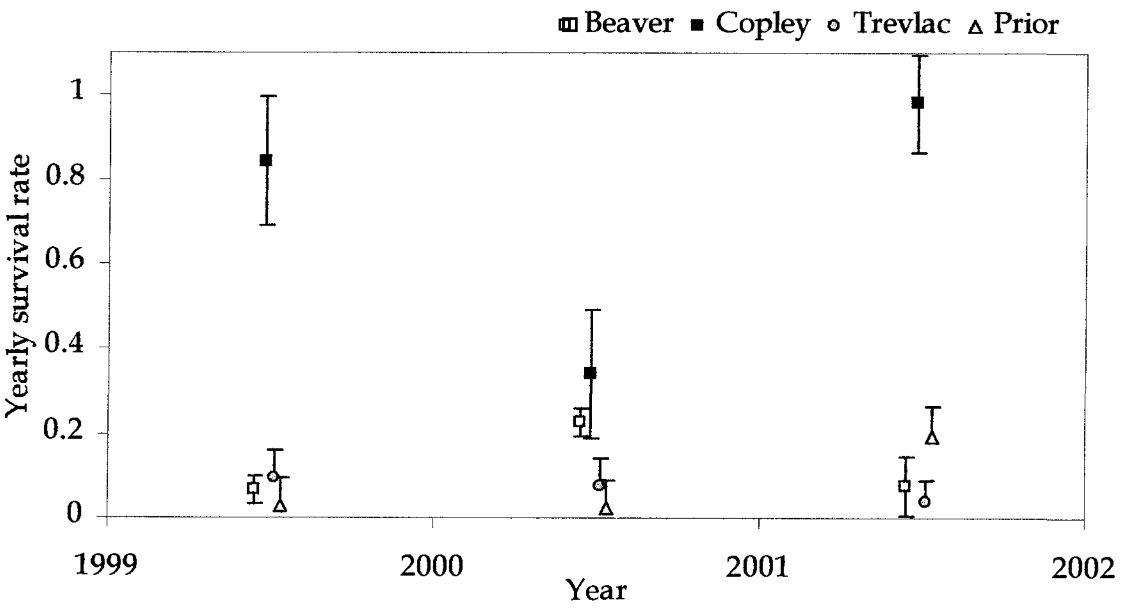


Figure 2: Yearly survival rate of post-metamorphic bullfrogs (>30g in size) in the four study ponds. Yearly survival rates varied asynchronously among ponds.

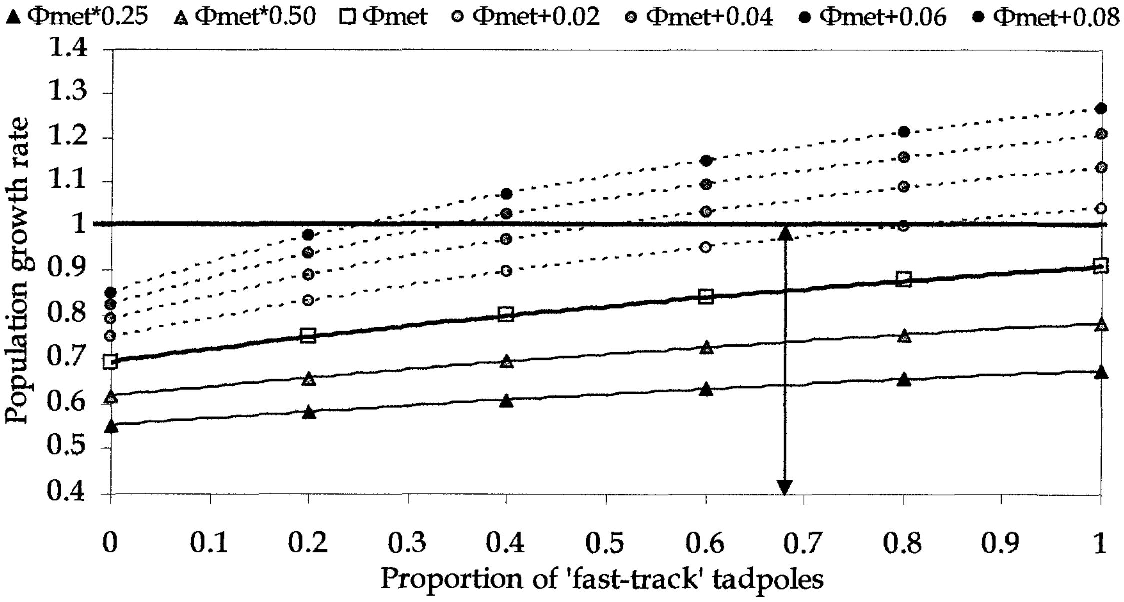


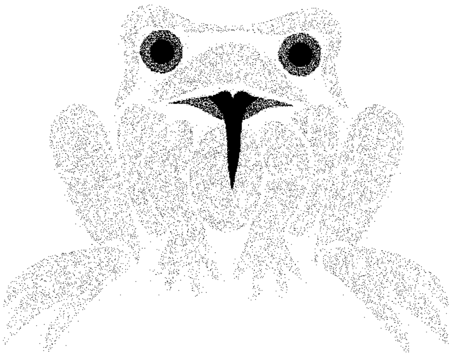
Figure 3: Simulation of the effect that increasing proportions of fast -track tadpoles has on projected population growth rate (open squares, bold line). The other vital rates are as estimated in the study. The two curves below the bold line indicate the same simulation but with metamorph survival rate (Φ_{met}=0.037) reduced to ½ and ¼ its current value through control efforts (triangle symbols, solid line). The four curves above the bold line indicate the same simulation but with metamorph survival rates increased by 2%, 4%, 6% and 8%, through successful inter-pond migration (circle symbols, dotted lines). The proportion of fast-track tadpoles observed in this study was 68% (double headed arrow).

Appendix 1: Methods for estimating transition probabilities for projection matrix.

The projection interval is one year, and vital rates are mean $\pm$ SE unless otherwise indicated. Embryo survival (ϕ_{embryo}) for ranid frogs is estimated at 0.92 ± 0.05 (SD) (Biek et al., 2002). I assumed that for the first two weeks after hatching bullfrog tadpoles < 1 cm ($\phi_{\text{v. s. tad}}$) would have survival rates similar to similarly sized *Hyla regilla* tadpoles (Chapter 3, 0.402 ± 0.03). Small tadpole and large tadpole summer survival rates ($\phi_{\text{s. tad}}$, 0.87 ± 0.07 and $\phi_{\text{l. tad}}$, 0.95 ± 0.05) and overwinter survival rates ($\phi_{\text{s. tad overwinter}}$ 0.23 ± 0.06 and $\phi_{\text{l. tad overwinter}}$, 0.26 ± 0.09) were estimated as mean rates from field enclosure competition studies (Werner 1994). Although these estimates were from enclosures with reduced predation and manipulation of competitor densities, overall they were similar to estimates generated by following tadpole cohorts to metamorphosis in whole pond studies (Cecil and Just, 1979). I assumed that bullfrog tadpoles were small (< 5 cm total length) until they emerged from their first hibernation. I estimated the probability of early or late metamorphosis ($\sigma_{\text{early}}/\sigma_{\text{late}}$) by sampling tadpoles in ponds in May (Beaver Pond: fast track = 60%, Trevlac Pond, fast track = 70%). Survival rates of the terrestrial stages were mean CMR survival rates from the four populations. Metamorphs grew to be larger than 30 grams two months following metamorphosis, after which they were treated as juveniles.

Transition	a_{ij}	Parameter estimation equation
Egg to tadpole survival	a_{21}	$\phi_{\text{embryo}} \times \phi_{\text{v. s. tad}} \times \phi_{\text{s. tad}} \times \phi_{\text{s. tad overwinter}} \times \phi_{\text{l. tad}}$ $0.92 \times 0.40 \times 0.87 \times 0.23 \times 0.95 = 0.0704$
Slow track - tadpole to tadpole	a_{32}	$\phi_{\text{l. tadpole}} \times \phi_{\text{l. tad overwinter}} \times \phi_{\text{l. tad}} \times \sigma_{\text{late}}$ $0.97 \times 0.26 \times 0.95 \times 0.325 = 0.0775$
Slow track - tadpole to juvenile	a_{43}	$\phi_{\text{met.}} \times \phi_{\text{met. overwinter}} \times \phi_{\text{juvenile}}$ $0.380 \times 0.097 \times 0.531 = 0.0196$
Fast track - tadpole to juvenile	a_{42}	$\phi_{\text{l. tad}} \times \phi_{\text{met}} \times \phi_{\text{met overwinter}} \times \phi_{\text{met}} \times \phi_{\text{juvenile}} \times \sigma_{\text{early}}$ $0.98 \times 0.62 \times 0.097 \times 0.62 \times 0.66 \times 0.68 = 0.0160$
Juvenile to adult	a_{54}	ϕ_{juvenile} 0.13 ± 0.03
Adult survival	a_{55}	ϕ_{adult} 0.32 ± 0.07
Fecundity	a_{15}	ϕ_{adult} x sex ratio x egg mass size $0.32 \times 0.5 \times 13{,}014 = 2082$

CHAPTER 7



INTRODUCED BULLFROGS IN BRITISH COLUMBIA: SUMMARY AND GENERAL DISCUSSION

Introduction

The enormity of the ecological and economic damage caused by introduced species has greatly increased the study of biological invasions (Oka 1983, Vitousek 1990, Vermeij 1991, Lodge 1993, Reichard and Hamilton 1997, Tilman 1997, Ricciardi and Rasmussen 1998, Perrings 2002). In this thesis I looked at one such invasion, that of the American bullfrog (*Rana catesbeiana*) in British Columbia. In spite of the long history of bullfrog introductions in western North America, studies on their ecology and their impacts are fairly recent. The stages of a biological invasion - arrival, establishment and impact on native species, and integration - provided a framework within which I addressed the following issues:

- The reasons for the successful establishment of bullfrogs in British Columbia.
- The potential reasons for its current range expansion in British Colombia.
- The extent of bullfrog impacts on two native species of frogs, focusing on direct and indirect competitive effects in the tadpole stage.
- The population dynamics of bullfrogs in British Columbia compared to those in their native range.

In the last section of this chapter, with the insight gained from the above studies and natural history observations, I propose a management strategy to control the spread of bullfrogs and mitigate their impacts in areas where they have become established.

Arrival and successful establishment of bullfrogs in British Columbia

The economic potential of frog farms was the main reason for the import of bullfrogs into British Columbia. Following arrival, the successful establishment of a viable population is thought to depend primarily on the number of times the species is repeatedly introduced, and the population size of these introductions (Williamson 1996, Hee et al. 2000). In the case of bullfrogs, the odds were biased in favour of success because of the number of frog farms and because stocks released from these farms probably included a number of breeding pairs. Since stochastic demographic processes strongly influence the establishment phase (Carrol and Dingle 1996, Vermeij 1996), the large size of the initial introduced populations and the high reproductive rates of bullfrogs were almost certainly instrumental in avoiding early extinction. As well, their ability to thrive in human modified habitats and their generalist diet favoured the establishment of sustainable populations.

Bullfrog populations are now well established in British Columbia. With the exception of one isolated population in the Okanagan, the bullfrog range is currently restricted to the southwestern corner of the province. In spite of this, bullfrogs are a conservation concern because their range overlaps regions of the province with the highest anuran diversity (Green and Campbell 1992). Although bullfrogs were first introduced in the 1930's and 1940's, large populations were not documented until the mid-1960's on Vancouver Island and the Lower Mainland (Green 1978, Green and Campbell 1992). The pattern of long quiescence prior to population density build-up is common for a number of introduced species (Williamson 1996), as well as for bullfrogs in other parts of their introduced range (Jennings and Hayes 1985).

Potential reasons for current bullfrog range expansion in British Columbia

Over the past decade there have been anecdotal reports of bullfrog range expansions in British Columbia. This could be due to observational bias. Bullfrogs have become more conspicuous with increased attention from the scientific community and the media. However, in the Greater Victoria area, bullfrogs have expanded their range by 1-5 km/year in the past eight years. Therefore, at least in this case, the range expansion is real.

The reasons for the recent range expansion could involve both intrinsic factors controlling the population dynamics of bullfrogs and extrinsic factors such as weather and habitat modification. It is unlikely to be intrinsic factors because of the high reproductive rate of bullfrogs and their capacity for rapid population increase. Of the two potential extrinsic factors, I suggest habitat modification rather than changed weather patterns as the more likely explanation. Long-term population trend data that would be required to rigorously evaluate the effects of weather patterns on bullfrog range do not exist for British Columbia. In their native range, bullfrogs can tolerate a wide range of weather conditions (Stebbins 1985, Bury and Whelan 1986) but are susceptible to harsh winters and drought (Howard 1981, Shirose et al. 1993, Shirose and Brooks 1995). In British Columbia, bullfrogs face milder weather conditions than in the northern parts of their native range in eastern North America. It is unlikely that their range in British Columbia is limited by weather conditions.

Bullfrogs are highly aquatic and inhabit warm, open, permanent ponds (Bruneau and Magnin 1980, Bury and Whelan 1986, Shirose and Brooks 1995). Given these habitat preferences, the large-scale conversion of forested habitats to agricultural uses in the Lower Mainland and southern Vancouver Island probably favoured the range expansion of bullfrogs (Jennings and Hayes 1985). Most farms and even rural residential properties have at least one irrigation pond. Irrigation ponds provide ideal habitat for bullfrogs. Often these ponds are within the migration distance of bullfrogs (preferably < 500 m) or are connected by migration corridors such as ditches and streams.

In addition, people continue to transport bullfrogs into new areas either intentionally (sport hunting, farming) or unintentionally (pets, 'live garden ornaments', discarded science projects). Once bullfrogs have established a viable population at these points of introduction, they then rapidly expand to occupy the suitable habitat within migration distance. Human-aided transport to modified habitats can account for the 'jump' pattern of range expansion of bullfrogs (Saurez et al. 2001). This pattern consists of pockets of expanding populations in widely separated suburban and rural areas close to human habitation. These newly recorded populations seem to be expanding while older populations from the 1960's remain stable. A global explanation such as changed weather patterns would require all populations to be expanding equally.

The recent range expansion of the bullfrogs in Victoria was probably caused by the establishment of a new migration route connecting existing populations to un-colonized suitable habitats. In Victoria, bullfrogs have been recorded in the Elk/Beaver area since the 1960's (Figure 1). However, they did not start to expand their range west towards Prospect Lake, and the surrounding agricultural lands until the early 1990's. This coincides with the time a beaver dam converted a seasonally flooded potato field to a permanent wetland (Viaduct Flats), mid way between the two areas. Once established in and around Prospect Lake, the bullfrogs were able to spread rapidly through the numerous irrigation ponds, small lakes, and wetlands to the Thetis Lake system.

Bullfrogs are currently expanding their range north on the Millstream and Todd Creek systems, and south towards Langford Lake.

The distance between ponds and availability of suitable migration routes can determine the rate of ranid frog range expansions (Holenweg Peter 2001, Semlitsch 2002). In suburban areas such as the Saanich Peninsula in the Greater Victoria area (Figure 1), seasonal roadside ditches and streams may serve as migration corridors. Due to this, rainfall patterns during the fall migration can have a strong influence on the rate of range expansion of bullfrogs. However, alternative hypotheses for the reasons of bullfrog range expansion in British Columbia remain to be tested.

Impact of bullfrogs on native frogs

In their native range, bullfrogs have a strong influence on the diversity and abundance of other pond-dwelling frog species (Werner et al. 1995, Hecnar and M'Closkey 1996). It is not surprising then that recent studies have documented impacts of introduced bullfrogs on native communities (Moyle 1973, Hayes and Jennings 1986, Kiesecker and Blaustein 1997, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001, Pearl et al. 2004). However, not all native species are equally affected (Fisher and Shaffer 1995, Pearl et al. 2004). I compared the effect of bullfrogs on two native frog species, the Pacific treefrog (*Hyla regilla*) and the red-legged frog (*Rana aurora*), focusing mainly on larval competition (Chapters 3 to 5). To summarize the results of the field and experimental mesocosm studies:

- Bullfrog tadpoles decreased the development rate of Pacific treefrog tadpoles but did not affect either their survival or growth rate.
- Bullfrog tadpoles had a stronger effect on red-legged frog tadpoles, decreasing both their growth rate and development but not their survival rate.
- Neither native species had an effect on bullfrog survival, growth or development rate.
- Indirect effects, mediated through the presence of predators, did not affect the competitive relationship between bullfrog and native tadpoles.

These experiments suggested that Pacific treefrog tadpoles, because of their small size, higher activity levels, higher growth and development rates and propensity to feed in the water column are less vulnerable to competition from bullfrog tadpoles. Red-legged frog tadpoles are more vulnerable because of their larger size, slower development and growth rates, lower activity levels, and benthic habits.

It is difficult to extrapolate the population level consequences of decreased development and growth rates of native tadpoles. Both decreased development and growth rates lead to increased time to metamorphosis. Given that mean daily survival rates of Pacific treefrogs ranged from 94% to 88% (Chapter 3), delayed metamorphosis results in fewer tadpoles surviving to metamorphosis. Also, decreased growth rate results in a longer period when tadpoles remain vulnerable to gape-limited predators (Van Buskirk 1988, Lardner 1998). Ultimately, lower growth rates lead to smaller size at metamorphosis. Small size at metamorphosis and delayed metamorphosis have been associated with lower survival and growth in the post-metamorphic stages (Berven and Gill 1983, Semlitsch et al. 1988, Berven 1990, Goater 1994, Beck and Congdon 1999, Alvarez and Nicieza 2002a, Altwegg 2003).

In addition to competitive effects on the tadpole stages, bullfrogs can directly decrease the survival of post-metamorphic stages of native frogs by preying on them (Werner et al. 1995, Pearl et al. 2004). Nearly half of the adult bullfrogs examined had frog remains in their stomachs (Chapter 2, Werner et al. 1995). Pacific treefrogs are mainly terrestrial but return to ponds to breed. Pacific treefrogs start to breed in March and are safe from predation by bullfrogs until the end of April when bullfrogs become active. However, treefrog breeding choruses continue well into June and during this time they are vulnerable to predation by bullfrogs. Pacific treefrogs are also vulnerable immediately following metamorphosis when they remain in the vicinity of the natal ponds. Red-legged frogs are more aquatic than Pacific treefrogs and may be vulnerable to predation by bullfrogs throughout their active season. Red-legged frogs are known to forage in upland sites along streams and in moist forests when such habitats are available (Licht 1974, 1986, Pearl et al. 2004). The predation rate of bullfrogs on post-metamorphic Pacific treefrogs or red-legged frogs is yet to be estimated.

Sensitivity analysis using population matrix models has shown that post-metamorphic survival rates have a strong influence on the population growth rate of frogs (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002). Therefore, larval competitive effects that translate to decreased performance in the post-metamorphic stages and the direct predatory effect of bullfrogs is expected to result in lower population growth of the two native frog species. Whether and under what conditions these decreased population growth rates result in local extinction of the native species remains unclear.

Demography of bullfrogs

Introduced species in novel environments, either exploiting new food sources or released from their normal competitors, predators, and parasites, sometimes exhibit marked deviations in life-history traits and vital rates (Carrol and Dingle 1996, Lampo and De Leo 1998, Mitchell and Power 2003, Torchin et al. 2003). These changes may lead to rapid population growth rate and high population densities, both of which can cause extensive economic and ecological damage (Schloesser et al. 1998, Alvarez and Cushman 2002). It has been suggested that bullfrogs reach unusually high population densities in their introduced habitat (Cohen and Howard 1958), and this is often attributed to the lack of predators. However, there has been little data on the demography of bullfrogs in their introduced range to validate this and other hypotheses.

In order to evaluate the demographic characteristic of the bullfrog populations in the study area, I used a combination of field observations and marked-population studies. To summarize:

- As is common for frog species, the bullfrog populations varied both temporally and spatially (Collins 1979, Berven 1990, Gibbons et al. 1997, Dodd and Cade 1998, Reaser 2000). However, the variation in adult body size, metamorph size, egg mass size, tadpole growth and size, tadpole density, size composition of terrestrial populations, and population density of metamorphs and adults were all within the range of variation observed in the native bullfrog range.

- Mean annual post-metamorphic survival rates estimated using Capture-Mark-Recapture methods, however, were lower than those estimated for bullfrogs in eastern North America using life-table analyses (Shirose et al. 1993).
- The life-cycle of bullfrogs in British Columbia consisted of two parallel trajectories where tadpoles either metamorphosed after one year (fast-track) or had to spend two years as tadpoles (slow-track). Loop analysis of the population matrix models indicated that bullfrog population growth rate was strongly influenced by the proportion of fast-tracking tadpoles. Tadpole development rate which determines the proportion of tadpoles in the two options, increases with temperature and decreases with increasing intra-specific density (Harkey and Semlitsch 1988, Werner 1994, Newman 1998, Blouin and Brown 2000, Alvarez and Nicieza 2002b).
- Metamorph and juvenile survival rates also had a strong influence on population growth rate. The strong influence of these vital rates has been shown to be a common pattern of anuran population dynamics (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002).
- The projected population growth rate using the matrix model suggested a stable or slightly declining population ($\lambda = 0.86$, bootstrap 95% CI: 0.58 to 1.12). However, I observed expanding bullfrog populations at the landscape level. Capture-Mark-Recapture methods are unable to discriminate between mortality and permanent emigration and therefore, underestimate survival rates. This leads to low λ estimates. Inter-pond migration in ranids can range from 8% to 12% (Willis et al. 1956, Shirose et al. 1993, Shirose and Brooks 1995, Holenweg Peter 2001). Increasing metamorph survival alone in the modelling to account for this migration results in population growth rates > 1. Migration between neighbouring ponds may therefore be important in maintaining bullfrog populations extant at the landscape level.
- Three factors that could potentially be very important in governing the population dynamics of bullfrogs are density dependence in the tadpole stages, trade-off between early metamorphosis and delayed metamorphosis, and

cannibalism of smaller bullfrogs by large bullfrogs. Further research into how these factors affect bullfrog population dynamics is required, particularly with reference to the culling of various life-stages in bullfrog population control efforts.

Overall, it appears that bullfrog population structure and dynamics in British Columbia were similar to those in the northern parts of their native range in eastern North America, even though the suite of competitors, predators, and parasites are different in the two regions. This suggests that the population dynamics of bullfrogs are controlled by abiotic factors such as weather, water temperature, and spatial distribution of ponds. Population growth self-regulation in the form of density dependent growth and survival in tadpoles and cannibalism in the post-metamorphic stages could also be important.

Control of bullfrogs and mitigation of impacts

The bullfrog range in British Columbia will most likely continue to expand because people still transport and release these frogs into new areas. Although regulations exist to prevent such introductions, these are rarely enforced. Public awareness of these regulations and of the ecological damage caused bullfrog introductions is minimal. I recommend that public education to prevent further range expansion should be the first step in a bullfrog management plan.

In areas where bullfrogs have already become established, the management program for bullfrogs and their impacts can be envisaged at three levels. Which level is chosen will depend not only on the extent of bullfrog populations and the resources available, but also on the level of conservation concern for the affected native species and the degree to which they would benefit from bullfrog control.

Level 1 - Eradication: In many respects, this is the ideal situation where, in the absence of other negative influences, native species are restored to original population levels once bullfrogs are removed.

Level 2 - Population control: When populations are wide spread and eradication is not possible, one management option would be to decrease bullfrog population size and density.

Level 3 - Mitigation of impacts: When bullfrog populations are well entrenched in the landscape and bullfrog population control is prohibitive in cost and effort, one management option would be to modify habitat in ways that create a refuge for native species. In the refuge, the impacts of bullfrogs are minimized, enabling native species to persist.

Eradication

To date, my work and that by others has shown negative effects of bullfrogs on the survival, growth and development rates of one or more life-stages of native frogs. Unless these lowered vital rates in one life-stage are compensated by higher growth or survival in other life-history stages, the presence of bullfrogs leads to lower population growth rates in the native frogs. It seems clear then that native frogs will benefit if bullfrogs are eliminated. However, because bullfrogs are so widespread and well established in British Columbia, elimination of all bullfrog populations at the landscape level will be prohibitive in cost and effort.

Eradication of small isolated populations, such as the one in the Okanagan, can still be attempted. Elimination of the one isolated bullfrog population in England, from a 80m x 20m pond, cost $72,000 (Banks et al. 2003). In British Columbia, such expenditure can only be justified if areas of high biodiversity are under imminent threat of colonization by bullfrogs or if bullfrogs are a direct threat to endangered species.

Bullfrog Population Control

Sensitivity analysis using population matrix models suggests that decreasing the proportion of tadpoles entering the fast-track option of the life-cycle and decreasing metamorph and juvenile survival rates will result in the largest declines in population growth rate. As discussed in Chapter 6, culling metamorphs and juveniles may be the most effective option in terms of cost and effort. Inter-pond migration has also been shown to be important in maintaining positive growth of bullfrog populations (Shirose and Brooks 1995). Identifying migration corridors and targeting these in control efforts may disrupt the meta-population dynamics of bullfrogs and cause the population to collapse.

As with eradication, bullfrog population control will be labour intensive and costly. Consequently, the expected benefits to native species and the extent of bullfrog population culling need to be defined. Bullfrog population control is uncertain in terms of benefits because the nature of the relationship between bullfrog population density and the magnitude of its negative impact is not known. In the simplest case, the relationship may be linear. Therefore, the lower the bullfrog density, the higher will be the benefit to native species. The relationship can also be a step-function where below a certain density bullfrogs have minimal effects but above that density the impacts are high. It is also possible that the impacts increase rapidly at low population densities but asymptote at higher densities. In this case, native species would not benefit at all until bullfrog populations have been decreased to very low levels. Niche overlap between bullfrogs and native species, and the response of native species to competitors and predators will determine the nature of this relationship. Some understanding of this relationship will be required in order to set the limits of bullfrog population control.

Unlike eradication that has a clearly defined end point, bullfrog population control is inherently open ended. In rare occasions, bullfrog population control can reduce numbers to such low levels that stochastic demographic processes lead to extinction. The likelihood of this happening is minimal given that even one breeding pair can restore population size within a few years. To maintain bullfrogs at lower than normal densities, culling will have to be repeatedly carried out every year. In the absence of clearly demonstrable benefits of bullfrog population control, the costs of such a long-term program will not be justified.

Mitigation of bullfrog impacts

In many cases, bullfrog populations are too well established and widespread to make even population control cost effective. In these circumstances, management efforts that enable affected species to co-exist with bullfrogs need to be devised. I discuss this with reference to Pacific treefrogs and red-legged frogs, the two species on which I focused my research. The Pacific treefrog is a common and abundant species in British Columbia and is not considered to be of conservation concern. The red-legged frog, on the other hand, is restricted to Vancouver Island and the southwest of the province, areas where bullfrogs are well established. Red-legged frogs are assessed to be of moderate conservation concern and are currently 'blue-listed' in provincial conservation lists and are a species of 'special concern' nationally.

Field surveys indicate that in most habitats Pacific treefrogs persist with bullfrogs (Fisher and Shaffer 1995, *unpublished data*), but anecdotal reports indicate that population densities and the magnitude of the treefrog breeding chorus are diminished in the years following the establishment of bullfrogs. Surveys in the Greater Victoria area show that red-legged frogs are extirpated from areas colonized by bullfrogs since the 1960's but red-legged frogs continue to persist in areas colonized by bullfrogs in the early 1990's. Under certain circumstances, the red-legged frogs are known to co-exist with long established populations of bullfrogs (Adams et al. 1998, Kiesecker et al. 2001, Pearl et al. 2004). If habitat features that permit coexistence between the species are identified, these can be incorporated into plans to mitigate the negative impact of bullfrogs.

During the post-metamorphic stage, the main effect of bullfrogs on the native frogs is through predation. Bullfrogs are highly aquatic and remain along the shores of permanent ponds. Pacific treefrogs, on the other hand, feed in terrestrial habitats and return to ponds only to breed. This habitat separation gives them some refuge from the predatory effects of bullfrogs. Red-legged frogs are more aquatic but will feed along stream courses and on the moist forest floor, if these habitats are available. However, in the absence of such upland habitat, red-legged frogs are forced to remain close to the margin of ponds where they are vulnerable to predation by bullfrogs.

In their larval stages, the three species interact as competitors for common resources. These interactions are mediated through the presence of predators and the interplay of abiotic factors such as pond drying (hydro-period) and water temperature (Wellborn et al. 1996). Bullfrogs are confined to permanent ponds because of their multi-year larval period. Bullfrog tadpoles are not vulnerable to fish predation but the tadpoles are very vulnerable to predation by dragonfly larvae (Werner and McPeek 1994). Bullfrog tadpoles also require water temperature between 15-32°C to maintain optimal development rates (Bury and Whelan 1986) and development stops below 13°C (Chapter 4, Willis et al. 1956, Viparina and Just 1975).

Pacific treefrogs can breed in short duration temporary ponds because of their rapid development rate. The high activity levels required for maintaining maximum growth and development rates makes them highly vulnerable to predation (Skelly 1994, Morin 1995). However, by breeding in temporary ponds with low densities of predators and by having short larval periods, treefrog tadpoles minimize exposure to high predation risk (Skelly 1996).

Red-legged frogs, because of their slower development rates, are confined to permanent ponds or to longer duration temporary ponds that hold water at least until mid-August. They are vulnerable to predation by introduced fish but because of their lower activity levels are not very susceptible to predation by invertebrate predators (Chapter 5). They breed very early in the season and are adapted to development in low water temperatures (John Adler et al. 1988). They can survive only in water < 21 °C (Licht 1974).

When the habitat requirements of the three species are examined, it is apparent that conversion of forested habitats to agricultural/residential uses, and the accompanying conversion of temporary wetlands to permanent irrigation/ornamental ponds favours bullfrogs over native frog species. Previous studies have shown that construction of permanent ponds in agricultural landscapes favour bullfrog tadpoles in competitive relationships with native tadpoles (Willis et al. 1956, Jennings and Hayes 1985, Adams 2000). These ponds are also suitable over-wintering habitat for bullfrogs and their close proximity increases metamorph survival during the fall migration. This, in turn, increases the probability of bullfrog population persistence and range expansion (Willis et al. 1956, Shirose and Brooks 1995).

The conversion of short hydro-period ponds to permanent ponds deprives Pacific treefrog populations of low predator density breeding sites. In addition, fish have been introduced to many permanent ponds for sport fishing or for mosquito control (Kiesecker and Blaustein 1998, Lawler et al. 1999). Many of the lakes and permanent ponds in the Pacific Northwest were naturally fishless or had native fish that are not dominant predators on tadpoles. Not only do fish directly prey on Pacific treefrog and red-legged frog tadpoles, but they also reduce the density of dragonfly larvae, the main predators of bullfrog tadpoles (Werner and McPeek 1994, Adams et al. 2003). Compared to bullfrog tadpoles, red-legged frog tadpoles are less vulnerable to invertebrate predators such as dragonfly larvae and diving beetle larvae that accumulate in these fishless ponds. The introduction of non-native fish has thus directly and indirectly facilitated the dominance by bullfrogs (Kiesecker and Blaustein 1998, Knapp and Matthews 2000, Kiesecker et al. 2001, Matthews et al. 2001, Adams et al. 2003).

Removal of the forest canopy results in loss of upland foraging sites for red-legged frogs. Canopy loss can also result in increasing water temperature in the breeding ponds of red-legged frogs above their thermal maximum (Halverson et al. 2003). Small streams in forested habitats that provide ideal migration routes are often converted to open roadside ditches or storm sewers, leading to habitat fragmentation for red-legged frogs.

It is clear that, in addition to the negative impacts of bullfrogs themselves, a number of habitat modifications have biased conditions against native frog species. In order to restore native frog populations these changes have to be reversed where possible. This could enable native frogs to persist in the landscape even in the face of negative impacts from bullfrogs. I suggest the following:

- The construction of short duration temporary ponds in rural landscapes. These provide alternative breeding sites for Pacific treefrogs away from permanent ponds dominated by bullfrogs and introduced fish.
- The planting of hedgerows and thickets which provide safe foraging sites for treefrog metamorphs emerging from these temporary ponds. This would increase the post-metamorphic survival rate, a vital rate with strong influence on population growth rate.
- The preservation of forested patches with longer hydro-period, cooler temperature ponds that favour red-legged frog tadpole survival and growth. It is important to ensure that these ponds remain free of introduced fish.
- The preservation and restoration of upland moist stream and forest foraging sites for red-legged frogs. This would minimize predation by bullfrogs.
- The establishment of forested stream habitats can also serve as migration corridors between remnant forest patches that still persist in rural landscapes.

To summarize: increasing public awareness to prevent the transport and further spread of bullfrogs in the province is the first step in a comprehensive management plan. When bullfrog populations are isolated or when they are in the proximity of highly endangered species, eradication should be attempted. In areas where they are well established, limited bullfrog population control to prevent further spread and habitat restoration to favour native species could be the long term solution.

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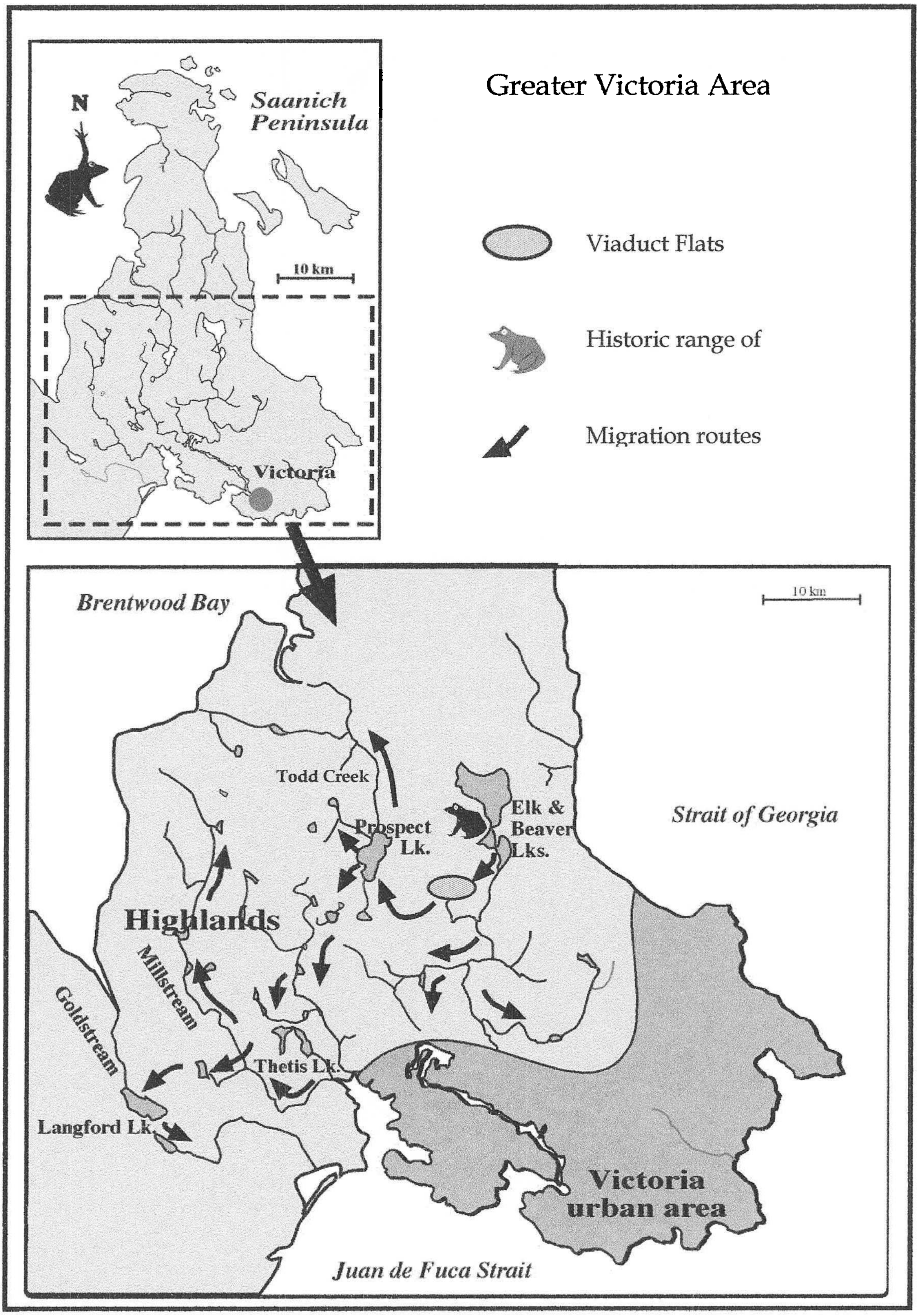

Figure 1: Bullfrog range expansion in the 1990's in the Greater Victoria Area.