A Comparative Ecology of *Rana aurora* Baird and Girard and *Rana catesbeiana* Shaw at Freshwater Lagoon, Humboldt County, California.

by

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A Comparative Ecology of

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Arts.

Major Professor

Approved by the Graduate Coordinator

Approved by the Graduate Dean

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I dedicate this thesis to my mother, my sister, and my niece.

Abstract

Populations of *Rana aurora* Baird and Girard (red-legged frog) and *Rana catesbeiana* Shaw (Bullfrog) were studied at Freshwater Lagoon from December 1990 through January 1991. Significant differences in habitat-use between species were confirmed using log-linear analysis. I found red-legged frogs most often on land, while bullfrogs were found most frequently in the water. An analysis of the stomach contents of bullfrogs provides proof that bullfrogs prey on red-legged frogs at Freshwater Lagoon. Bullfrogs were shown to also feed on the highly toxic *Taricha granulosa* (Skilton) (rough-skinned newt). I examined the seasonal activities of both species, and I found that adult male and sub-adult red-legged frogs are absent from the lagoon after bullfrogs emerge from hibernation. Interspecific amplexus between male red-legged frogs and sub-adult and juvenile bullfrogs was observed on 31 separate occasions. Estimates of the population structure of bullfrogs confirm that it is well established at Freshwater Lagoon. Although the differences in habitat use between red-legged frogs and bullfrogs at Freshwater Lagoon appear to be great enough to alleviate the effects of predation and interspecific amplexus on the population of red-legged frogs, the two populations should be monitored through time to see if they are increasing or decreasing relative to one another.

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Introduction

Global declines in amphibian populations have raised the concerns of researchers worldwide (Blaustein and Wake, 1990). Apparently, not all species and regions are affected. Reasons for declines are not always discernible. Dramatic fluctuations in amphibian populations may, at times, be natural phenomena. Separating natural events from human-caused events is difficult without long-term studies (Barinaga, 1990).

Native ranid populations have suffered decreases throughout western North America. Herpetologists are in general agreement that there has been a widespread decline of populations of red-legged frogs *(Rana aurora* Baird and Girard) in California over the past 50 years (Anderson, 1983; McKeown, 1974). Declines of western ranids have been attributed to alteration of habitats (Banta and Morafka, 1966; Moyle, 1973; Hammerson, 1982), predation by fishes (Hammerson, 1982; Grinnell and Storer, 1924), and the introduction of bullfrogs, potential competitors and predators (Jameson, 1956; Dumas, 1966; Black, 1969; Moyle, 1973; Licht, 1974; Hayes and Jennings, 1986).

Documented field evidence that bullfrogs *(Rana catesbeiana* Shaw) prey on California ranids is unavailable (Jennings and Hayes, 1985). The only published study of comparative habitat use between bullfrogs and a native rapid, *Rana boylii* Baird, was conducted by Moyle (1973). To my knowledge, no such study comparing the bullfrog and the red-legged frog has been done.

Well-established populations of red-legged frogs and bullfrogs exist in Freshwater Lagoon (Humboldt Co., CA). Bullfrog populations have existed in coastal Humboldt County for at least the past 40 years (Houck, pers. com.). During a casual visit to Freshwater Lagoon in September of 1990, I observed juvenile red-legged frogs and adult bullfrogs along the shore. Many juvenile red-legged frogs were on land, while all observed bullfrogs were in the water. These and other observations during subsequent visits suggested that the two species might utilize the available habitat differently, thus significantly reducing predation pressure if bullfrogs actually prey on red-legged frogs.

I conducted research at Freshwater Lagoon with the following objectives:

1) To collect data to evaluate whether red-legged frogs and bullfrogs use the habitat differently.

2) To look for evidence of predation on red-legged frogs by bullfrogs.

3) To observe both species throughout the year to assess their seasonal activities.

4) To examine the population structure (maturity classes) of both species by their physical characteristics, and to determine which sub-species of red-legged frog occurs at Freshwater Lagoon.

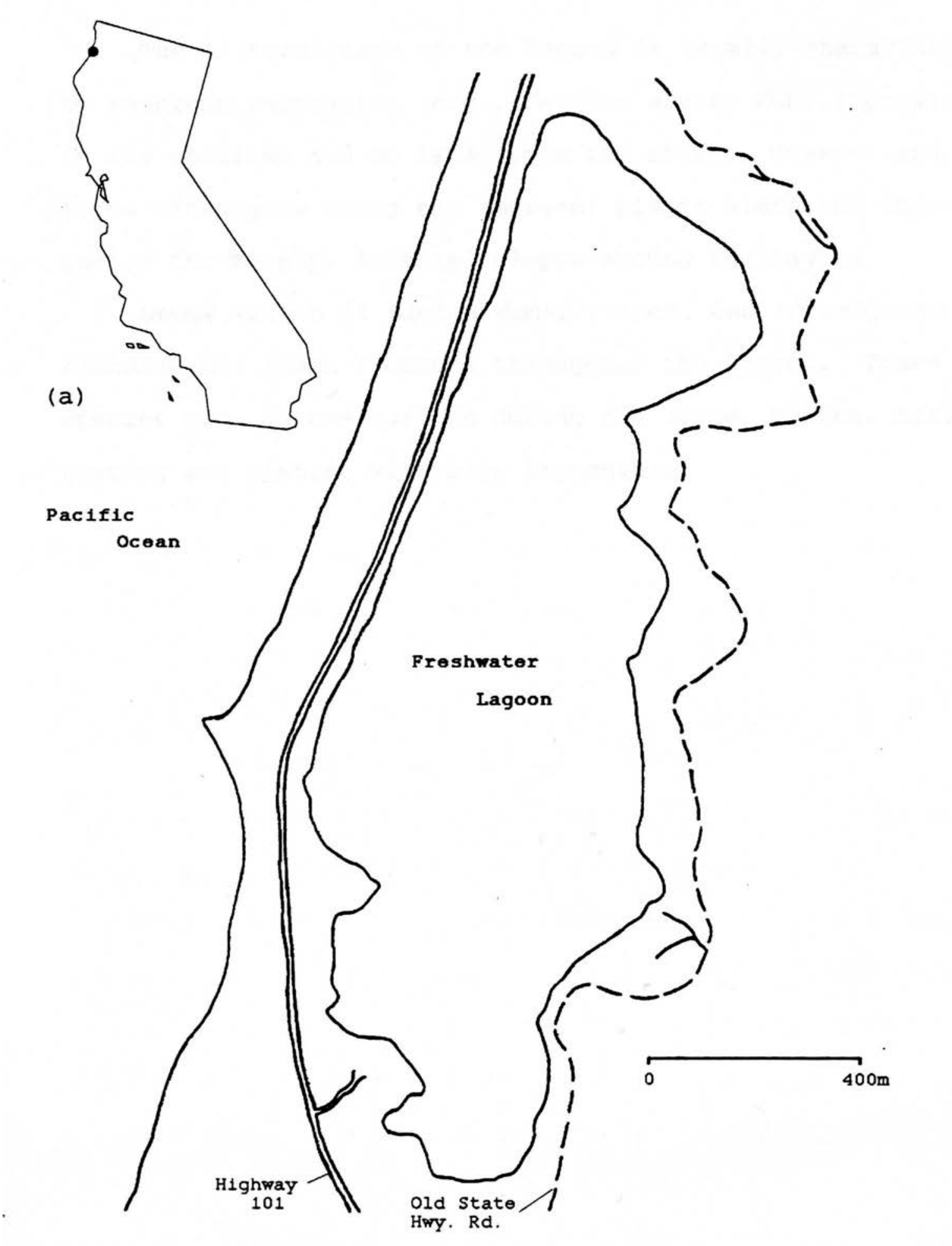
5) To estimate the size and age structure of the population of bullfrogs.

Description of Study Site

Freshwater Lagoon is located 72 km north of Eureka, California in Humboldt County (Figure 1). Because of the presence of the Highway 101 roadbed, breaking out (breaching) has been rare in the past, and the lagoon's water is fresh, not brackish like that of Big Lagoon and Stone Lagoon to the south (Kimsey, 1952).

Maximum length of Freshwater Lagoon is 1.6km, and maximum width is 0.4km. Surface area has been estimated at 99 hectares (245 acres). The lagoon basin is trough-like, relatively uniform in depth. Kimsey (1952) calculated a mean depth of 14 ft (4.3m) with a maximum depth of 17ft (5.2m). Area of the lagoon's drainage-basin has been estimated at 5.7 sq. km. (Merrit et al.,1987).

Until the early 1940's, a forest of Sitka spruce *(Picea sitchensis* (Bong.)), Douglas fir *(Pseudotsuga Menziesii* (Mirb.)), and some coastal redwood *(Sequoia sempervirens (D.* Don.)) surrounded the lagoon on three sides. After the area was logged in the early 1940's, red alder *(Alnus oregona* Nutt.) became the dominant tree species, with an extensive understory of brush. Vegetation is sparse along the western shore, where a sand spit approximately 100m wide and Hwy 101, separate the lagoon from the Pacific Ocean.



(b)

Figure 1: Location map (a), and site map (b) of Freshwater Lagoon, Humboldt Co., California, 1991.

The littoral zone of the lagoon is usually characterized by emergent vegetation (e.g., *Scirpus acutus* Muhl.) growing in the shallows and on land along the shore. Grasses and forbs often grow among the emergent plants along the shore and on the brushy, forested slopes around the lagoon.

Dense growth of *Elodea densa* Planch. and *Potamogeton richardsonii* (Benn.) occurs throughout the lagoon. These species grow to the surface during the summer months, making boating and fishing virtually impossible.

Materials and Methods

Observations of seasonal activity and habitat-use

Observations of frogs were made in two ways. Over a period of 14 months, I made an average of four visits per month to observe and record the presence or absence, the movements, and the life-histories of red-legged frogs and bullfrogs at Freshwater Lagoon. Both day and evening visits were conducted, and observations were made while walking along the shore in selected areas and from an inflatable kayak. The date, time of day, weather, air and water temperatures, and relative humidity were recorded during each visit to the lagoon. I used a battery powered head-lamp during evening visits.

To objectively study the use of habitat by red-legged frogs and bullfrogs, I used systematically placed sampling plots for collecting data. With a 50m measuring tape, I placed station markers (survey flagging) every 100m around the perimeter of the lagoon. These markers facilitated the placement of plots as follows. I considered ten plots per sampling run manageable in terms of time and effort. I divided the total shoreline (perimeter) distance, 5386m, by ten to determine the spacing between adjacent plots in a given run (538.6m). I determined placement of the first plot of a run by multiplying the spacing distance by a random number. If the spacing distance (e.g., 538.6m) was multiplied by the random number 0.50, the first plot of the run would be placed 269.3m clockwise from station marker 0. Subsequent plots would be positioned every 538.6m from the first plot. Plot width comprised 10m of shoreline. attempted to sample at least 100 sq. m. of habitat (both in water and on land) in each plot. I visually estimated the area of each habitat-type sampled per plot to compare the habitat available versus the habitat used by the frogs. Care was taken to keep the sampling effort per plot as constant as possible (e.g., search time).

Systematic sampling was used for a number of reasons. This sampling technique is faster and easier to execute than is simple random sampling (Cochran, 1977. p. 205). When studying behavior I did systematic sampling to ensure statistical independence by maintaining an adequate distance between plots. In other words, the behavior of frogs in one plot will not be altered by my sampling activities in an adjacent plot. Altered behavior could lead to biased results for habitat-use if frogs were disturbed to the point of hiding or changing their position. I used a new random start for each sampling run, so that no area of the lagoon would be sampled more than once. If the same plots had been used throughout the study, the behavior of frogs could have been altered by my repeated disturbances. Frogs might become increasingly wary, thus biasing observations. Systematic sampling also aided in making observations throughout the entire lagoon while I traveled between sample sites.

Plot sampling was conducted from 23 July 1991 through 22 September 1991 after red-legged frog tadpoles had metamorphosed. I sampled 50 different plots, 32 during the day and 18 at night. In addition to these plots, a 200m stretch of shoreline consisting of rocky, spike-rush, and grass/forbs habitats was sampled once during the day and once at night in order to increase the sample size for these habitats. An estimated total of roughly 8400 sq. m. of habitat was sampled in and around Freshwater Lagoon (Figure 2). Some of the shoreline (1130m) could not be sampled, because the vegetation (bulrushes) was too dense for me to search effectively.

I recorded the following categorical variables for each frog sighted in each plot:

1) Frog species [red-legged frog (Ra) or bullfrog (Rc)].
2) Time (day or night).
3) Habitat type [surface vegetation, bulrushes *(Scirpus acutus),* spike rushes *(Heleocharis* sp.), grass/forbs, rocky, no cover].
4) Position (in water or on land).

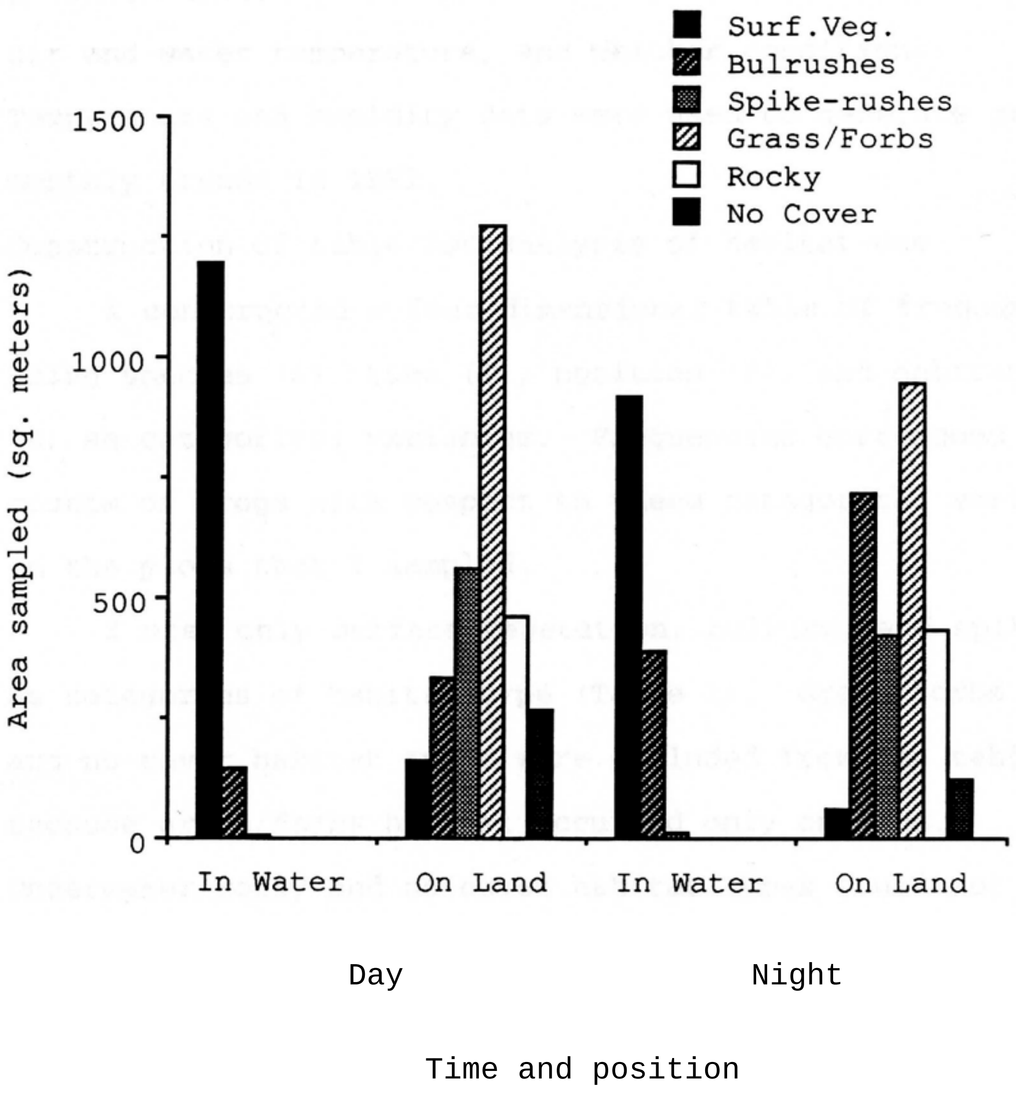


Figure 2: Total area of each habitat type sampled with respect to time (day or night) and position (in water or on land) at Freshwater Lagoon 1991.

Additional information recorded for each plot included plot location, date, start and stop times, relative humidity, air and water temperature, and weather conditions. Temperature and humidity data were used to generate graphs of monthly trends in 1991.

Construction of table for analysis of habitat-use

I constructed a four-dimensional table of frequencies using species (S), time (T), position (P), and habitat type (H) as categorical variables. Frequencies correspond to counts of frogs with respect to these categorical variables in the plots that I sampled.

I used only surface vegetation, bulrush, and spike-rush as categories of habitat-type (Table 1). Grass/forbs, rocky, and no-cover habitat types were excluded from the table, because grass/forbs habitat occurred only on land. Underwater rocky and no-cover habitat types could not be adequately sampled from shore or inflatable kayak due to the obstruction of view by submerged vegetation.

Log-linear modeling

I tested a series of different models, including the model of complete variable independence ({S}{P}{T}{H}), for goodness of fit using log-linear analysis (Table 2). Any significant differences in use of habitat within or between frog species can be revealed by an acceptable model, where expected frequencies are good approximations of the observed frequencies within the table. An acceptable model expresses

Table 1: Observed and expected (parentheses) frequencies of frogs with respect to species [red-legged frog (Ra) or bullfrog (Rc)], position, time, and habitat type. Expected frequencies are based on the model:{SP} {ST} {SH} {HP} {PT} {HT) (see also Figures 6 and 7).

Habitat	Time	Position	Species Ra	Species Rc
Surface Vegetation	Day	In Water	40 (42.2)	195 (194.1)
		On land	82 (76.3)	17 (21.4)
	Night	In Water	65 (66.0)	169 (166.8)
		On land	2 (4.5)	2 (0.7)
Bulrushes	Day	In Water	8 (8.3)	21 (20.4)
		On land	13 (11.6)	0 (1.7)
	Night	In Water	27 (28.6)	40 (38.7)
		On land	2 (1.5)	0 (0.1)
Spike-Rushes	Day	In Water	7 (6.1)	7 (7.0)
		On land	188 (193.5)	18 (13.4)
	Night	In Water	17 (12.9)	3 (8.0)
		On land	16 (15.5)	1 (0.6)

Table 2: Tests of significance of log-linear models for four-dimensional frequency table of species, position (in water or on land), time (day or night), and habitat types (surface vegetation, bulrushes, and spike-rushes).

Model	d.f	L^2	p-value
{ S }	22	1579.95	< 0.0001
{ T }	22	1511.60	< 0.0001
{p}	22	1508.26	< 0.0001
{H}	21	1223.70	< 0.0001
{S} {T} {P} {H}	18	1083.54	< 0.0001
{ST} {P} {H}	17	1051.08	< 0.0001
{S} {P} {HT}	16	984.65	< 0.0001
{S} {H} {PT}	17	844.56	< 0.0001
{SH} {P} {T}	16	840.23	< 0.0001
{SP} {T} {H}	17	722.04	< 0.0001
{S} {T} {HP}	16	680.30	< 0.0001
{ST} {HP}	15	647.84	< 0.0001
{SP} {HT}	15	623.16	< 0.0001
{SH} {PT}	15	601.25	< 0.0001
{ST} {SP} {PT}	17	825.57	< 0.0001
{ST} {SH} {HT}	14	808.52	< 0.0001
{PH} {TH} {PT}	14	425.67	< 0.0001
{SP} {SH} {HP}	14	349.71	< 0.0001
{SP} {ST} {SH} {HP} {HT}	10	177.88	< 0.0001
{ST} {SH} {HP} {PT} {HT}	10	177.77	< 0.0001
{SP} {ST} {SH} {PT} {HT}	11	154.99	< 0.0001
{SP} {ST} {HP} {PT} {HT}	11	50.35	< 0.0001
{SP} {ST} {SH} {HP} {PT}	11	28.55	0.0027
{SP} {SH} {HP} {PT} {HT}	10	26.65	0.0030
{SP} {ST} {SH} {HP} {PT}	9	16.46	0.0578
{SPH} {T}	10	271.58	< 0.0001
{PTH} {S}	11	425.23	< 0.0001
{SPT} {H}	14	467.67	< 0.0001
{STH} {P}	11	736.21	< 0.0001

how observed frequencies are affected by individual variables (main effects) and combinations of variables (interaction effects) (Zar, 1984).

A better understanding of log-linear modeling might be gained by a comparison with chi-square contingency analysis. Log-linear modeling is used for analysis of contingency tables with three or more dimensions. Hence, log-linear modeling picks up where chi-square contingency analysis leaves off. The methods are similar in that potential associations of variables (interactions) may be explored. However, approaches to finding associations are fundamentally different. Using the chi-square test for independence of variables, rejection of the null hypothesis of no association between variables is declared when the chi-square statistic (X^2) is large relative to the degrees of freedom. Finding a suitable log-linear model requires acceptance of the hypothesized model, where the log-likelihood ratio statistic [$L^2 = 2\sum f_{ij} \ln(f_{ij}/F_{ij})$] is small relative to the degrees of freedom (Knoke and Burke, 1980).

The major advantage of log-linear analysis over chi-square contingency analysis is that the effects, which are log-transformed, are additive in the former, while they are multiplicative in the latter. In other words, the contribution of effects in a log-linear model may be evaluated independently of one another (Alford and Crump, 1982). These same evaluations can not be accomplished using chi-square contingency analysis. Knoke and Burke (1980) may be consulted for a relatively thorough discussion of log-linear models. Their discussion includes mathematical derivations for the effect-parameters used in generating expected cell frequencies for a given model.

Before I describe the building and testing of models, a discussion of log-linear model notation is warranted. Let A, B, and C represent categorical variables. A model that expresses complete independence of variables is represented by the following notation: {A} {B} {C}. Since A, B, and C are to act independently of one another, they are all separated by braces. This model is the hypothesized model of complete independence in a traditional chi-square contingency analysis. All three are considered single-variable (main) effects. {AB} {C} represents a model where variables A and B are associated to produce an interaction effect, in addition to their being main effects. Variable C acts as a main effect, but is independent of the other two variables and their association.

I used the "Multiway Frequency Tables" computer program of the BMDP statistics software package to perform log-linear analyses of the habitat-use data collected at Freshwater Lagoon. This program uses a model-fitting procedure similar to stepwise regression (Green and Macdonald, 1987). Models are tested from the simplest (complete independence) to the most complex models having interaction effects. Hence, there is a progression from models containing only main effects to models with interaction effects. Models of increasing complexity are tested until a non-significant L^2 value results ($p > 0.05$). Model selection is based on parsimony, on the assumption that the simplest explanation is the best one. Analysis of the diet of bullfrogs

Twenty-two bullfrogs were collected for analysis of stomach contents after population estimates had been completed. I pithed specimens in the field and transported them to the Fred Telonicher Marine Laboratory (Trinidad, CA) where their stomachs and intestines were removed and dissected. Prey items were identified and tallied.

Snout-vent length, and weight measurements

I periodically captured different maturity classes of each species to record snout-vent length (SVL) and weight. SVL was measured to the nearest millimeter with a metric ruler. Smaller frogs were weighed to the nearest gram using a 30g or 50g Pesola scale. Juvenile red-legged frogs were weighed to the nearest 0.1g. I weighed large bullfrogs to the nearest gram with a 2000g Ohaus scale.

I sexed adult red-legged frogs by size (males are noticeably smaller than females) and by the presence of nuptial tubercles (swollen thumb bases) of males.

Adult bullfrogs are easily sexed by comparing the diameter of the tympanum to the diameter of the eye. The tympanum is larger than the eye in adult males, roughly equal in size in adult females (Stebbins, 1985, p. 93).

Maturity classes of bullfrogs were based on snout-vent length. Bullfrogs 125mm snout-vent length or longer were classified as adults, since the smallest male bullfrog encountered was 127mm SVL. Bullfrogs 65mm to 124mm SVL were classified as sub-adults, since the largest juvenile I encountered was 64mm in length. I could distinguish smaller sub-adult bullfrogs from larger juveniles by stoutness of digits and skin coloration and texture. Juveniles had smooth skin, ranging in color from yellow-green to light green. The skin of sub-adults had a roughened appearance. Skin color of sub-adult bullfrogs was a darker green.

Estimation of population size/structure of bullfrogs

I captured bullfrogs, using a pair of fish-landing nets and marked them by toe-clipping the fourth digit of the left hind foot, to estimate population size and structure. Stage 44 and 45 froglets were included in the juvenile class for population estimates (Gosner, 1960), since these stages are very close to completing metamorphosis. I saw no signs of regeneration of toes on marked frogs that were recaptured, so toe-clipping was a reliable technique for identifying animals.

I made three mark-and-recapture runs at night. Three nights were required to sample the entire lagoon for one run of capturing and marking frogs Population sizes of bullfrog adults, sub-adults, and juveniles were estimated using the Schnabel method, which involves a series of two or more mark-and-recapture runs (Krebs, 1989). These multiple samples are, essentially, a series of Petersen samples (Schnabel, 1938). A weighted average of Petersen estimates provides a population estimate: $\text{N-hat} = \sum(C_t M_t)/\sum R_t$ where:

C_t represents the number of animals captured at time t, M_t represents the number of animals marked previous to time t, and

R_t is the number of marked animals re-captured at time t.

The assumptions of the Petersen method and Schnabel method are the same. Size of the population is assumed to be constant with no recruitment or loss of individuals. Sampling is assumed to be random. All individuals are assumed to have an equal chance of being captured in a given sampling run (Krebs, 1989).

I chose not to attempt an estimate of the population size of red-legged frogs, primarily because of its migratory behavior. A significant proportion of the population may be absent from the lagoon at any given time, and the understory of brush in the forest is too dense to sample the population away from the lagoon.

Results

Observations of habitat use prior to plot sampling

Habitat use by each species was recorded during observations made before plot sampling was started. Both species tended to use the same habitat types when in the water. Most of the adult and sub-adult red-legged frogs that I observed through spring and early summer were found in bulrushes when in the water or on land. No bullfrogs were seen on land during February and March. All eight bullfrogs sighted before May were associated with bulrushes in the water.

Adult female red-legged frogs were observed most often in surface vegetation from August through September. Of 149 females, 77% (115) were observed in surface vegetation. The remaining 23% (34) were associated with surface vegetation among bulrushes. I observed only two adult males during the same time period.

Habitat-use from plot samples

A total of 1125 different frog sightings was recorded from sampling plots (Figures 3 and 4). Most of the red-legged frogs that I counted in plots were juveniles. More red-legged frogs were observed on land by day, while most bullfrogs were observed in the water (Figure 5). Very few

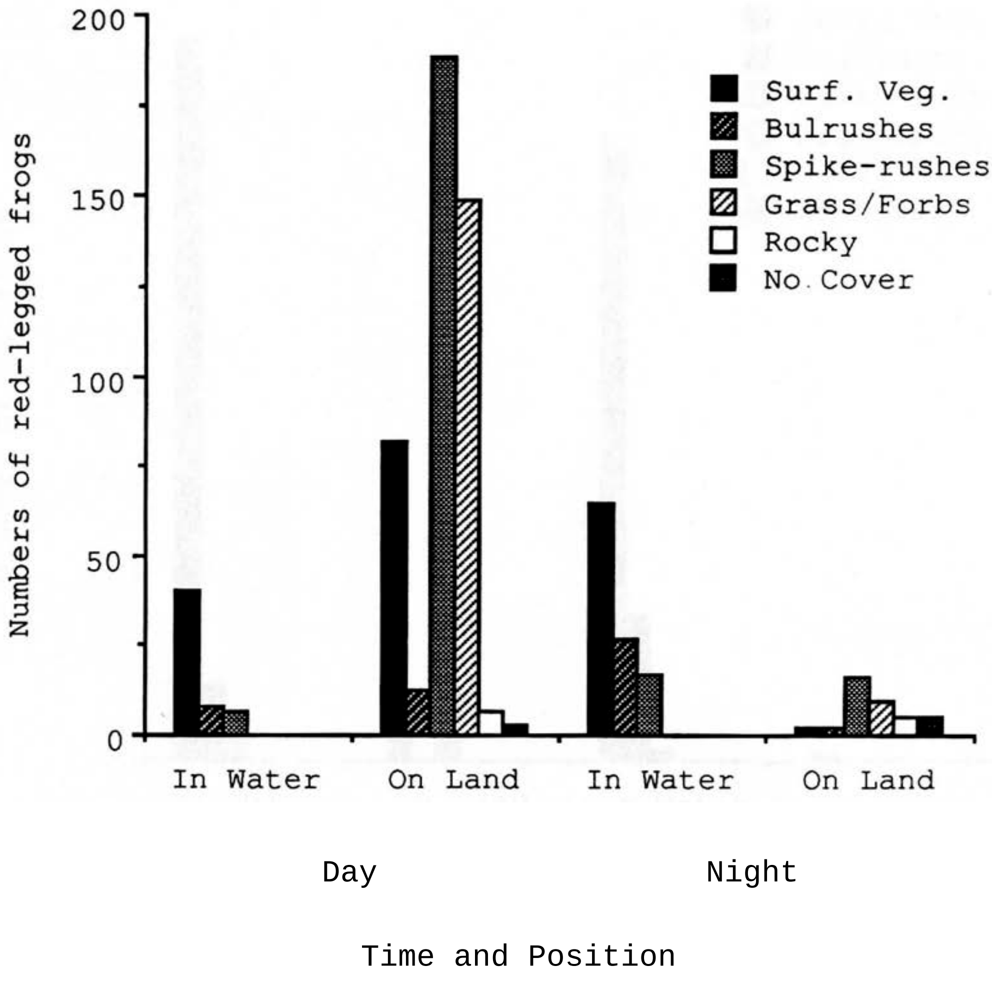
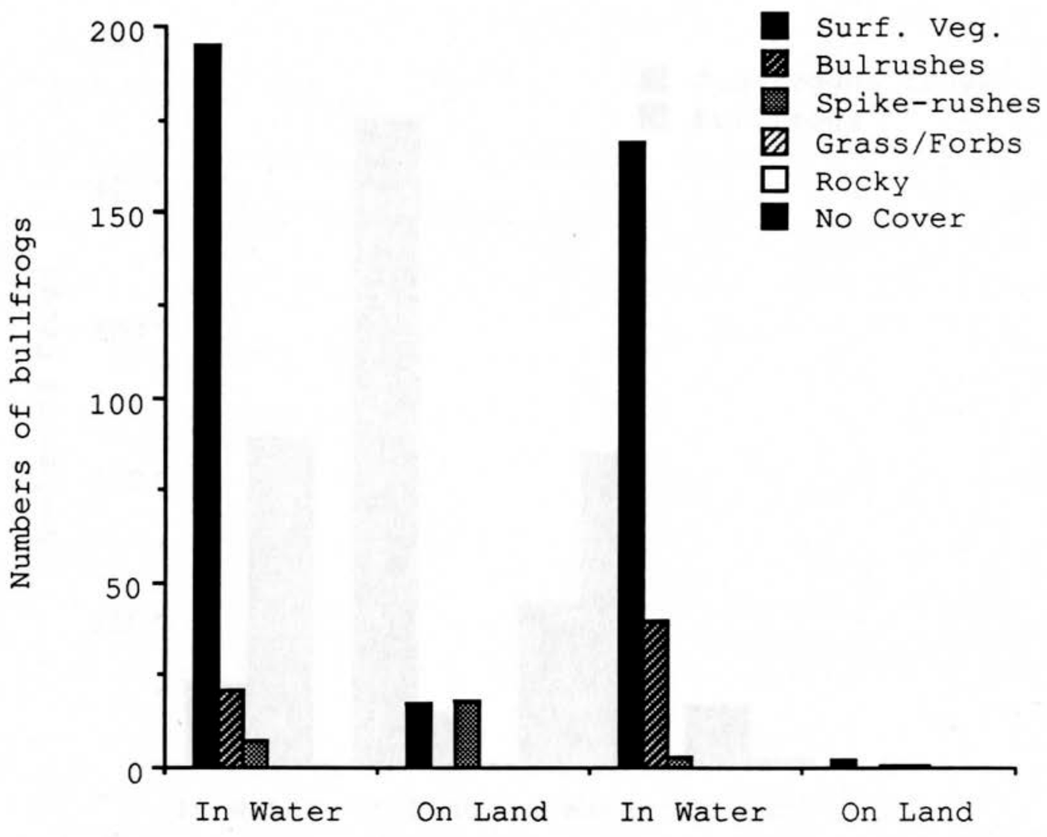


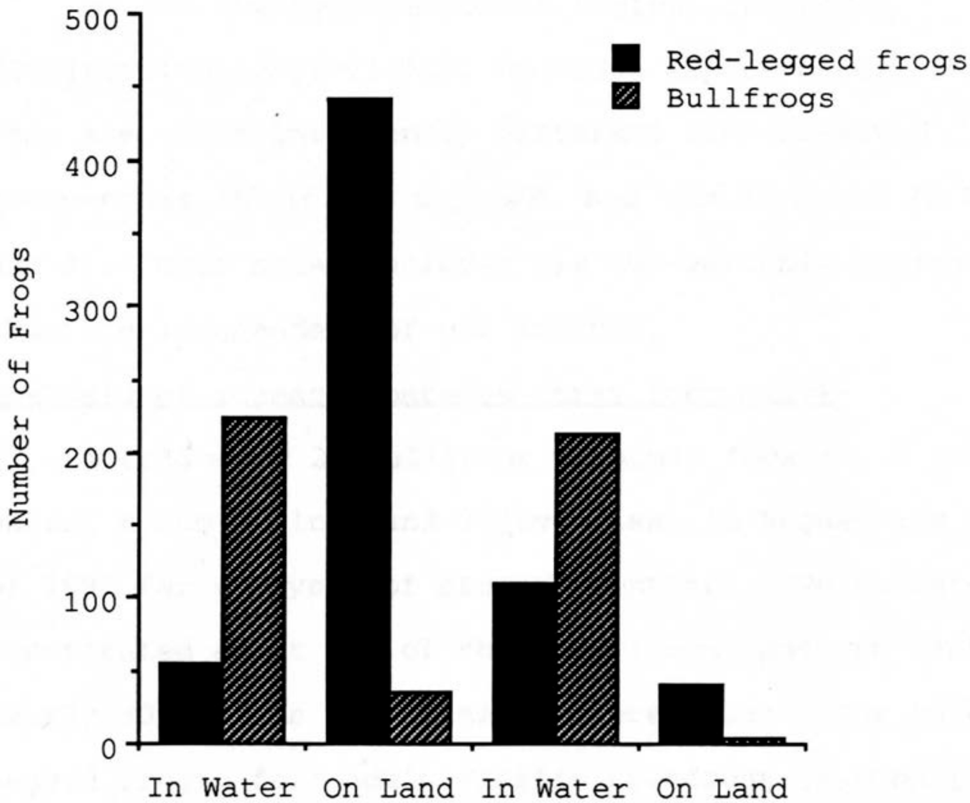
Figure 3: Red-legged frog sightings from sampling plots in different habitat types with respect to time (day or night) and position (in water or on land) at Freshwater Lagoon 1991.



Day Night

Time and Position

Figure 4: Bullfrog sightings from sampling plots in different habitat types with respect to time (day or night) and position (in water or on land) at Freshwater Lagoon 1991.



Day Night

Time and Position

Figure 5: Counts of frogs with respect to species, time, and position at Freshwater Lagoon 1991.

bullfrogs were seen on land. On land, I saw red-legged frogs most frequently in spike rush habitat.

<u>Log-linear models</u>

Of the twenty-nine models tested, one model ({SP} {ST} {SH} {PH} {PT} {TH}) provides expected cell frequencies that are not significantly different from observed frequencies ($L^2=16.46$, $p=0.578$ OK!, see Tables 1 and 2, Figures 6 and 7). This model includes six two-variable interactions that are independent of one another.

<u>Analysis of stomach contents (prey frequency)</u>

I collected 22 bullfrogs (4 adult females, 3 adult males, 6 sub-adults, and 9 juveniles) in August and September of 1991 for analysis of stomach contents. Vertebrates constituted about 36% of the prey items consumed (Table 3). Nearly 30% of the prey consumed were frogs: four juvenile red-legged frogs, four adult Pacific treefrogs *(Pseudacris regilla* (Baird and Girard)), one juvenile bullfrog, and four unidentified frogs. One adult and two juvenile rough-skinned newts *(Taricha granulosa)* were consumed. The skin of the adult newt had been completely digested.

Invertebrates made up 64% of the prey items. Various kinds of insects, one large banana slug, and four aquatic snails were identified. Of the identifiable arthropods, dragonflies were most abundant.

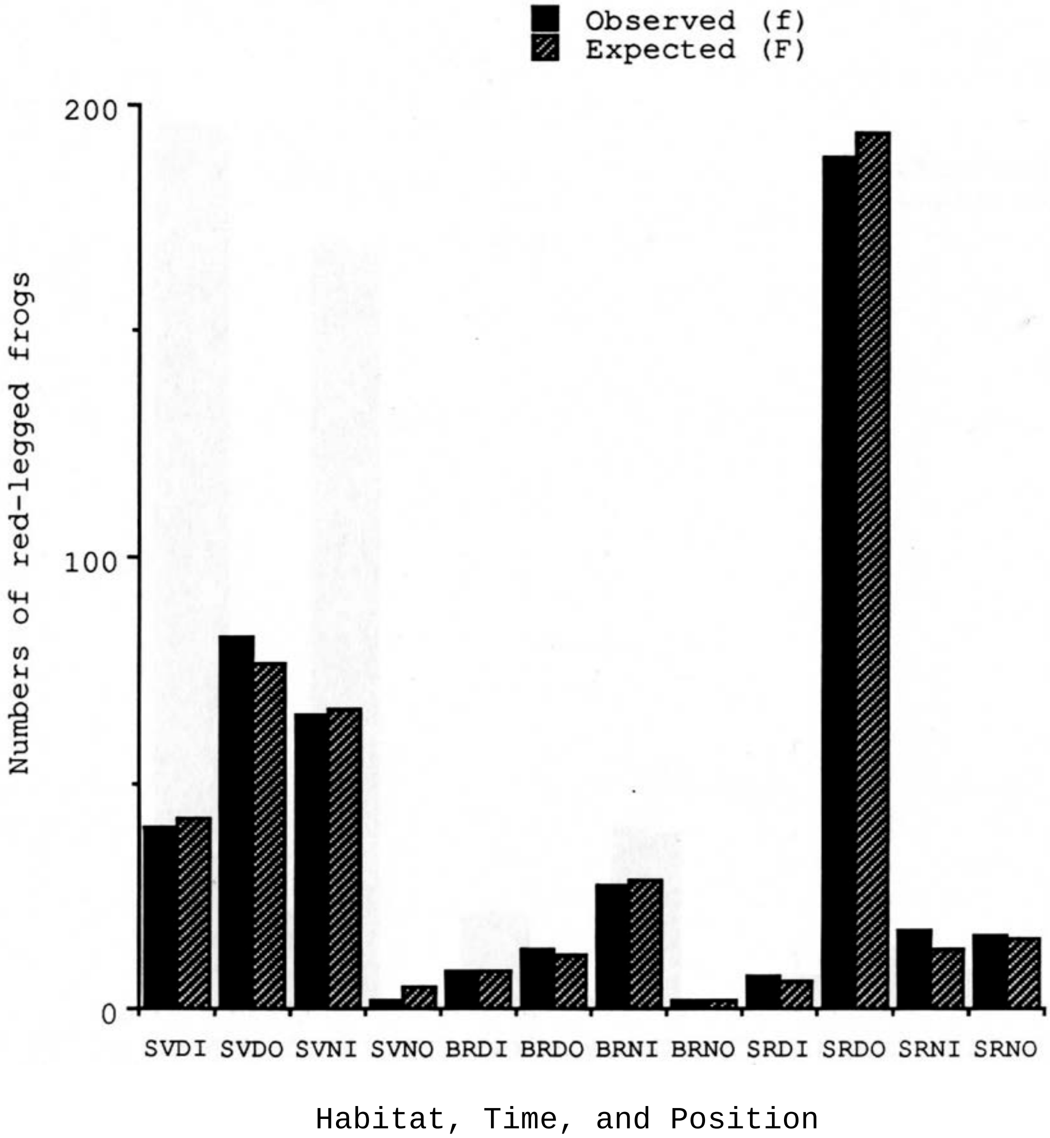


Figure 6: Observed and expected frequencies of red-legged frogs with respect to habitat type, position, and time at Freshwater Lagoon 1991. Expected frequencies are based on the model: {SP} {ST} {SH} {HP} {PT} {HT}

SV=surface vegetation; BR=bulrushes; SR=spike rushes; DI=in water during the day; DO=on land during the day; NI=in water at night; NO=on land at night.

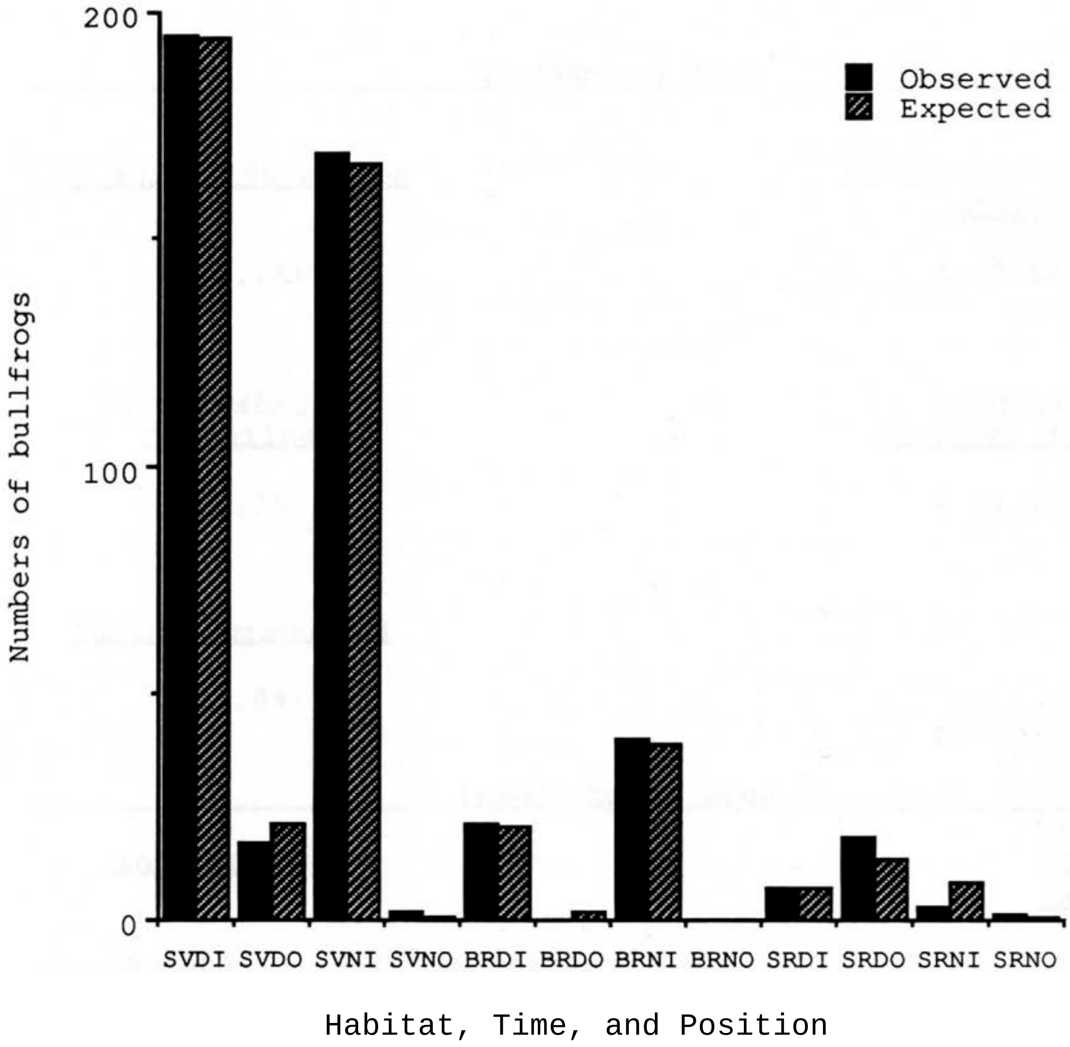


Figure 7: Observed and expected frequencies of bullfrogs with respect to habitat type, position, and time at Freshwater Lagoon 1991. Expected frequencies are based on the model: {SP} {ST} {SH} {HP} {PT} {HT).

SV=surface vegetation; BR=bulrushes; SR=spike rushes; DI=in water during the day; DO=on land during the day; NI=in water at night; NO=on land at night.

Table 3: Prey items of bullfrogs collected at Freshwater Lagoon in August and September of 1991. Percentages of total prey count (44) are in parentheses.

R. aurora juveniles	*Pseudacris regilla* adults
4 (9.1%)	4 (9.1%)
R. catesbeiana juveniles	Anurans (unidentified)
1 (2.3%)	4 (9.1%)
Taricha aranulosa	
3 (6.8%)	

Invertebrate prey

Insects			Count (and %)
O. Odonata	S.O. Anisoptera		6 (13.6%)
	S.O. Zygoptera		3 (6.8%)
O. Hemiptera		F. Notonectidae	1 (2.3%)
		F. Belostomatidae	1 (2.3%)
O. Diptera			1 (2.3%)
O. Coleoptera		F. Dytiscidae	1 (2.3%)
unidentified insects			10 (22.7%)
Molluscs			
Cl. Gastropoda			5 (11.4%)

Seasonal activity patterns

I visited the lagoon 63 times from 1 September 1990 through 18 January 1992. Observations during these visits provided important information on the seasonal activities of red-legged frogs and bullfrogs throughout the year.

Both male and female red-legged frogs were frequently sighted along shore and along the Old State Highway Road throughout January and February of 1991 and 1992, during or after evening rains.

I found egg masses of red-legged frogs in the lagoon on 21 January 1991 and on 12 January 1992, indicating that breeding occurs in the first half of January. A total of 66 egg masses was located in two days of searching in January 1991. Egg masses were not counted in 1992. Mean number of eggs per mass was 471 (s= 134, n= 8). Egg masses were usually attached to submerged vegetation *(Elodea densa* Planch), and many were located about 1m below the surface.

I did not encounter amplectic pairs of red-legged frogs prior to the discovery of egg masses. Interspecific amplexus was observed during six different months (Table 4). I counted a total of 31 cases of male red-legged frogs in amplexus with bullfrogs.

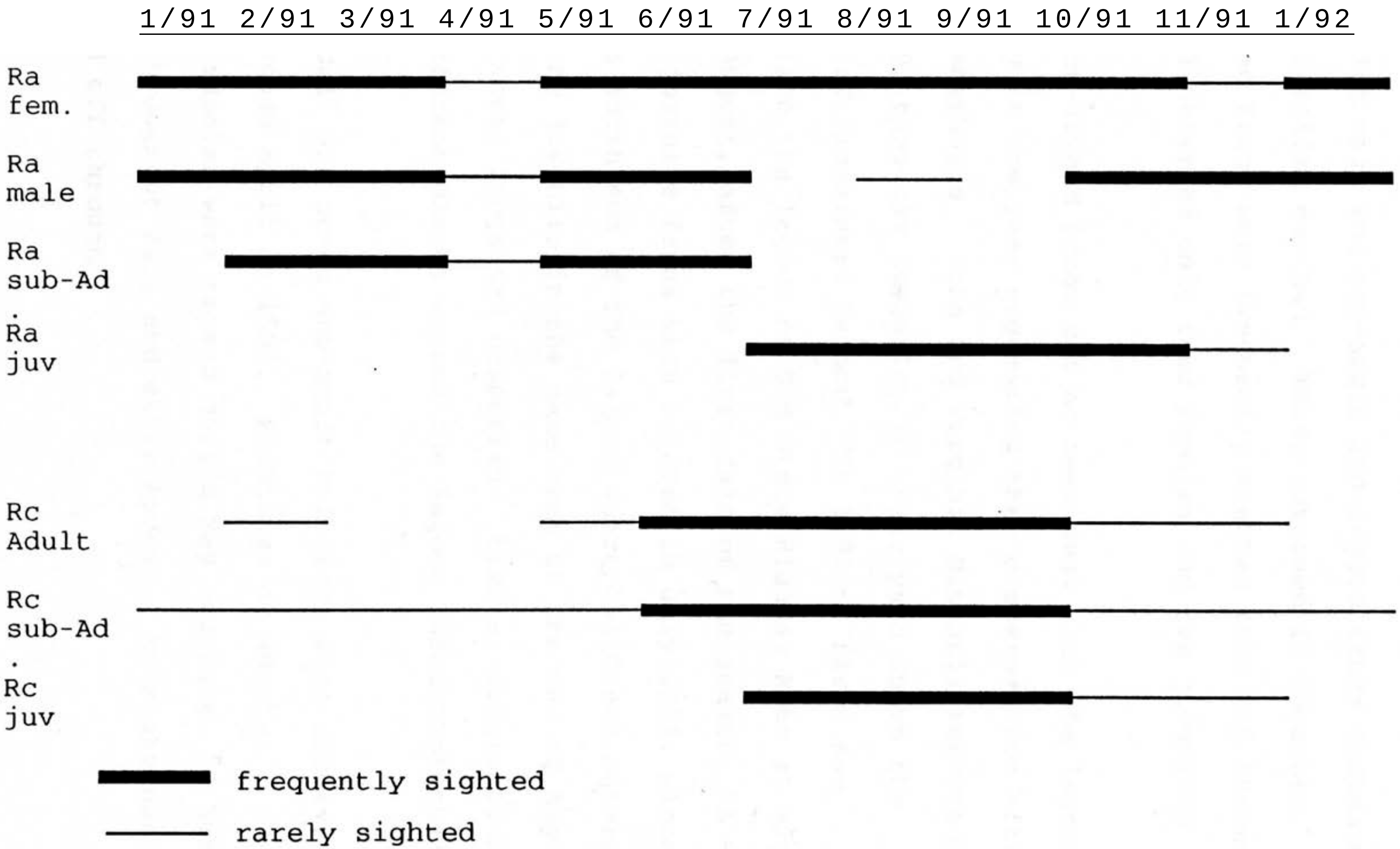
Adult and sub-adult (classification based on relative size) red-legged frogs were frequently found from February through March 1991 (Figure 8). Many fewer of both age classes were observed in April, coincident with a marked drop

Table 4: Cases of interspecific amplexus between *R. aurora* (Ra) males and *R. catesbeiana* (Rc) adult females (AdFem), sub-adults (sub-Ad), and juveniles (juv.) at Freshwater Lagoon 1991 and 1992. Snout-vent lengths (SVL) were recorded for some frogs.

Date	Ra		*Rc*
1/16/91	1 Ad	on	1 sub-Ad
	SVL: 56mm		SVL: 64mm
	1 Ad	on	1 Ad
2/21/91	1 Ad	on	1 sub-Ad
	SVL: 57mm		SVL: 67mm
	3 Ad	on	1 sub-Ad
	SVL: 60mm		SVL: 97mm
	SVL: 65mm		
	SVL: 55mm		
	1 Ad	on	1 sub-Ad
	SVL: 50mm		SVL: 79mm
3/10/91	1 Ad	on	1 Adfem.
			SVL-150mm
	1 Ad	on	1 sub-Ad
5/11/91	1 Ad	on	1 sub-Ad
	SVL: 54mm		SVL: 64mm
5/26/91	1 Ad	on	1 sub-Ad
11/2/91	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
11/25/91	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.
	1 Ad	on	1 juv.

Date	RA		Rc
1/2/92	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
1/12/92	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
1/18/92	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad
	1 Ad	on	1 sub-Ad

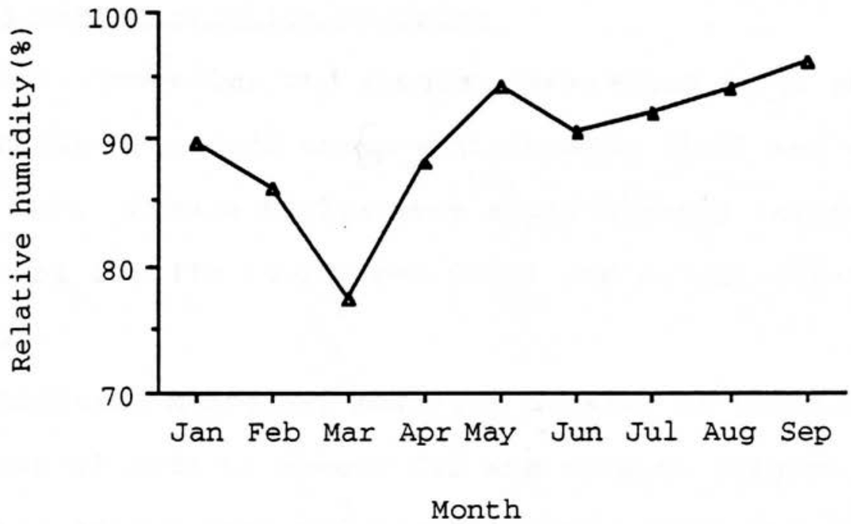
Figure 8: Seasonal trends in sightings of different stages of red-legged frogs (Ra) and bullfrogs (Rc) at Freshwater Lagoon from January 1991 through January 1992. Observations were not made in December of 1991.



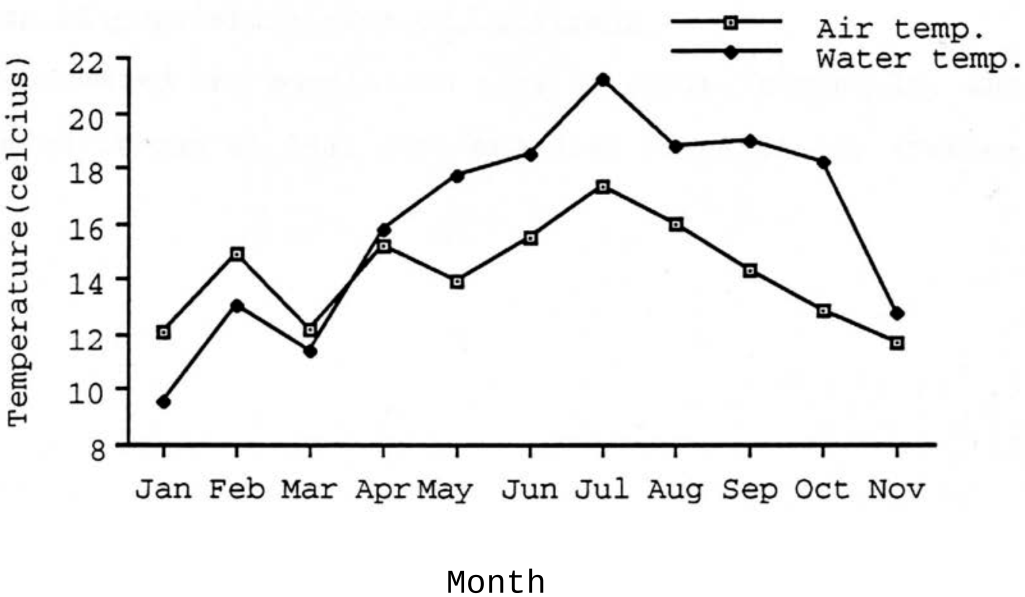
in relative humidity, air temperature, and water temperature in March (Figure 9). Sightings increased again through May and June. My encounters with male and sub-adult red-legged frogs decreased in July, when juveniles emerged. Males returned in November. Female red-legged frogs were frequently sighted from May through October, while I observed only four females and two juveniles in November.

Juvenile red-legged frogs can be seen away from the lagoon relatively early in the year suggesting they disperse soon after completing metamorphosis. John and Virginia Mitchell reported that in May 1990, they saw juveniles in their yard above the southwest shore of Freshwater Lagoon. In 1991, I first saw juveniles away from the lagoon on Old State Highway Road at night on the 27th of August, after the first rain of the season. A large number of juvenile frogs were located in July 1991, along the shore at the south end of the lagoon where Owl Creek enters, but I saw only one juvenile in the same area at the end of August, suggesting that these frogs had dispersed. Similar observations were made in different places around the lagoon throughout the summer and fall.

Only one adult and seven sub-adult bullfrogs were observed from January through April in 1991. Sightings of adults, sub-adults and tadpoles were common during May and June. I heard bullfrog calls throughout July and early August. My sightings of tadpoles tapered off through



(a)



(b)

Figure 9: Trends in relative humidity (a), and air and water temperatures (b) at Freshwater Lagoon 1991. Relative humidity was not recorded from October through December, and temperatures were not recorded in December.

September and October. By November, very few bullfrogs were seen (Figure 10).

Physical characteristics of frogs

Adult, juvenile, and froglet red-legged frogs were captured periodically to record snout-vent lengths (SVL) and weights (Figure 11). Female adults were significantly larger than males in terms of SVL ($T= 14.16$, $p<0.0001$) and weight ($T=-15.59$, $p<0.0001$).

I captured different maturity classes of bullfrog throughout the summer of 1991 to record SVL and weights (Figure 12). Male and female adults were not significantly different in SVL ($T=-0.73$, $p=0.5$) or weight ($T=-0.73$, $p=0.5$).

Estimates of population size of bullfrogs

I estimated the population size of adult, sub-adult, and juvenile bullfrogs at 143, 255, and 3198 respectively (Tables 5-7).

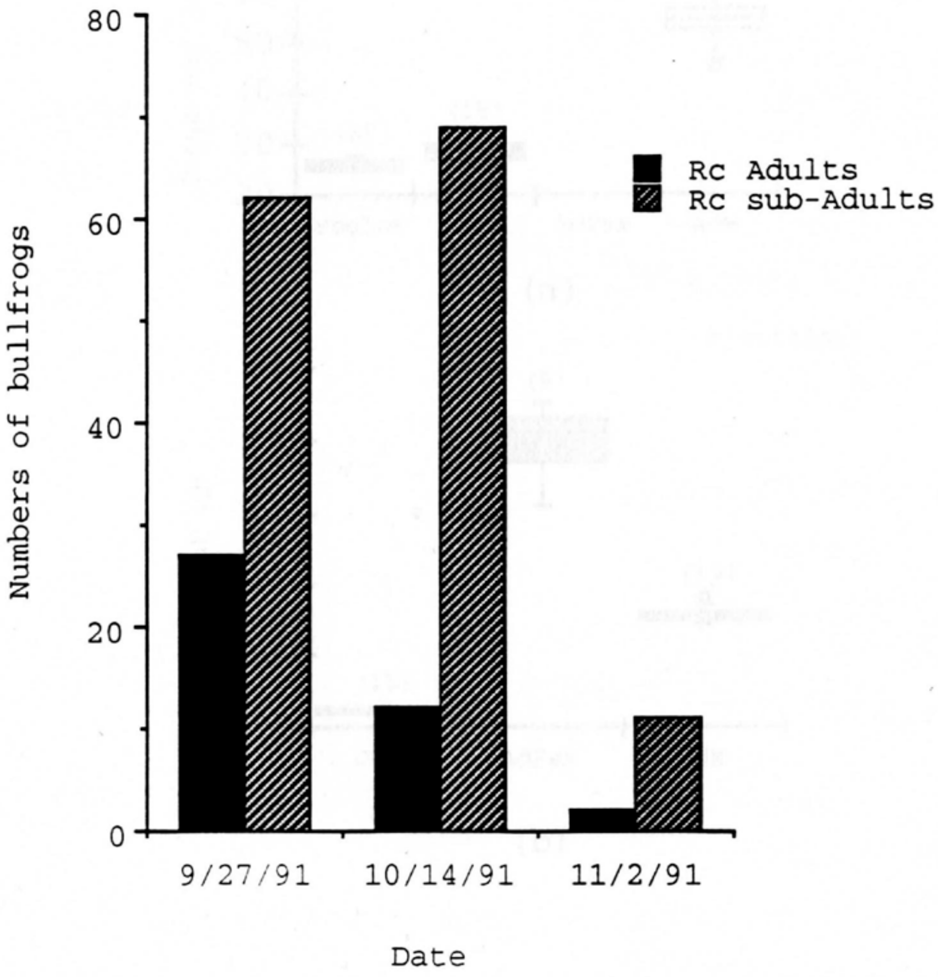


Figure 10: Counts of bullfrogs made while kayaking around the perimeter of Freshwater Lagoon 1991.

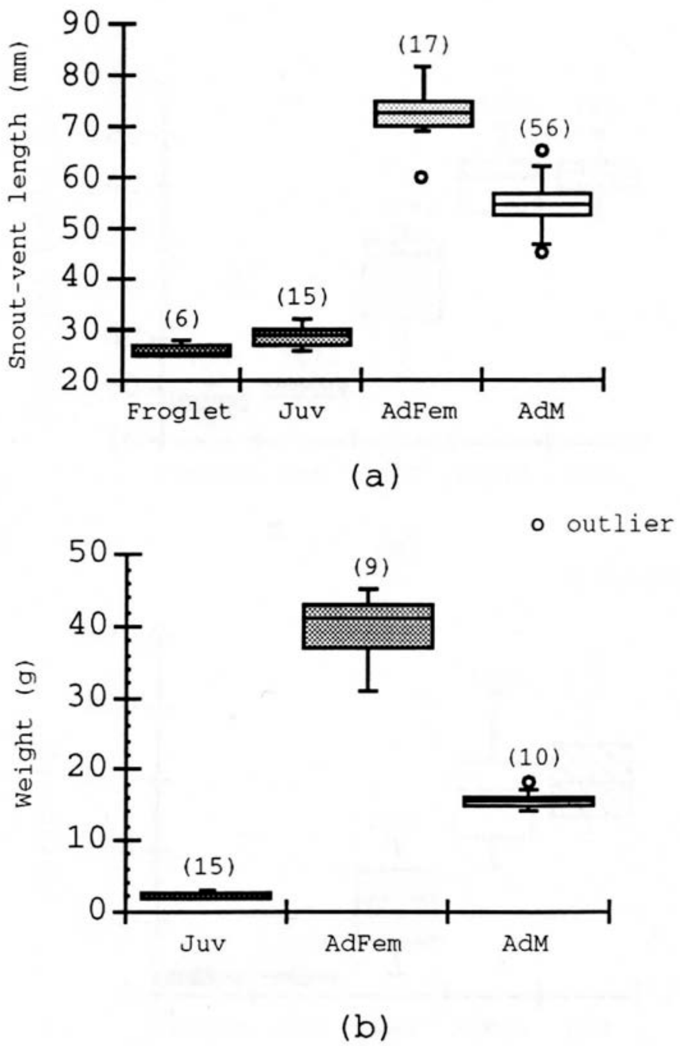


Figure 11: Mean snout-vent length (a) and mean weight (b) of different maturity classes of red-legged frog at Freshwater Lagoon 1991, 1992.

Juvenile (Juv); sub-adult (sAd); adult female (AdFem); adult male (AdM).

Boxes represent 95% confidence limits, and bars represent two standard deviations about the mean. Sample sizes are in parentheses.

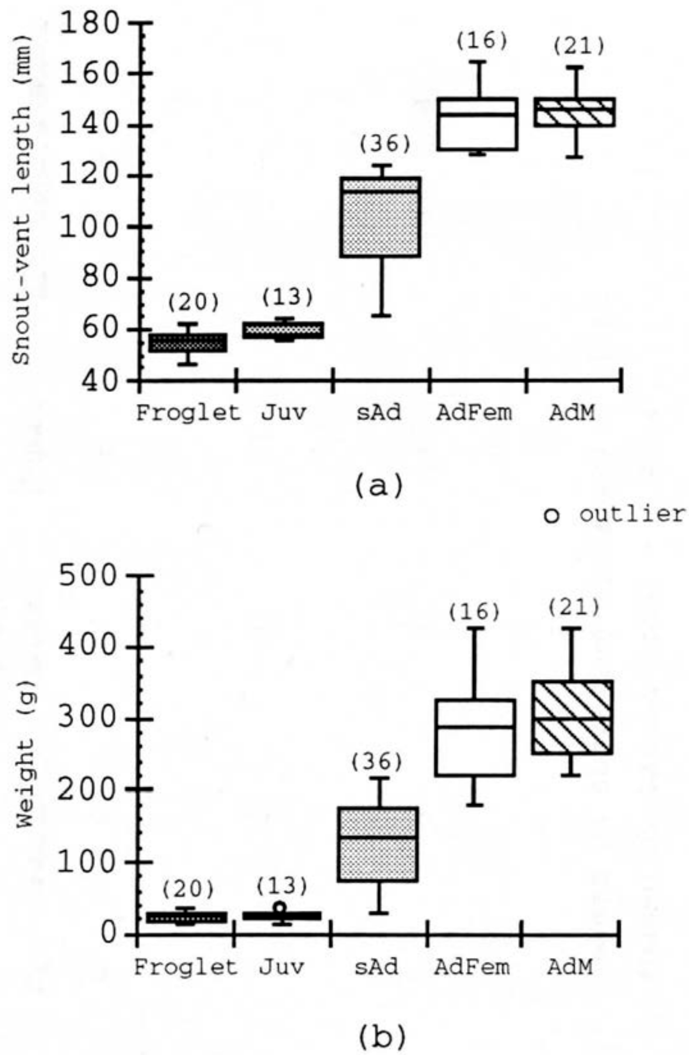


Figure 12: Mean snout-vent length (a) and mean weight (b) of different matuity classes of *Rana catesbeiana* at Freshwater Lagoon 1991.

Juvenile (Juv); sub-adult (sAd); adult female (AdFem); adult male (AdM).

Boxes represent 95% confidence limits, and bars represent two standard deviations about the mean. Sample sizes are in parentheses.

Table 5: Mark-and-recapture statistics for adult bullfrogs at Freshwater Lagoon 1991. Mi= number of marked frogs at start of ith run; Ci= number of captures in ithrun; Ri= recaptures in ith run; N-hat= population estimate for ith run.

Date	Ni	Mi	MiCi	Ri	sum (Ri)	Nwly marked	N-hat	95% conf.limits
8/12 8/17 8/18	0	14	0	0	0	14	-	-
8/22 8/23 8/26	14	11	154	3	3	8	51	-
8/29 8/30 9/1	22	32	704	3	6	0	143	(67, 328)

Estimates of population density: (based on shoreline distance) = 26/km

(based on lagoon area) = 1.4/ha

Table 6: Mark-and-recapture statistics for sub-adult bullfrogs at Freshwater Lagoon 1991. Mi= number of marked frogs at start of ith run; Ci= number of captures in ith run; Ri= recaptures in ith run; N-hat= population estimate for ith run.

Date	Eli	Ci	MiC1	Ri	sum_(Ri)	Newly marked	N-hat	95% conf.limits
8/12 8/17 8/18	0	4	0	0	0	4	-	-
8/22 8/23 8/26	4	MiCi	Ri	0	0	22	undefined	-
8/29 8/30 9/1	26	26	676	3	3	0	255	(94, 934)

Estimates of population density: (based on shoreline distance) -= 47/km

(based on lagoon area) = 2.6/ha

Discussion

Interpretation of the log-linear model (Red-legged frogs and bullfrogs use habitat differently at Freshwater Lagoon

Interpretation of the accepted log-linear model [{SP} {ST} {SH} {HP} {PT} {HT}] for the observed frequencies of frogs in sampling plots provides statistical support for differences habitat use, both within and between species, with respect to time, position, and habitat type. The accepted model appears complex, and includes six interaction effects. However, these interactions are relatively straightforward.

{SP}, {ST}, and {SH} are effects indicative of differences in use of habitat between species.

1) The effect {SP} asserts that the species that I was likely to find depended on where I was looking, in the water or on land (refer to Figures 3 and 4). The majority of red-legged frogs were seen on land, and the majority of bullfrogs were seen in the water. I have seen bullfrogs on shore throughout the Central Valley and in the Sierra Nevada foothills of California. The relative humidity during summer in the central valley is generally much lower than it is in coastal areas like Freshwater Lagoon. Summer air and water temperatures, on the other hand, are higher in the Central Valley than at Freshwater Lagoon. The lower air temperatures

of summer at Freshwater Lagoon may explain why bullfrogs do not leave the water. Lillywhite (1970) studied the behavioral regulation of body temperature in bullfrogs at two ponds in southern California. He found that they maintained their body temperatures between 26^{0}C and 33^{0}C by posturing and by moving between water and land. The highest air temperatures at Freshwater Lagoon occurred in July, but they never exceeded 22^{0}C. Therefore, no thermal benefit would be gained by leaving the water.

2) {ST}: The species I was likely to find depended on when I was looking (day or night). I saw many fewer red-legged frogs than bullfrogs at night, and more red-legged frogs than bullfrogs during the day.

3) {SH}: The species that I was likely to find depended on the type of habitat in which I was looking. Red-legged frogs were frequently observed in spike-rushes (and grass/forb habitats), while bullfrogs were not. I saw bullfrogs much more frequently than red-legged frogs in surface vegetation.

{HP}, {PT], and {HT} are effects indicating differences in use of habitat independent of species.

4) {HP}: The type of habitat in which I saw frogs depended on whether I was looking in the water or on land. This effect is obvious on examination of Figure 2. Very little surface vegetation was sampled on land where it is rare. For similar reasons, very little spike-rush habitat

was sampled in the water. I was likely to find frogs (primarily red-legged frogs) in spike-rushes on land. In the water, I was likely to find frogs of either species in surface vegetation.

5) {PT}: The position where I was likely to find frogs depended on whether I was looking during the day or at night. More frogs were seen on land during the day, while more were seen in the water at night. That I saw so few red-legged frogs at night suggests that these frogs may be less active after dark.

6) {HT}: The type of habitat in which I found frogs depended on the time of searching (day or night) (Figure 3). During the day, frogs (primarily red-legged frogs) were seen most frequently in spike-rushes. At night, I saw frogs most frequently in surface vegetation.

Analysis of stomach contents [Bullfrogs prey on red-legged frogs]

My analysis of stomach contents shows that vertebrates make up a significant portion of the diet of bullfrogs at Freshwater Lagoon during the summer. Adult bullfrogs have been reported to feed on their own species as well as on mice, moles, bats, snakes, and birds (Bury and Whelan, 1984). Cohen and Howard (1958) found small fishes, tadpoles, and salamanders in the stomachs of bullfrogs from the San Joaquin valley in California. I found four juvenile red-legged frogs in bullfrog stomachs. The importance of predation on red-legged frogs by bullfrogs can not be assessed by the analysis of stomach contents without a reliable estimate of the population size of *R. aurora* (Hayes and Jennings, 1986).

My observation that rough-skinned newts *(Taricha granulosa* (Skilton)) had been eaten by *R. catesbeiana* is surprising, considering the reported toxicity of this species. An intraperitoneal injection of as little as 0.00005 cc of skin from *T. granulosa* can kill white mice within 15 minutes (Brodie, et al. 1974). An adult Bobcat ~~lynx~~ *(Lynx* rufus ~~*canadensis*~~ Kerr.) died within 13 minutes after receiving an intraperitoneal injection of only 0.15 cc of newt skin (Brodie, 1968). The skin of this newt contains a neurotoxin that is identical to the tetrodotoxin of the puffer fish, *Takifugu rubripes* (Temminck and Schlegel). The symptoms of tetrodotoxin poisoning are: (a) muscular weakness, leading to splayed gait: (b) loss of righting reflex: (c) convulsions: (d) gasping, gaping, and vomiting: (e) paralysis and fall in blood pressure: (f) death. Brodie (1968) force fed a rough-skinned newt to a bullfrog. Within ten minutes, the bullfrog was dead. The newt crawled from the frog's mouth five minutes after the frog's death, apparently unharmed.

The three newts that I recovered from the stomachs of three different bullfrogs were all dead. All three frogs were healthy when captured, showing no signs of illness. They were apparently unaffected by the skin toxin of the newts they had ingested. The skin of the adult newt had been completely digested.

The only vertebrate reported to have an effective resistance to the tetrodotoxin of *T. granulosa* is the common garter snake, *Thamnophis sirtalis* Garman found sympatrically with the newt (Brodie and Brodie, 1990). These researchers provide evidence that the common garter snake may have evolved a resistance to tetrodotoxin as an adaptation for preying on rough-skinned newts where the two species occur together. An extensive study of the diet of bullfrog populations throughout their range of sympatry with newts might provide evidence of resistance to tetrodotoxin in bullfrogs as well.

Seasonal patterns of activity

The absence of adult male and sub-adult red-legged frogs from the lagoon throughout most of the summer and fall suggests that intraspecific habitat/ resource partitioning may be occurring. Initially an adaptive response to intraspecific competition, an increase in carrying capacity could be a consequence of this resource partitioning (Simon and Middendorf, 1976).

Migration to and from breeding sites is a normal part of the life-history of the northern red-legged frog (Licht, 1969). It is interesting that the departure of adult males and sub-adults from the lagoon is coincident with the emergence of bullfrogs from hibernation. Coincidental or otherwise, the dispersal of adult males and sub-adults, along with juveniles, from the lagoon most certainly alleviates potential predation by bullfrogs. Adult female red-legged frogs, unlike adult males and sub-adults, remain in the lagoon throughout the summer. Their larger size may allow adult females to effectively avoid predation by bullfrogs. To remain in the lagoon during the summer may be important to the reproductive success of the population, off-setting the risk of predation by bullfrogs. Water temperatures tended to be warmer than air temperatures from May through October of 1991 (Figure 10). The warmer water could increase the metabolism of mature females, thereby decreasing the time required for the development of eggs within their ovaries. Thus, the warmer temperatures, coupled with an abundant food supply (i.e., insects) in the lagoon, could help to ensure the readiness of females for breeding the following season.

Subspecies of red-legged frog at Freshwater Lagoon

The size and reproductive behavior of the red-legged frogs at Freshwater Lagoon indicate that the population is of the sub-species *Rana aurora aurora* Baird and Girard (northern red-legged frog). Snout-vent lengths of male and female northern red-legged frogs from Canada range from 45mm to 60mm and 62mm to 80mm, respectively (Licht, 1974 in Hayes and Miyamoto, 1984). Storm (1960) found that the SVL of male and female northern red-legged frogs in Oregon range from 49mm to 65mm and from 72mm to 93mm, respectively. I found that the

SVL of male and female red-legged frogs at Freshwater Lagoon ranges from 45mm to 65mm, and from 60mm to 82mm, respectively. Adults of *R. a. draytonii* Baird and Girard (California red-legged frog) in populations to the south are significantly larger. Hayes and Miyamoto (1984) found that male and female California red-legged frogs from San Luis Obispo, CA range in length from 78mm to 116mm and from 91mm to 138mm, respectively. These frogs are, obviously, much larger than adults from Freshwater Lagoon.

The choice of submerged oviposition sites by female red-legged frogs at the lagoon is consistent with the reproductive behavior of the northern red-legged frog (Licht, 1969; 1971; Storm, 1960). In contrast, female California red-legged frogs deposit their eggs on emergent vegetation at the surface of the water (Hayes and Miyamoto, 1984; Jennings, 1988). It is likely that I did not observe adults in amplexus during the breeding season in 1991 or 1992 because the sub-species is *R. a. aurora*. Male *R. a. aurora* are known to call under water to attract females; mating occurs at the calling site (Licht, 1971), hence, amplexus occurs in submerged positions. Amplexus occurs at the water's surface in the California red-legged frog (Jennings, 1988). <u>Inter-specific amolexus</u>

I observed interspecific amplexus between male red-legged frogs and sub-adult and juvenile bullfrogs at Freshwater Lagoon during the 1991 and 1992 breeding seasons of red-legged frogs. Such a phenomenon could lead to a decrease in reproductive success if it occurred frequently enough. Interspecific amplexus has been reported for other anuran species. Reading (1984) observed numerous incidents of interspecific spawning between male *R. temporaria* L. and female *Bufo bufo* L. at a small, man-made pond in Portland, Dorset (England). Brown (1977) observed a male *B. boreas* (Baird and Girard) in amplexus with a female red-legged frog on 26 April 1973 near Bellingham, WA, at least one month after the breeding season of red-legged frogs. Interspecific amplexus between red-legged frogs and bullfrogs has been reported in the past from Oregon (Storm, 1953). Mark Jennings and Mark Hayes have observed amplexus between these species in southern California (pers. comm.). Since the breeding season of the northern red-legged frog occurs in early to mid-January at Freshwater Lagoon when the majority of bullfrogs are hibernating, I doubt that the few cases of interspecific amplexus during January have any significant impact on the reproductive success of the population. There are probably more than enough males to mate with mature females in a given breeding season (pers. obs.). The possibility that interspecific amplexus contributed to the demise of native ranid populations elsewhere can not be ruled out, particularly in places where bullfrogs emerge from hibernation before the breeding season of another frog begins.

Population size of bullfrogs

My population estimates confirm that bullfrogs are well established at Freshwater Lagoon. While studying bullfrog populations in California canals, Treanor (1975) found that population densities ranged from 6.6 frogs (2.1 adults) to 119 frogs (108.7 adults) per kilometer of shoreline in control areas. I found the population densities of adult and sub-adult bullfrogs at Freshwater Lagoon to be 26 adults/km of shoreline and 47 sub-adults/km of shoreline, which are within the range of densities reported by Treanor. My estimate of the overall density of bullfrogs at the lagoon, (~35 frogs/ha), is comparable to population densities reported for bullfrogs in a 7 ha Illinois lake (Durham and Bennett, 1963).

Summary

Red-legged frogs and bullfrogs use the habitat differently enough at Freshwater Lagoon to allow their co-existence, in spite of: a) the inter-specific amplexus that occurs; and b) the predation on red-legged frogs by bullfrogs.

Predation could have played a significant role in the decline of populations of red-legged frogs in warmer/drier climates where frogs would be more confined to permanent water. There appear to be no such barriers to dispersal for red-legged frogs at Freshwater Lagoon. Relative humidity remains high, and temperatures remain mild throughout the summer.

Interspecific amplexus might also have contributed to declines in populations of other species of frog where the bullfrogs emerge from hibernation before or during the breeding season of the other species. These factors should be examined in greater detail where bullfrogs have been introduced.

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Appendix A

Table A.1: Snout-vent lengths (SVL) of all male and female *Rana aurora* measured at Freshwater Lagoon 1991 and 1992.

Adult males
SVL (mm)

49	52	53	57	54	52	51	56	57	55
60	65	55	52	45	55	56	62	50	50
48	57	55	55	59	61	54	54	59	55
54	54	57	53	53	53	57	53	58	57
56	57	56	54	53	56	58	54	50	55
54	50	60	50	60	47				

Adult females
SVL (mm)

69	80	74	73	72	74	75	70	76	72
72	70	70	60	78	82	74			

Appendix A (continued)

Table A.2: Snout-vent lengths (SVL) and weights of *Rana aurora* adults captured at Freshwater Lagoon in January 1992.

Adult males		Adult females	
SVL (mm)	Weight (g)	SVL (mm)	Weight *(g)*
59	16	69	31
55	15	80	45
54	14	74	41
54	16	73	36
57	17	72	44
53	15	74	42
53	15	75	39
53	14	70	37
57	18	76	43
53	16		

Appendix A (continued)

Table A.3: Snout-vent lengths (SVL) and weights of *Rana aurora* juveniles captured at Freshwater Lagoon on 5 August 1991.

Juveniles			
SVL (mm)	weight (q)	SVL (mm)	Weight (g)
30	2.0	31	3.0
29	2.0	26	1.9
30	2.9	32	2.5
30	2.4	29	2.4
29	2.4	30	2.2
26	1.7	30	2.7
27	1.7	27	2.5
27	1.8		

Appendix A (continued)

Table A.4: Snout-vent lengths (SVL) and weights of *Rana catesbeiana* adults captured at Freshwater Lagoon 1991.

Male		Female	
SVL (mm)	Weight (g)	SVL (mm)	Weight (g)
146	275	142	300
143	287	142	270
127	220	138	250
146	325	150	325
137	225	152	400
132	225	165	425
140	300	152	325
140	250	145	315
142	250	130	210
149	340	145	300
159	390	130	225
150	350	128	180
135	250	148	370
140	265	136	220
163	425	128	200
150	325	145	275
147	375		
157	370		
130	225		
150	350		
155	350		

Appendix A (continued)

Table A.5: Snout-vent lengths (SVL) and weights of *Rana catesbeiana* sub-adults captured at Freshwater Lagoon 1991.

SVL	Weight (a)	SVL (mm)	Weight (a)
75	38	100	102
80	51	74	41
108	125	110	150
112	135	73	33
123	200	117	175
119	125	112	125
124	200	65	28
71	37	117	125
122	175	108	125
120	175	104	100
116	160	115	130
88	75	120	150
75	49	82	66
122	175	103	140
116	150	118	175
114	125	110	150
115	165	117	175
123	215	121	175

Appendix A (continued)

Table A.6: Snout-vent lengths (SVL) and weights of *Rana catesbeiana* juveniles and froglets captured at Freshwater Lagoon 1991.

Juvenile		Froglet	
SVL (mm)	Weight (a)	SVL (mm)	Weight (a)
56	22	56	22
58	24	57	24
57	24	57	30
62	24	62	35
57	30	62	23
62	23	57	27
57	27	52	18
57	16	58	25
58	23	51	18
58	19	60	28
56	21	58	22
64	27	55	24
		56	28
		55	28
		55	22
		54	20
		56	33
		47	14
		50	16
		51	19