Demographic analysis of the Columbia spotted frog (*Rana luteiventris*): case study in spatiotemporal variation

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Abstract: This study examined size, mass, sex ratios, and age structure of the Columbia spotted frog (*Rana luteiventris*) at seven sites in the Toiyabe Range in central Nevada from 1994 through 1996. Age structure was estimated using skeletochronology. Demographic composition was found to be significantly different among sites, suggesting that localized factors influence recruitment and mortality rates. Demographics among years at the sites were also significantly different, indicating that the population dynamics of this system are complex and are also driven by one or more temporal factors. Knowledge of local land-use patterns and anecdotal observations were incorporated in an attempt to identify potential stress agents in need of further research and possible intensive management. Differences in recruitment, survivorship, and mortality rates among sites may be due to microclimate, food availability, and predation rates. Introduction of exotic trout and cattle are likely the most important anthropogenic factors limiting the distribution and persistence of *R. luteiventris* in the study area. Extreme variations in annual weather patterns may account for many differences observed at some sites. This study demonstrates that adequate assessment of amphibian population status requires knowledge of subpopulation demographics across a broad landscape.

Résumé : La taille, la masse, les rapports mâles:femelles et la structure de la population en fonction de l'âge ont été déterminés chez la grenouille *Rana luteiventris* à sept sites dans les monts Toyabee, dans le centre du Nevada, de 1994 à la fin de 1996. La structure de la population en fonction de l'âge a été étudiée par squelettochronologie. La composition démographique s'est avérée significativement différente d'un endroit à l'autre, ce qui semble indiquer que des facteurs locaux influencent le recrutement et les taux de mortalité. Les facteurs démographiques différaient significativement aussi d'une année à l'autre; il semble donc que la dynamique de population dans ce système soit complexe et régie par un ou plusieurs facteurs temporels. La connaissance des patterns d'utilisation du terrain et des observations anecdotiques ont été incorporées aux analyses dans le but d'identifier d'éventuels agents de stress qui doivent faire l'objet de recherches plus poussées et qui nécessitent peut-être aussi d'être régis de façon plus rigoureuse. Les différences d'un site à l'autre quant au recrutement, à la survie et aux taux de mortalité peuvent être attribuables au microclimat, à la disponibilité de la nourriture et aux taux de prédation. L'introduction de truites exotiques et de bétail sont probablement les facteurs anthropogènes les plus influents sur la répartition et la continuité de *R. luteiventris* dans la zone d'étude. Des variations climatiques annuelles extrêmes peuvent expliquer plusieurs des différences observées entre les sites. Cette étude démontre qu'une estimation juste du statut des populations d'amphibiens suppose la connaissance des variables démographiques des sous-populations dans un paysage à grande échelle.

[Traduit par la Rédaction]

Introduction

Studies of frogs have shown that populations of a species at different locations may differ in variables that influence life history, such as egg size (Pettus and Angleton 1967; Berven 1995), egg development rates (Ruibal 1955), clutch size, length of larval period, size at metamorphosis (Berven 1995; LeClair and Laurin 1996), and age and size at maturity (Tilley 1973; Berven 1995; LeClair and Laurin 1996).

Many local differences, including female size (a rough measure of fecundity); larval, juvenile, and adult growth rates; and age at maturity influence the demographic dynamics and structure of amphibian populations (Cole 1954; Gadgil and Bossert 1970; Berven 1988, 1990) and are determined at least in part by local environmental conditions (Gill et al. 1983).

Because amphibian life-history traits are closely linked to the environment, the growth rates and age composition of an amphibian population may reflect the condition of the local habitat. Populations may experience birth and death rates that vary from area to area. When this occurs, reproductive surpluses from productive source habitats may sustain subpopulations in sink habitats, where local recruitment fails to keep pace with mortality (Pulliam 1988). Misyura (1989), for example, analyzed the age composition of subpopulations of *Rana temporaria* under the influence of runoff water from chemical and metallurgy industries and found elevated young-of-the-year mortality rates in contaminated ponds.

Fig. 1. Distribution of the *Rana pretiosa* complex (*Rana luteiventris* (hatched), *Rana pretiosa* (stippled)). The numbers correspond to the Toiyabe Range (1), Jarbidge Mountains/ Independence Range (2), Ruby Mountains (3), West Desert (4).
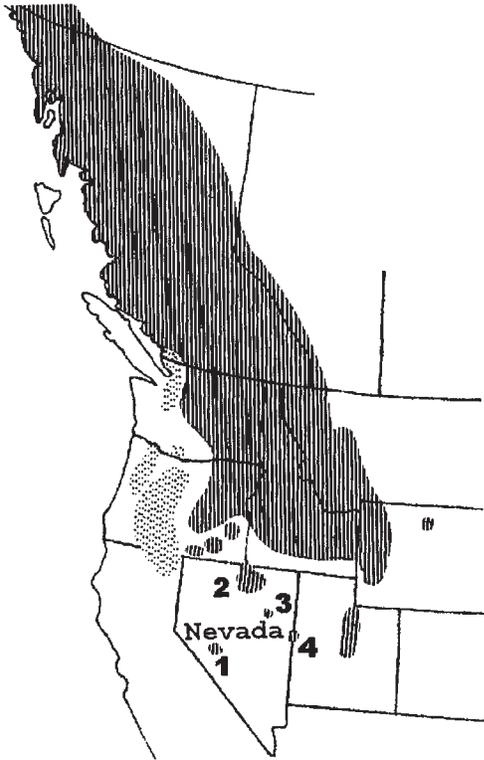
Thus, his findings indicate a variation in the source–sink potential of different sites.

Knowledge of demographic patterns of amphibian subpopulations is essential in identifying stress agents in the environment, setting management priorities to protect critical source habitat, and monitoring recovery efforts. In particular, monitoring demographic patterns and land-use and climate variables could lead to improved techniques for preventing the gradual depauperation of communities, and eventually to improved management of communities and ecosystems under stress.

Reaser (1997) conducted a survey of the status of the Columbia spotted frog, *Rana luteiventris*, in Nevada and found that the frog had disappeared from more than 50% of its historically occupied sites. Persistent frogs were clustered in four population units (Fig. 1).

To evaluate the population status and determine possible factors driving population declines, the demographic patterns of seven "subpopulations" of *R. luteiventris* in the Toiyabe Range in central Nevada were investigated. If the frogs at these sites showed similar demographic patterns, then it would be apparent that the dynamics were predominantly influenced by one or more factors operating at the regional level. Alternatively, if the demographic compositions were significantly different, then it could be assumed that localized factors are influencing recruitment and mortality rates. If significant differences were found among years, then it would be likely that the population dynamics of this system are complex and that any short-term evaluation must

be viewed with caution when applied to conservation planning.

Knowledge of local land-use patterns and anecdotal observations were incorporated into the study in an attempt to identify potential stress agents in need of further research and possible intensive management. While a quantitative comparison of land-use patterns and frog demographic trends would be ideal, records on land use in this region are incomplete and often do not reflect the actual timing, extent, and degree of use (J. Brack, personal communication; J.K. Reaser, personal observation). This is due in part to the remoteness of the area and paucity of land management personnel. Thus, comparisons of land-use patterns and frog demographic trends are limited largely to the discussion.

Materials and methods

Natural history

Rana luteiventris is a member of the cryptic western spotted frog (*Rana pretiosa* complex) that also includes the Oregon spotted frog (*R. pretiosa*) in south-central Washington, the Cascade Mountains of Oregon, and extreme southwestern British Columbia. The range of *R. luteiventris*, as currently recognized, extends northward from isolated relict populations in Nevada and Utah, through parts of eastern Oregon, northern and central Idaho, northwestern Wyoming, eastern Washington, western Montana, and much of British Columbia, to extreme southwestern Yukon (Fig. 1; Green et al. 1996, 1997; Reaser and Pilliod 2000).

The *R. pretiosa* complex is one of many groups of frogs experiencing declines in the western United States (Corn 1994; Stebbins and Cohen 1995; Reaser and Pilliod 2000). Documented rarity and loss of populations (Turner 1962; Dumas 1966; Nussbaum 1983; Hovingh 1993; McAllister et al. 1993; Reaser 1997) and increasing land-use pressures, such as urbanization and irrigation, have qualified spotted frogs in the Great Basin (Nevada and southern Idaho), West Desert (Utah), and Wasatch Front (Utah), as well as along the west coast (western Washington and Oregon) for protection under the federal Endangered Species Act (Worthing 1993).

Rana luteiventris in Nevada are found at sites characterized by low water-flow rates, little shade, cool clear water, and other habitat variables associated with slow moving and (or) pooled water. Populations persist at elevations ranging from 1700 to 2650 m above sea level (mean of 2200 m) with midday summer water temperatures ranging from 6 to 24°C (mean of 15°C) and midday summer air temperatures ranging from 16 to 36°C (mean of 26°C) (Reaser 1997). Anecdotal observations suggest that *R. luteiventris* in central Nevada are generally active from midspring through midfall. Breeding activity occurs soon after emergence from hibernation (Turner 1958; Reaser and Pilliod 2000).

Field sampling

This study was undertaken in conjunction with a broad-scale investigation of the current status of *R. luteiventris*, during which a large team of biologists conducted visual-encounter surveys (Heyer et al. 1994) of the species at wetland sites throughout central and northern Nevada from mid-June to late August, 1993–1996 (Reaser 1997).

This paper focuses on the intensive study of demographics of *R. luteiventris* at seven sites in the Toiyabe Range of Nye County, in central Nevada. These sites were identified in 1993 as the only locations in the Toiyabe Range where *R. luteiventris* was predictably located. The sites are listed and described in Table 1 and will be referred to by their corresponding abbreviations throughout the remainder of the paper. Each site was visited approximately every

Table 1. Sites intensively surveyed for *Rana luteiventris* in the Toiyabe Range, Nye County, Nevada.

Site name and location[a]	Elevation (m)	Flow status	Predominant vegetation	*Rana luteiventris* density (no./150 m)[b]	Other vertebrates[c]
Illinois Creek (ILC), T12N R40E S24 SW1/4 NW1/16	2200	Permanent	*Salix* spp., Rosaceae, *Artemisia* spp., *Chrysothamnos nauseosus*	2	*Salvelinus fontinalis, Oncorynchus mykiss, Thamnophis elegans, Bos taurus*
Indian Creek Ditch (ICD), T11N R40E S5 NE1/4 NE1/16	2200	Permanent	*Rannunculus aquaticus, Salix* spp., Rosaceae, *Artemisia* spp.	10	*Rhinichthys osculus, T. elegans, B. taurus*
Indian Creek, permanent transects (IC), T11N R40E S17 SE1/4 SW1/16	2250	Permanent	*Rannunculus aquaticus, Potamogeton foliosis, Spyrogyra* spp., *Artemisia* spp., *Chrysothamnos nauseosus*	20	*R. osculus, Catostomus tahoensis, T. elegans, Lagurus curtatus*
Indian Creek at RO Ranch (RO), T11N R40E S20 NE1/4 NW1/16	2250	Ephemeral	*Rannunculus aquaticus, Spyrogyra* spp., *Artemisia* spp., *Chrysothamnos nauseosus*	9	*R. osculus, T. elegans, B. taurus*
Cow Canyon Creek (CCC), T11N R40E S27 NE1/4 SW1/16	2300	Ephemeral	*Salix* spp., Rosaceae, *Artemisia* spp., *Chrysothamnos nauseosus*	6	*R. osculus, T. elegans, B. taurus*
Farrington Ranch Pond (FRP), T9N R40E S5 NE1/4 NE1/16	2150	Permanent	*Spyrogyra* spp., *Salix* spp., Rosaceae, *Artemisia* spp., *Chrysothamnos nauseosus*	24	*T. elegans*
Upper Reese River (URR), T11N R41E S34 SW1/4 SE1/16	2700	Permanent	*Salix* spp., *Artemisia* spp.	4	Trout spp., *T. elegans*

[a]Linear sites consisted of a 750 m transect divided into 150 segments. Average site width of creeks is at 1 m and for the river is at 2 m. Surface area of FRP is 56.8 × 37.5 m, with a maximum depth at 1.75 m.

[b]Average midseason (1996) densities of *Rana luteiventirs* for 150-m transects in linear habitats and time-constrained search at FRP.

[c]Other predominant vertebrates observed on site.

10 days from mid-June to late August. At the streams, two-person teams employed transects to conduct visual-encounter surveys as they walked upstream in unison, on opposite banks, for a distance of 150 m over approximately a 20-min period. The teams captured frogs and placed them in individually marked bags. A series of environmental variables were measured and noted (e.g., air and water temperatures; stream widths, depths, and flow rates; presence and numbers of other species; vegetative cover). All frogs were processed (see below) and returned to their original sites of capture.

The surveys covered up to six continuous transects per site, or a potential 750 m/day. This was the maximum distance that could be effectively covered at sites where frogs were relatively abundant, and it also represented the maximum stream length available midseason at ephemeral sites. The pond was divided into four equally sized quadrats, and each quadrat was surveyed during a 20-min period by two individuals on an inflatable raft.

Size (snout–vent length; SVL) and mass were measured for each captured animal, and sex was determined for mature frogs. Examination of voucher specimens revealed that the sex of adult *R. luteiventris* could be confidently determined through the evaluation of external morphology; males have an enlarged first finger (thumb) and relatively shorter, more robust forelimbs than females.

One toe was obtained from each animal for skeletochronological analysis and placed in individually marked microvials containing 10% buffered formalin. In 1994, animals were individually marked through toe clipping (see Reaser and Dexter 1996*b*). In 1995 and 1996, the third toe from the thumb on the frog's right forefoot was clipped (RF3 position; Donnelly 1989).

Museum specimens

The author located 58 historical voucher collections (1912–1973) with specimens identified as *R. pretiosa* (= *R. luteiventris*) from Nevada. Of these vouchers, one series of 11 vouchers col-

lected at Indian Creek (IC) in 1938 provided a direct comparison of age and size of *R. luteiventris*. Each voucher specimen was measured as in the field procedure and the RF3 toe excised for skeletochronological analysis.

Age estimation

Many age-estimation methods commonly used for amphibians (e.g., size–age comparisons, size at sexual maturity, extrapolation from size-frequency data) are based on the assumption that there is a strong predictable correlation between size and age, at least for adult amphibians. Halliday and Verrell (1988), however, questioned this assumption and determined that in the majority of species reviewed, growth rate prior to age of first reproduction is a much more significant source of variance in body size than age. They concluded that only two methods, mark–release–recapture studies and skeletochronology, are reliable for aging amphibians. Mark–release–recapture studies can provide precise data on a wide variety of demographic measures over a specific time interval, but the technique is labor intensive and requires many years of sampling before definitive analysis is possible.

Skeletochronology has been conducted for several amphibian species (see reviews by Halliday and Verrell 1988; Smirina 1994; Russell et al. 1996) and indicates that amphibian growth may actually be punctuated, with each unit of time recorded as a band of tissue separated by a line marking a period of arrested growth (e.g., hibernation or estivation). Investigators typically assume that a single growth band is laid down annually, and therefore the number of growth bands accurately reflects chronological age, at least past metamorphosis, in amphibians.

Slide preparation of toe samples for skeletochronological analysis requires that a long bone (in this case, the toe) is decalcified, cross-sectioned, and stained. Then individual sections are mounted. This procedure was conducted by a commercial laboratory (Mat-

Table 2. Summary of *R. luteiventris* caught in the Toiyabe Range, 1994–1996.

	Total no.	%	SVL (cm)[b]			Mass (g)		
			$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Females[a]	424	47	5.7	1.3	3.0–9.0	21.2	14.2	3.0–68.0
Males	303	34	5.4	0.9	3.3–7.1	17.3	8.0	3.5–4.1
Juveniles	154	17	3.5	0.7	2.1–5.1	4.9	1.9	1.0–9.0

[a]SVL and mass for all animals combined ($F = 5778.8$, $P < 0.0001$), for females ($F = 2524.9$, $P < 0.0001$), males ($F = 1063.1$, $P < 0.0001$), and juveniles ($F = 134.1$, $P < 0.0001$).
[b]Females were significantly larger and heavier than males (SVL: $F = 7.0$, $P < 0.008$; mass: $F = 18.2$, $P < 0.001$).

son's Laboratory, Milltown, Mo.) for this study, generally following published protocols (e.g., Hemelaar and Van Gelder 1980; LeClair and Castanet 1987; Kusano et al. 1995; Russell et al. 1996).

Several cross sections from each specimen were viewed under a compound microscope and photographed. Age assigned to each specimen was determined from the number of lines of arrested growth (LAGs) visible in the photographs. Each LAG was assumed to indicate one annual hibernation event. The outer boundary of the periosteum was not counted because it represents growth that occurred during the season of field sampling.

In any study utilizing skeletochronological data, a number of potential sources of error should be considered, including evaluation of cross sections containing an incomplete complement of LAGs, miscounting of LAGs, and resorption of LAGs (see discussion in Russell et al. 1996; review by Smirina 1994). Serial sectioning of five phalanges revealed that only a 0.5-mm segment at the phalanx midpoint contained all bone layers. Therefore, only mid-diaphyseal sections were evaluated in this study.

LAGs were defined in this study as darkly stained, robust lines that were continuous around much of the phalanx. Occasional small, faint, incomplete lines between the darkly stained LAGs were not counted. Control for errors in counts of LAGs included the examining of sections by independent observers (the author and one assistant) and the disregarding of six sections in which the number of LAGs was uncertain. Partial resorption of the innermost LAGs was apparent in many samples, but only four were excluded because of the reorganization or resorption of bone that completely eliminated one or more LAGs.

Statistical procedures

Statistical analyses were employed to test the hypotheses that there are significant differences in SVL, mass, and longevity among male, female, and juvenile *R. luteiventris* in the Toiyabe Range, and that demographic measures (sex ratio, SVL, mass, longevity, and age structure) are significantly different (*i*) among sites in the same year, (*ii*) among years at the same site, and (*iii*) within the same cohort among sites and years. Linear regression was conducted to compare continuous variables, and a *F* test was conducted. *P* values based on the *F* ratio were examined to test the strength of the association, and a logistic regression was used to evaluate continuous factors for categorical responses. A one-way analysis of variance (ANOVAs) was used to evaluate the means of noncategorized variables and the *F* test, as well as to calculate standard deviation (SD) from the mean. Contingency table analysis was used to examine categorical responses to categorical factors. All statistical analyses used JUMPIN (Sall and Lehman 1996) statistical software.

Results

Across population

Over the course of this study, 887 *R. luteiventris* individuals were captured (Table 2). Skeletochronology was conducted for approximately 82% of all individuals sampled

Table 3. Sex ratios of *R. luteiventris* among sites in the Toiyabe Range, 1996.

Sex	Sites						
	ILC	ICD	IC	RO	CCC	FRP	URR
Males	1	8	102	9	17	68	0
Females	2	16	145	12	54	43	8
Juveniles	0	20	28	19	0	51	3

Note: Refer to Table 1 for site abbreviations. Sites have a $P < 0.0001$.

and for 83% of females (354 individuals), 78% of males (235 individuals), and 86% of juveniles (132 individuals). Females were estimated to have lived up to 7 years ($\bar{x} = 2.0$ years, SD = 1.2 years), but males did not exceed 5 years ($\bar{x} = 1.7$ years, SD = 0.91 years). Eighty-six percent of the juveniles were metamorphosis-year animals, the remainder having experienced one hibernation. SVL and mass were significantly correlated with number of LAGs (age) for all animals combined (SVL: $F = 812.9$, $P < 0.0001$; mass: $F = 719.3$, $P < 0.0001$), as well as for females (SVL: $F = 365.7$, $P < 0.0001$; mass: $F = 396.2$, $P < 0.0001$) and males (SVL: $F = 67.0$, $P < 0.0001$; mass: $F = 69.2$, $P < 0.0001$). SVL was significantly correlated with number of LAGs in juveniles ($F = 10.1$, $P < 0.002$), but mass was not ($F = 2.6$, $P < 0.1$). There was substantial overlap in size among age-classes.

Demographic variation among sites

No site had a 1:1 sex ratio of *R. luteiventris*, and sex ratios were significantly different among sites ($P < 0.0001$; Table 3). Males were more frequently detected than females at Farrington Ranch pond (FRP), but females dominated elsewhere. Males were not detected at Upper Reese River (URR). Juveniles were not detected in any year at either Cow Canyon Creek (CCC) or Illinois Creek (ILC). Males were significantly different in SVL and mass, but not age structure (Table 4). Females and juveniles were significantly different in all demographic measures among all sites (Table 4). Differences in SVL and mass are generally explained by variations in age structure. In 1996, no males were found to be older than 3 years of age, but cohorts of 4-, 5-, and (or) 6-year-old females were detected everywhere but ICD.

Demographic variation among years

Sex ratios tended to vary among 3 years at IC (1994–1996; $P < 0.0001$) but were similar between 1995 and 1996 at FRP ($P < 0.5$; Table 5). Females dominated in 1994 and 1996 at IC, but sex ratios were nearly equal in 1995. Males were more commonly detected than females at FRP. All demographic measures were significantly different among years for both sexes at IC, and mean SVL was significantly

Table 4. Traits of *R. luteiventris* among sites in the Toiyabe Range, 1996.

Subpopulation and sex	N	SVL (cm)[a]				Mass (g)[b]				Age structure (year)[c]							
		Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	0	1	2	3	4	5	6	N
ILC																	
Male	1	5.8	5.8	5.8	—	21.0	21.0	21.0	—	0	—	—	—	—	—	—	—
Female	2	7.1	7.6	7.4	0.35	37.0	38.0	37.5	0.71	0	—	—	—	1	—	—	1
ICD																	
Male	8	4.4	5.6	5.0	0.38	7.5	18.0	12.3	3.39	0	3	—	—	—	—	—	3
Female	16	4.0	7.0	5.5	1.13	5.0	32.0	17.6	10.55	0	8	2	1	—	—	—	11
IC																	
Male	102	4.1	6.9	5.3	0.61	6.0	22.7	15.0	5.63	2	44	24	4	—	—	—	74
Female	145	3.4	8.3	5.8	1.10	4.0	49.0	20.8	11.08	4	47	34	34	5	2		126
RO																	
Male	9	4.6	6.0	5.5	0.59	10.0	21.0	16.0	4.04	1	2	2	1	—	—	—	6
Female	12	4.5	7.6	5.8	1.16	9.0	50.0	20.9	12.72	0	6	2	2	—	—	1	11
CCC																	
Male	17	4.8	6.5	5.8	0.61	8.0	29.0	20.3	6.86	0	3	4	3	—	—	—	10
Female	54	4.3	8.2	6.3	1.24	8.0	58.0	28.8	14.93	0	10	3	18	8	1	—	39
FRP																	
Male	68	3.6	7.1	6.1	0.76	4.0	38.0	24.1	7.52	5	17	12	6	—	—	—	50
Female	43	3.9	9.0	6.0	1.38	5.0	68.0	25.3	17.32	9	11	2	6	2	1	—	30
URR																	
Male	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Female	8	5.9	7.9	7.0	0.67	25.0	46.0	38.8	8.32	0	—	2	1	3	—	1	7

[a]Male, $P < 0.0001$; female, $P < 0.002$.
[b]Male, $P < 0.0001$; female, $P < 0.0001$.
[c]Female, $P < 0.0001$.

greater in females and males collected at IC in 1938 versus those captured during this study (Table 6). At IC cohorts progressed in age and the age distribution broadened from 1994 through 1996, but males sharply declined in the subpopulation (or at least the site) at age 3 (3 LAGs; Fig. 2). The population at FRP also showed variation (Table 7), but it was not significant for SVL and mass of males between years. At FRP, both males and females in the upper age-classes disappeared from the site between 1995 and 1996 (Fig. 3), resulting in a significantly more truncated age structure.

Demographic variation within a cohort among sites and years

Only FRP and IC showed consistent annual recruitment for both sexes, dating back to 1991 for females and 1993 for males. Samples taken in 1996 were statistically large enough for comparison with the 1993 cohort among the CCC, FRP, and IC sites. There was a significant difference in sex ratios ($P < 0.002$) and mass ($F = 3.4$, $P < 0.03$), but not SVL ($F = 1.87$, $P < 0.16$) among sites. FRP had approximately a 1:1 sex ratio, while CCC and IC had 6.0 and 8.5 times as many females as males, respectively. In a comparison of 3-year-old *R. luteiventris* sampled at IC in 1938, 1995, and 1996 (sample size was only 1 male and 3 females for 1994), I found no significant differences in SVL and mass among females (SVL: $F = 1.69$, $P < 0.18$; mass: $F = 1.15$, $P < 0.3$) and males (SVL: $F = 0.82$, $P < 0.5$; mass: $F = 1.6$, $P < 0.26$).

Discussion and conclusions

The finding that demographic composition varies significantly among sites suggest that localized factors are influ-

Table 5. Sex ratios of *R. Luteiventris* among years at IC and FRP.

	IC[a]	FR
1938		
Male	11	—
Female	9	—
Juvenile	?	—
1994		
Male	43	—
Female	80	—
Juvenile	0	—
1995		
Male	55	12
Female	29	7
Juvenile	8	4
1996		
Male	205	68
Female	145	43
Juvenile	22	41

[a]Sex ratios for all years at IC with a $P < 0.0001$.

encing recruitment and mortality rates. That differences among years at the same site are also significant indicates that the population dynamics of this system are complex and are being driven by one or more factors that also vary temporally.

Local demographics, local determinants

Two sites in this study, ILC and CCC, may be characteristic sink habitats (Pulliam 1988), as no recruitment was appar-

Fig. 2. Age structure of female (*a*) and male (*b*) Columbia spotted frogs at IC in the Toiyabe Range, 1994–1996.
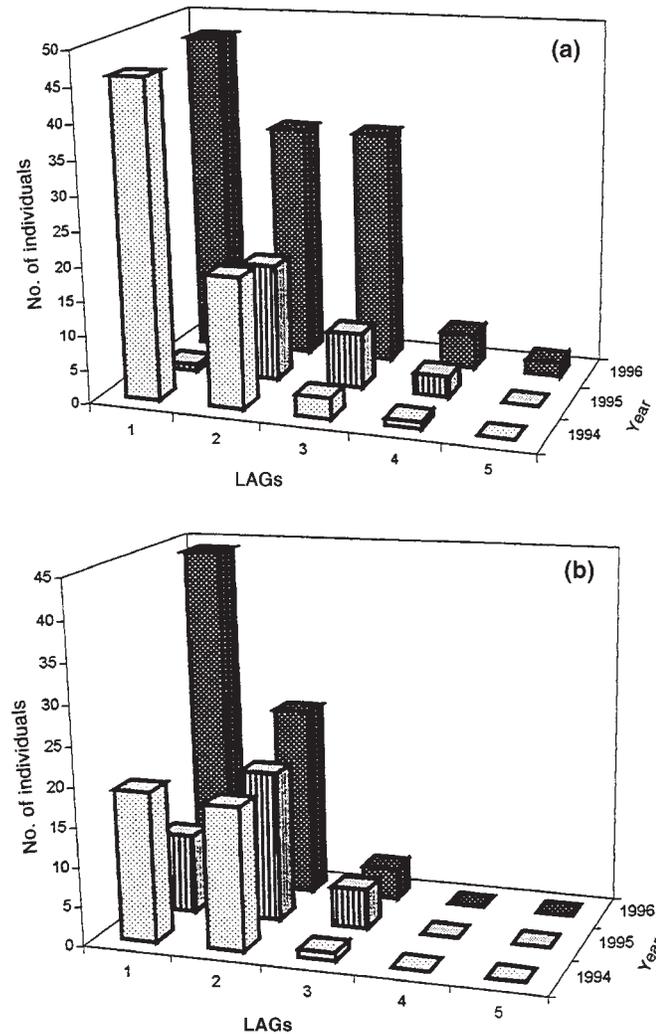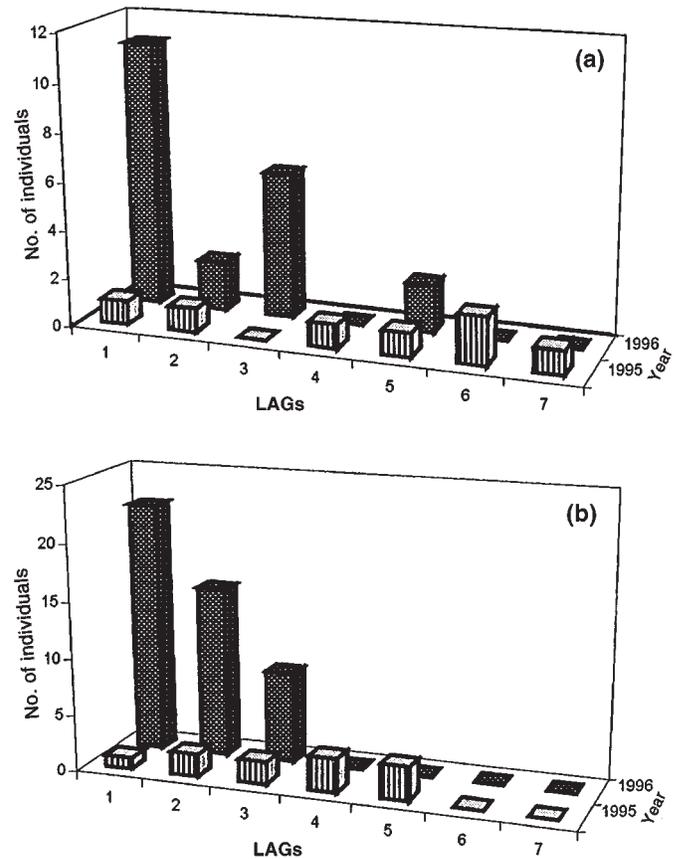

Fig. 3. Age structure of female (*a*) and male (*b*) Columbia spotted frogs at FRP in the Toiyabe Range, 1995–1996.

ent over the course of this study or these sites may be acting as critical corridors for the dispersal of frogs between high elevation URR and many lower elevation sites. FRP is the only known site in which breeding occurs in its drainage, and it may be an important source habitat for maintaining *R. luteiventris* at the southernmost extent of the species' range. Because tadpoles are found in IC and the backwaters of the Reese River, breeding must be occurring along these waterways. However, in the absence of breeding site information, defining specific source habitat is difficult. Neither tadpoles nor metamorphs were encountered at regularly visited sites until August, strongly suggesting that tadpoles move up and down the stream from sites where eggs were oviposited in late winter – early spring (February–April, depending on weather patterns).

Differences in recruitment, survivorship, and mortality rates among sites may be due to several variable factors, including microclimate, food availability, and predation rates. Each of these factors is influenced by land-use practices at the different sites. No data are currently available for com-

paring microclimate and food availability among sites, but it is likely that microclimate is more stable and prey abundance is highest at IC and FRP because of the permanent and pooled nature of the aquatic habitat at those two sites.

Sexual dimorphism is characteristic of many amphibian species (Duellman and Trueb 1986). In this study, the smaller size of males is probably responsible for the fact that they have a shorter life-span than females. Predation by wandering terrestrial garter snakes (*Thamnophis elegans vagrans*) is a common cause of natural mortality, both directly through consumption and indirectly through attack-invoked injury (Reaser and Dexter 1996*a*). The largest garter snakes in the Toiyabe Range are approximately 59.0 cm SVL (range = 22.0–59.0 cm, $\bar{x}$ = 32.0 cm), and field observations and gut content analysis indicate that they consume Columbia spotted frog tadpoles, as well as adult frogs up to approximately 5.0 cm.[2] Thus, most male *R. luteiventris* are always potential prey for snakes, while the majority of the female frogs are beyond the gape width of snakes within a year or two after metamorphosis. The garter snake population is highest at IC, but because of the availability of numerous other prey items (e.g., *Rhinichthys oscusus*, *Lagurus curtatus*) at that site and the generalist diet of this snake (Koch and Peterson 1995), predation on *R. luteiventris* is probably no higher than that at the other sites.[2]

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[2]J.K. Reaser and M.A. Hagerty. Dependence of the wandering terrestrial garter snake (*Thamnophis elegans vagrans*) on the Columbia spotted frog (*Rana luteiventris*) in Nevada, U.S.A. In preparation.

Table 6. Traits of *R. luteiventris* at IC in the Toiyabe Range, 1994–1996.

Year and sex	N	SVL (cm)[a]				Mass (g)[b]				Age structure (year)[c]							N
		Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	0	1	2	3	4	5	6	
1938																	
Male	11	5.0	7.0	5.9	0.57	—	—	—	—	—	—	3	6	—	—	—	9
Female	9	5.9	7.9	7.1	0.53	—	—	—	—	—	—	1	5	2	—	1	9
1994																	
Male	43	3.3	5.5	4.3	0.63	3.5	18.5	8.9	3.72	0	19	18	1	—	—	—	38
Female	80	3.0	7.0	4.2	0.91	3.0	34.0	8.6	6.22	2	46	19	3	1	—	—	71
1995																	
Male	34	4.9	6.5	5.6	0.39	10.0	29.0	18.2	4.30	0	10	19	5	—	—	—	34
Female	29	4.7	7.1	5.9	0.65	11.0	41.0	22.7	8.23	0	1	17	8	3	—	—	29
1996																	
Male	102	4.1	6.9	5.3	0.61	6.0	22.7	15.0	5.63	2	44	24	4	—	—	—	74
Female	145	3.4	8.3	5.8	1.10	4.0	49.0	20.8	11.08	4	47	34	34	5	2	—	126

[a]Male, $P < 0.0001$; female, $P < 0.0001$.
[b]Male, $P < 0.0001$; female, $P < 0.0001$.
[c]All male, $P < 0.0001$; males from 1994–1996, $P < 0.02$; females, $P < 0.001$.

Table 7. Traits of *R. luteiventris* at FRP in the Toiyabe Range, 1995–1996.

Year and sex	N	SVL (cm)[a]				Mass (g)[b]				Age structure (year)[c]								N
		Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	0	1	2	3	4	5	6	7	
1995																		
Male	12	3.7	6.8	6.0	1.11	6.0	41.0	25.3	12.13	1	1	2	2	3	3	—	—	12
Female	7	4.2	8.5	7.2	1.73	6.0	65.0	44.1	24.00	0	1	1		1	1	2	1	7
1996																		
Male	68	3.6	7.1	6.1	0.76	4.0	38.0	24.1	7.52	5	22	15	8	—	—	—	—	50
Female	43	3.9	9.0	6.0	1.38	5.0	68.0	25.3	17.30	9	11	2	6	—	2	—	—	30

[a]$P < 0.05$.
[b]Female, $P < 0.01$.
[c]Male, $P < 0.0001$; female, $P < 0.003$.

Table 8. Weather during the period of the study showing extremes in temperature and precipitation.

Water year[a]	Temperature (°C)			Precipitation (cm)			
	$\bar{x}$/year	Rank[b]	Percentage	$\bar{x}$/month	Total/year	Rank[b]	Percentage
1993	11	88	86	1.2	14.4	24	24
1994	10	54	53	2.4	29.1	97	95
1995	12	101	99	1	12.6	12	12

[a]The water year is from August 1993 to July 1995.
[b]Rank is out of 102 water years as recorded by the National Climate Data Center.

The introduction of exotic trout and cattle are likely the two most important anthropogenic factors limiting the distribution and persistence of *R. luteiventris* in the Toiyabe Range. Many species of fish, especially trout, are voracious aquatic predators that are capable of eliminating larval amphibians from aquatic sites (Macan 1966; Voris and Bacon 1966; Heyer et al. 1975; Semlitsch 1993). Although no direct evidence has been gathered in this study relative to the negative impact of introduced trout on *R. luteiventris*, these observations suggest that one reason Columbia spotted frogs are limited in distribution is the extensive occurrence of these fish (Reaser 1997). It is possible that no recruitment is occurring at ILC because, unlike at URR, breeding sites are not available away from the main water course where tadpoles can be consumed by trout. This conclusion is consistent with the findings of other researchers (D.S. Pilliod, personal communication; J. Munger, personal communication)

who have found that introduced trout species have negatively affected the distribution and abundance of Columbia spotted frogs (technical reports reviewed in Reaser and Pilliod 2000).

Cattle grazing can have a negative impact on spotted frog populations (Worthing 1993; Ross et al. 1999). While changes in water quality (Buckhouse and Gifford 1976), chemistry (Jefferies and Klopatek 1987), and temperature (Van Velson 1979) caused by grazing may be subtle, they are cumulative over a long time (Elmore and Beschta 1987) and can, in effect, create an entirely new aquatic ecosystem (Kauffman and Krueger 1984). Livestock trampling can cause injury, and likely mortality, in *R. luteiventris* (Ross et al. 1999). Based on comparisons of the sites sampled in this study, it appears that grazing history explains, at least in part, the density and age distribution of Columbia spotted frogs. IC and FRP have the highest densities of *R. luteiventris* and the broadest age distributions, and have been rested from graz-

ing the longest. At the time of the study, Indian Creek at RO Ranch (RO) was still subject to intensive mid and late summer grazing. In May, tadpoles were found upstream of RO, but it appears that recruitment may be extremely low because later in the season the pools that they inhabit were trampled and destroyed (J.K. Reaser, personal observation). RO, therefore, may be largely maintained as a site for *R. luteiventris* through the persistence of a few adults and the occasional immigration of juveniles from IC. ILC and Indian Creek Ditch (ICD) are still subject to short-term late-season cattle grazing and, as at RO, have significantly truncated age distributions of *R. luteiventris*. This suggests that recruitment is low and (or) mortality and (or) emigration rates are high. CCC was grazed heavily until recently. Its stream course has been channeled and the water table has dropped to such an extent that the system no longer holds water throughout the season. Reproduction may no longer be taking place at CCC because critical habitat for breeding is no longer present.

Subpopulation persistence

An equilibrium can be ecologically and evolutionarily stable for animals exhibiting active habitat selection when both source and sink habitats are occupied (Pulliam 1988). Still, large fluctuations in the dynamics of subpopulations should be expected given the temporal changes in weather and land use typical of the study area. If this system operates as a functional metapopulation (Levins 1969, 1970), then loss of one or more subpopulations is not a threat to *R. luteiventris* in the Toiyabe Range. Frogs from other locations would be expected to recolonize sites where subpopulations have succumbed to local extinction or to colonize new habitat as it becomes available (McCullough 1996; Hanski and Gilpin 1997). Indeed, subpopulations of many amphibian species experience periodic extinctions and recolonizations, thus seeming to display population dynamics in keeping with nonequilibrium models (e.g., Corn and Fogleman 1984; Sjögren 1991; Weitzel and Panik 1993; Blaustein et al. 1994). However, recolonization depends on the existence of functional corridors. In the Toiyabe Range, drainages that once may have served as avenues for dispersal are now either stocked with trout or completely dry across large reaches (Reaser 1997). This study system, it appears, is at best a contracting metapopulation.

The problem of behavior

The activity patterns of *R. luteiventris* warrant caution in interpreting these findings. Although this study was conducted over a 3-year period, the window on the life of *R. luteiventris* is narrow. The author observed frogs only during the nonbreeding season and, by necessity, at a limited number of sites. Males, females, and juveniles may have different site selection criteria. Loman (1978) found that subadult *Rana arvalis* and *R. temporaria* did not segregate in forest and meadow habitats, while adult frogs did. In meadow habitat, females of *R. arvalis* were found higher in the vegetation than males. Site-selection criteria may change throughout the season, depending on the habitat requirements for breeding, foraging, predator avoidance, and hibernation. Individuals might also move in response to acute stress, such as the seasonal drying of aquatic habitats or the temporary grazing of livestock. Therefore, assuming dispersal of individual *R. luteiventris* at any life stage, it is possible that the subpopulation dynamics I observed may hold only for the nonbreeding season and are influenced as much by the proximity and type of other habitats as by on-site characteristics.

Extreme variations in annual weather patterns may account for much of the differences observed among years at IC and FRP. The National Climate Data Center's data for August through July for 102 years, from 1895 through 1996, show that the Toiyabe region of Nevada experienced extremes in both temperature and precipitation during the years in which the study was conducted (Table 8). More surface water was available throughout the summer of 1995 (1994 water year) than in any other year of this study. It is plausible that *R. luteiventris* take advantage of wetter years by dispersing into potentially colonizable regions, across a landscape that is usually too dry to be inhabited. Small, ephemeral creeks in the spring of 1995 may have served as corridors for movement among sites (Reaser 1996), resulting in a broader dispersion of frogs than is typical. Based on the FRP subpopulation, it appears that the oldest frogs may have been induced to breed in 1995 (Table 7) and their absence in 1996 may indicate that they have something other than an annual breeding cycle, either as a response to weather conditions or because of the physiological demands of breeding.

The findings of this study suggest that multiple-year mark–release–recapture studies, coupled with land-use stress experiments, are needed to further elucidate *R. luteiventris* activity patterns. If monitored continuously, the demographics of the Columbia spotted frog should provide resource managers with an index for assessing the impact of their recovery efforts on the Columbia spotted frog, as well as on the aquatic systems that these animals inhabit.

Furthermore, this study demonstrates that adequate assessment of amphibian population status requires knowledge of subpopulation demographics across a broad landscape. Studies of amphibian declines in which the authors suggest that amphibian populations have been significantly reduced in numbers may actually document site-specific declines in subpopulations. Such losses may be of little concern if the subpopulations are part of a functional metapopulation. Given the trends in aquatic habitat destruction and degradation, however, losses of subpopulations are increasingly likely to represent permanent local extinctions.

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