Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin

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Abstract: Information on how animals partition their activities and travel among complementary resources, such as breeding or overwintering habitats, is needed for species conservation. In a mountain basin at 2500 m elevation in central Idaho, we studied the habitat use and movement patterns of 736 marked and 87 radio-tagged Columbia spotted frogs (*Rana luteiventris*) from 1995 to 1998. The goals of this study were to (*i*) identify and characterize *R. luteiventris* breeding, summer foraging, and overwintering habitats, (*ii*) describe the movement patterns of juvenile, male, and female *R. luteiventris* among these resources, and (*iii*) determine migration routes. Juvenile and adult *R. luteiventris* occupied a variety of widely distributed wetlands from late June to September. On average, 1–32% of juvenile, 6–11% of male, and 16–51% of female frogs moved from breeding ponds to summer habitats. Migratory males remained within 200 m of the breeding sites, whereas females traveled up to 1030 m to reach summer habitats. From late August through September, frogs migrated to deep (>3 m) lakes to overwinter. Frog migrations occurred quickly and often followed shortest-distance travel routes through dry, open forest even when stream corridors were available nearby. This study exemplifies the need to protect both complementary resources and the corridors connecting these anuran habitats.

Résumé : La protection d'une espèce requiert qu'on sache comment elle répartit ses activités et ses déplacements parmi les ressources complémentaires, comme les territoires de reproduction et les quartiers d'hiver. Nous avons étudié l'utilisation de l'habitat et les patterns des déplacements de 87 individus munis d'un émetteur-radio et de 736 individus marqués de la grenouille maculée de Columbia (*Rana luteiventris*) dans un bassin hydrographique de montagne du centre de l'Idaho, à 2500 m d'altitude. Nous avons tenté (*i*) d'identifier et de caractériser les aires de reproduction, les territoires d'alimentation d'été et les quartiers d'hiver, (*ii*) de décrire les patterns des déplacements des grenouilles juvéniles et des adultes mâles et femelles parmi ces ressources et (*iii*) de déterminer leurs routes de migration. Les juvéniles et les adultes de *R. luteiventris* occupent un éventail de terres humides dispersées sur un grand territoire de la fin de juin à septembre. En moyenne 1–32 % des juvéniles, 6–11 % des mâles et 16–51 % des femelles migrent des aires de reproduction aux quartiers d'été. Les mâles migrateurs restent à moins de 200 m des territoires de reproduction, alors que les femelles peuvent parcourir jusqu'à 1030 m pour gagner les quartiers d'été. De la fin d'août à la fin de septembre, les grenouilles migrent vers des lacs de profondeur supérieure a 3 m pour passer l'hiver. Les migrations se font rapidement et les grenouilles empruntent les chemins les plus courts à travers les boisés secs et ouverts, même lorsqu'il existe des corridors d'eau courante dans le voisinage. Cette étude souligne l'importance de protéger à la fois les ressources complémentaires et les corridors qui relient les habitats de ces anoures.

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Introduction

As scientists search for factors to explain regional amphibian declines (e.g., climate change, increased UV-B, pathogens), local habitat destruction, modification, and isolation continue to reduce many amphibian populations (Alford and Richards 1999; Corn 2000; Marsh and Trenham 2001). De-spite growing awareness of these local threats to amphibian communities, the development of management plans is often hampered by a lack of information on amphibian natural history, especially regarding habitat requirements and the relevant spatial scales. If we are to conserve amphibian populations, better information on their spatial ecology is needed, including (*i*) the spatial distribution of resources critical to sur-

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vival, (*ii*) the seasonal use and movement patterns of animals among these habitats, and (*iii*) the factors that contribute to habitat loss and fragmentation. In this paper, we address these topics for the Columbia spotted frog (*Rana luteiventris*), a species widely distributed throughout northwestern North America.

Information on the habitat requirements of anurans in heterogeneous landscapes is somewhat limited, mostly because of the tendency for field studies to focus on activities around breeding sites (Sinsch 1990; Dodd 1996; Pope et al. 2000). In a review of anuran migration, Sinsch (1990) suggested that biotopes must provide four major resources for the annual activities of anurans: reproduction, nutrition acquisition, hibernation, and estivation. In some circumstances, these resources may be located in the same habitat patch (such as a breeding pond with adequate summer and winter habitat), but for many north temperate anurans, some or all of these resources are spatially separated, requiring seasonal migrations among different habitat patches. For the use of spatially separated, non-substitutable resources, or those resources that are critical to the survival of an animal and that can only be found in specific habitat patches, the term landscape complementation was coined by Dunning et al. (1992). We use the term complementary resources in this regard. Few studies have identified complementary resources (breeding, summer, and winter habitats) for anurans in a landscape. Such information is crucial for adequate analysis of the impacts of management decisions and for implementing appropriate habitat protection measures (Sinsch 1990).

Ranids are ubiquitous in and around mountain lakes in western North America, yet surprisingly little is known about what habitats they require to survive under such harsh conditions or to what extent they move among water bodies seasonally. A recent study in a high mountain basin in the Sierra Nevada, California, demonstrated that mountain yellow-legged frogs (*Rana muscosa*) traveled up to 1 km from breeding ponds to reach overwintering sites (Matthews and Pope 1999). We were curious as to whether *R. luteiventris*, one of the most common lentic-breeding amphibians found at high elevations throughout northwestern North America (Reaser and Pilliod 2003), also traveled as extensively through alpine environments. Seasonal movements of *R. luteiventris* among spatially separated habitats had been previously documented (Turner 1960; Hollenbeck 1974; Patla 1997), but not in the steep, inhospitable terrain that is characteristic of many of the mountain ranges of the West (i.e., areas where *R. luteiventris* are widespread and abundant).

The goals of our study were to (*i*) identify and characterize *R. luteiventris* breeding, summer foraging, and overwintering habitats in a mountain basin near the altitudinal limits of the species, (*ii*) describe the movement patterns of juvenile, male, and female *R. luteiventris* in relation to complementary resources in a landscape, and (*iii*) determine migration routes. This information should prove useful for agencies responsible for developing conservation plans for this species. *Rana luteiventris* is locally threatened in various parts of its range because of the widespread introduction of nonnative trout, cattle grazing, water diversions, and habitat fragmentation (Patla 1997; Bull and Hayes 2000; Reaser 2000; Pilliod and Peterson 2001).

Materials and methods

Study area

This project was conducted in Skyhigh Basin, a large (1128 ha), glacial cirque in a region of the Salmon River Mountains known as the Bighorn Crags. The steep, granitic peaks of the Bighorn Crags rise to 3073 m, forming a crest between the Middle Fork and Main Salmon River drainages in the Frank Church – River of No Return Wilderness, Idaho, U.S.A. (Fig. 1). Skyhigh Basin drains into Wilson Creek, a tributary of the Middle Fork of the Salmon River. The basin contains 16 permanent alpine and subalpine lakes and ponds, four flooded meadows, and five ephemeral ponds at elevations ranging from 2323 to 2634 m.

The climate of the study area is characterized by long, cold winters and cool, dry summers. Standing water was ice-free from mid-June to mid-October 1995–1998. Average daily air temperatures ranged from 1.3 to 16.6°C (average 9.0°C) from June through September, the period when frogs were active, and from –25.1 to 9.6°C (average –4.5°C) from October through May. Hourly air temperatures were highly variable during the active season, ranging from –3.3 to 30.6°C. The region receives approximately 80 cm of precipitation annually, but only about 5 cm falls as rain during July and August. Most of the surface water comes as a pulse in the spring when the snowpack, which can reach up to 250 cm deep, begins to melt in late May and June (Finklin 1988). The two permanent and six intermittent headwater creeks that fed and connected many of the wetlands reached peak flows during snowmelt in late June but were mostly dry by the middle of August. Correspondingly, water levels in many lakes dropped as much as 2 m by August, and pools in flooded meadows often dried up by mid-August.

This cool, dry, subalpine climate results in fairly open forests of subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) with sparse understory vegetation composed mostly of grouse whortleberry (*Vaccinium scoparium*) in the dry uplands and beargrass (*Xerophyllum tenax*) in areas inundated by spring runoff. Engelmann spruce (*Picea engelmanni*), alpine rhododendron (*Rododendrous altiflorum*), and sedges (*Carex* sp.) are found along the margins of lakes and ponds and within flooded meadows.

We chose Skyhigh Basin as the study area for this project because it contained several breeding populations of *R. luteiventris* and was mostly undisturbed by human recreation. The area is protected by wilderness regulations, is free from livestock grazing, and is located approximately 19 km from the nearest trailhead. Non-native cutthroat trout (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) continue to be stocked in nine lakes every 3 years and are found in all permanent streams downstream from lakes with fish (Pilliod and Peterson 2001).

Surveys and marking

All lentic water bodies and streams in Skyhigh Basin were located, mapped, and surveyed for amphibians. At each lake and pond, two trained observers conducted visual searches for all life stages of *R. luteiventris* along the entire shoreline. Surveyors walked approximately 2 m apart, with one person in the water and the second person on the shore. Observers searched streams by walking their entire length, one observer

Fig. 1. Map of Skyhigh Basin showing the distribution of *Rana luteiventris* breeding (solid fill), summer (no fill), and winter (shaded fill) habitats. Sites L3 and L8 were both breeding and overwintering sites for *R. luteiventris*, indicated by their shaded fill and solid border. Fish symbols indicate sites with fish (*n* = 7). All solid-fill sites are fishless. Perennial streams are represented by solid lines and intermittent streams (June and July only) by broken lines. Lentic water bodies (sites) are numbered as lacustrine (L1–L11) and palustrine (P1–P15). Contour intervals of 100 m are shown (2400–2900 m). Inset photograph illustrates the topographical relief of Skyhigh Basin.
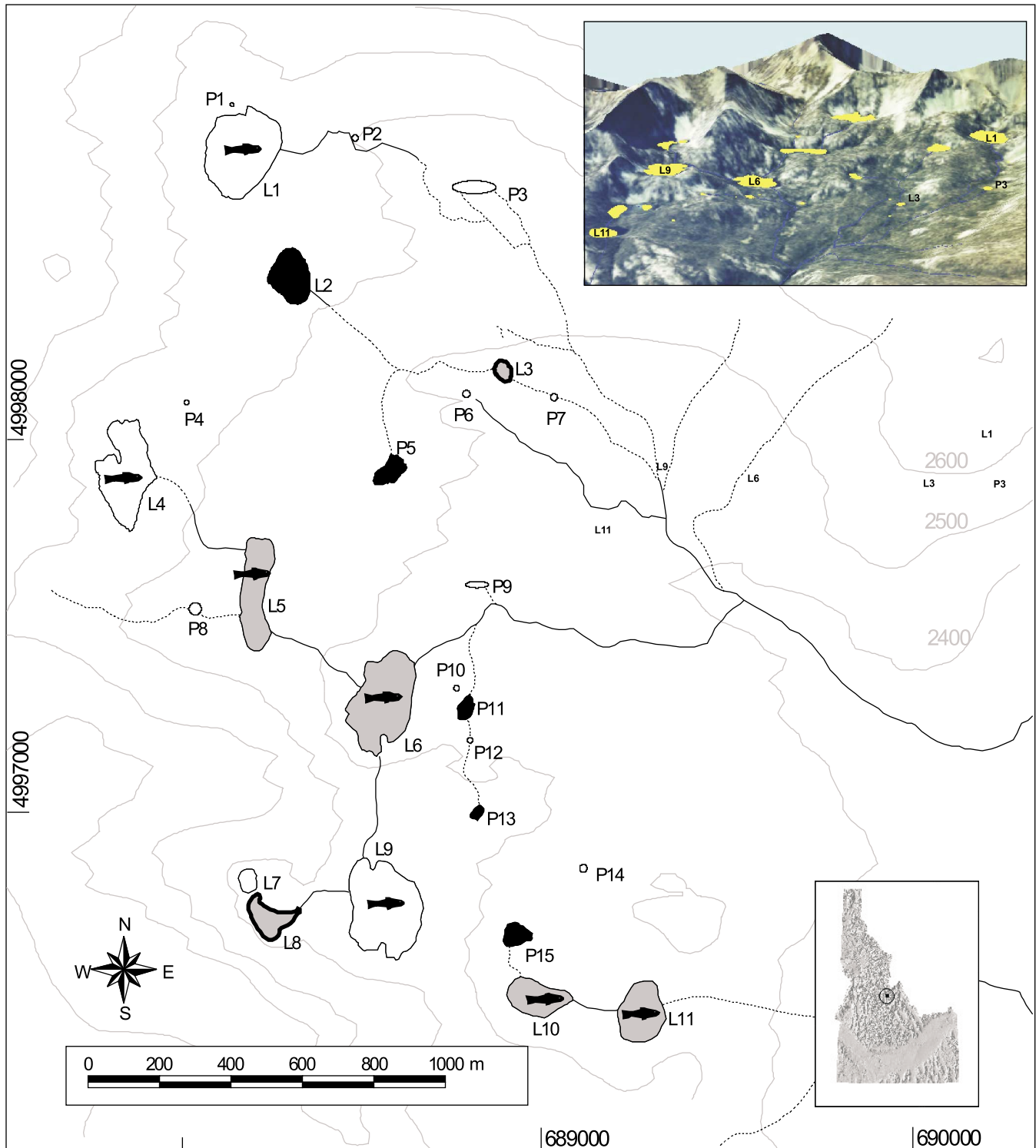
along each bank (usually within 2 m of each other). Meadows were searched using a zigzag pattern (Thoms et al. 1997). Where aquatic or terrestrial grasses and sedges were present, dipnets were used to sweep the vegetation for frogs.

Complementary resources for *R. luteiventris*, including breeding, summer foraging, and overwintering habitats, were identified using surveys, mark–recapture, and radiotelemetry. To identify breeding sites, we searched all water bodies for *R. luteiventris* egg masses and tadpoles in the first week in July 1995–1998, about 1–2 weeks after surface ice had melted. Based on resurveys of all sites in early August 1995 and observations of postbreeding movements to nonbreeding habitats in 1995–1997, we identified summer foraging areas. Finally, we identified winter habitats as those areas to which frogs migrated or where frogs congregated in late August and early September 1995–1997 and October 2001.

We attempted to capture all frogs observed, either by hand or by net. Frogs were held in nets or nylon bags for 2–15 min during data collection and were released at their capture locations. For each frog captured, snout–vent length was measured with calipers (SVL, ±1 mm), mass was measured with a Pesola spring scale (±0.5 g, Forestry Suppliers, Jackson, Miss.), and sex of frogs >46 mm was determined by the presence of nuptial pads on males. Based on size, mass, and sexual maturity, we grouped individuals into three size classes: young of the year (YOY), <20 mm; juveniles, 20–46 mm; adults, >46 mm.

To document gross movement of frogs among habitats, we marked as many juvenile and adult frogs as possible at each lotic and lentic water body from 1995 to 1997. To reduce stress on metamorphosing frogs, we did not mark YOY frogs as they left the breeding ponds. At breeding ponds, juvenile frogs (following their first winter) and adult frogs were marked with a site-specific toe-clip pattern to identify the location at first capture. We clipped toes at the second tarsal or carpal joint with disinfected fine-point, electrical wire clippers or stainless-steel cuticle clippers following toe-clip patterns modified from Donnelly (1989). Frogs captured at breeding sites had two toes clipped, each on different limbs and not including thumbs. We marked frogs in summer habitats with individual codes using three toe clips and recorded recapture locations. Frogs that were marked at breeding sites and later recaptured at a new site were given an additional toe clip to differentiate them from other frogs in the event that they returned to the site where they were originally marked.

We summarized movements as the percentage of juvenile, male, or female frogs that moved away from breeding sites and the average and maximum distances traveled 4–6 weeks after initial marking in 1995 and each year thereafter. We calculated the straight-line distance traveled by males and females from their first capture location to the farthest recapture location using the animal movement module (Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska) in a geographic information system (ArcView 3.1, ESRI, Redlands, Calif.). Because the greatest potential for marking errors were right–left confusions, we only included frog movements between sites that could not have been a right–left marking error. This was a conservative approach to reduce error rates. Thus, the movement results presented are minimum estimates of actual movement rates.

To determine seasonal habitat use patterns, we first recorded the capture and recapture of *R. luteiventris* in lentic and lotic habitats. We then summed the number of juvenile, male, and female frogs captured in lacustrine (deep lakes without fish, deep lakes with fish), palustrine (shallow ponds, ephemeral ponds, flooded meadows), and riverine (creeks without fish, creeks with fish) habitats each year. The percentage of juvenile or adult frogs captured in each of these habitats was calculated by dividing the number captured in each habitat by the total number captured each year. To calculate the percentage of individuals recaptured at breeding and summer habitats where first marked (did not move away from pond), we divided the number of *R. luteiventris* recaptured at each habitat type by the total number captured. Differences in seasonal use of habitats by male and female frogs were expressed by dividing the number of male or female frogs captured in either breeding or summer habitats in July surveys each year by the total number of adult frogs captured in July surveys each year.

To calculate the percentage of individuals that had migrated from breeding habitats annually, we first calculated the cumulative number of juvenile, male, or female *R. luteiventris* captured in breeding and nonbreeding habitats and differentiated individuals that had been marked in breeding sites or nonbreeding sites originally. The minimum annual migration estimates were then calculated as a percentage of the number of frogs marked in breeding sites that were recaptured in other habitats >100 m away divided by the total number of captured frogs that carried a breeding-site mark in the basin during the annual census. Hence, the minimum migration estimates were based only on those individuals that were marked at breeding sites and later recaptured in summer habitats. The maximum annual migration estimates were calculated as a percentage of the sum of the number of frogs marked in breeding sites that were recaptured in other habitats >100 m away plus the number of frogs that were first captured and marked in these nonbreeding habitats divided by the total number of frogs captured in the basin during the annual census. Thus, the maximum migration estimates included individuals that were first captured and marked in summer habitats during our first year of surveys. This upper estimate assumes that unmarked frogs captured in summer habitats had already migrated from breeding or overwintering sites earlier that year. In support of this assumption, we rarely found frogs during the earliest surveys of summer habitats in July but subsequently encountered steadily increasing numbers of frogs at these sites as the summer progressed.

Radiotelemetry

Radiotelemetry of 81 females (65–85 mm SVL, 26–65 g) and 6 males (51–73 mm SVL, 26–34 g) was used to study the movement routes and habitats occupied by *R. luteiventris* between the months of July and September from 1995 to 1997. The transmitters (BD-2T transmitters, Holohil Systems Ltd., Carp, Ont.) were attached to the frogs using a lightweight belt-type harness made of surgical polyethylene tubing (Bartelt and Peterson 2001) or polyester ribbon that fit around the waist of the frog. Frogs carried transmitters for an average of 24 days (range of 2–57). An additional 29 frogs (3 in 1995, 4 in 1996, and 22 in 1997) were excluded

from the analyses because they dropped their transmitter and harness before being relocated.

We located radio-tagged frogs every 1–3 days with a Telonics TR4 or TR2 receiver (Telonics, Inc., Mesa, Ariz.) and an "H" directional antenna. Initial frog locations, final locations, and all movements greater than 100 m were determined to the nearest 3 m using a differentially correctable global positioning system (GPS, GeoExplorer II, Trimble Electronics, Sunnyvale, Calif.). We mapped shorter movements using a compass and 30-m tape. To avoid excessive injury to the frogs, we captured radio-tagged frogs weekly to check for abrasions or lacerations caused by the transmitter harness. Abrasions were treated with Neosporin ointment and often healed without further complications. The harness and transmitter were removed if lacerations penetrated the skin.

The selection of frogs to be radio-tagged was not random, and our site selection and frog mass limitation criteria resulted in biasing our telemetry study toward female frogs. We intentionally placed more transmitters on frogs in summer habitats, such as flooded meadows, to increase our chance of observing movement. This selection likely underestimated the total distance traveled per season. To reduce the potential effect on frog mobility and behavior, we did not place transmitters on any frogs weighing less than 26 g.

Habitat data collection

To characterize breeding, summer, and winter habitats, we collected and summarized habitat data. We recorded elevation from 1 : 24 000 U.S. Geological Survey topographic maps. Lentic habitats were classified as lacustrine or palustrine, based on size (all <8 ha) and depth (>2 and <2 m, respectively; Cowardin 1979). Lake surface area was calculated from aerial photographs in a geographic information system (ArcView 3.1, ESRI). Maximum water depth was determined from bathymetric transects and sonar. We collected shoreline water temperature at 1 m from shore and 5 cm from the surface and used the average water temperature per site across all visits for analyses. The shoreline vegetation was mapped and categorized as forest, shrub, or grass–graminoid. We then estimated the percentage of each vegetation type by dividing the total amount (metres of shoreline) of each by the total perimeter of the site. A similar approach was used for aquatic substrates, which included silt–sand or rock (gravel, cobble, and boulder). For flooded meadows, we visually estimated the percent cover of the area. We recorded the presence of perennially flowing springs, inlets, and outlets. The presence of fish was determined from 12 h overnight gillnet sets in all lakes and ponds.

Statistical procedures

To examine the qualitative differences among the types of wetland habitats used by *R. luteiventris* for breeding, summer foraging, and overwintering sites, we first reduced the number of measured habitat variables into composite factors using a principal components analysis (PCA) on the correlation matrix. Principal axes with eigenvalues >1 were retained. To achieve simple structure and increase interpretability, we rotated the components using the orthogonal Varimax rotation method with Kaiser normalization. We considered variables with component scores in excess of 0.50 (~30% overlapping variance) to be good measures of the factor (Comrey and Lee 1992).

To compare the distance traveled by recaptured male and female frogs, we first recorded the straight-line distance from the original mark-and-release site to the farthest recapture location for each frog and then analyzed mean distances moved by each sex using a Mann–Whitney U test. The heteroscedasticity of our movement data warranted use of this nonparametric test. Because animal size can influence mobility, we also examined the linear relationship between the straight-line distance traveled and the SVL of male versus female frogs. To control for the influence of sexual dimorphism, we reran the previous analysis using only male and female frogs of similar size (58–70 mm SVL) with ANOVA. We did not use circular statistics in our analyses of frog dispersal direction because of inadequate numbers of capture locations (Zar 1984). All statistical tests were performed on SPSS v.10.0 (SPSS Inc., Chicago, Ill.). We used $P < 0.05$ to indicate statistical significance.

Results

Complementary resources and habitat use patterns

In Skyhigh Basin, we identified 5 breeding, 13 summer foraging, and 4 overwintering habitats (Fig. 1). We also found two water bodies that were used for each of these functions (Fig. 1). All breeding habitats were occupied by frogs from early July to late August and thus provided summer habitats for many frogs. Breeding sites were mostly small, silt-bottomed, fishless ponds, but frogs also bred in larger, rock-bottomed lakes with little emergent vegetation or silt substrate (Table 1). Summer habitats were occupied by juveniles and adults from early July to late August and included all types of wetland habitats (Table 1). In mid-August, juvenile and adult frogs began congregating at overwintering sites, which were mostly large, deep (all >3 m), rocky lakes with perennially flowing outlets (Table 1). Four of six overwintering sites contained introduced trout (Fig. 1). Of the two water bodies used for breeding, summer foraging, and wintering, one of these (L3) was a source population and a hotspot of migratory activity in the basin, whereas the other (L8) was an isolated population with very low productivity. Hence, this paper highlights the habitat characteristics (Table 1) and functional role of site L3.

To characterize the seasonal habitat associations of *R. luteiventris*, we created four composite factors of the measured habitat variables that explained a total of 82% of the variance in the data (Table 2). Factor 1 explained 27% of the variability in habitat and characterized large, deep, rocky lakes with fish that had at least 5% of the littoral zone with emergent vegetation and perennially flowing outlet streams (Table 2). Factor 2 explained an additional 26% of the variance in habitat and characterized warm ponds with grass- or sedge-covered shorelines, emergent vegetation, silt substrate, and not rocky substrates (Table 2). Overwintering sites were positively associated with factor 1, whereas breeding sites tended to be negatively associated with this factor (Fig. 2). Neither breeding nor wintering sites was associated with factor 2 (Fig. 2). However, site L3, the largest frog population in the basin and one of two sites that provided all complementary resources, was positively associated with factor 2

Table 1. Characteristics of breeding, summer, and winter habitats used by *Rana luteiventris* in Skyhigh Basin, 1995–1998.[a]

Habitat variable	Breeding and summer	Summer only	Winter only[b]	Site L3[c]
Number of sites	5	13	4	1
Sites with perennial outlets (%)	0	46	100	100
Sites with inlets or springs (%)	0	46	100	100
Sites with trout present (%)	0	15	100	0
Elevation (m)				
Median	2505	2549	2467	2484
Range	2463–2606	2463–2634	2463–2536	
Surface area (ha)				
Median	0.39	0.02	1.93	0.21
Range	0.10–1.30	0.003–4.29	1.30–3.68	
Maximum depth (m)				
Median	2.0	0.4	8.4	3.1
Range	1.6–8.0	0.2–24.3	6.0–11.9	
Water temperature (°C)				
Median	16.3	14.8	16.3	20.7
Range	15.2–17.3	9.7–24.0	13.5–20.1	
Forest shoreline (%)				
Median	51	30	46	0
Range	0–86	0–93	25–68	
Shrub shoreline (%)				
Median	15	0	40	0
Range	0–44	0–70	25–61	
Grass shoreline (%)				
Median	5	10	8	100
Range	0–10	0–100	5–13	
Rock substrate (%)				
Median	5	0	50	0
Range	0–77	0–100	26–75	
Silt substrate (%)				
Median	74	100	46	100
Range	10–100	0–100	2–74	
Emergent vegetation (%)				
Median	10	20	40	100
Range	0–40	0–100	24–54	

[a]Site L8 was not included in this table because this lake barely supported a frog population and only one male and one female frog left this pond from 1995–2001.

[b]A few juveniles and adults were found at these sites during the summer, suggesting that they may occasionally be used as summer foraging areas.

[c]Site L3 was used for breeding, summer, and winter habitats and supported the majority of frogs in the basin.

(Fig. 2). In contrast, the other breeding–summer–winter site (L8) was negatively associated with factor 2 and only supported one breeding pair in 1995 and 1997. Summer habitats tended to be negatively associated with factor 1 and positively associated with factor 2, with some exceptions (Fig. 2). The range of conditions in breeding, summer, and winter habitats is summarized in Table 1.

In Skyhigh Basin, *R. luteiventris* were easily captured and frequently recaptured. From 1995 to 1997, 736 postmetamorphic *R. luteiventris* were captured and marked in 24 of 27 lentic sites and 7 of 8 streams in Skyhigh Basin. For the duration of the study, the basin population appeared to be closed, as we did not observe the emigration of marked frogs out of Skyhigh Basin or the immigration of marked frogs from surrounding basins. Furthermore, total recapture rates of adults generally increased over time. After the first year of the study, 54–77% of the males and 73–85% of the females captured were frogs that had been previously captured

and marked. Because of annual recruitment of unmarked YOY, recapture rates of juveniles did not exceed 36% after the first year.
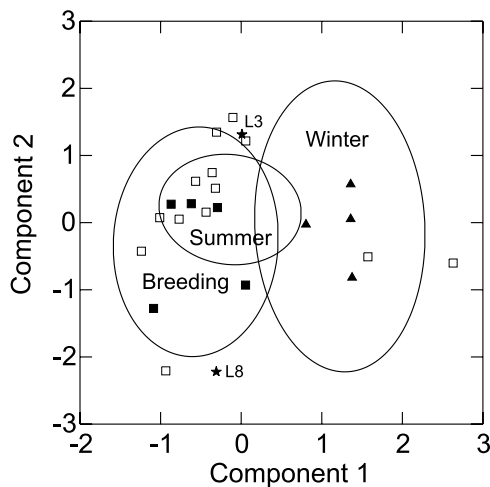
Rana luteiventris seasonal habitat occupancy varied depending on the age and sex of the animal (Figs. 3 and 4). Most frogs were captured in deep lakes without fish and in shallow ponds (Fig. 3), and most of these frogs were first captured and marked in breeding sites (Table 3). Site L3, a deep, fishless lake, contained the majority of frogs in Skyhigh Basin, including 11–64% of the juveniles and 48–69% of the adult frogs captured during July surveys in 1995–1998. In early summer, juveniles were also occasionally captured in two deep lakes with fish (sites L10 and L11), whereas adults were rarely captured in these habitats during the summer (Fig. 3) and only moved into these lakes in the fall to overwinter. Juveniles were not captured more than 350 m from breeding sites. During the active season, males were less widely distributed than female frogs in Skyhigh Basin

Table 2. Scoring coefficients from rotated pattern matrix showing the strength and direction of association between habitat variables measured in 24 water bodies in Skyhigh Basin and the orthogonal components (with eigenvalues >1) generated in a PCA.

| Habitat variable	Component			
	1	2	3	4
Perennial outlets	**0.643**	0.065	**0.587**	0.256
Inlets or springs	0.421	0.421	**0.622**	0.402
Trout	**0.895**	–0.131	–0.028	0.233
Elevation	0.114	–0.451	0.232	**–0.734**
Surface area	**0.889**	–0.302	–0.016	0.047
Maximum depth	**0.800**	–0.468	–0.106	–0.178
Water temperature	0.029	**0.749**	0.184	0.106
Forest shoreline	0.166	0.195	**–0.905**	0.037
Shrub shoreline	0.280	–0.282	0.175	**0.781**
Grass shoreline	–0.194	0.565	**0.679**	–0.339
Rock substrate	0.318	**–0.854**	0.104	0.044
Silt substrate	–0.365	**0.845**	–0.031	–0.060
Emergent vegetation	**0.582**	**0.536**	–0.076	0.093
Variance explained	27%	26%	17%	12%

Note: Variables that loaded high on a component are in bold. The percent of variance in the data explained by each component is shown at the bottom. The habitat variable units used in the PCA are shown in Table 1.

Fig. 2. Plot of component 1 (deep, rocky, fish lakes with perennially flowing outlets and shrub shorelines) versus component 2 (warm ponds with perennially flowing inlets, emergent sedges, and grass–sedge shorelines) from a PCA of measured habitat variables in all sites where *R. luteiventris* bred and summered (solid squares), summered (open squares), or overwintered (solid triangles) in Skyhigh Basin. Sites L3 and L8 (stars) were used for breeding, summering, and overwintering. Confidence ellipses (95%) for breeding, summering, and overwintering habitats are shown. See Table 2 for scoring coefficients.

Fig. 3. The percentage of juvenile (A) and adult (B) *R. luteiventris* captured in different habitat types in Skyhigh Basin between 1 July and 15 August 1995–1998. Error bars (±1 SE) represent annual variation.
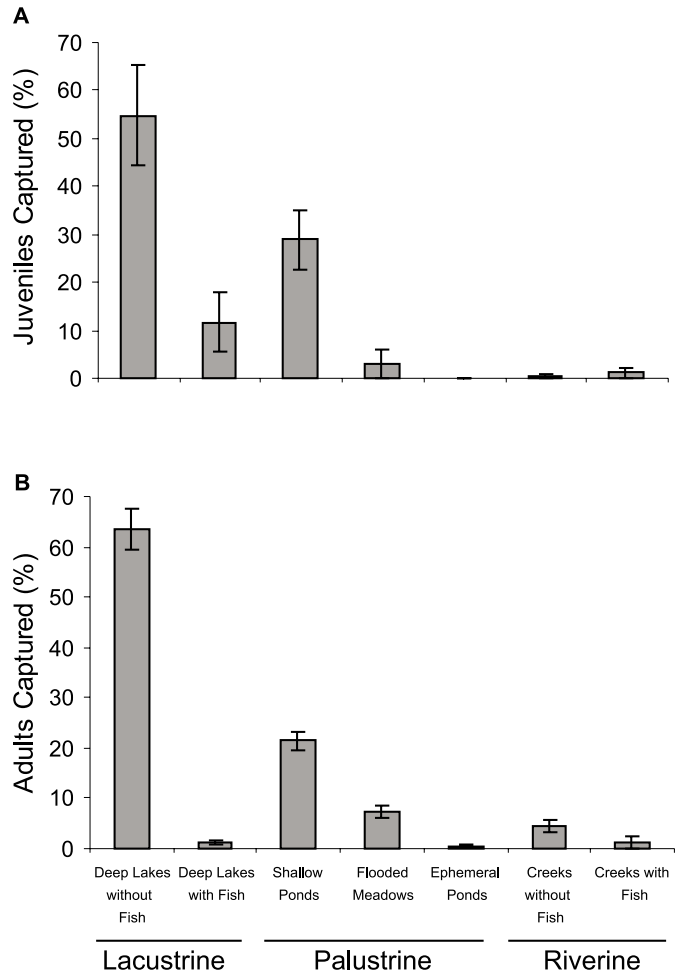
the exception of adults near site L3 and females during the migratory period (Figs. 3 and 4).

Both sexes showed strong site fidelity to breeding sites, whereas only females tended to return to their summer habitats. From 1995 to 1998, about 66% of the males and 56% of the females marked in breeding sites were recaptured in subsequent years at the same sites (Table 3). The few males that were marked in summer habitats had low recapture rates (~9%) compared with females (~53%) (Table 3). Of 32 individually marked female frogs in P3 (a site where females congregated in the summer), we found that up to 75% returned each year. Conversely, at two sites where male frogs congregated in the summer, only 15% (2 of 15) of individually marked males were recaptured in subsequent years.

Migration patterns and travel routes

Migration to summer habitats

In early July, shortly after egg deposition, adult frogs began migrating from breeding and wintering sites to summer habitats (Figs. 5 and 6), with noticeable differences between juvenile and adult frogs and male and female frogs (Table 4). On average, only 6–11% of males migrated from

and generally remained at breeding sites or occupied flooded meadows within 200 m of breeding ponds (Table 3, Fig. 4). Similar to males, most female frogs were captured at breeding sites, but they also occupied flooded meadows, lakes, and ponds throughout the basin (Table 3, Fig. 4). Adults and juveniles were rarely found along the edges of streams, with

Fig. 4. Maps of all male (triangles) (A) and all female (circles) (B) *R. luteiventris* capture and recapture locations in Skyhigh Basin, 1995–1998. Note that one individual could be represented by more than one symbol. Frogs that moved from one site to another are shown as straight solid lines (one per frog moved). Site fill patterns are the same as those used in Fig. 1.
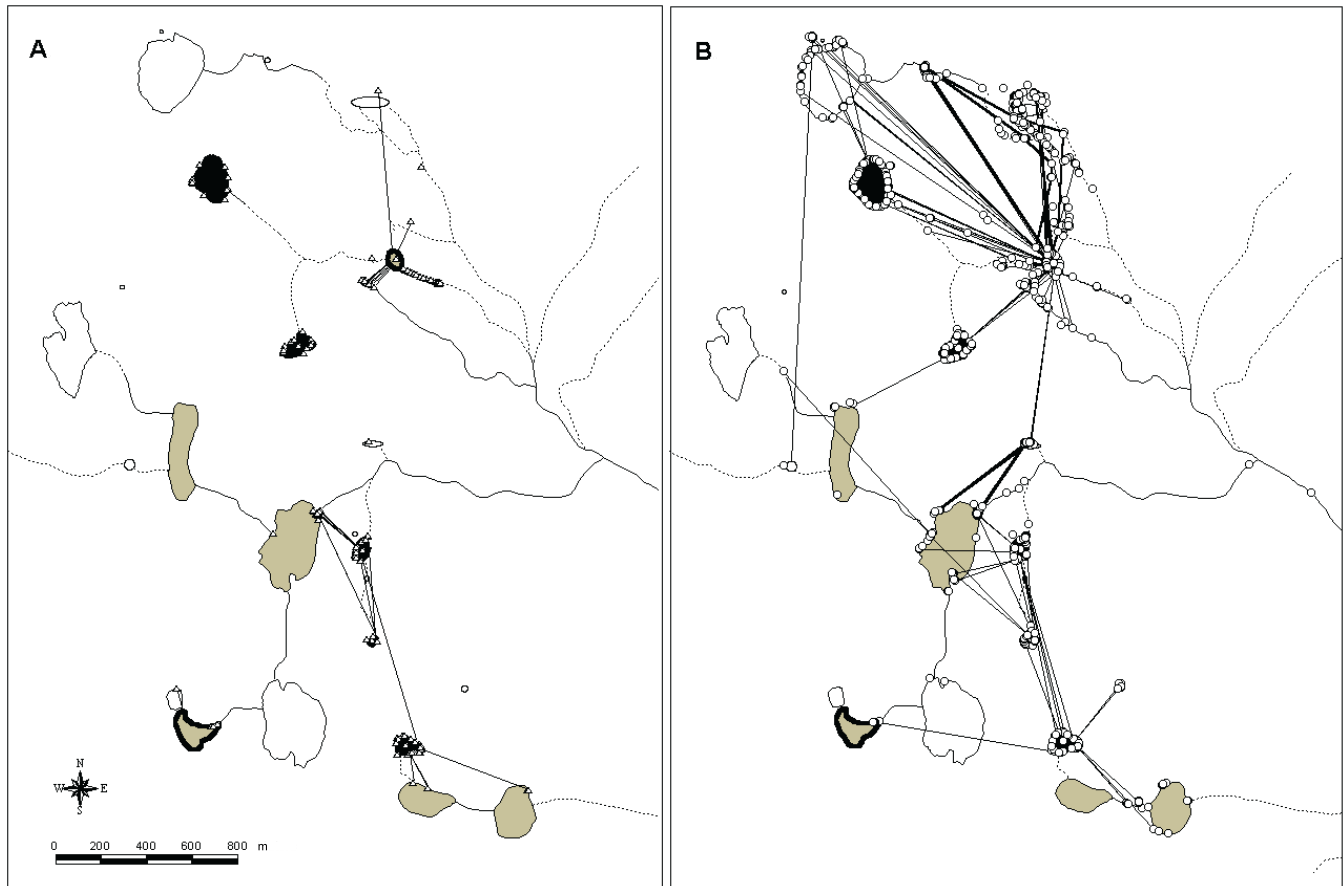

Table 3. Summary of juvenile (J), male (M), and female (F) *R. luteiventris* captured in breeding and nonbreeding summer habitats in Skyhigh Basin during five sampling periods.

Sample period	Sex	Number captured		Percent recaptures[a]	
		Breeding	Summer	Breeding	Summer
July 1995	J	63	34		
	M	185	5		
	F	89	23		
August 1995	J	67	17	42	12
	M	142	14	68	0
	F	88	66	55	29
July 1996	J	20	1	10	0
	M	151	6	52	17
	F	77	45	52	62
July 1997	J	10	12	30	16
	M	76	5	71	20
	F	59	72	61	51
July 1998	J	17	5	24	20
	M	61	2	74	0
	F	26	13	58	69
Average	J			26	12
	M			66	9
	F			56	53

[a]Percent recaptures is the proportion of juvenile, male, or female frogs that were captured in breeding or nonbreeding summer habitats (number captured) that had been previously captured and marked in a particular site.

Fig. 5. Examples of seasonal and annual migratory patterns *R. luteiventris* between breeding, summer foraging, or overwintering sites in Skyhigh Basin from 1995 to 1998. The chronologically numbered dates for the four males (triangles) and five females (circles) shown are the first dates that these individuals were captured at each site each year. We documented many frogs migrating between these (and other) sites but used these examples to illustrate the general patterns. Site fill patterns are the same as those used in Fig. 1.
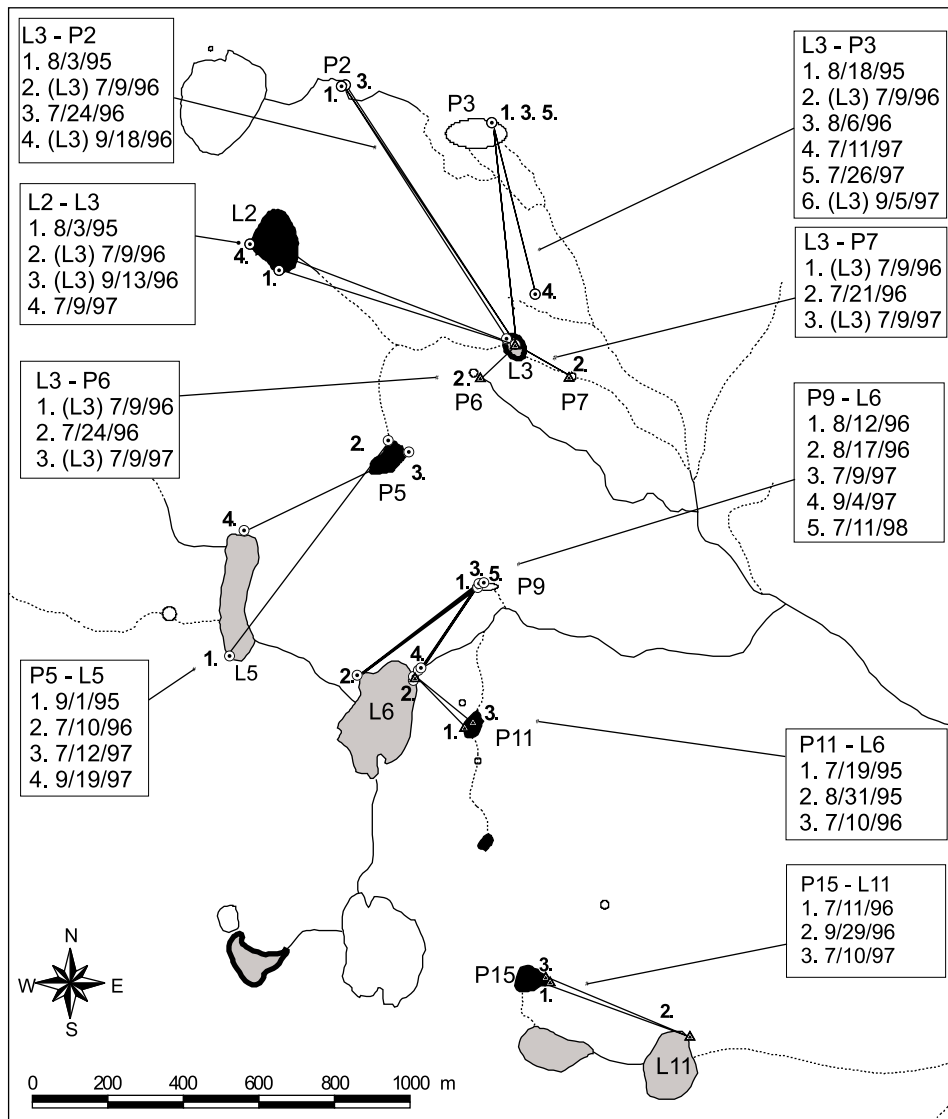
breeding or wintering sites to summer habitats compared with 1–32% of juveniles and 16–51% of female frogs (Table 4). In August 1995, just 4 weeks after we initially marked frogs, males were recaptured up to a straight-line distance of 424 m from breeding ponds, whereas females were recaptured up to 1033 m away (Table 5). Individual movements varied and not all frogs moved away from breeding ponds during the summer (Table 3). Of the frogs that migrated, male *R. luteiventris* moved among complementary habitats (summer foraging and overwintering) that were closer to breeding sites, whereas females migrated considerably farther to reach summer foraging areas and overwinter habitats (Table 5; $F_{[1,112]} = 47.2$, $P < 0.001$). In general, larger frogs moved longer distances from the breeding ponds (adjusted $R^2 = 0.33$, $F_{[1,66]} = 34.7$, $P < 0.001$). When males ($n = 12$) and females ($n = 16$) of similar size (58–70 mm SVL) were compared, there was no difference in migratory distances

between the sexes ($\male \overline{X} = 367$ m, SD = 304 m; $\female \overline{X} = 354$ m, SD = 259 m, $F_{[1,26]} = 0.27$, $P = 0.61$). Male *R. luteiventris* are capable of moving long distances, e.g., one individual was captured nearly 2000 m from where it was marked, and in an adjacent basin, an adult male traveled 1500 m between lakes. Nonetheless, on an annual basis, more female than male frogs migrated distances more than 500 m from breeding sites. Frogs marked at the same breeding site did not all move to the same summer range (Fig. 5). For example, frogs marked at L3 were recaptured at nine different water bodies (Fig. 4).

Migration to winter habitats

Beginning in mid-August and continuing until late September, adult frogs began migrating from breeding sites and summer habitats to overwintering sites (Figs. 5 and 6). During September surveys of overwintering sites, frogs were

Fig. 6. Examples of *R. luteiventris* migration routes and timing of migration in Skyhigh Basin based on locations of eight radio-tagged female frogs in 1996 and 1997. Site fill patterns are the same as those used in Fig. 1.
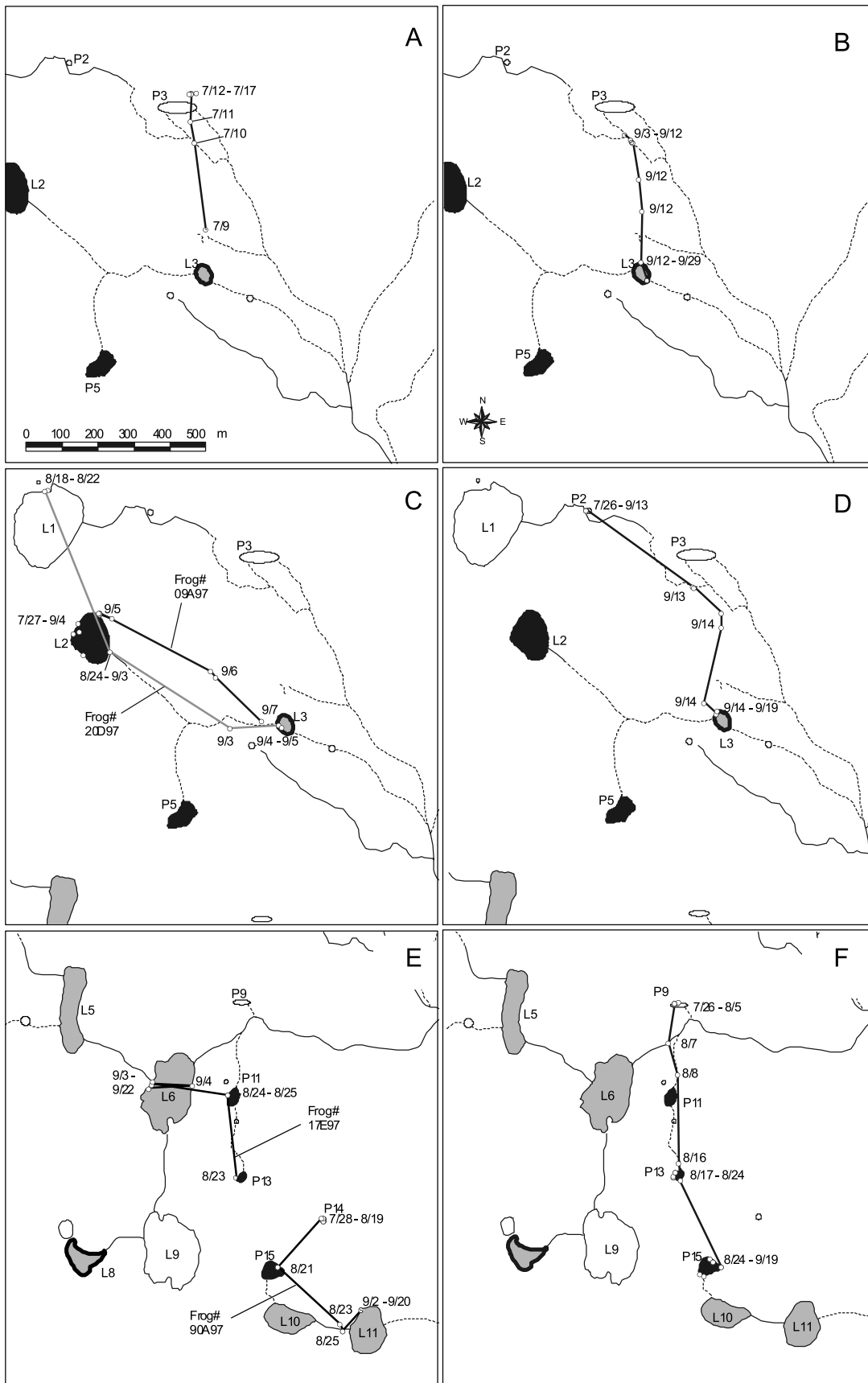
Table 4. Percentages of *R. luteiventris* migrating from breeding and overwintering sites to summer habitats in Skyhigh Basin, 1995–1998.

Year	Juveniles (%)		Males (%)		Females (%)	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
1995	0	35	9	17	15	52
1996	5	10	3	7	9	43
1997	0	60	8	14	15	62
1998	0	23	3	6	23	49
Mean	1	32	6	11	16	51

Note: The minimum annual migration estimates were calculated as a percentage of the number of frogs marked in breeding sites that were recaptured in other habitats >100 m away divided by the total number of captured frogs that carried a breeding-site mark in the basin during the annual census. The maximum annual migration estimates were calculated as a percentage of the number of frogs marked in breeding sites that were recaptured in other habitats >100 m away plus the number of frogs that were first captured and marked in these nonbreeding habitats divided by the total number of frogs captured in the basin during the annual census.

Table 5. Summary of straight-line distances between first capture locations and farthest recapture locations (in same or subsequent years) for *R. luteiventris* that migrated from breeding or overwintering sites to summer foraging areas in Skyhigh Basin, 1995–1997.

Year	Males				Females			
	n	$\overline{X}$	SE	Maximum	n	$\overline{X}$	SE	Maximum
1995	17	161	21	424	21	470	62	1033
1996	17	196	38	525	22	450	65	925
1997	14	123	34	525	27	430	44	998

Note: *N*, number of *R. luteiventris* recaptured in summer foraging areas during August surveys; $\overline{X}$, average of maximum straight-line distances (in metres) between initial capture locations and recapture locations; SE, 1 standard error of the straight-line distances (in metres); Maximum, maximum straight-line distances (in metres).

usually found at the inlets or outlets of larger lakes. In L3, we could not identify one area of the lake where frogs were congregating, but the numerous springs in and around the lake probably provided numerous overwintering opportunities. In October 2001, we observed juvenile and adult frogs moving through shallow water under 1 cm of surface ice along the shoreline of L3. Some frogs also may have overwintered in a large spring (P6) about 100 m from L3.

After metamorphosis, YOY frogs also migrated from shallow breeding ponds to deeper lakes to overwinter, although this usually occurred weeks later than adult migrations. In September 1997 and October 2001, we observed a mass movement of 26 and 103 recently metamorphosed frogs (~20 mm SVL, ~0.8 g) from a shallow breeding pond (P15) into two nearby overwintering sites (L10, L11). To reach the lakes, the YOY frogs traveled about 100 m over dry land and up to 350 m total distance. We were unable to witness the fall migration of metamorphs from other shallow breeding ponds, but numbers of YOY frogs steadily declined in these ponds in September.

Although most of the frogs in a particular site migrated to the same overwintering area, some individuals moved to completely different locations to overwinter. For example, one frog at P5 moved to and overwintered at L5 in 1995 and 1997, whereas other frogs in P5 moved down to L3 to overwinter (Fig. 5). Although most male and some female frogs had to migrate 450 m or less between the breeding and overwintering sites (up to 900 m annually), female frogs that

had migrated to distant summer ranges were forced to make long-distance return migrations to reach overwintering sites in the fall. The longest annual female migration observed was a round trip of at least 2066 m, between sites L3 and L1 (Fig. 6C). This long-distance migration was completed by at least three to five female frogs annually.

Travel rates and conditions

Depending on the distances between spatially separated summer and fall ranges (from 100 to 1030 m), frogs completed their migrations in 1–2 days, traveling up to 708 m in a day. Of the radio-tagged frogs, 8 of the 10 fastest migration rates (50–160 m/h) were observed between 20:00 and 06:45, when air temperatures were between 3 and 10°C. During fall migrations, radio-tagged frogs generally traveled the farthest at night and during or shortly after rain events. However, many frogs were also observed migrating along dry streambeds and through uplands during the day and during dry periods.

Travel routes

We documented the migration of 37 radio-tagged *R. luteiventris* between breeding and summer habitats or summer and winter habitats, with 13 captured in route. Based on these 13 female frogs, travel routes were fairly direct, approximating the shortest linear distances (Figs. 6A, 6B). Frogs that migrated to summer habitats in the spring (*n* = 2 observations; Fig. 6A) followed similar routes back to winter habitats in the fall (*n* = 6 observations; Fig. 6B). Stream corridors were followed when streams traveled along the migratory route, but for the most part, frogs did not follow streams. For example, frogs traveled across dry land to move from L1 to L3 (Fig. 6C) and from P2 to L3 (Fig. 6D). This route was taken despite the available streams connecting the water bodies. By using shortest-distance terrestrial travel routes instead of only following the streams, these frogs reduced their travel distance by more than 1 km. This migratory behavior resulted in frogs traveling at least 500 m across dry, upland habitat and through subalpine fir and lodgepole pine forests with sparse grouse whortleberry and bear grass understory vegetation. When available, frogs stopped at seeps, springs, lakes, and isolated pools of intermittent streams when traveling through uplands between distant habitats that lacked direct stream connections (Figs. 6E, 6F).

Discussion and conclusions

This study reveals that many *R. luteiventris* in Skyhigh Basin used spatially separated, specific habitat patches for breeding, foraging, and hibernating and that individuals could migrate hundreds to thousands of metres annually among these complementary resources. Although seasonal migrations have been previously reported for this species (Turner 1960; Hollenbeck 1974; Patla 1997; Bull and Hayes 2001; Engle 2001), this study provides the first evidence that *R. luteiventris* is capable of extensive annual migrations among distant water bodies, even in steep, arid mountain ranges at the altitudinal limit of the species. The results of this study have important implications for the conservation of montane *R. luteiventris* populations in relation to their habitat requirements and recolonization capabilities. Our study adds to a growing body of evidence that amphibian conservation requires the protection of groups of diverse water bodies and the upland or riparian habitats that connect them (Semlitsch 2002).

Habitat requirements of *R. luteiventris* vary seasonally, but the factors responsible for individual variation in habitat selection and migratory patterns remain unclear. The spatial arrangement of breeding, foraging, and overwintering sites in Skyhigh Basin required many frogs to undertake annual migrations, sometimes among distant water bodies. Yet it is interesting that a site that provided all of the seasonal habitat requirements (L3) contained the vast majority of frogs in the basin. This site was noticeably different from the other breeding and overwintering habitats in the basin (see Fig. 2) in that it was deeper than 3 m and fishless but also surrounded by extensive mats of vegetation and algae covered by shallow water flowing from numerous perennial springs. These unique habitat characteristics may explain why frogs from a large portion of the basin migrated to this site to overwinter and possibly breed. Despite this ideal "frog pond", nearly half of the female frogs at L3 migrated over 500 m to reach summer habitats. In contrast, male frogs remained at or close to L3. This difference in migratory patterns between males and females was consistent among the breeding sites in this study and is a pattern congruent with other studies on this and closely related species (Hollenbeck 1974; Licht 1974).

The long-distance summer migrations made by female but not male frogs suggests either a physical limitation for males, based on size differences (female frogs were 16% larger than males), or different life-history strategies. In this study, larger frogs moved longer distances from the breeding ponds. Furthermore, when males were compared with females of similar size (i.e., small females), there was no difference in migratory distances between the sexes. This implies that long-distance annual migrations may only be possible for larger individuals (and thus probably older females). However, we also observed some males traveling up to 1500 m between lakes that had no riparian corridor, a distance comparable to female migrations in Skyhigh Basin. Therefore, we suspect that migration distance is related more to behavioral differences between the sexes than to morphological or physiological limitations. For example, males may remain near breeding sites to compete for females each spring, causing them to forgo traveling to preferred foraging sites. Males may also require less energy than reproductive females because female *R. luteiventris* lose

25–35% of their body mass during egg deposition (Engle 2001). In the short active season and cool temperatures of this high-elevation basin, female frogs may need to reach high-quality foraging habitat or areas with less competition to regain fat reserves needed for egg development. At higher elevations, female *R. luteiventris* are thought to reproduce every 3–4 years (Turner 1960), although females that migrate to prey-rich areas may be able to reproduce more frequently (D.S. Pilliod, unpublished data).

The migratory movements between complementary resources in this study are more than twice the migratory distances previously reported for *R. luteiventris* (Turner 1960; Hollenbeck 1974; Patla 1997; Bull and Hayes 2001, 2002; Engle 2001). At 2390 m elevation in Yellowstone National Park, Turner (1960) described *R. luteiventris* moving from breeding ponds into foraging pools and meadows 100–200 m away and later from meadows along intermittent streams for 50–450 m to overwinter in a permanent stream and springs. Hollenbeck (1974) reported annual movements to and from breeding areas ranging from 40 to 550 m in a population of *R. luteiventris* at 2070 m elevation near Hyalite Reservoir in south-central Montana. Based on reported straight-line movements among breeding, foraging, and wintering areas, we estimate that frogs migrating among complementary resources in Turner's and Hollenbeck's study areas did not travel more than about 1200 m annually.

Ranids are certainly capable of traveling farther than the migratory distances reported here, even through apparently inhospitable terrain (e.g., see Table 1 in Dodd 1996 and Table 3 in Marsh and Trenham 2001, as well as Reaser 1996 and Hayes et al. 2001). A year after being marked and released, a 2-year-old *R. luteiventris* was recaptured 6.5 km downstream from its natal pond in the arid Owyhee Uplands of southwestern Idaho (Engle 2001). This is the longest dispersal distance recorded for this species. Other studies on *R. luteiventris* report maximum dispersal distances of less than 1.3 km (Turner 1960; Hollenbeck 1974; Patla 1997; Bull and Hayes 2001, 2002). We captured a male and a female *R. luteiventris* after they had traveled more than 1800 m from breeding ponds into areas that were not associated with other migratory patterns. We are uncertain whether these movements were unidirectional dispersal events or multiyear long-distance migrations. The duration of this study may have been insufficient to record migratory patterns that occurred over several years. For example, a 4-year study of *R. luteiventris* in southwestern Idaho revealed that young female frogs did not return to breeding ponds for several years until sexually mature (Engle 2001).

We are uncertain why juvenile recapture rates (as juveniles or later as adults) were so low. This result made interpretation of juvenile movements difficult. We suspect that juvenile mortality in Skyhigh Basin is very high, possibly as a result of late-season migrations to overwintering areas and predation by introduced trout in overwintering sites (Pilliod and Peterson 2001). Because juvenile frogs were never captured more than 350 m from breeding sites, we conclude that juveniles may not be able to travel as far as adults in the steep topography and harsh environmental conditions of Skyhigh Basin. Contrary to our findings, other studies have found that juvenile ranids move further than adults, traveling from 2 to 5 km from their natal pond (Dole 1971; Berven

and Grudzien 1990; Seburn et al. 1997). Movement patterns of juvenile *R. luteiventris* need to be further investigated.

Surprisingly few studies have described amphibian movement patterns to overwintering sites, and consequently, very little is known about the winter habitat requirements of amphibians, especially at high elevations (but see Bradford 1983 and Matthews and Pope 1999). In a recent study of *R. luteiventris* overwintering habitat at lower elevations (915–1800 m), Bull and Hayes (2002) followed 66 radio-tagged *R. luteiventris* as they migrated 15–1200 m to reach overwintering sites in northeastern Oregon. Forty-four percent of tagged frogs used ice-covered ponds with a mean surface area of 2.2 ha and a depth of 2.4 m. The rest overwintered in partially frozen ponds, lotic habitats, backwaters, and seeps. In our study, most, if not all, frogs overwintered in ice-covered lakes with a mean surface area of 1.7 ha (±1.2 ha (SD)) and a depth of 8.4 m (±3.6 m (SD)). These winter habitats were mostly rocky lakes with perennially flowing outlets. Small, organically rich ponds, like those used for *R. luteiventris* reproduction, probably become anoxic during winter and thus are unsuitable habitats for overwintering. During September surveys of our study basin, frogs were found at inlets and outlets of overwintering sites, possibly to take advantage of flowing, oxygenated water. Frogs that overwinter under ice appear to select areas with the highest dissolved oxygen levels but not necessarily the highest water temperatures (Bull and Hayes 2002).

Our data suggest that *R. luteiventris* prefer certain habitats for overwintering and that individuals have strong preferences, or at least drives (environmental cues and (or) learned migratory routes), to specific wintering sites. Fidelity to specific hibernacula may be fairly typical in landscapes that offer few suitable overwintering sites, such as at high altitudes or latitudes where lakes can remain frozen for more than 9 months each year. At 3470 m elevation in the Sierra Nevada, 97% of 500 marked *R. muscosa* overwintered in the same lake in 2 consecutive years (Matthews and Pope 1999). One of the best studies of fall migrations to winter habitat is that of the Manitoba toad (*Bufo hemiophrys*), which migrates to communal overwintering sites in northwestern Minnesota (Breckenridge and Tester 1961; Kelleher and Tester 1969). Studies spanning a decade found that 88–95% of toads that had bred in various prairie potholes migrated to the same terrestrial "Mima-type" mounds for hibernation each year. In our study, all marked frogs returned to the same overwintering sites year after year, even when other deep lakes were closer. The mass migration of frogs from two breeding ponds and six summer habitats to site L3 in fall was the most striking example of the attraction of a suitable wintering site. Given the number of frogs that use this site, L3 is clearly a critical resource for frogs in Skyhigh Basin. These data suggest that the carrying capacity of Skyhigh Basin may be strongly influenced by the location and quality of wintering sites. The relationship between winter habitat quality and the local abundance of north-temperate anurans needs further examination.

The migration travel rates of adult *R. luteiventris* in this study were considerably greater than those previously reported for this species and other ranids in western North America. We found maximum travel rates of up to 160 m/h and at least 700 m/day by a female spotted frog. Turner (1960) reported maximum rates of travel of 50–189 m/day for adult *R. luteiventris* in Yellowstone National Park. Other studies of *R. luteiventris* report maximum travel rates of less than 100 m/day (Hollenbeck 1974; Patla 1997; Engle 2001). Adult northern leopard frogs (*Rana pipiens*) have been found to travel from 40 to 160 m/day (Dole 1965), whereas the much larger adult bullfrogs (*Rana catesbeiana*) travel up to 229 m/day (Raney 1940). We suspect that the travel rates of ranid frogs may be underestimated, possibly as a result of the traditional techniques used (mark–recapture) and the landscapes studied.

We were particularly surprised when frogs migrated along fairly linear routes through dry uplands when streams were available. *Rana luteiventris*, like most ranids in western North America, are rarely found far from water and are generally considered to rarely move across upland habitats. Early accounts describe numerous *R. luteiventris* along high mountain streams (Wright and Wright 1933), the most obvious travel corridor for a species closely associated with water. Turner (1960) thought that most *R. luteiventris* movements were restricted to streams or intermittent watercourses in the latter part of the summer (fall migration), and he believed that appreciable cross-country movements only occurred earlier in the season. Other studies have found that *R. luteiventris* generally travel along riparian corridors but also report occasional movements of 400–500 m across dry, grazed grasslands and sagebrush uplands (Reaser 1996; Bull and Hayes 2001). In Skyhigh Basin, most migrating frogs were captured in and along streams, but frogs were also captured moving through dry open forests and were frequently recaptured in distant water bodies with no water connectivity. Our data suggest that *R. luteiventris* readily migrates between habitats separated by 500 m or more of dry, coniferous forests. Movements through these upland habitats often occurred at night and during rain events, but frog migrations were not restricted to these conditions. Long-distance navigation and the ability to move quickly and use microclimates to reduce water loss may be critical to the survival of ranids in harsh high-elevation environments where annual migrations among complementary resources are necessary.

These data suggest that protecting breeding sites for montane populations of *R. luteiventris* is not sufficient protection for the species. In some areas, spatially separated breeding, summer, and winter habitats may all be essential for the persistence of *R. luteiventris* populations. Identifying these critical habitats requires a better understanding of the local habitat use patterns of frog populations. In areas where amphibian conservation is a priority, we recommend a shift in management focus from protecting only breeding ponds to protecting groups of diverse water bodies and surrounding uplands within 1 km of breeding ponds.

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