

Herpetologica, 58(3), 2002, 354–363
© 2002 by The Herpetologists' League, Inc.

INFLUENCE OF ANURAN PREY ON THE CONDITION AND DISTRIBUTION OF *RANA MUSCOSA* IN THE SIERRA NEVADA

KAREN L. POPE¹ AND KATHLEEN R. MATTHEWS

USDA Forest Service Pacific Southwest Research Station, P.O. Box 245, Berkeley, CA 94701, USA

ABSTRACT: Mountain yellow-legged frogs (*Rana muscosa*) at high elevations of the Sierra Nevada must obtain enough food during summer to survive 7–9 winter months when their aquatic habitats are frozen and food is presumably unavailable. Adults of *R. muscosa* prey on a variety of organisms, including aquatic and terrestrial invertebrates and anuran larvae. To determine if anuran larvae influence the condition, distribution, and survival of adults of *R. muscosa*, we assessed body condition (variation from the expected mass for given length) and distribution of *R. muscosa* in relation to abundance and distribution of larval *Hyla regilla*, *Bufo canorus*, and *Bufo boreas*. Using three years of mark-recapture data, we found that abundance of larval *H. regilla* in a water body was positively correlated with the condition of *R. muscosa*. Moreover, *R. muscosa* had higher relative mass (W_r) values in areas with other anuran larvae than in areas with no other amphibian species. High W_r values significantly increased the probability of recapturing frogs in following years. Using surveys of over 1700 lakes and ponds in the John Muir Wilderness and Kings Canyon National Park, we also found that the presence of larval *H. regilla* or *Bufo* in a water body was a significant indicator of the presence of adults of *R. muscosa* after accounting for significant habitat and isolation variables. These findings taken together suggest that some adults of *R. muscosa* actively seek out water bodies with other anuran species during the critical summer months and that the anuran larvae provide a nutritious food source that increases the body condition and, therefore, survival of the frogs.

Key words: Anuran predation; Condition; Frog predation on tadpoles; High elevation anurans; *Rana muscosa*; Relative mass; Sierra Nevada amphibians

AMPHIBIANS at high elevations or latitudes exhibit annual cycles in energy intake and expenditure (Jørgensen, 1992). During summer months, they feed, grow, and store energy to survive the long winter months when their aquatic habitats are frozen and food is presumably unavailable. In this short activity period, amphibians must obtain enough nutritious prey to create fat stores for maintenance of metabolic needs over winter, support gamete production, and support post-thaw breeding activities (Jørgensen, 1992).

The body condition (variation from the expected mass for given length) of an an-

imal is often assumed to reflect its amount of fat stores, health, and reproductive state, as well as environmental characteristics such as habitat quality and prey availability (Anderson and Gutreuter, 1983; Ney, 1993). Condition measurements are easily calculated from routinely collected mass and length data and measure the “plumpness” of an animal (Liao et al., 1995). Condition indices have been widely used as field assessment tools for determining relationships of fish populations and environmental conditions including prey concentrations (Liao et al., 1995; McGurk et al., 1993; Murphy et al., 1991), but they are just beginning to be used for assessing relationships between amphibian

¹ CORRESPONDENCE: e-mail, kpope@fs.fed.us

populations and environmental conditions (Docherty et al., 1995; Reading and Clarke, 1995).

The mountain yellow-legged frog (*Rana muscosa*) occurs in aquatic habitats in the Sierra Nevada Mountains of California and Nevada at elevations of 1370–3700 m, where it must obtain enough food during 3–5 mo in the summer to survive the long frozen winter months of the high Sierra (Bradford, 1983). Like other ranid frogs, mountain yellow-legged frogs are primarily sit-and-wait predators and opportunistically seize their prey when it comes into range (Stebbins and Cohen, 1995; Zwiefel, 1955). To be successful with this technique, frogs would be expected to position themselves in areas with high densities of prey, thus increasing the chances of prey entering their range. Those frogs occurring in areas with abundant prey would likely take more prey and, therefore, have higher body condition than frogs occurring in areas with low numbers of prey, assuming other environmental conditions are constant.

Because *R. muscosa* has declined throughout its range in the Sierra Nevada (Bradford et al., 1994; Drost and Fellers, 1996; Knapp and Matthews, 2000a) and is currently petitioned for federal listing as endangered, it is important to understand the relationship between it and other organisms on which it depends. The body condition and distributional relationship between adults of *R. muscosa* and important prey sources will provide valuable information when assessing the viability of habitats as reserve areas for this declining species.

Although very little is known about the feeding habits of *R. muscosa* in the Sierra Nevada, adults have been reported feeding on tadpoles of *Bufo canorus* (Mullally, 1953) and *Hyla regilla* (Pope, 1999a), as well as aquatic and terrestrial invertebrates (Mullally, 1953; Zwiefel, 1955). Juvenile and subadult frogs feed on smaller invertebrate prey, and adult frogs, if possible, supplement their invertebrate diet with larger tadpole prey. The tadpoles of *H. regilla*, *B. canorus*, and *B. boreas* form aggregations during the daytime in warm

shallow waters along the margins of lakes and ponds (Ultsch et al., 1999) and, in these habitats, are vulnerable to predation (Alford, 1999). Stomach analyses of several adults of *R. muscosa* collected from a pond with numerous tadpoles of *B. canorus* revealed that *B. canorus* made up a large proportion of the stomach contents (Mullally, 1953). In addition to actual feeding behavior, a recent study provided evidence that movement patterns of adults of *R. muscosa* may be related to the distribution and abundance of tadpoles of *H. regilla* during mid-summer when foraging is the primary activity (Pope and Matthews, 2001).

Based on an assumed predator/prey relationship between *R. muscosa* and other anuran larvae in the Sierra Nevada, we used two study techniques (small-scale, long-term mark-recapture and large-scale, short-term survey) to determine if (1) body condition of adults of *R. muscosa* is positively related to abundance of *H. regilla* in a water body, (2) body condition affects the probability of recapture after the winter season, and (3) the distribution of adults of *R. muscosa* is related to the distribution of other anuran larvae (*H. regilla*, *B. canorus*, and *B. boreas*) in the Sierra Nevada. We predicted that, if anuran tadpoles are an important prey source, we would find increased body condition in areas with abundant anuran prey, we would more likely recapture frogs that had high body condition the previous summer because fatter frogs would more likely survive the winter months, and we would detect an association between the distribution of adults of *R. muscosa* and other anuran larvae. To account for possible confounding habitat, isolation, and temporal and spatial effects, we used generalized additive regression models (Cleveland and Devlin, 1988; Hastie and Tibshirani, 1991) for the analyses.

MATERIALS AND METHODS

To determine if body condition of *R. muscosa* is related to abundance of larval *H. regilla* and if body condition affects the probability of recapture, we conducted a 3-yr mark-recapture study of *R. muscosa*

in Dusy Basin (3470 m), Kings Canyon National Park (KCNP), California. Both species were abundant there, and we observed *R. muscosa* feeding on tadpoles of *H. regilla* on numerous occasions (Matthews and Pope, unpublished data; Pope, 1999a). The general study area covers approximately 1.0 km² and includes five stream segments and 11 lakes and ponds. The main lake in the basin (10 m deep, 5.3 ha) supports a self-sustaining population of hybrid rainbow-golden trout (*Oncorhynchus mykiss* × *O. aguabonita*), but most of the smaller neighboring ponds (<2.5 m deep, area <3000 m²) do not support any fish. The presence of trout in Dusy Basin is a result of past stocking by the California Department of Fish and Game, which was terminated in the basin in the early 1980s. Interspersed among the lakes and granite outcroppings, alpine fell field vegetation occurs with low-growing herbaceous plants and shrubs and few krummholzed white-bark pines (Holland and Keil, 1995).

During summers of 1997 and 1998, a total of 500 adults (>40 mm SVL) of *R. muscosa* were individually marked in the basin using passive integrated transponders (PIT tags) (Pope, 1999b; Pope and Matthews, 2001). Recapture surveys were conducted in 1997–1999 by systematically revisiting all water bodies in the study area and capturing all adult frogs possible. The PIT tag number, location of capture, mass, length, and sex were recorded for all frogs. We conducted seven recapture surveys in each body of water in the study area in 1997, 15 in 1998, and eight in 1999.

To compare frog condition to an area without any other anuran prey, an additional 81 mountain yellow-legged frogs were PIT tagged and surveyed in an isolated lake (1805 m²) approximately 1 km from the study basin at an elevation of 3450 m where no other amphibian species were found. The lake is 4 m deep, does not support fish, and has similar near-shore substrate to lakes and ponds within the study area. Frogs in this lake have been observed foraging on terrestrial invertebrates both on the surface of the wa-

ter and in an adjacent wet meadow (Pope and Matthews, unpublished data).

Visual encounter surveys (Crump and Scott, 1994) were conducted periodically throughout summers to assess the relative number of amphibian larvae in each water body in the basin. The surveys involved one person walking the perimeter of a lake or stream and counting all species and numbers of tadpoles seen. The shoreline habitat features, including substrate characteristics and vegetation of all lakes in the study area, were mapped using GPS.

To determine if the landscape-scale distribution of adults of *R. muscosa* in the Sierra Nevada is related to the distribution of other anuran larvae, we used a data set that included 1728 lakes in the John Muir Wilderness (JMW) and neighboring KCNP. The lakes were surveyed between 1995 and 1997 as a part of a larger study to determine the effect of introduced trout on native biota (Knapp and Matthews 2000a,b; Matthews and Knapp, 1999). Lakes and ponds were identified from U.S. Geological Survey (USGS) 1:24,000 topographic maps and included 669 and 1059 water bodies in the JMW and KCNP study areas, respectively. Surveys were conducted during summer months when water bodies were ice-free and amphibians were active. The JMW and KCNP study areas encompass a total of approximately 100,000 ha and are managed by the U.S. Forest Service and the National Park Service, respectively. With the exception of introduced fishes and low impact recreation, both areas are relatively undisturbed.

The species and number of amphibians at each water body were determined using visual encounter surveys. Potential amphibians in the sampled lakes were *R. muscosa*, *H. regilla*, *B. canorus*, and *B. boreas*. The presence or absence of trout (*Oncorhynchus mykiss* × *O. m. aguabonita* hybrids, *Salvelinus fontinalis*, and *Salmo trutta*) was determined at each water body using visual encounter surveys in shallow ponds or gillnets in deep lakes. Information was also collected on the physical attributes of each water body, including water body elevation, surface area, maximum depth, littoral zone (i.e., near-

shore) substrate composition, number of inlet streams, and isolation from other water bodies (see Knapp and Matthews, 2000a, for methodological details).

Data Analysis

To measure the variation in mass of *R. muscosa* from Dusy Basin in terms of abundance of larval *H. regilla* while accounting for length and possible confounding environmental effects, we used a generalized additive model (GAM; Cleveland and Devlin, 1988; Hastie and Tibshirani, 1991). The use of a GAM allowed us to assess directly the linear or nonlinear effects of potential sources of variation on the mass of frogs without assuming a linear or other simple parametric relationship and while controlling for the other covariates including length. The GAMs relax the assumption that the relationships between the dependent and independent variables are linear by using a nonparametric smoothing function (e.g., loess) to determine the fitted model that best fits the independent variables (Cleveland and Devlin, 1988; Hastie and Tibshirani, 1991). Therefore, instead of assuming that the dependent variable is a parametric function of the significant independent variables, one assumes only that it is a sum of the smooth functions for each of these variables. By using a GAM, use of a specific condition index was unnecessary to determine the effects of specific variables. We used the regression equation

$$\begin{aligned} \log W = & \alpha + \beta \log L + \text{snowfall} \\ & + \text{sex} + \text{lo}(X_1) + \text{lo}(X_2) \\ & + \text{lo}(X_3) + \epsilon \end{aligned} \quad (1)$$

where W = wet weight (mass), L = snout-vent length (SVL), and β = slope of L and represents the exponent of length ($\beta = 3$ for isometric growth) in the weight-length equation (LeCren, 1951). *Snowfall* is a categorical variable indicating the percent of normal winter snowfall recorded at the Bishop Pass Station located about 0.60 km from the Dusy Basin study site (California Department of Water Resources, <http://cdec.water.ca.gov>) for 1996/1997 (117%), 1997/1998 (177%), and 1998/1999 (74%).

The covariates X_1 , X_2 , and X_3 represent log of number of larval *H. regilla*, number of days from thaw, and maximum water body depth; and *lo* is a nonparametric loess smooth function of the covariates (Hastie and Tibshirani, 1991). The random error term, ϵ , is assumed to represent white noise. The number of days from thaw was calculated by subtracting the date when 0 mm of snow was first recorded at the Bishop Pass Station from the date of the frog's recapture. Additional variables (presence/absence of fish, and near-shore substrate) were initially analyzed but were not included in the final regression model because they were not found to be statistically significant. The data for this analysis were collected over three summer seasons (1997–1999), and repeated measurements of individuals were included if at least 25 days had passed between captures. We used the likelihood ratio test and the Akaike information criteria (AIC) (Linhart and Zucchini, 1986) to estimate the significance and relative importance of each covariate in the presence of all other covariates.

We then used the relative mass (W_r) condition index (Wege and Anderson, 1978) to compare condition of frogs in water bodies with and without larvae of *H. regilla* and to assess whether or not body condition affected the probability of recapturing frogs from year to year. The W_r index was calculated for all frogs with the equation

$$W_r = 100 \frac{W}{W_s} \quad (2)$$

where W is the wet mass of the frogs and W_s is the expected length-specific mass predicted from a linear regression of mass ($\log_{10}W$) on length ($\log_{10}L$) for all frogs. The estimated regression line for length-specific mass for Dusy Basin mountain yellow-legged frogs was determined to be

$$\log W_s = -3.76 + 2.85 \log L + \epsilon \quad (3)$$

W_s was then multiplied by 1.003 based on the Baskerville bias correction (Baskerville, 1972), $e^{mse/2}$, for log normal regression where *mse* is the mean sum of squares of the linear regression. Consequently, $W_s =$

$e^{-3.76 + 2.85\log L + 1.003}$ and the resulting values were used to calculate W_r values (equation 2) for individual frogs.

To compare body condition in lake basins with and without other anuran prey, summer 1998 and 1999 W_r values for PIT-tagged frogs captured in the isolated lake 1 km from the main study basin were compared to W_r values for frogs captured in the main study area lakes during the same period using the Wilcoxon rank-sum test. We used the nonparametric Wilcoxon test because the data failed the normality test ($P < 0.001$), and it was not possible to normalize distributions via transformations.

To quantify the effect of body condition on the probability of recapturing frogs from year to year while accounting for potentially confounding effects, we used nonparametric logistic regression with the equation

$$\Pr(Y = 1) = \frac{e^\theta}{1 + e^\theta} \quad (4)$$

where $\Pr(Y = 1)$ is the probability of recapturing a frog the following year and the linear predictor $\theta = \alpha + \log(W_r) + \text{SVL} + \text{day} + \text{over-wintering lake} + \text{frog sex} + \text{year}$. The W_r and SVL values used in the equation were the last values collected for a frog before winter in 1997 and 1998, and day was the day of survey (day number starting from 1 January). The variable SVL was included in the equation in addition to W_r because there is evidence that larger frogs have a better chance of being recaptured after the winter season than smaller frogs (Pope, 1999b). Over-wintering lake was the expected lake (either 1 or 5) used for over-wintering based on locations of recaptured frogs prior to lakes freezing and immediately after the thaw (Pope and Matthews, 2001).

The survey data from the 1728 water bodies in the JMW and KCNP were first used to determine if an association between the distribution and abundance of adults of *R. muscosa* and other anuran species could be found. In water bodies where adults of *R. muscosa* were identified, we compared the mean number of adults of *R. muscosa* in water bodies with

other species versus water bodies with only *R. muscosa* using the Wilcoxon rank-sum test. We then used the JMW and KCNP survey data to determine if the presence/absence of larvae of *H. regilla* or *Bufo* spp. influenced the probability of adults of *R. muscosa* presence/absence in water bodies on a landscape scale. We used nonparametric logistic regression (equation 4) for the analysis in order to assess the effect of larval presence/absence while accounting for potentially confounding habitat and isolation effects. In this equation, $\Pr(Y = 1)$ is the probability of presence of adults in a water body and the linear predictor $\theta = \alpha + \text{larvae} + \text{fish} + \log(X_1) + \dots + \log(X_6)$ where larvae and fish were categorical variables indicating presence/absence of larval *H. regilla* or *Bufo* spp. and presence/absence of fish, respectively. The covariates X_1, \dots, X_6 were maximum lake depth, lake elevation, % near-shore silt, UTM coordinates, number of lakes within 1 km, and number of inlets. These variables were chosen to reduce collinearity and because most had been found to be significant variables in a previous analysis on the effect of trout on presence/absence of larval *R. muscosa* (Knapp and Matthews, 2000a). The spatial surface, represented by $\log(\text{UTM}_e, \text{UTM}_n)$, can be viewed as a surrogate for any habitat characteristics at locations with coordinates $(\text{UTM}_e, \text{UTM}_n)$ that were not measured but that might have an effect on adult *R. muscosa* occurrence (Hobert et al., 1997).

If an observed distributional relationship between adults of *R. muscosa* and other amphibians is based on a predator/prey relationship as our hypothesis predicts and our model accounts for other important explanatory variables, we would not expect to see as strong a relationship between larval *R. muscosa* and other amphibian larvae since the larvae are primarily herbivores (Stebbins and Cohen, 1995). To test this, we substituted the adults of *R. muscosa* dependent variable with larval *R. muscosa* presence/absence in the nonparametric logistic regression model. We then compared the significance values for the independent variable *H. regilla* or

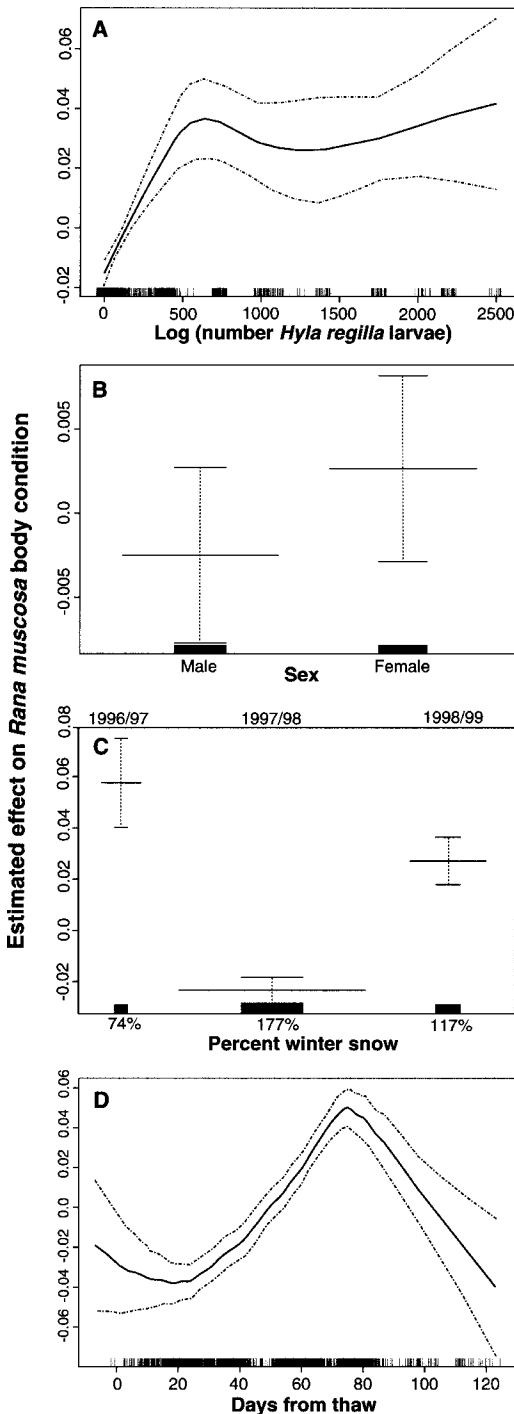


FIG. 1.—Estimated effects of (A) number of *Hyla regilla*, (B) frog sex, (C) percent winter snowfall, and (D) number of days from thaw on the body condition [log(W) while accounting for log(L)] of *Rana muscosa*. For A and D, dotted lines represent approxi-

Bufo spp. presence/absence in the two models.

RESULTS

In Dusy Basin, we found that the abundance of larval *H. regilla* in a water body positively influences the mass of *R. muscosa* when length is held constant (Fig. 1A). The overall regression model of log mass was highly significant ($n = 2530$, $P < 0.001$, $R^2 = 0.88$) as was the individual effect of the relative number of larval *H. regilla* ($P < 0.001$). Based on the AIC, the relative importance of significant ($P < 0.05$) independent variables influencing condition (not including length) was % winter snowfall, number of larval *H. regilla*, and number of days from thaw. Sex did not significantly influence body condition ($P = 0.18$, Fig. 1B). The condition of frogs was lower ($P < 0.001$) in the summer after the winter of 1997–1998 with 177% of normal snowfall compared to the more “normal” winters of 1996–1997 (117%) and 1998–1999 (74%, Fig. 1C). The relationship between body condition and number of days from thaw had a nonlinear contribution ($P < 0.001$) with condition peaking approximately 70 days after thaw (Fig. 1D).

A comparison of W_r values for frogs in the isolated lake with no amphibians other than *R. muscosa* and the Dusy Basin study area lakes during mid-summer (August and early September) 1998 and 1999 revealed that frogs in the Dusy Basin study area had a significantly higher condition in both 1998 ($n = 111$, $\bar{x} = 95.2 \pm 0.99$) and 1999 ($n = 232$, $\bar{x} = 105.4 \pm 0.90$) than did frogs in the isolated lake (1998: $n = 28$, $\bar{x} = 85.0 \pm 2.22$; 1999: $n = 96$, $\bar{x} = 92.3 \pm 1.62$) (Fig. 2).

The logistic regression model assessing the probability of recapturing Dusy Basin PIT-tagged frogs after the 1997–1998 and 1998–1999 seasons was highly significant ($n = 737$, $P < 0.001$) as was the individual effect of frog W_r values recorded before the winter seasons ($P < 0.001$, Table 1).

←

mate 95% confidence intervals, and hatch marks at the bottom of the graphs represent data points.

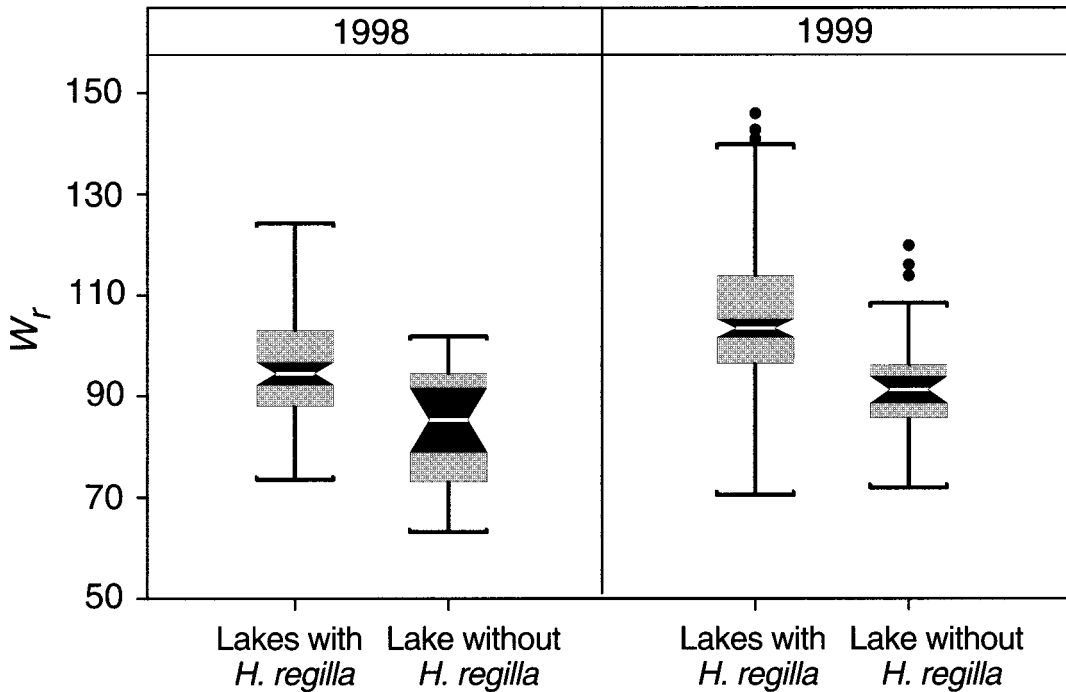


FIG. 2.—Box plots showing the relative mass (W_r) of *Rana muscosa* in the study lakes with *Hyla regilla* versus the isolated lake without *H. regilla* for summers of 1998 and 1999. The bottom and top of each box indicate the 25th and 75th percentiles, respectively; the black notched area represents the 95% confidence interval; the line within each box marks the median; and the whiskers below and above each box indicate the 10th and 90th percentiles, respectively. Observations falling outside these percentiles are shown as points above and below the whiskers. For 1998, $n_{\text{with } H. \text{ regilla}} = 111$ and $n_{\text{without } H. \text{ regilla}} = 28$ (Wilcoxon rank-sum test: $z = 3.70$, $P = 0.0002$). For 1999, $n_{\text{with } H. \text{ regilla}} = 332$, and $n_{\text{without } H. \text{ regilla}} = 96$ (Wilcoxon rank-sum test: $z = 5.76$, $P < 10^{-5}$).

Frogs with low W_r values were less likely to be recaptured after the winter season than frogs with high W_r values when all other variables were held constant. In ad-

dition, frogs with large SVL and frogs that over-wintered in the deepest lake (10 m) had a higher probability of being recaptured compared to frogs with small SVL

TABLE 1.—Regression coefficient (β), standard error of β , test statistic, statistical significance (P value), and direction of effect of the variables in the linear regression model assessing the probability of recapturing PIT-tagged frogs after the winter seasons.

Variable	β	SE $_{\beta}$	t Test statistic	P value	Direction of effect
Relative weight when last recaptured before winter	0.04	0.01	5.53	<0.001	+
Snout-vent length	0.10	0.02	6.17	<0.001	+
Over-wintering lake (1 or 5)*	-0.75	0.18	-4.11	<0.001	**
Survey year	-1.12	0.22	-5.02	<0.001	***
Calendar day last recaptured before winter	0.01	0.00	1.94	0.05	+
Frog sex	0.01	0.20	0.07	0.94	NA

* Test statistic = t value.

* Specific lake where frog was assumed to over-winter based on recapture history of the individual (Pope and Matthews, 2001). Lake 1 is 53,187 m² and 10 m deep; lake 5 is 1028 m² and 1.4 m deep.

** Probability of recapture was higher for frogs that over-wintered in lake 1 than in lake 5.

*** Probability of recapture was higher in 1998 than in 1999.

and frogs that over-wintered in a more shallow lake (1.4 m) (Table 1).

Within the JMW and KCNP study areas, 356 of the 1728 water bodies surveyed were found to have at least one adult mountain yellow-legged frog. Of these, 134 (38%) also had at least one other anuran species present (*H. regilla*, *B. boreas*, or *B. canorus*). Adults of *R. muscosa* were more abundant in lakes with other anuran species ($n = 134$, $\bar{x} = 46.2 \pm 9.90$) than in lakes with no other species ($n = 221$, $\bar{x} = 26.6 \pm 2.99$; Wilcoxon rank-sum test $z = 2.007$, $P = 0.04$).

The overall logistic regression model of adults of *R. muscosa* occurrence in a water body was highly significant ($n = 1728$, $P < 0.001$) and presence or absence of larval *H. regilla* or *Bufo* spp. was found to be a significant indicator ($P = 0.05$) of occurrence of adults of *R. muscosa*. When the dependent variable (adults of *R. muscosa*) in the logistic regression model was replaced with larval *R. muscosa* and the covariates remained constant, the presence/absence of *H. regilla* or *Bufo* spp. was not found to be a significant indicator of the presence of larval *R. muscosa* ($P = 0.19$).

DISCUSSION

Our results indicate that individuals of *R. muscosa* have higher body conditions in areas with high numbers of larval *H. regilla* when compared to areas with low numbers and that the presence of larval *H. regilla* or *Bufo* spp. in a water body significantly increases the abundance and probability of finding adults of *R. muscosa* in the water body. In addition, based on recapture surveys, *R. muscosa* with high body condition seem to have a better chance of surviving winter than frogs with low body condition. It appears that some adults of *R. muscosa* actively seek out water bodies with other amphibian species during summer months and that these anuran larvae provide a nutritious food source that increases the body condition and, thus, survival of the frogs.

Throughout the summer of 1998, after a winter with 177% normal precipitation, body condition of frogs in Dusy Basin remained significantly lower compared to

summers of 1997 and 1999. Although survival of adult frogs was high after the extreme winter (Pope and Matthews, 2001), the frogs were unable to regain mass-to-length ratios comparable to 1997 and 1999 in the 2.5 mo before winter began. Recapture rates were lower in 1999 compared to 1998 and, when the site was first surveyed in early summer 1999, bodies of several winter-killed *R. muscosa* were observed (Pope and Matthews, unpublished data) and may have been caused by starvation (no signs of disease were observed). There may have been a delayed effect of the extraordinary 1997–1998 winter, where frogs used up fat reserves for winter survival and reproduction and then were not able to obtain enough nutrition in the shortened summer (breeding occurred in late July 1998) to survive the following winter.

This study assumes that the increased body condition of adults of *R. muscosa* in areas with abundant anuran larvae is due to increased body fat from eating more nutritious prey than in areas with fewer anuran larvae. However, we do not have direct evidence (fat body organ comparisons) that the high condition in areas with abundant anuran prey is directly reflective of increased fat body size. While acknowledging this deficiency, we believe that the development of condition models is an important noninvasive tool that can provide insight on the ecological relationships and fitness of declining or endangered amphibian populations.

This research highlights the importance of a specific prey type for adult mountain yellow-legged frogs but does not suggest that other prey types are not important. To understand the relative importance of prey, the different nutritional needs of growing young and adult frogs and the seasonal shifts in composition and abundance of prey must be considered (Donnelly, 1991). Small juvenile and subadult mountain yellow-legged frogs likely rely heavily on aquatic and terrestrial invertebrates instead of large tadpole prey due to their gape restrictions. Suitable invertebrate prey (e.g., ants, grasshoppers, wasps, butterflies, caddisflies, and mayflies) are abundant and widespread throughout the Si-

erra Nevada (Storer and Usinger, 1966) and are probably a more consistent food source for the frogs throughout summer, especially when tadpoles are not present (early and late in the summer season). However, during periods when tadpole prey are abundant, they are likely more energetically profitable (lower search and capture costs per calorie gained) for adult frogs than are invertebrates, and they provide an important supplemental food source.

Although we have observed *R. muscosa* feeding on tadpoles on numerous occasions, we have not observed this species feeding on larval *R. muscosa*. There appears to be a division between the daytime tadpole microhabitats of the different species (Matthews and Pope, unpublished data; Mullally, 1953), and we have observed adults of *R. muscosa* moving to different water bodies after breeding is completed (Pope, 1999b). These behaviors may result in a reduction in cannibalism.

This is the first study showing a relationship between the distribution and body condition of adults of *R. muscosa* and other amphibian species. Understanding this relationship may aid managers in designating successful reserve areas for *R. muscosa* and other amphibians in the Sierra Nevada. In addition to mountain yellow-legged frogs, Yosemite toads (Drost and Fellers, 1996; Sherman and Morton, 1993) and Pacific treefrogs (Matthews et al., 2001) have also declined in the high Sierra Nevada, at least partially due to the widespread introduction of nonnative fish (Knapp, 1996). Fish-free reserve areas with a range of aquatic habitats that support as many native amphibians as possible may be the only way to maintain natural aquatic food webs in the high Sierra Nevada.

Acknowledgments.—We are indebted to H. Preisler who helped with statistical analysis. We extend gratitude to 28 excellent field assistants. We thank D. Graber for permitting and encouraging this research in Kings Canyon National Park. The research was funded by the US Forest Service Pacific Southwest Research Station, US Forest Service Region 5 Ecosystem Conservation Group, and a Region 5 Fish Habitat Relationship grant.

LITERATURE CITED

- ALFORD, R. A. 1999. Ecology: resource use, competition, and predation. Pp. 240–278. *In* R. W. McDiarmid and R. Altig (Eds.), *Tadpoles: the Biology of Anuran Larvae*. University of Chicago Press, Chicago, Illinois, U.S.A.
- ANDERSON, R. O., AND S. J. GUTREUTER. 1983. Length, weight, and associated structural indices. Pp. 283–300. *In* L. A. Nielson and D. L. Johnson (Eds.), *Fisheries Techniques*. American Fisheries Society, Bethesda, Maryland, U.S.A.
- BASKERVILLE, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forest Research* 2:49–53.
- BRADFORD, D. F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. *Ecology* 64:1171–1183.
- BRADFORD, D. F., D. M. GRABER, AND F. TABATABAI. 1994. Population declines of the native frog, *Rana muscosa*, in Sequoia and Kings Canyon National Parks, California. *Southwestern Naturalist* 39:323–327.
- CLEVELAND, W. S., AND S. J. DEVLIN. 1988. Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association* 83:596–610.
- CRUMP, M. L., AND N. J. J. SCOTT. 1994. Visual encounter surveys. Pp. 84–91. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (Eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington D.C., U.S.A.
- DOCHERTY, S., P. J. BISHOP, AND N. I. PASSMORE. 1995. Calling behavior and male condition in the frog *Hyperolius marmoratus*. *Journal of Herpetology* 29:616–618.
- DONNELLY, M. A. 1991. Feeding patterns of the strawberry poison frog, *Dendrobates pumilio* (Anura: Dendrobatidae). *Copeia* 1991:723–730.
- DROST, C. M., AND G. M. FELLERS. 1996. Collapse of a regional frog fauna in the Yosemite area of the California. *Conservation Biology* 10:414–425.
- HASTIE, T., AND R. TIBSHIRANI. 1991. *Generalized Additive Models*. Chapman and Hall, London, U.K.
- HOBERT, J. P., N. S. ALTMAN, AND C. I. SCHOFIELD. 1997. Analysis of fish species richness with spatial covariate. *Journal of the American Statistical Association* 92:846–854.
- HOLLAND, V. L., AND D. J. KEIL. 1995. *California Vegetation*. Kendall/Hunt Publishing Company, Dubuque, Iowa, U.S.A.
- JØRGENSEN, C. B. 1992. Growth and reproduction. Pp. 439–466. *In* M. E. Feder and W. W. Burggren (Eds.), *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago, Illinois, U.S.A.
- KNAPP, R. A. 1996. Non-native trout in the natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. Pp. 363–390. *In* *Sierra Nevada Ecosystem Project, Final Report to Congress, Vol. 3*. Center for Water

- and Wildland Resources, University of California, Davis, California, U.S.A.
- KNAPP, R. A., AND K. R. MATTHEWS. 2000a. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conservation Biology* 14:428–438.
- . 2000b. Effects of nonnative fishes on wilderness lake ecosystems in the Sierra Nevada and recommendations for reducing impacts. Proceedings: Wilderness Science in a Time of Change, Proc. RMRS-P-00. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, U.S.A.
- LECREN, E. D. 1951. The length-weight relationship and seasonal cycle of gonad weight and condition in the perch *Perca fluviatilis*. *Journal of Animal Ecology* 32:359–365.
- LIAO, H., C. L. PIERCE, AND D. H. WAHL. 1995. Relative weight (W_r) as a field assessment tool: relationships with growth, prey biomass, and environmental conditions. *Transactions of the American Fisheries Society* 124:387–400.
- LINHART, H., AND W. ZUCCHINI. 1986. Model Selection. John Wiley & Sons, New York, New York, U.S.A.
- MATTHEWS, K. R., AND R. A. KNAPP. 1999. A study of high mountain lake fish stocking effects in the U.S. Sierra Nevada wilderness. *International Journal of Wilderness* 5:24–26.
- MATTHEWS, K. R., K. L. POPE, H. K. PREISLER, AND R. A. KNAPP. 2001. Effects of non-native trout on Pacific treefrogs (*Hyla regilla*) in the Sierra Nevada. *Copeia*:1130–1137.
- MCGURK, M. D., A. J. PAUL, K. O. COYLE, D. A. ZIEMANN, AND L. J. HALDORSON. 1993. Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasii*, larvae in an Alaska subarctic embayment. *Canadian Journal of Fish and Aquatic Science* 50: 163–180.
- MULLALLY, D. P. 1953. Observations on the ecology of the toad *Bufo canorus*. *Copeia* 1953:182–183.
- MURPHY, B. R., M. L. BROWN, AND T. A. SPRINGER. 1991. The relative weight index in fisheries management: status and needs. *Fisheries* 16:30–38.
- NEY, J. J. 1993. Practical use of biological statistics. Pp. 137–158. In C. C. Kohler and W. A. Hubert (Eds.), *Inland Fisheries Management of North America*. American Fisheries Society, Bethesda, Maryland, U.S.A.
- POPE, K. L. 1999a. *Rana muscosa*: feeding. *Herpetological Review* 30:163–164.
- . 1999b. Mountain Yellow-legged Frog Habitat Use and Movement Patterns in a High Elevation Basin in Kings Canyon National Park. M.S. Thesis, California Polytechnic State University, San Luis Obispo, California, U.S.A.
- POPE, K. L., AND K. R. MATTHEWS. 2001. Movement ecology and seasonal distribution of mountain yellow-legged frogs, *Rana muscosa*, in a high elevation Sierra Nevada basin. *Copeia* 2001:787–793.
- READING, C. J., AND R. T. CLARKE. 1995. The effects of density, rainfall and environmental temperature on body condition and fecundity in the common toad, *Bufo bufo*. *Oecologia* (Berlin) 102:453–459.
- SHERMAN, C. K., AND M. L. MORTON. 1993. Population declines of Yosemite toads in the eastern Sierra Nevada of California. *Journal of Herpetology* 27:186–198.
- STEBBINS, R. C., AND N. W. COHEN. 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, New Jersey, U.S.A.
- STORER T. I., AND R. L. USINGER. 1966. *Sierra Nevada Natural History*. University of California Press, Berkeley, California, U.S.A.
- ULTSCH, G. R., D. F. BRADFORD, AND J. FREDA. 1999. Physiology: coping with the environment. Pp. 189–214. In R. W. McDiarmid and R. Altig (Eds.), *Tadpoles: the Biology of Anuran Larvae*. University of Chicago Press, Chicago, Illinois, U.S.A.
- WEGE, G. J., AND R. O. ANDERSON. 1978. Relative weight (W_r): a new index of condition for largemouth bass. Pp. 79–91. In G. Novinger and J. Dillard (Eds.), *New Approaches to the Management of Small Impoundments*. Transactions of the American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland, U.S.A.
- ZWIEFEL, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. *University of California Publications in Zoology* 54: 207–292.

Accepted: 5 October 2001

Associate Editor: Carl Anthony