

Site fidelity of the declining amphibian *Rana sierrae* (Sierra Nevada yellow-legged frog)

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Abstract: From 1997 to 2006, we used mark–recapture models to estimate the site fidelity of 1250 Sierra Nevada yellow-legged frogs (*Rana sierrae*) in Kings Canyon National Park, California, USA, during their three main activity periods of overwintering, breeding, and feeding. To quantify site fidelity, the tendency to return to and reuse previously occupied habitats, we used multistrata models (with water bodies as the strata) and potential function analyses. The probability of returning to previously used water bodies during all activity periods was typically greater than 80% and always greater than the probability of moving to other water bodies. Site fidelity models (with lake-specific movement transitions) were favored over those models that held movement transitions equal between lakes. Potential function analyses demonstrated that frogs were most strongly attracted to their original capture lakes rather than moving to the nearest available breeding or overwintering lake. Under current disturbances in high-elevation Sierra Nevada lakes (exotic trout, climate change), site fidelity is problematic because frogs return to lakes subject to drying or those with fish rather than dispersing to other lakes. Future recovery of declining species will need to focus efforts towards restoring habitats when animals maintain strong site fidelity even when their habitats deteriorate.

Résumé : De 1997 à 2006, des modèles de marquage-recapture nous ont servi à estimer la fidélité au site de 1 250 grenouilles à pattes jaunes de la Sierra Nevada (*Rana sierrae*) dans le parc national de King's Canyon, Californie, É.-U., durant leur trois principales périodes d'activité, soit l'hivernage, la reproduction et l'alimentation. Afin de quantifier la fidélité au site, c'est-à-dire la tendance à retourner dans des habitats utilisés antérieurement et à les exploiter de nouveau, nous utilisons des modèles à strates multiples (les plans d'eau représentant les strates) et des analyses fonctionnelles potentielles. La probabilité de retourner dans un plan d'eau déjà utilisé est, dans l'ensemble des périodes d'activité, généralement de plus de 80 % et toujours plus élevée que la probabilité de se déplacer vers un autre plan d'eau. Nous préférons les modèles de fidélité au site avec des transitions de déplacement spécifiques à chaque lac aux modèles qui présupposent que les transitions de déplacement sont égales pour tous les lacs. Les analyses fonctionnelles potentielles montrent que les grenouilles sont beaucoup plus fortement attirées vers le lac de leur première capture que portées à se déplacer vers le lac le plus proche de reproduction ou d'hivernage. Dans les conditions actuelles de perturbations dans les lacs de haute altitude de la Sierra Nevada (truites exotiques, changement climatique), la fidélité au site pose des problèmes parce que les grenouilles peuvent retourner à des lacs sujets à la dessiccation ou des lacs contenant des poissons, plutôt que se disperser vers d'autres lacs. La récupération future des espèces en déclin devra concentrer ses efforts sur la restauration des habitats lorsque les animaux conservent une forte fidélité au site même quand leurs habitats se détériorent.

[Traduit par la Rédaction]

Introduction

Site fidelity, the tendency to return and reuse previously occupied habitats (Switzer 1993), occurs in a wide variety of animals including amphibians (Baker 1978). Movement and site fidelity have important ecological and evolutionary implications and are considered important life history strategies for increased survival because animals will efficiently relocate and use habitats for important activities such as breeding, feeding, and overwintering. Possible benefits of site fidelity include familiarity with winter cover, prey, predators, return routes, and specific habitat features that could lead to increased survival or reproductive success (Baker

1978). The relationship between site fidelity and increased survival or breeding success is poorly understood for amphibians. Although site fidelity might increase the efficient relocation of previously used sites, one potential problem is if the site deteriorates or has a new disturbance, then frogs could be selectively returning to inferior habitats. Ganter and Cooke (1998) predicted that site fidelity of lesser snow geese (*Chen caerulescens caerulescens*) should be reduced if their habitats deteriorate; however, they did not detect reductions in a 10-year study once habitats became degraded.

The Sierra Nevada yellow-legged frog (*Rana sierrae*) (previously called the mountain yellow-legged frog) is endemic to the Sierra Nevada and was historically a common

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inhabitant of lakes and ponds from 1400 to 3700 m (Grinnell and Storer 1924). Despite its habitat being within national park and national forest wilderness areas, *R. sierrae* has been extirpated from more than 90% of its historic localities (Drost and Fellers 1996; Jennings 1996; Vredenburg et al. 2007). It was recently found warranted but precluded for federal Endangered Species Act protection (US Fish and Wildlife Service 2003). *Rana sierrae* habitat has undergone widespread deterioration with the introduction of nonnative trout (Knapp and Matthews 2000) and other stressors such as pesticide drift from central California agriculture (Davidson and Knapp 2007). Trout introductions typically occur in large, deep lakes so that stocked fish can survive over winter. Because of the widespread introduction of trout into the larger lakes, frogs are relegated to fishless but inferior habitats such as shallow, ephemeral lakes that may dry in the summer. *Rana sierrae* breeding success depends on perennial water bodies for tadpoles and requires 3 or 4 overwintering years before metamorphosis. Thus, when breeding occurs in shallow lakes prone to summer drying, several year-classes of tadpoles die if there is no connectivity to adjacent water bodies. Many deeper lakes have been stocked with trout, which prey on all *R. sierrae* life history stages (eggs, tadpoles, and adults) (Knapp and Matthews 2000). Thus, site fidelity could be problematic for these frogs if their current breeding, feeding, and overwintering sites have deteriorated (i.e., stocked with fish or dry due to climate change).

Site fidelity is common in many organisms, but most quantitative studies have focused on birds (Hestbeck et al. 1991; Cooch et al. 1993; Lindberg and Sedinger 1998). For amphibians, many site fidelity studies are qualitative and observational and there is no consistent quantitative analysis. Nevertheless, many studies have documented breeding site fidelity in amphibians reporting that they seldom move between sites within the breeding season and typically return to same breeding lake or stream year after year (Sinsch 1990; Vasconcelos and Calhoun 2004), but little work has been done on feeding or overwintering site fidelity. Berven and Grudzien's (1990) study of marked wood frogs (*Rana sylvatica*) showed that 100% of marked adults were faithful to the ponds where they first bred. In their study, no quantitative analyses or comparisons using other sites were needed because all frogs returned to their original breeding site. Pope and Matthews (2001) reported that *R. sierrae* had different and specific overwintering, breeding, and feeding areas and showed site fidelity, but the study was only conducted for 2 years. Site fidelity may be an important strategy especially for high-elevation species such as *R. sierrae* that have a short active season (typically July–October) because breeding, feeding, and overwintering success could be improved by efficiently relocating previously used sites. Limitations of many breeding site fidelity studies include the studies being conducted over limited time periods (1–2 years) and not sampling all sites to determine whether amphibians move between sites during breeding. A consistent and quantitative way of determining site fidelity is necessary.

Multistate models are an extension of the open-population mark–recapture Cormack–Jolly–Seber models (Lebreton et al. 1992) and use mark–recapture data from multiple survey

sites to simultaneously obtain maximum likelihood estimates of encounter or recapture, survival, and movement probabilities. Recent improvements of robust estimates of movement probabilities using data from marked animals allow estimates of these probabilities from several locations (Nichols et al. 1992; Nichols and Kendall 1995) such that quantitative comparisons of probabilities of returning to or staying at sites (site fidelity) versus moving to new sites (dispersal or no site fidelity) can be made. Many quantitative studies have focused on bird and fish site fidelity (Hestbeck et al. 1991; Lindberg and Sedinger 1998), but these techniques have not been widely used in amphibian studies.

Our objective was to determine the degree of site fidelity of a population of high-elevation *R. sierrae* over a decade. We used mark–recapture surveys to examine year-to-year water body occupancy and quantified the tendency for individual frogs to return to specific water bodies during their important activity periods. We used Cormack–Jolly–Seber and multistate (strata) models (White et al. 2006) and potential function (Preisler et al. 2006) analyses of 10 years of mark–recapture data during breeding, feeding, and overwintering periods to estimate probabilities of returning to previously used locations (as an estimate of site fidelity) or moving to and being recaptured at other sites. From our mark–recapture surveys, we could directly estimate movement probabilities between the water bodies and determine whether the probability of returning to previously used water bodies is higher than being found at a new water body during each activity period.

Materials and methods

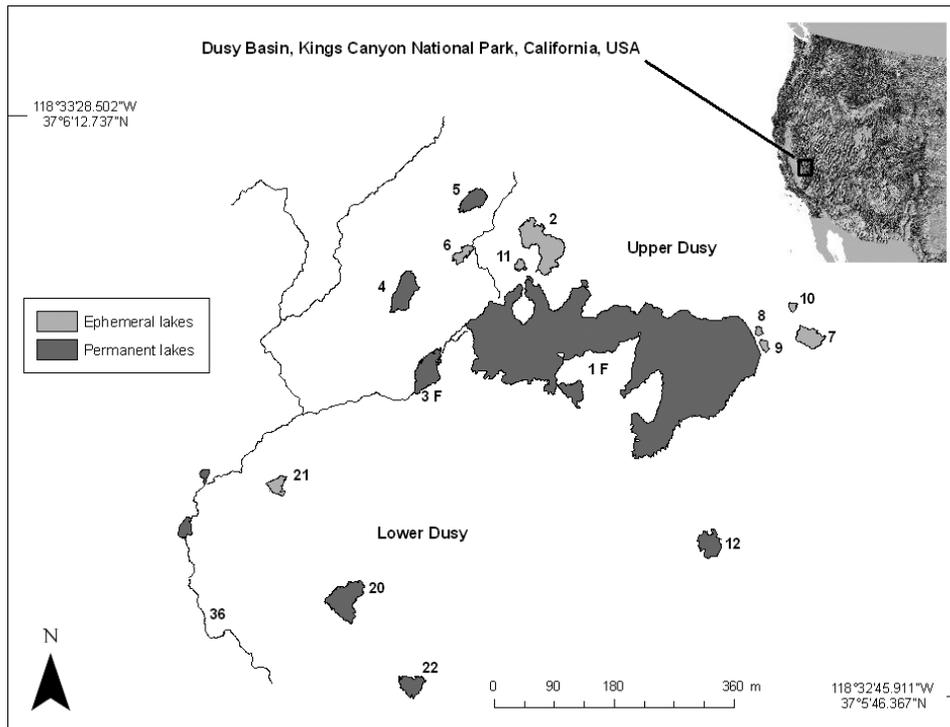
Study site and data collection

The study area was in the upper and lower Dusy Basin at an elevation of about 3470 m in Kings Canyon National Park, California (37°5'40"N, 118°33'45"W) (Fig. 1). The basin supports alpine vegetation with low-growing herbaceous plants, dwarf shrubs, and occasional whitebark pines (*Pinus albicaulis*) (Holland and Keil 1995). The general study area covers approximately 0.8 km² and includes 12 lakes and ponds and adjacent streams in upper Dusy Basin (1–12) and three lakes and adjacent stream in lower Dusy Basin (20–22) (Fig. 1).

All bodies of water within the study area were mapped (Fig. 1) using a Trimble Pro XRS GPS (global positioning system) accurate to 1 m. The largest lake (lake 1) in the basin (5.3 ha, 10 m deep) and lake 3 support a self-sustaining population of hatchery-stocked, hybrid rainbow trout–golden trout (*Oncorhynchus mykiss* × *Oncorhynchus aquabonita*), but all of the smaller neighboring ponds have no fish. In California, the National Park Service no longer allows fish stocking and is actively removing exotic trout from some water bodies.

Rana sierrae (originally *Rana muscosa*; Vredenburg et al. 2007) is endemic to the Sierra Nevada and Transverse ranges of California and Nevada (Zweifel 1955). In the Sierra Nevada, it was historically a common inhabitant of lakes and ponds at elevations of 1400–3700 m (Grinnell and Storer 1924), nearly all of which were naturally fishless. All life history stages (eggs, tadpoles, and adults) are found either in or close to water. Adults are always near water and

Fig. 1. Map of Dusy Basin study site showing lakes 1–12 in upper Dusy Basin and lakes 20–22 in lower Dusy Basin. The darker shaded lakes are deeper than 1.3 m and permanently held water year-round. The lighter shaded lakes are less than 1.3 m deep and were dry in low-snowpack years. Inset at the top right shows the location of Dusy Basin in Kings Canyon National Park, California, USA.



do not have a terrestrial phase. In addition, the aquatic larvae require two or more summers to develop and metamorphose. *Rana sierrae* larvae and adults are therefore restricted primarily to distinct habitat patches (lakes and ponds) (Bradford et al. 1993).

Captured frogs greater than 40 mm snout–vent length (SVL) were individually tagged with a passive integrated transponder (PIT) (Destron, 12 mm, 125 KHz) and we surveyed from 1997 through 2006 (no surveys in 2004). The tags have a life span of 50–100 years allowing for subsequent reidentification of tagged animals. Tags were inserted under the skin of each frog by hand through a V-shaped incision made at the sacral hump with a pair of sharp scissors. The small nick was allowed to heal without glue or closing. Recapture surveys were conducted throughout the summer by revisiting all water bodies in the study area and capturing by hand or net all frogs possible. The PIT tag number, location of capture, mass, length, and sex were recorded for each frog. Each frog was measured for SVL (millimetres) using calipers and mass (grams) was recorded using Pesola spring scales. Sex was determined by the enlarged nuptial pad at the base of the innermost finger found on males. If a frog had no nuptial pad, it was categorized as a female. Timing and number of surveys differed each year because of variable snowpack. To explore whether frogs found at lake 1 were of breeding size, we compared the sex, length, and mass of captured frogs during breeding with frogs found at lake 2.

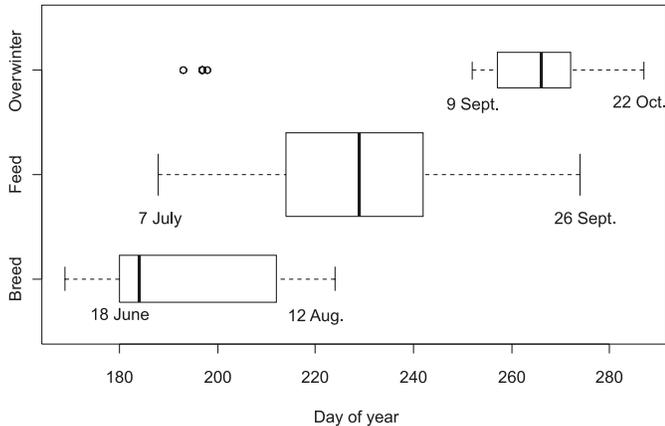
Snowpack was measured at the Bishop Pass weather station approximately 300 m from lake 20 (California Department of Water Resources; <http://cdec.water.ca.gov>) and reported for 1997–2006. The amount of snowpack influ-

enced whether some lakes dried up or underwent natural drawdown during the summer. We recorded the lake and stream water levels at the end of each summer during the 1997–2006 surveys and documented any lake drying. Another ongoing study in Dusy Basin found significantly reduced *R. sierrae* recruitment in low-snowpack years when several water bodies dried (Lacan et al. 2008).

Data analysis

We quantified site fidelity separately for each activity period defined below. Breeding, feeding, and overwintering dates varied each year due to the amount of snowpack and time of lake thawing. The active period for *R. sierrae* typically starts in early summer (late June–July) just after snowmelt and lasts until fall (October–November) when lakes start to freeze. We defined the breeding period as the period when surveyors found egg masses and amplexing frogs, typically just after the lakes thawed. We did not observe individual tagged frogs laying eggs, but there was a strong correlation between the number of frogs observed at lakes with the number of egg masses in count surveys (K.R. Matthews, unpublished data). It is unknown whether *R. sierrae* breed yearly or intermittently. We defined the feeding period as that time when egg masses were no longer found until overwintering started. Overwintering (when frogs are inactive and typically under ledges or vegetation) activity could be observed twice yearly: early in the season before breeding begins as lakes are thawing when only a few surveys were completed ($n = 3$) and after the feeding period. The overwintering period started after feeding in September or October when daytime temperatures dropped below 10 °C and frogs were more difficult to locate. The periods esti-

Fig. 2. Box plots showing the range of dates for breeding, feeding, and overwintering activity periods for the 1997–2006 study period. Bars inside a box are the median day of year, extended lines are the entire range of days, the length of a box is the interquartile range, and the width of a box is proportional to the number of observations.



dated for breeding, feeding, and overwintering are summarized for the 1997–2006 survey years in Fig. 2. Breeding times were related to the previous winter's snowpack.

From the recapture data, we summarized the tag information (individual PIT number and their length, mass, and sex) and the water bodies where frogs were recaptured during each specific activity period.

Mark–recapture models

We used open-population mark–recapture models (Cormack–Jolly–Seber; Lebreton et al. 1992) and program Mark (White et al. 2006) to obtain maximum likelihood estimates of the following probabilities: apparent survival (ϕ is the probability that a frog survives and is present at the site) and capture probability (p is probability of being captured given the animal was alive and present in the study area). We made encounter histories from the 1997–2006 surveys ($n = 1250$ individual frogs) for each individual tagged frog for 9 years (no surveys in 2004) of observed (1) or not observed (0) and whether the frog was male or female.

We tested the fit of the global starting model (Cormack–Jolly–Seber) to our mark–recapture data and estimated the amount of overdispersion or variance inflation factor (\hat{c}) using Program Release within Mark. If the goodness-of-fit test showed significant differences between the model fit and mark–recapture data, we adjusted the Akaike information criterion (AIC_c) with the \hat{c} estimates if they were less than 3.0.

We then used multistate models (Hestbeck et al. 1991; Nichols et al. 1992; Clobert 1995) and program Mark to estimate movement probabilities during specific activity periods (breeding, feeding, and overwintering). Multistate models are an extension of the Cormack–Jolly–Seber models that use mark–recapture data from marked individuals to simultaneously obtain maximum likelihood estimates of encounter or recapture, survival, and movement probabilities. Movement probability is the probability of moving between water bodies from one sampling period (survey) to the next given that the frog survives (Hestbeck et al. 1991; Lebreton

et al. 1992). We report separate analyses for breeding, feeding, and overwintering.

We first obtained maximum-likelihood estimates for three strata-specific probabilities: (i) ϕ_i^s is the probability that a frog in water body s at time i survives (i.e., and is recaptured at a later time), (ii) ψ_i^{rs} is the probability of a frog being in site s in year $i + 1$ after being seen in site r in year i and survived to year $i + 1$, and (iii) p_i^s is the probability that a marked frog alive in site (water body) s at time i is recaptured. We cannot distinguish between frogs staying at the breeding site from one year's survey to the next versus frogs that move to another site for feeding or overwintering and then return in the following year to the breeding site. We tested biologically relevant models incorporating various combinations of water body and time dependence in survival, recapture, and movement parameters. Because frog activity periods differed from year to year, the time intervals between our recapture occasions were not constant. In upper Dusy Basin, we completed 13 breeding, 31 feeding, and 16 overwintering surveys, and we often had multiple surveys for each activity period within a year. In lower Dusy Basin, we conducted 6, 18, and 10 breeding, feeding, and overwintering surveys, respectively. We pooled multiple surveys (see Hargrove and Borland 1994) from within one activity period in the multistrata analysis.

Site fidelity

Site fidelity (philopatry) was then defined as the probability of being at water body r in year $i + 1$ for frogs that were at water body r in year i and had survived to $i + 1$ (i.e., ψ_i^{rr}). Dispersal (ψ_i^{rs}) or no site fidelity would be the probability of not being at the same water body in year $i + 1$ instead being found at s . Probabilities of site fidelity estimate whether during an activity period, such as breeding, tagged frogs are more likely to be found at the same water body.

We modeled movement probabilities and tested whether movement between sites was equal or whether there was fidelity to a site by comparing models with no constraints (model $\psi_{\text{site fidelity}}$, separate transition probabilities for each pair of lakes) with a model with all movement parameters set equal (ψ_{equal} , transition probabilities between any two lakes = $1/\text{number of sites tested}$), i.e., whether the probability of returning or reusing previous sites (site fidelity) is greater than a model holding movement between all suitable sites equally probable. For model testing, we combined males and females because there were little differences in their survival, recapture, and movement. We estimated overdispersion and goodness-of-fit of our general model to the multistate mark–recapture data by estimating \hat{c} in program U-Care (Choquet et al. 2005).

For the multistate analyses, we used live encounter data from lakes commonly used for breeding, feeding, and overwintering activity periods. For the breeding analyses in upper Dusy Basin, we included lakes 1, 2, 5, and 7 because these lakes represented where most of the breeding activity occurred. We made this judgment based on count surveys of egg masses and where adult frogs were found during breeding. Count surveys conducted yearly in Dusy Basin (Lacan et al. 2008; K.R. Matthews, unpublished data) found most egg masses at lakes 2 (64%), 5 (20%), 7 (8%), and 1 (2%). Although adult frogs are commonly found at the larg-

est lake 1 during breeding periods (330 recaptures during the breeding season), egg masses were rare, presumably due to the introduced trout eating the eggs. Egg predation may be rare in other amphibians (see review by Gunzburger and Travis 2005) but we have observed trout eating *R. sierrae* eggs (K.R. Matthews, unpublished data). We included lake 1 frogs in our analyses because they may breed there even though eggs may be eaten by trout and not detected in surveys, so we wanted to assess frog fidelity. In lower Dusy Basin, we used all three lakes in the breeding analysis. For overwintering, we only used lakes 1, 4, and 5 in upper Dusy Basin where we had adequate sample sizes. During feeding periods, frogs were most numerous at lakes 1, 2, 4, 5, and 7 in upper Dusy Basin and lakes 20, 21, and 22 and stream 36 in lower Dusy Basin, and these water bodies were included in the feeding analyses. Separate analyses were done for upper and lower Dusy Basin because of the distance between the areas, and we detected little movement between upper and lower Dusy Basin. We also included distance as a covariate in analyses for all activity periods to determine if distance between lakes improved the model's ability to explain the movement probability.

For evaluating models, we used AIC_c if corrected for small sample sizes or $QAIC_c$ if corrected for overdispersion. For model selection and hypothesis testing, we relied on ΔAIC_c , a measure of each model relative to the best model in the candidate set, and AIC_c weights (Burnham and Anderson 2002). Models with the lowest values of AIC_c were retained as good candidate models. We selected models that incorporated variation in capture, survival, and movement probabilities. We report those competitive models with the lowest AIC_c that tested legitimate a priori survival and movement hypotheses but also report on the equal probability of movement models for comparison.

Potential surface model

In this section, we will further explore the effect of distance between lakes and estimate the “force of attraction” to a given lake or region during the transition period between each of the three activity periods. For example, for a frog captured at location x, y (latitude, longitude of water body midpoint) during a feeding season, how strong is the force of attraction on this frog to move to its preferred overwintering lake as opposed to the attraction to the nearest suitable overwintering lake? Here, the “preferred” lake for a frog during a given activity is the lake suitable to that activity where it was first seen. Because some frogs were captured over 300 m from their “preferred” lake, are these frogs more likely to travel over 300 m to get back to their preferred lake or is the force of attraction just as strong to the nearest suitable lake for that activity?

We estimated a surface whose gradient is assumed to be the magnitude and direction of the attraction. We used the potential function model (Brillinger et al. 2001; Preisler et al. 2004; Brillinger 2007) where the word “potential” refers to the potential of an animal or an object to move in a given direction. The model assumes that each frog is moving in a hypothetical surface, with the lowest point on the surface being the lake or region of its choice during that season. If the potential surface is flat, then the frog is not attracted to or repelled from any part of the surface; consequently,

movements will resemble a random walk. Surfaces with steeper gradients represent stronger attractions to a point or region. Potential functions have been used to model motion in Newtonian dynamics (Goldstein 1950). More recently, they have been used to describe movements of elk (Brillinger et al. 2001; Preisler et al. 2004, 2006) and elephant seals (Brillinger et al. 2007).

The statistical formulation for estimating a potential surface given successive locations of a frog is as follows. Let $\mathbf{r}_t = (x_t, y_t)$ be the coordinates of a frog at time t . We will assume that a potential surface exists that may be approximated by a smooth function of the distance between the frog and the point of attraction (e.g., center of a breeding lake). Specifically, let the potential surface be defined as

$$(1) \quad H(\mathbf{r}_t) = \beta_0 + \sum_{m=1}^M \beta_m u_t^m$$

where the distance between a frog and a point of attraction is

$$u_t = \sqrt{(x_t - a)^2 + (y_t - b)^2}$$

and where (a, b) are the coordinates of point of attraction, M is the degree of the polynomial being used, and $\beta_0, \beta_1, \dots, \beta_M$ are the intercept and slope parameters to be estimated from the movement data. The negative of the partial derivatives, $(\frac{\partial H(\mathbf{r})}{\partial x}, \frac{\partial H(\mathbf{r})}{\partial y})$, of $H(\mathbf{r})$ with respect to x and y are the expected distances traveled by the frog in the x and y directions. Assuming that the time between two captures is one unit of time, regardless of the number months or years between captures, then the distances traveled by a frog in the x and y directions are

$$(2) \quad \begin{aligned} x_t - x_{t-1} &= -u_x \sum_{m=1}^M m \beta_m u^{m-1} + \varepsilon_t \\ y_t - y_{t-1} &= -u_y \sum_{m=1}^M m \beta_m u^{m-1} + \varepsilon_t \end{aligned}$$

where $(u_x, u_y) = (\frac{x-a}{u}, \frac{y-b}{u})$ are the partial derivatives of the distance u with respect to x and y and where ε_t are random error terms. The continuous case of eq. 2 corresponds to a mean-reverting Ornstein–Uhlenbeck process (Dunn and Gipson 1977) where particles are attracted to a central point (a, b) . If all the β s in eq. 2 are zero, then the potential function (eq. 1) is equal to β_0 , which corresponds to a random walk process where particles are moving at random with no drift or attraction to a particular point.

Given a set of consecutive capture locations for a sample of frogs, the parameters β_1, \dots, β_M in eq. 2 were estimated using a linear mixed-effect regression routine (R Development Core Team 2004). A mixed-effect model with random frog effect was necessary to account for possible spatial correlations between observations on the same frog. Substituting the estimated parameter values into eq. 1 gives an estimate of the potential surface up to the constant β_0 .

During breeding season, we estimated a potential function with u equal to the distance of the frog to the midpoint of the first breeding lake where it was initially found. For the alternative hypothesis, we estimated the potential function with u equal to the distance of the frog from the nearest pos-

sible breeding lake. A similar procedure was used to decide whether a frog prefers a particular lake during the overwintering season or simply tends to go to the nearest suitable overwintering lake. During feeding season, frogs were found in most lakes and were not as selective as for breeding or overwintering. Consequently, during feeding season, we compared the model where a frog is reverting to the same region where it was captured the first time against an alternative model that assumes frogs moving randomly with no attraction to a particular region (random walk model). In terms of the parameters in eq. 1, a model is a random walk model if all of the β s except β_0 are assumed to be zero.

The “distance traveled” between captures was calculated as follows. For each frog, we calculated the step size (in the x and y directions of the water body midpoint) between consecutive captures. If the second capture was during the breeding season, then that information was used in the estimation of the potential function for the breeding season. A similar procedure was used to decide which data points are included in the estimation of the potential functions for the overwintering and feeding seasons. The AIC was used to compare different models.

Results

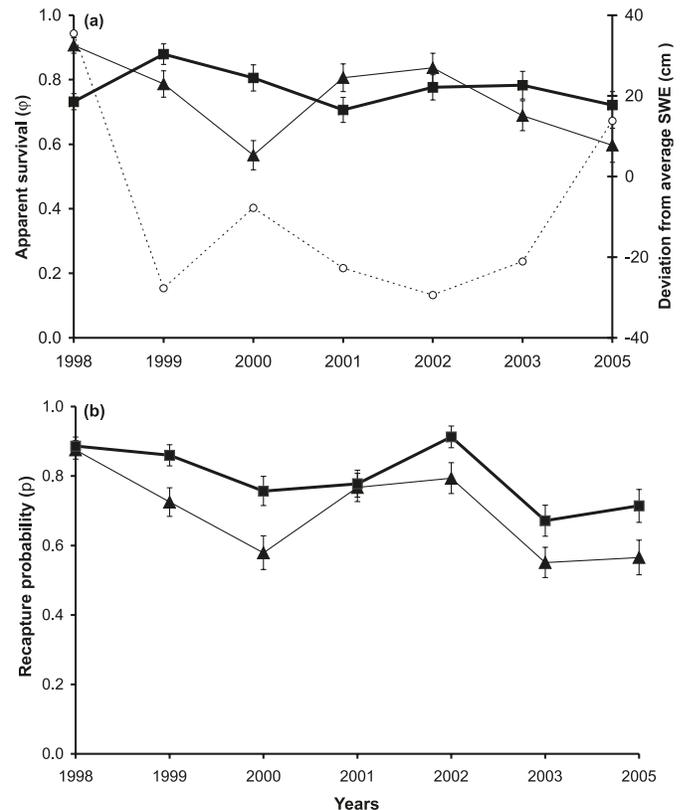
Between 1997 and 2006, we tagged 1250 frogs in upper and lower Dusky Basin; 1009 of the 1250 tagged frogs have been recaptured at least once (81%). We recaptured 1009 frogs for a total of 6877 recaptures; 851 frogs (68%) were recaptured more than 1 year (from 2 to 9 years). In upper Dusky Basin, we completed 13 breeding surveys (pooled into seven yearly surveys: 1998–2003 and 2006), 31 feeding surveys (pooled into nine yearly surveys: 1997–2003 and 2005–2006), and 16 overwintering surveys (pooled into eight yearly surveys: 1997–1998, 2000–2003, and 2005–2006). In lower Dusky Basin, we completed six breeding surveys (five years: 1998, 2001–2003, and 2006), 18 feeding surveys (nine years: 1997–2003 and 2005–2006), and 10 overwintering surveys (nine years: 1997–1998, 2000–2003, and 2005–2006).

From the capture data, we collected length ($n = 6645$ frogs) and mass ($n = 6644$). Females ($n = 3323$) ranged from 34 to 85 mm SVL and had a mean SVL = 63.5 mm. Females mass ($n = 3322$) ranged from 5 to 58 g with mean mass = 25.4 g. Males ($n = 3322$) ranged from 37 to 74 mm SVL with mean = 55.9 mm and mass ($n = 3322$) ranged from 5 to 34 g with mean = 16.8 g.

Over the 10-year study, individual frogs were found in two to six different water bodies in 51.2% of recaptures and recaptured in only one water body in 48.8% of recaptures. The longest distance moved from one observation to the next was 729 m (lake 20 in lower Dusky Basin to lake 7 in upper Dusky Basin); 11 frogs (0.008% of 1250 frogs tagged) moved between upper and lower Dusky Basin, over 500 m.

Seasonal use of different water bodies was detected from recaptures; frogs were found in more water bodies during feeding periods and in fewer during breeding and overwintering periods. Most recaptures during the overwintering period ($n = 924$) were found in lakes 1, 5, and 20. During the breeding season, over 50% of the recaptures ($n = 1795$) were found in lakes 1, 4, 5, 6, and 20. During feeding peri-

Fig. 3. (a) Estimated year-to-year apparent survival (± 1 SE) for male (triangles) and female (squares) frogs and deviation from the 1930–2006 average snow water equivalent (SWE) (circles) from 1997 to 2005 (Cormack–Jolly–Seber models). Survival estimates are not available for 2004. (b) Estimated recapture probabilities (± 1 SE) for male (triangles) and female (squares) frogs, 1997–2005 (Cormack–Jolly–Seber models). In the Cormack–Jolly–Seber models, parameters for the last transition (2005–2006) are not estimable and were not included.



ods ($n = 3785$), frogs were more dispersed than in breeding and overwintering periods and found throughout the basin in the greatest number of lakes, with over 50 recaptures in 16 water bodies.

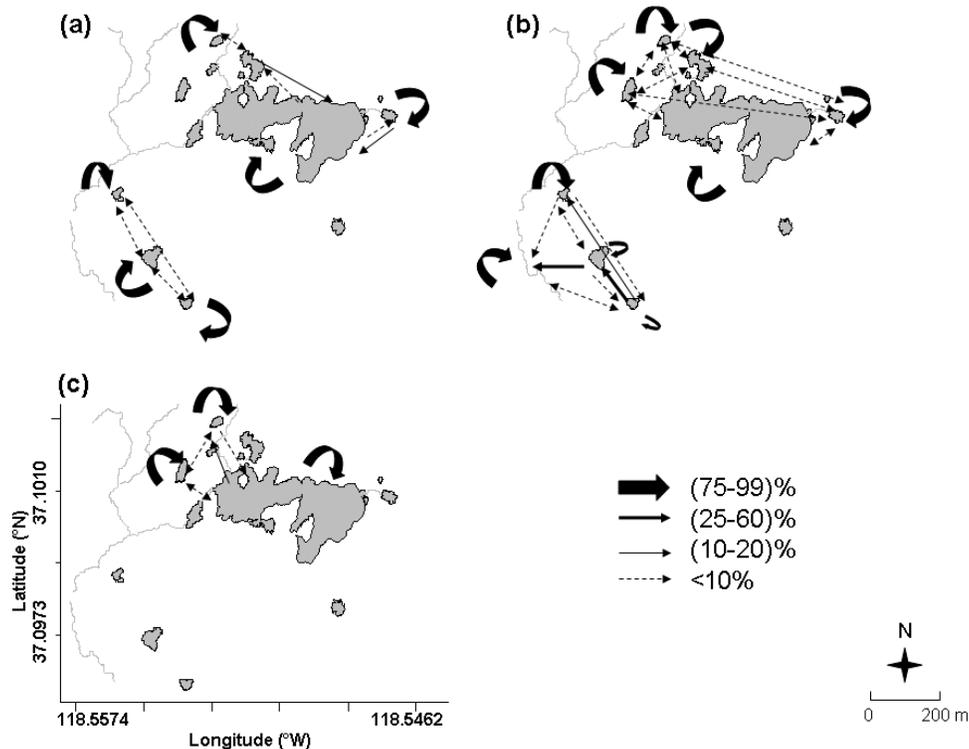
To explore whether the frogs found at lake 1 were of breeding sizes, we compared the sex, length, and mass of captured frogs during breeding with those of frogs found at lake 2 during the same surveys. The 174 individual frogs (91 females and 83 males) recaptured at lake 1 were smaller than the 194 individuals (94 females and 100 males) caught at lake 2. Lake 1 females were 62.4 mm SVL (range 45–81 mm) and males were 56.7 mm SVL (range 42–64 mm) and average female mass was 21.6 g (range 6–54 g) and average male mass was 16.1 g (range 7–27 g). In comparison, during breeding surveys, females in lake 2 were 67.7 mm SVL (range 47–82 mm) and males were 59.0 mm SVL (range 42–71 mm); average mass was 26.9 g (range 8–40 g) for females and 18.0 g (range 7–27 g) for males.

Year-to-year (1997–2005, the last transition 2005–2006 was not estimable) apparent survival probabilities (Cormack–Jolly–Seber models in program MARK) were similar (overall mean = 0.74) for males (mean = 0.74 \pm 0.042 SE) and females (mean = 0.75 \pm 0.037 SE) (Fig. 3a). We

Table 1. Akaike information criterion corrected for overdispersion (QAIC_c, $\hat{c} = 2.7$), Δ QAIC_c, QAIC_c weights, and number of parameters (*K*) used to estimate apparent survival (ϕ), capture probability (*p*), and snowpack from all surveys conducted, 1997–2006.

Model		QAIC _c	Δ QAIC _c	QAIC _c weight	<i>K</i>
$\phi_t p_t$	General model: survival and recapture varied with time	1148.2	0	0.41	17
$\phi_t p_{t+\text{snowpack}}$	Survival and recapture varied with time, recapture includes snowpack	1149.8	1.6	0.40	18
$\phi_{t+\text{snowpack}} p_{t+\text{snowpack}}$	Survival and recapture varied with time and snowpack	1150.2	2.0	0.14	19
$\phi_{t+\text{snowpack}} p_t$	Survival and recapture varied with time, survival includes snowpack	1152.2	4.1	0.05	18

Fig. 4. Map summarizing probabilities of lake to lake movement transitions for upper (lakes 1, 2, 5, and 7) and lower (lakes 20, 21, and 22) Dusy Basin during (a) breeding, (b) feeding, and (c) overwintering. Curved arrows depict movement back to that lake. The largest return arrows depict movement transitions (ψ) of 75%–99%, medium solid arrows of 25%–60%, small solid arrows of 10%–20%, and broken line arrows of <10%.



combined males and females in the models because their survival estimates were similar. Survival declined over two periods: 1999–2000 survival dropped to 0.56 for males and 0.70 for females and 2003–2005 (no surveys in 2004) dropped to below 0.60 for both males and females. Adult survival did not appear to be affected by low snowpack (Fig. 3a). We used goodness-of-fit to test whether the global model was a reasonable fit to the mark–recapture data; the global model was rejected by the goodness-of-fit test ($\chi^2 = 54.2209$, *df* = 20, *p* = 0.0001). However, the variance inflation factor ($\hat{c} = 2.7$) indicated minor overdispersion, so we used \hat{c} to adjust all parameter estimates (QAIC_c) (Table 1). Survival was average and ranged from 0.68 to 0.83 in the years with lowest snowpack, and incorporating snowpack as a covariate did not improve the models’ ability to account for survival (Table 1). Overall recapture probabilities were slightly higher for females (mean = 0.80 ± 0.030 SE) than for males (mean = 0.70 ± 0.042 SE) (Fig. 3b).

PIT tags did not seem to affect frog survival adversely: after the first year of tagging, we recaptured 87% of the

390 frogs tagged in 1997, suggesting that the PIT tags were not shed and they were not harming the frogs. We did not double-tag the frogs, which would have given more information to determine tag loss, as we were concerned about the impact to frogs. Forty-four frogs of the 390 originally tagged in 1997 (11.3%) were recaptured in 2006; these frogs were at least 10 years old.

Snowpack collected at the Bishop Pass site showed considerable variation during the study period; 5 of the 10 years had lower than average (1930–2006) snowfall (Fig. 3a); 2006 snowfall (not in the figure) was 29.6 cm higher than average. Most lakes held water by the end of the summer but lakes 2 and 7–9 were dry by the end of the summer in the lowest snowpack years. Lake 2, where most of the egg masses were found, was dry in 5 of the 10 study years.

Site fidelity

From the multistate analyses, we found that site fidelity was high for breeding, feeding, and overwintering: the movement probability (ψ) of being found at the same lake (site fidelity) was always higher than the probability of

Table 2. Akaike information criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (*K*) used to examine movement probabilities (ψ), apparent survival (ϕ), and capture probability (*p*) during breeding periods (*n* = 13 surveys for 1998–2006 pooled into seven yearly surveys: 1998–2003 and 2006) in upper Dusy Basin at lakes 1, 2, 5, and 7 for male and female frogs combined.

Model	Description	AIC _c	ΔAIC _c	AIC _c weight	<i>K</i>
$\psi_g p_g \phi_g$	General model, all strata different, constant over time	1184.7	0.0	0.96	20
$\Psi_g p \phi_g$	Constant recapture, group differences in movement and survival	1192.1	7.41	0.02	17
$\psi_{g \times \text{distance}} p_g \phi_g$	General model, all strata different, constant over time, movement dependent on distance between lakes	1192.5	7.8	0.01	21
$\psi_g p_g \phi$	Constant survival, group/strata differences in movement and recapture	1204.0	19.3	0.001	17
$\psi_g p \phi$	Constant survival and recapture, group/strata difference in movement	1211.4	26.7	0.0	14
$\psi_{0.25} p_g \phi_g$	Movement set equal for all lakes = 0.25, group/strata differences in recapture and survival	1361.4	176.7	0.0	9
$\psi p_g \phi_g$	Constant movement, group/strata differences in survival and recapture	1376.8	192.1	0.0	9

Table 3. Akaike information criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (*K*) used to examine movement probabilities (ψ), apparent survival (ϕ), and capture probability (*p*) during breeding periods (*n* = 6 surveys pooled into five yearly surveys: 1998, 2001–2003, and 2006) in lower Dusy Basin at lakes 20, 21, and 22 for male and female frogs combined.

Model	Description	AIC _c	ΔAIC _c	AIC _c weight	<i>K</i>
$\psi_g p_g \phi_g$	General model, all strata different, constant over time	80.6	0.0	0.34	12
$\psi_g p \phi_g$	Constant recapture, group/strata differences in movement and survival	81.1	0.5	0.27	10
$\psi_g p_g \phi$	Constant survival, group/strata differences in movement and recapture	81.6	0.9	0.22	10
$\psi_{g \times \text{distance}} p_g \phi_g$	General model, all strata different, constant over time, movement dependent on distance between lakes	82.9	2.2	0.11	13
$\psi p_g \phi_g$	Constant movement, strata differences in survival and recapture	90.0	10.35	0.002	7
$\psi_{0.33} p_g \phi_g$	Movement set equal for all lakes = 0.33, group/strata differences in recapture and survival	91.8	11.1	0.001	7

Table 4. Akaike information criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (*K*) used to examine movement probabilities (ψ), apparent survival (ϕ), and capture probability (*p*) during feeding periods (*n* = 31 surveys for 1997–2006 pooled into nine yearly surveys: 1997–2003 and 2005–2006) in upper Dusy Basin at lakes 1, 2, 4, 5, and 7 for male and female frogs combined.

Model	Description	AIC _c	ΔAIC _c	AIC _c weight	<i>K</i>
$\psi_g p_g \phi_g$	General model, all strata different, constant over time	2275.6	0.0	0.92	30
$\psi_g p \phi_g$	Constant recapture, group/strata differences in movement and survival	2280.5	4.9	0.08	27
$\psi_{g \times \text{distance}} p_g \phi_g$	General model, all strata different, constant over time, movement dependent on distance between lakes	2304.1	28.5	0.0	31
$\psi_g p_g \phi$	Constant survival, group/strata differences in movement and recapture	2304.4	28.8	0.0	26
$\psi_{0.20} p_g \phi_g$	Movement set equal for all lakes = 0.20, group/strata differences in recapture and survival	3198.3	922.74	0.0	11
$\psi p_g \phi_g$	Constant movement, group/strata difference in survival and recapture	3199.4	923.8	0.0	11

being found at other lakes (Fig. 4). Once frogs were caught during breeding surveys in upper Dusy Basin at the commonly used lakes (1, 2, 5, or 7), the probability of being found there again in subsequent breeding surveys was always higher than being found at another lake (ψ ranged from 0.78 ± 0.048 SE to 0.86 ± 0.078 SE) (Fig. 4a). For example, when examining lake 2 recaptures from the 1998–2006 breeding surveys, we found that the probability was higher ($\psi = 0.80 \pm 0.048$ SE) that frogs would be recaptured in subsequent surveys at lake 2 compared with the probability of being found at the other suitable breeding lakes (1, 5, or 7) (ψ ranged from 0.01 ± 0.019 SE to 0.16 ± 0.048 SE) for each possibility of moving from lake 2 to lake 1, 5, or 7 (Fig. 4a). A similar pattern of higher probabilities (and high site fidelity) was observed for tagged frogs during breeding in lower Dusy Basin lakes, feeding periods at both lower and upper Dusy Basin, and during overwintering at upper Dusy Basin (Figs. 4a–4c). Because most frogs were found

at only three lakes during overwintering surveys, we compared movement probabilities for lakes 1, 4, and 5. We again found that the probability was higher for $1 > 1$ transition ($\psi = 0.87 \pm 0.103$ SE), $4 > 4$ ($\psi = 0.99 \pm 0.0001$ SE), and $5 > 5$ ($\psi = 0.92 \pm 0.068$ SE) compared with movement probabilities to other water bodies ($\psi < 0.20 \pm 0.00001$ – 0.068 SE). The low sample sizes at lower Dusy Basin during overwintering surveys precluded analyses.

Multistate general models were assessed (U-Care) to determine their fit to the mark–recapture data during each activity period. All variance inflation factors (\hat{c}) were less than 1, and goodness-of-fit tests reported no significant difference ($p > 0.05$) between the general models and the mark–recapture data, so no adjustments of AIC_c were necessary.

When examining multistate movement models as a function of apparent survival, recapture, year, site (water body), and distance, the most plausible models (those with the lowest AIC_c values and highest Akaike AIC_c weights) were

Table 5. Akaike information criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) used to examine movement probabilities (ψ), apparent survival (φ), and capture probability (p) during feeding periods (n = 18 surveys pooled into nine yearly surveys: 1997–2003 and 2005–2006) in lower Dusy Basin at lakes 20, 21, and 22 and stream 36 for male and female frogs combined.

Model	Description	AIC _c	ΔAIC _c	AIC _c weight	K
$\psi_g p_g \phi_g$	General model, all strata different, constant over time	688.3	0.0	0.5	20
$\psi_g p_g \phi$	Constant survival, group/strata differences in movement and recapture	688.5	0.12	0.48	17
$\psi_{g \times \text{distance}} p_g \phi_g$	General model, all strata different, constant over time, movement dependent on distance between lakes	694.8	6.5	0.02	21
$\psi_g p \phi_g$	Constant recapture, group/strata differences in movement and survival	697.1	8.8	0.01	17
$\psi_g p \phi$	Constant recapture and survival, group/strata difference in movement	698.6	10.3	0.0	14
$\psi p_g \phi_g$	Constant movement	767.4	79.0	0.0	9
$\psi_{0.25} p_g \phi_g$	Movement set equal for all lakes = 0.25, group/strata differences in recapture and survival	771.2	82.8	0.0	9

Table 6. Akaike information criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) used to examine movement probabilities (ψ), apparent survival (φ), and capture probability (p) during overwintering periods (n = 16 surveys pooled into seven yearly surveys: 1997–1998, 2000–2003, and 2005–2006) in upper Dusy Basin at lakes 1, 4, and 5 for male and female frogs combined.

Model	Description	AIC _c	ΔAIC _c	AIC _c weight	K
$\psi_g p_g \phi_g$	General model, all strata different, constant over time	128.5	0.0	0.55	12
$\psi_{g \times \text{distance}} p_g \phi_g$	General model, all strata different, constant over time, movement dependent on distance between lakes	129.5	1.1	0.33	13
$\psi_g p_g \phi$	Constant survival, group/strata differences in movement and recapture	130.5	2.0	0.17	10
$\psi_g p \phi_g$	Constant recapture, group/strata differences in movement and survival	132.6	4.2	0.06	10
$\psi_g p \phi$	Constant recapture and survival, group/strata difference in movement	133.4	4.9	0.04	8
$\psi_{0.25} p_g \phi_g$	Movement set equal for all lakes = 0.33, group/strata differences in recapture and survival	144.2	15.7	0.0	7
$\psi p_g \phi_g$	Constant movement	161.2	32.7	0.0	7

Table 7. Estimated Akaike information criterion statistics for two models and three seasons tested in the potential function analyses.

	Season		
	Breeding	Feeding	Overwintering
Model 1	21 967	60 399	10 725
Model 2	25 188	61 848	13 756

Note: Model 1 uses distance to site where a frog was first captured during that season. Model 2 uses distance to the nearest lake for the breeding and overwintering seasons and no distance for feeding season.

those where movement was site specific (i.e., different for each water body to water body transition) and where time was held constant (Tables 2–6). Including distance as a variable did not improve the models (Tables 2–6) during any activity period tested. The least plausible models in the set held movement probabilities constant and set movement transitions equal (i.e., no site fidelity) (Tables 2–6).

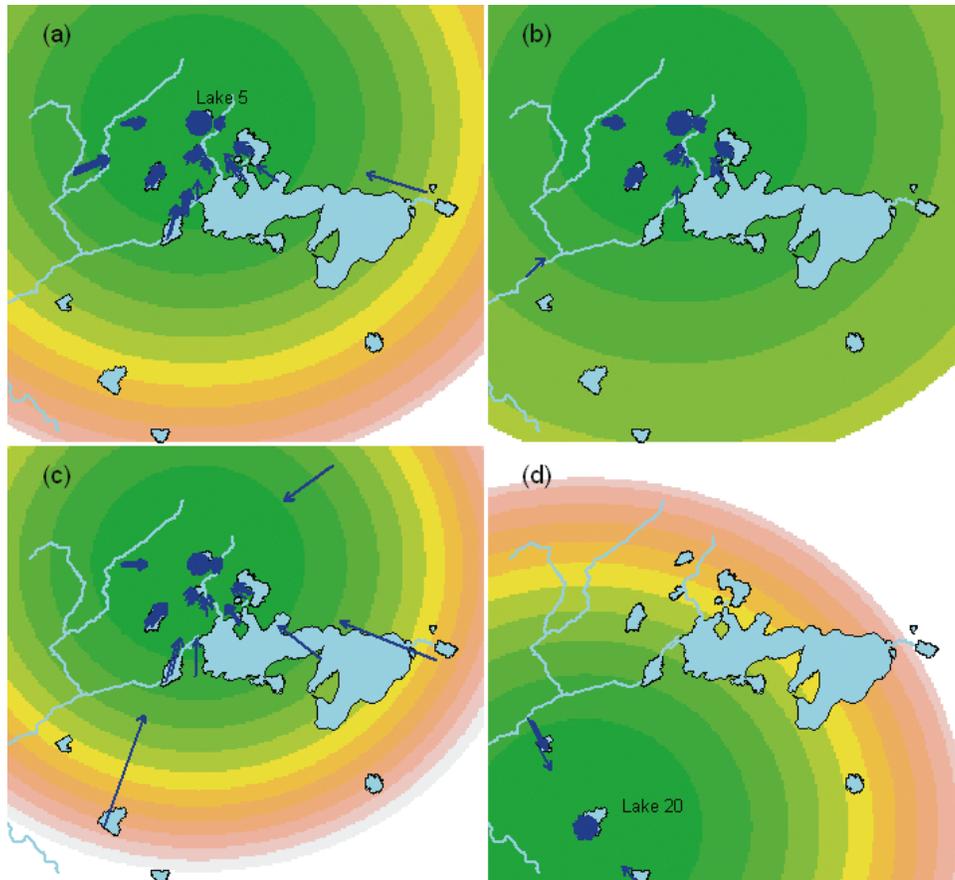
For all activity periods, the best supported models (lowest AIC_c values and highest AIC_c weights) were those that had lake-specific survival, recapture, and movement (Tables 2–6). The contribution of survival and recapture probabilities (apparent survival ranged from 0.46 to 0.91) to movement models differed for activity and sites (Tables 2–6). Holding survival and recapture probabilities constant generally did not improve the models’ ability to explain the different movement transitions.

Overall model selection showed the most support for site-specific movement when compared with movement transitions being held equal or constant. We compared a fidelity

model with no constraints on movement (i.e., movement probabilities varied depending on site to site transitions) with a model with all movement parameters set equal (1/ number of sites tested). For breeding, we compared movement between the most commonly used breeding lakes (1, 2, 5, and 7) and the model with no site constraints had the lowest AIC_c values (Table 2) and the highest AIC_c weight (0.96). The model with ψ set equal for the four sites (0.25) had the highest AIC_c values and an AIC_c weight of zero. Therefore, the model with equal movement probabilities had the least support from the data. Similar tests were conducted for all other activity periods in lower and upper Dusy Basin with the same result (Tables 2–6).

In the potential function analysis, we further explored site fidelity by testing if a potential surface with a point of attraction being the lake where a frog was initially captured was a better fit than a potential surface with the point of attraction being the nearest suitable breeding, feeding, or overwintering water body. For breeding and overwintering, models that had frogs moving the distance to the original capture site (even when distance was greater than moving to another closer, suitable breeding lake) gave a better fit than those using distance to the nearest lake appropriate for that activity (Table 7). This stronger attraction (site fidelity) is seen in the potential surfaces evaluated for each season and for a specific lake (Fig. 5). The potential surfaces for breeding and overwintering seasons seem to indicate that frogs were attracted to the lake where they had been originally captured (in this case, lake 5). During the feeding season, the attraction to any given region seems minimal as indicated by the almost flat potential surface. Thus, the po-

Fig. 5. Estimated potential surfaces for (a) breeding, (b) feeding, and (c) overwintering seasons for frogs that were initially captured in lake 5 and (d) those initially captured during breeding at lake 20. Estimated movement arrows (each arrow is a recapture), plotted for actual locations of frogs captured during preceding season, demonstrate the “strength” and direction of movement. The lengths of the arrows indicate the “strength” of a hypothetical force of attraction on a frog towards its preferred site for the upcoming season. Steeper surfaces (green is the flattest and orange the steepest) indicate stronger attraction to the lowest point on the surface. The estimates were evaluated up to a distance of 600 m from the lake, the maximum observed distance between captures for the overwintering season.



tential function analysis indicated that frogs are most strongly attracted to their original site for overwintering and breeding and have less attraction to the original site during the feeding season.

Discussion

Over this 10-year study, *R. sierrae* exhibited strong site fidelity and high probability of returning to previously used sites, especially for breeding and overwintering. Pilliod et al. (2002) noted that site fidelity might be fairly typical in landscapes that offer few suitable areas in winter and breeding periods, such as at high altitudes or latitudes where some lakes can remain completely frozen for more than 9 months each year. Multistate models and potential function analyses provided quantitative assessments of movement and site fidelity for *R. sierrae* and will be useful for other amphibian site fidelity studies. The strength of these analyses is the ability to quantify and model the tendency of frogs to return to lakes and compare this with other dispersal possibilities. The advantages of site fidelity in many species are well described (Baker 1978; Sinsch 1990; Duellman and Trueb 1994), suggesting that benefits exist for returning to previ-

ously used sites. Multistate and potential function analyses offer a robust way to use longer-term mark–recapture data to quantify site fidelity and provide a consistent manner to quantify site fidelity.

Our study demonstrated that *R. sierrae* has strong site fidelity, which is usually an effective life history strategy that maximizes an animal’s ability to efficiently relocate important habitats. However, site fidelity to degraded habitats may be further stressing *R. sierrae* populations throughout the Sierra Nevada. Presumably, this life history strategy was advantageous before fish were introduced into the high-elevation Sierra Nevada ecosystems. Introduced exotic fish are now a dominant predator in many basins throughout the Sierra Nevada (Knapp and Matthews 2000). *Rana sierrae* also exhibited high site fidelity for lakes that dry after low-snowpack years (Lacan et al. 2008) even though they require perennial water for successful tadpole development, which can take up to 4 years. When a lake dries, then up to four year-classes of tadpoles are lost. It is currently unknown whether *R. sierrae* is also breeding in lakes prone to drying throughout the Sierra Nevada and should be the topic of future research. Historically, frogs presumably bred in many lake types throughout the basin, and low survival in

lakes that dry would be offset by recruitment from larger lakes not subject to drying. Currently, the largest, deepest lake not susceptible to drawdown or snowpack variability is unfavorable for successful breeding because of exotic trout. Frogs are presumably breeding in lake 1 but low survival due to trout predation renders this lake unimportant for breeding, especially considering that this is the largest lake in the basin. It is not known at what age and size *R. sierrae* begins breeding. However, recent metamorphs typically range from 20–40 mm SVL and at that size, sex cannot be determined (no nuptial pads) (Matthews and Miaud 2007). A reasonable estimate would be that frogs might start breeding at around 40 mm SVL when nuptial pads are detectable. Frogs are smaller and possibly younger at lake 1, but based on the length and mass measurements, they range in age from 2 to 10 years (Matthews and Miaud 2007), so would be considered of breeding size. Some frogs are breeding in lake 1 because we did find some egg masses and tadpoles but substantially fewer than in lakes 2, 5, and 7.

Breeding in ephemeral ponds may have been successful historically when the larger fish-free lakes provided recruitment opportunities to offset recruitment failures in low-snowpack years when ephemeral lakes dry and tadpoles do not survive (Lacan et al. 2008). Current breeding site fidelity to ephemeral ponds and lakes with fish will likely result in further population declines of this imperiled frog. The most commonly used breeding site (lake 2) in upper Dusy Basin is now a sink habitat (Pulliam 1988) where many age-classes of tadpoles (2–3 years) are lost each time the lake dries. This breeding lake can produce substantial recruitment of *R. sierrae* but only when it experiences 3–4 years of above-average snowpack (Lacan et al. 2008). Reproductive surpluses from productive source habitats can sustain sink habitats where local recruitment fails to keep pace with mortality (Pulliam 1988). However, due to exotic trout in the largest lake and repeated drying of fish-free lakes, upper Dusy Basin currently has no source habitat for breeding. Many studies have concluded that amphibian eggs are unpalatable to trout (Gunzburger and Travis 2005); however, in Dusy Basin, we have observed trout eating egg masses (K.R. Matthews, unpublished data). Also, restoration projects have removed nonnative trout from lakes in the Sierra Nevada and *R. sierrae* adults and tadpole abundance quickly increased, indicating that trout have been limiting frog populations (Knapp et al. 2007).

One implication of maintaining site fidelity in deteriorating habitats is the possible decline due to increased mortality from overwintering in a lake with trout and decreased recruitment from breeding at a lake that often dries. Over time, site fidelity to degraded habitats could result in local extirpation. Before fish were introduced, Dusy Basin frog abundance was likely much higher. Surveys of lakes and basins in the Sierra Nevada (Knapp and Matthews 2000; Knapp et al. 2001) found the highest abundance and densities of *R. sierrae* in areas with no fish. Once fish were introduced, ongoing fidelity to both overwintering and breeding lakes has likely reduced the overall Dusy Basin population. Future restoration plans in Dusy Basin will remove nonnative trout and the frog abundance will likely increase, similar to other fish removal projects (Knapp et al. 2007). In contrast, if *R. sierrae* had no site fidelity, then

after habitat changes, frogs could increase survival over time by dispersing and breeding in lakes not prone to drying and overwintering in lakes without fish. Maintaining site fidelity to disturbed and deteriorating habitats is a reason why some have suggested that this life history strategy could be maladaptive (Levin et al. 1984). Ganter and Cooke (1998) predicted that lesser snow geese site fidelity would decrease after their habitats became deteriorated but did not observe a decline over their long-term study. They speculated that site fidelity has always been a better strategy because relocating has too many risks and that longer time periods may be required before a change in site fidelity occurs in altered habitats. In contrast, Schlupp and Podlucky (1994) reported that common toads (*Bufo bufo*) with strong site fidelity could change their behavior and become attached to a substitute breeding pond by using barriers to their old sites. Switzer (1997) found that past reproductive success influenced site fidelity and speculated that dragonflies might have sensitivity to disturbed sites and chose to change sites.

Annual *R. sierrae* recapture rates were high (0.55–0.91), presumably indicating high survival, low emigration out of the basin and the tendency to be in or near water making them easy to find and recapture. Only recently have researchers been using more quantitative assessments of survival and recapture probabilities of amphibians (Wood et al. 1998; Sagar et al. 2007) over multiple years, so it is difficult to make comparisons. Apparent survival rates were also high (0.52–0.90) and not affected by low-snowpack years; low snowpack primarily affects larval stages during the summer when lakes dry and tadpoles die (Lacan et al. 2008). Long winters and heavy snowpack also did not result in lower adult survival as was predicted in other studies (Bradford 1983; Corn 2003).

Understanding and incorporating site fidelity into future restoration strategies will be crucial. It is important to restore at least some basins to historical status and remove fish so that breeding and overwintering sites can offer survival for all life history stages. Restoration projects in Kings Canyon National Park and elsewhere have already begun removing nonnative trout (Knapp et al. 2007), and future plans may allow the removal of trout from Dusy Basin. Future studies will reveal if site fidelity remains strong and breeding success returns when trout are removed. While there is some evidence of finding trout and *R. sierrae* co-occurring, it is uncommon and typically is found when trout abundance is low. The low probability of being found at other lakes (i.e., dispersal) indicates that once frogs breed in a lake, regardless of success, in future years, they will likely return even if the lake may ultimately dry. Conservation strategies for this imperiled amphibian require restoring the ecological integrity of these high-elevation aquatic ecosystems so that site fidelity is once again a strategy for survival.

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References

- Baker, R.R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London, U.K.
- Berven, K.A., and Grudzien, T.A. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution*, **44**(8): 2047–2056. doi:10.2307/2409614.
- Bradford, D.F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. *Ecology*, **64**(5): 1171–1183. doi:10.2307/1937827.
- Bradford, D.F., Tabatabai, F., and Graber, D.M. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conserv. Biol.* **7**(4): 882–888. doi:10.1046/j.1523-1739.1993.740882.x.
- Brillinger, D.R. 2007. Learning a potential function from a trajectory. *IEEE Signal Process. Lett.* **14**(11): 867–870. doi:10.1109/LSP.2007.900032.
- Brillinger, D.R., Preisler, H.K., Ager, A.A., and Kie, J. 2001. The use of potential functions in modelling animal movement. *In* Data analysis from statistical foundations. Edited by A.K.Md.E. Saleh. Nova Science Publishers, Inc., Huntington, N.Y. pp. 369–386.
- Brillinger, D.R., Stewart, B., and Littnan, C. 2007. Three months journeying of a Hawaiian monk seal. *IMS Collect. Prob. Stat.* **2**: 246–264. doi:10.1214/193940307000000473.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O., and Pradel, R. 2005. U-Care users's manual. CEFE, Montpellier, France. Available from <http://www.cefe.cnrs.fr/biom/pdf/Choquet-USER%20MANUAL%20U-CARE%202.2.pdf>.
- Clobert, J. 1995. Capture–recapture and evolutionary ecology: a difficult wedding? *J. Appl. Stat.* **22**(5–6): 989–1008. doi:10.1080/02664769524757.
- Cooch, E.G., Jefferies, R.L., Rockwell, R.F., and Cooke, F. 1993. Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia (Berl.)*, **93**(1): 128–138.
- Corn, P.S. 2003. Amphibian breeding and climate change: the importance of snow in the mountains. *Conserv. Biol.* **17**(2): 622–625. doi:10.1046/j.1523-1739.2003.02111.x.
- Davidson, C., and Knapp, R.A. 2007. Multiple stressors and amphibian declines: dual impacts of pesticides and fish on yellow-legged frogs. *Ecol. Appl.* **17**(2): 587–597. doi:10.1890/06-0181. PMID:17489262.
- Drost, C.M., and Fellers, G.M. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. *Conserv. Biol.* **10**(2): 414–425. doi:10.1046/j.1523-1739.1996.10020414.x.
- Duellman, W.E., and Trueb, L. 1994. Biology of amphibians. Johns Hopkins University Press, Baltimore, Md.
- Dunn, J.E., and Gipson, P.S. 1977. Analysis of radio telemetry data in studies of home range. *Biometrics*, **33**(1): 85–101. doi:10.2307/2529305.
- Ganter, B., and Cooke, F. 1998. Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of lesser snow geese. *Auk*, **115**(3): 642–652.
- Goldstein, H. 1950. Classical mechanics. Addison-Wesley, New York.
- Grinnell, J., and Storer, T.I. 1924. Animal life in the Yosemite. University of California Press, Berkeley, Calif.
- Gunzburger, M.S., and Travis, J. 2005. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. *J. Herpetol.* **39**(4): 547–571. doi:10.1670/1-05A.1.
- Hargrove, J.W., and Borland, C.H. 1994. Pooled population parameter estimates from mark–recapture data. *Biometrics*, **50**(4): 1129–1141. doi:10.2307/2533449. PMID:7786993.
- Hestbeck, J.B., Nichols, J.D., and Malecki, R.A. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. *Ecology*, **72**(2): 523–533. doi:10.2307/2937193.
- Holland, V.L., and Keil, D.J. 1995. California vegetation. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- Jennings, M.R. 1996. Status of amphibians. *In* Sierra Nevada ecosystem project: final report to Congress. II:31. Centers for Water and Wildland Resources, University of California, Davis, Calif. pp. 921–944. Available from <http://ceres.ca.gov/snep/pubs/v2s3.html>.
- Knapp, R.A., and Matthews, K.R. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conserv. Biol.* **14**(2): 428–438. doi:10.1046/j.1523-1739.2000.99099.x.
- Knapp, R.A., Matthews, K.R., and Sarnelle, O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecol. Monogr.* **71**(3): 401–421.
- Knapp, R.A., Boiano, D.M., and Vredenburg, V.T. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). *Biol. Conserv.* **135**(1): 11–20. doi:10.1016/j.biocon.2006.09.013. PMID:17396156.
- Lacan, I., Matthews, K.R., and Feldman, K.V. 2008. Interaction of an introduced predator with future effects of climate change in the recruitment dynamics of the imperiled Sierra Nevada Yellow-legged Frog (*Rana sierrae*). *Herpetol. Conserv. Biol.* **3**(2): 211–223.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**(1): 67–118. doi:10.2307/2937171.
- Levin, S.A., Cohen, D., and Hastings, A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* **26**(2): 165–191. doi:10.1016/0040-5809(84)90028-5.
- Lindberg, M.S., and Sedinger, J.S. 1998. Ecological significance of brood-site fidelity of black brant: annual, spatial, and age-related variation. *Auk*, **115**(2): 436–446.
- Matthews, K.R., and Miaud, C. 2007. A skeletochronological study of the longevity and age structure of the mountain yellow-legged frog, *Rana muscosa*, in the Sierra Nevada. *Copeia*, **2007**(4): 984–991.
- Nichols, J.D., and Kendall, W.L. 1995. The use of multi-state capture–recapture models to address questions in evolutionary ecology. *J. Appl. Stat.* **22**(5–6): 835–846.
- Nichols, J.D., Sauer, J.R., Pollock, K.H., and Hestbeck, J.B. 1992. Estimating transition probabilities for stage-based population projection matrices using capture–recapture data. *Ecology*, **73**(1): 306–312. doi:10.2307/1938741.
- Pilliod, D.S., Peterson, C.R., and Ritson, P.I. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. *Can. J. Zool.* **80**(11): 1849–1862. doi:10.1139/z02-175.
- Pope, K.L., and Matthews, K.R. 2001. Movement ecology and seasonal distribution of mountain yellow-legged frogs, *Rana muscosa*, in a high-elevation Sierra Nevada basin. *Copeia*, **2001**(3): 787–793. doi:10.1643/0045-8511(2001)001[0787:MEASDO]2.0.CO;2.
- Preisler, H.K., Ager, A.A., Johnson, B.K., and Kie, J.G. 2004. Modelling animal movements using stochastic differential equations. *Environmetrics*, **15**(7): 643–657. doi:10.1002/env.636.
- Preisler, H.K., Ager, A.A., and Wisdom, M.J. 2006. Statistical

- methods for analyzing responses of wildlife to human disturbance. *J. Appl. Ecol.* **43**(1): 164–172. doi:10.1111/j.1365-2664.2005.01123.x.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* **132**(5): 652–661. doi:10.1086/284880.
- R Development Core Team. 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from www.R-project.org.
- Sagar, J.P., Olson, D.H., Schmitz, R.A., and Beaupre, S.J. 2007. Survival and growth of larval coastal giant salamanders (*Dicamptodon tenebrosus*) in streams in the Oregon Coast Range. *Copeia*, **2007**(1): 123–130. doi:10.1643/0045-8511(2007)7[123:SAGOLC]2.0.CO;2.
- Schlupp, I., and Podlousky, R. 1994. Changes in breeding site fidelity: a combined study of conservation and behaviour in the common toad *Bufo bufo*. *Biol. Conserv.* **69**(3): 285–291. doi:10.1016/0006-3207(94)90428-6.
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. *Ethol. Ecol. Evol.* **2**: 65–79.
- Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**(6): 533–555. doi:10.1007/BF01237820.
- Switzer, P.V. 1997. Past reproductive success affects future habitat selection. *Behav. Ecol. Sociobiol.* **40**(5): 307–312. doi:10.1007/s002650050346.
- US Fish and Wildlife Service. 2003. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the Sierra Nevada distinct population segment of the mountain yellow-legged frog (*Rana muscosa*). *Fed. Regist.* **68**: 2284–2303.
- Vasconcelos, D., and Calhoun, A.J.K. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *J. Herpetol.* **38**(4): 551–561. doi:10.1670/157-03A.
- Vredenburg, V.T., Bingham, R., Knapp, R., Morgan, J.A.T., Moritz, C., and Wake, D. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. *J. Zool. (Lond.)*, **271**(4): 361–374. doi:10.1111/j.1469-7998.2006.00258.x.
- White, G.C., Kendall, W.L., and Barker, R.J. 2006. Multistate survival models and their extensions in program Mark. *J. Wildl. Manag.* **70**(6): 1521–1529. doi:10.2193/0022-541X(2006)70[1521:MSMATE]2.0.CO;2.
- Wood, K.V., Nichols, J.D., Percival, H.F., and Hines, J.E. 1998. Size-sex variation in survival rates and abundance of pig frogs, *Rana grylio*, in northern Florida wetlands. *J. Herpetol.* **32**(4): 527–535. doi:10.2307/1565206.
- Zweifel, R.G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boyleii* group. *Univ. Calif. Publ. Zool.* **54**: 207–292.