
FROGS ON THE BEACH: ECOLOGY OF CALIFORNIA RED-LEGGED FROGS (*RANA DRAYTONII*) IN COASTAL DUNE DRAINAGES

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Abstract.—California Red-legged Frogs (*Rana draytonii*) are typically regarded as inhabitants of permanent ponds, marshes, and slow-moving streams, but their ecology in other habitats, such as drainages among coastal dunes, remains obscure. Because coastal dune ecosystems have been degraded by development, off-highway vehicle use, stabilization, and invasive species, these unique ecosystems are the focus of restoration efforts. To better understand the ecology of California Red-legged Frogs in coastal dune ecosystems and to avoid and minimize potential negative effects of dune restoration activities on these rare frogs, we studied their spatial ecology, habitat selection, and survival in coastal dune drainages at Point Reyes National Seashore, California, USA. All 22 radio-marked frogs remained in their home drainages throughout the spring and summer of 2015 and, with some notable exceptions, most remained close to water. Local convex hull home ranges of four out of five California Red-legged Frogs with > 20 observations in dunes were < 1,600 m². At the population level, frogs were 1.7 (95% credible interval, 1.2–4.4) times more likely to select sites 1 m closer to water, and were 83 (2.0–17,000) times more likely to select sites with 10% greater percentage cover of logs that served as refuges from environmental extremes and predators. On average, California Red-legged Frogs avoided the invasive plants Iceplant (*Carpobrotus edulis*) and European Beachgrass (*Ammophila arenaria*). Frogs were 0.68 (0.32–0.89) and 0.55 (0.24–0.75) times as likely to select areas that had 10% greater cover of these plants, respectively. Assuming constant risk of mortality, California Red-legged Frogs had an annual survival rate of 0.70 (0.27–0.96) in coastal dune drainages. Our results indicate that coastal dune drainages provide a locally important habitat for California Red-legged Frogs. Restoration practices that maintain wetted drainages with logjams are likely to benefit California Red-legged Frogs.

Key Words.—amphibian; habitat selection; home range; invasive species; movement; Point Reyes National Seashore; restoration; survival

INTRODUCTION

California Red-legged Frogs (*Rana draytonii*; Fig. 1) are typically regarded as inhabitants of permanent ponds, marshes, and slow-moving streams (Hayes and Jennings 1988; Stebbins 2003). The use of other habitats by California Red-legged Frogs has received much less attention, despite calls for understanding site-specific autecology of this federally listed as threatened species (Fellers and Kleeman 2007). Although California Red-legged Frogs occur in coastal dune drainages (Halstead and Kleeman, In press), little has been published about the ecology of California Red-legged Frogs in this imperiled ecosystem.

Coastal dune ecosystems on the Pacific Coast of the United States were once widespread. The extent and quality of dunes for flora and fauna adapted to this dynamic ecosystem have declined because of residential and commercial development, off-highway vehicle use, and stabilization (Pickart 1988). Thousands of hectares

of Pacific Coast sand dunes were stabilized with non-native plants by the middle of the twentieth century. European Beachgrass (*Ammophila arenaria*) is native to European coastal dunes, and it was introduced to San Francisco in the late 1800s (Pickart 1997). European Beachgrass has extensive roots and rhizomes, by which it readily spreads (Pickart 1997). Shoots form dense clusters in dunes, and monocultures of European Beachgrass often replace native foredune communities (Pickart 1997). Iceplant (*Carpobrotus edulis*), which is native to South Africa, was introduced to the United States in the early 1900s (D'Antonio 1993). This species forms dense mats; a single plant can be up to 20 m wide and 50 cm deep (D'Antonio 1993). Few native plants can become established or grow under these dense mats (D'Antonio 1993).

The stabilization of dunes by these invasive plants has widespread negative consequences for dune biota (D'Antonio 1993; Wiedemann and Pickart 1996; Pickart 1997; Mack and D'Antonio 1998). For example,



FIGURE 1. An adult California Red-Legged Frog, *Rana draytonii*. (Photographed by Patrick M. Kleeman).

arthropods adapted to dune ecosystems have lower diversity in dunes invaded by European Beachgrass than those dominated by native vegetation (Slobodchikoff and Doyen 1977). Because of invasive plants and other dune degradation, dune-dependent species such as the federally listed as endangered Tidestrom's Lupine (*Lupinus tidestromii*; Dangremond et al. 2010) and the federally listed as threatened Western Snowy Plover (*Charadrius nivosus nivosus*; Muir and Colwell 2010; Zarnetske et al. 2010) also have declined. Invasive dune vegetation also can affect native species indirectly. For example, densities of North American Deermice (*Peromyscus maniculatus*) increase in the presence of European Beachgrass, increasing seed predation on and limiting the distribution and abundance of native dune plants (Boyd 1988). To aid recovery of listed species and improve the overall health of coastal dunes, efforts are underway to restore this unique ecosystem (Pickart 1988; Wiedemann and Pickart 1996; Pickart 1997; Pickart et al. 1998). Typical dune restoration activities focus on removing invasive plants manually, mechanically, or chemically (Wiedemann and Pickart 1996; Pickart 1997; National Park Service 2015).

Restoration of coastal dunes for conservation of some species might have a negative effect on other species inhabiting the dune ecosystem. To avoid and minimize potential negative effects of restoration activities, it is necessary to understand how species of conservation concern use coastal dunes in their present state. We studied the spatial ecology, habitat selection, and survival of California Red-legged Frogs in coastal dune drainages at Point Reyes National Seashore, California, where more than 60% of the 890 ha of coastal dune, bluff, and scrub habitat had been invaded by European Beachgrass and Iceplant by 2009 (National Park Service 2015). We expected that frogs would avoid xeric areas of dunes dominated by invasive plants and remain in dune drainages throughout the summer, unless drying

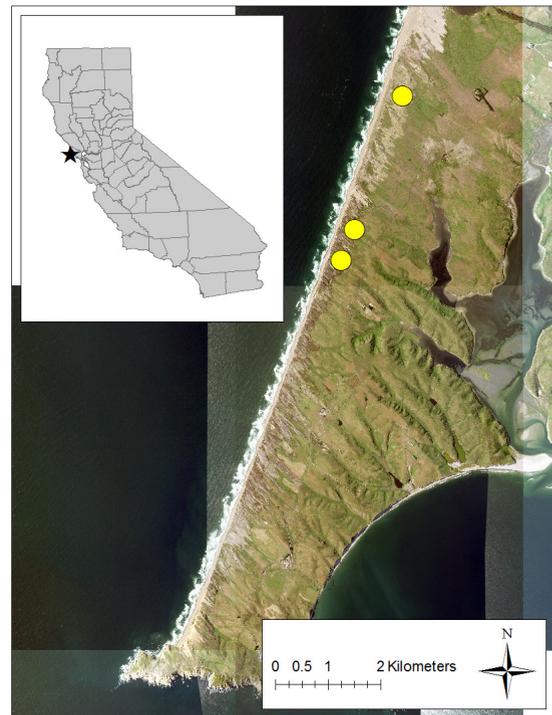


FIGURE 2. Locations of dune drainages along the Great Beach, Point Reyes National Seashore, California, USA, in which California Red-legged Frogs (*Rana draytonii*) were radio-tracked from April through September, 2015.

conditions forced them to migrate to nearby (< 1,500 m) stock ponds. Relative to available habitats, we expected that frogs would select locations near surface water and those that provided cover and moisture, such as logs and emergent aquatic vegetation. Finally, we expected that survival in dune drainages would be lower than in stock ponds that have longer hydroperiods. Our results will enable resource managers to restore habitat for rare plants and birds while avoiding or minimizing potential negative effects to a threatened amphibian.

MATERIALS AND METHODS

Study site.—Our study site was located along the Great Beach at Point Reyes National Seashore, California, USA. The Great Beach is a 12.5 km long, straight beach oriented in a NNE to SSW direction. Twenty-one dune drainages ranging from shallow, ephemeral streams to spring-fed systems with semi-permanent pools occur along the Great Beach; we conducted our study in three of the latter drainages where we could reliably obtain California Red-legged Frogs for study (Fig. 2). Drainages selected for study were 630 and 2,700 m from the nearest study drainage, and 300, 480, and 1,200 m from the nearest other drainage (Fig. 2).

Field methods.—We used radiotelemetry to study the spatial ecology of individual California Red-legged Frogs in coastal dune ecosystems from April through September, 2015. We captured adult California Red-legged Frogs greater than 40 g in the three drainages with the largest counts of frogs (Halstead and Kleeman, In press), and fitted them with a radio transmitter (Model BD-2; 2.1 g; Holohil Systems, Inc., Carp, Ontario, Canada) using a beaded chain belt (Rathbun and Murphey 1996). We captured the frogs approximately every two weeks to ensure that the belt fit properly and was not causing abrasions or other injury. We tracked 22 frogs, and located them approximately twice weekly until the transmitter fell off (12 individuals), the signal was lost (likely because of premature transmitter failure; two individuals), the individual died (two individuals), or the study ended (six individuals). We gave some individuals a new transmitter after the initial one fell off or prior to its expected battery failure. We conducted most frog observations during the day, but we made some observations and all examinations for injury and proper fit at night.

At each frog observation, we measured several variables to estimate space use, movements, and habitat selection of California Red-legged Frogs. In particular, we recorded the location of the frog using handheld Global Positioning System (GPS) receivers (UTM Zone 10; Garmin eTrex; Garmin Ltd., Kansas City, Missouri, USA) with 3–5 m accuracy, and we noted frog behavior (signal or frog stationary, jumped into water, sitting on or in land, log, or water, etc., fleeing, etc.), position (bottom [relatively flat area at the bottom of the cross-section] or sides [steep slopes on sides of cross-section] of drainage, top of dune, in pasture), and substrate (terrestrial, underground, surface of water, or underwater). We measured time; air, water, and substrate temperatures; wind speed; and sky condition (e.g., sunny, foggy, cloud cover, rain) to characterize the conditions under which we made observations. For most frog observations, we visually estimated the percentage cover of different structural microhabitats within a 0.5 m radius of the location of the frog. We chose habitat components to characterize structural composition of microhabitat we believed to be relevant to frogs (for example, proximity to water, logs, and emergent vegetation were hypothesized to be selected by frogs, whereas bare soil and invasive plants were hypothesized to be avoided by frogs), rather than the taxonomy of vegetation. Microhabitat categories recorded in the field included open water, bare ground, bare sand, rock, logs (> 5 cm diameter), litter, terrestrial clumped graminoids, terrestrial single-stemmed perennial graminoids, terrestrial single-stemmed annual graminoids, terrestrial turf grasses, terrestrial forbs, terrestrial shrubs, terrestrial succulents, emergent aquatic clumped graminoids,

emergent aquatic single-stemmed graminoids, emergent aquatic forbs, emergent aquatic shrubs, submerged aquatic vegetation, and floating aquatic vegetation. In addition to percentage of cover types, we also recorded the position in the drainage (bottom, sides, top of dune), slope, and aspect. Distance to open surface water was measured with a range finder (Bushnell Yardage Pro, Bushnell Outdoor Products, Overland Park, Kansas, USA) in the field for short distances (< 100 m), but we used mapping software (National Geographic TOPO!, Magellan, Santa Clara, California, USA) for greater distances. For each frog observation at which we collected habitat data, we selected a random point at a uniform (minimum = 1, maximum = 360) azimuth and uniform (2, 25) m distance from the location of the frog. We collected habitat information identical to that collected at frog locations at each random location.

Data analysis.—We used 12 analyses to examine the spatial ecology, habitat relations, and survival of California Red-legged Frogs in coastal dune drainages. We used hierarchical logistic regression to estimate the probability of frogs being found in the terrestrial environment or at the bottom of dune drainages, and the difference in this probability between diurnal and nocturnal observations. To examine the distances at which frogs were found from water, we used a hierarchical linear model that examined whether the log-transformed distance from water varied between diurnal and nocturnal observations. We estimated the effects of date, sex, and body length on log-transformed movement distances and rates between successive observations using hierarchical linear regression with random individual intercepts and slopes. We estimated non-breeding home range and core use areas using adaptive local convex hulls (*a*-LoCoH; Getz and Wilmers 2004; Getz et al. 2007) and minimum convex polygons (MCP). We estimated habitat selection of California Red-legged Frogs using hierarchical case-control logistic regression. To estimate survival of California Red-legged Frogs in coastal dune drainages, we used a time-to-event model with a constant hazard. We describe each of these models in more detail below.

We examined the proportion of observations in terrestrial habitats and in the bottoms of drainages (rather than sides of drainages or tops of dunes) using hierarchical binomial models. We used an intercept-only hierarchical logistic regression to describe the proportion of locations in terrestrial habitats and at the bottoms of drainages. This model had the form

$$\text{logit}(p_{ij}) = \alpha + \eta_j,$$

$$y_{ij} \sim \text{Bernoulli}(p_{ij}),$$

where y_{ij} was the habitat type (0 = aquatic, 1 = terrestrial) or location in the drainage (0 = bottom of drainage, 1 = elsewhere) of frog j at observation i , p_{ij} was the probability that observation i of frog j would be in the terrestrial environment or at a location other than the bottom of the drainage, α was the logit-scale intercept for the population average probability, and $\eta_j \sim \text{normal}(\text{mean} = 0, \text{SD} = \sigma_{ind})$ was the logit-scale random intercept for frog j . We used an uninformative (on the probability scale; Lunn et al. 2013) normal(0, 1.65) prior for α , and gave σ_{ind} an uninformative uniform(0, 5) prior.

We expanded the above Bernoulli model to estimate differences in the probability of frogs being in terrestrial habitats and at the bottom of drainages during the day and at night. This model took the form

$$\text{logit}(p_{ij}) = \alpha + \beta \times x_i + \eta_j,$$

$$y_{ij} \sim \text{binomial}(n_i, p_{ij}),$$

where y_{ij} was the count of observations of frog j in terrestrial habitats or at the bottom of drainages at time x_i (0 = day, 1 = night), n_i was the number of observations of frog j at time x_i , p_{ij} was the probability that observation i of frog j was in terrestrial habitats or at the bottom of a drainage, α was the logit-scale intercept for the population average probability of being in a terrestrial environment or at the bottom of a drainage, β was the effect of time x_i on the probability of being in a terrestrial environment or at the bottom of a drainage, and $\eta_j \sim \text{normal}(0, \sigma_{ind})$ was the logit-scale random intercept for frog j . We chose priors for this model to be uninformative, with priors for α and β specified as normal(0, 1.65), and priors for σ_{ind} specified as uniform(0, 5). From this model, we calculated the probability of adult frogs being terrestrial or at the bottom of a drainage during the day and at night, and calculated the odds ratio for being in the terrestrial environment or at the bottom of a drainage at night relative to during the day as e^β . We used a posterior predictive check for goodness-of-fit of this model using a χ^2 discrepancy measure, and derived a Bayesian P -value from the χ^2 discrepancy measures (Kéry and Royle 2016).

We further examined the locations of frogs by describing the distance from open surface water of frog observations for those locations not in the water or at the edge of the water. We used hierarchical linear regression on log-transformed distance as follows:

$$\mu_{ij} = \alpha + \omega_1 \times \beta_1 \times \text{night}_i + \omega_2 \times \beta_2 \times \text{date}_i + \eta_j,$$

$$y_{ij} \sim \text{normal}(\mu_{ij}, \sigma),$$

where y_{ij} was the log-transformed distance from surface water of frog j at observation i ; μ_{ij} was the

expected distance from water for frog j at observation i , given that the frog was away from water; σ was the residual error in the linear regression model; α was the intercept, or the population average distance from water during the day, given that the frog was away from water; β_1 was the effect of night on the distance from water; β_2 was the effect of Julian date on the distance from water; ω_1 and ω_2 were indicator variables used in model selection; and $\eta_j \sim \text{normal}(0, \sigma_{ind})$ was the random intercept for frog j . We selected priors for this model to be uninformative, with priors for α specified as uniform(0, 1,000), β s specified as normal(0, 31.6), σ specified as uniform(0, 50), σ_{ind} specified as uniform(0, 100), and ω s specified as Bernoulli(0.5). We used a posterior predictive check for goodness-of-fit of this model using a sum-of-squares discrepancy measure, and derived a Bayesian P -value from the sum-of-squares discrepancy measures (Kéry 2010).

To examine how frogs moved through the dune landscape, we calculated the distance between successive locations of frogs and the rate of movement between locations. We examined effects of sex, body length, Julian date, and a quadratic function of Julian date on movement distances and rates using log-linear hierarchical models with an individual random intercept. Variable selection was accomplished with the use of indicator variables on model coefficients (Kuo and Mallick 1998; Royle and Dorazio 2008). The form of the model was

$$\mu_{ij} = \alpha + \sum_{k=1}^{K} (\omega_k \times \beta_k \times x_{i,k}) + \eta_j,$$

$$y_{ij} \sim \text{normal}(\mu_{ij}, \sigma),$$

where y_{ij} was log-transformed movement distance or rate for frog j at observation i , σ was the residual error of the linear regression model, ω_k was an indicator variable for the inclusion of predictor variable k in the model, β_k was the effect of predictor variable k on movement distance or rate, $x_{i,k}$ was the value of predictor variable k at observation i , and $\eta_j \sim \text{normal}(0, \sigma_{ind})$ was the random intercept for frog j . We chose priors to be uninformative: normal(0, 100) for α , hierarchical t(mean = 0, SD = σ_β , df = 1) for β_k , uniform(0, 100) for σ , uniform(0, 10) for σ_β , and Bernoulli(0.5) for each ω_k . We used a Bayesian P -value based on a sum-of-squares discrepancy measure to assess model fit (Kéry 2010).

In addition to estimating frog movement distances and rates, we estimated non-breeding (spring-summer) home ranges for frogs with ≥ 20 observations ($n = 5$) using the a -LoCoH estimate (Getz and Wilmsers 2004; Getz et al. 2007). For the parameter a , which defines clusters of points such that the sum of distances between a root point and all points within a sphere is less than a (Getz et al. 2007), we examined a minimum of 10 values

for a centered around the maximum distance between two points for each individual (a_1), and spanning a range from less than half a_1 to more than double a_1 . Plots of 50%, 90%, and 95% isopleth areas against a_1 were then examined for asymptotes. If a_1 appeared in a region of stable area at the specified isopleths and no increase in area appeared above a_1 , we used a_1 as the parameter a for home range estimation (Getz et al. 2007). Because of the small sample size for home range estimates, we reported means and ranges of core areas (50% isopleths; where estimable) and home ranges (100% isopleths), and we plotted individual home ranges. We also estimated MCP home range areas because of their common use in the amphibian literature.

We evaluated habitat associations of California Red-legged Frogs in the coastal dune ecosystem by pairing observations of habitat components used by frogs fitted with radio transmitters with observations of habitat components available at nearby random locations. We analyzed the paired habitat use-availability data using hierarchical case-control logistic regression. This model had the form

$$\text{logit}(p_i) = \sum_{k=1}^K (\beta_{j,k} \times x_{i,k}),$$

$$y_i \sim \text{Bernoulli}(p_i),$$

where y_i was a vector of ones for each observation pair i , $\beta_{jk} \sim \text{normal}(\mu_k, \sigma_k)$ was a matrix of individual frog j and habitat variable k specific coefficients, and $x_{i,k}$ was a matrix of the differences between used and available habitats for each observation pair i and each variable k . The hierarchical structure of β accounts for varying numbers of observations per individual frog and quantifies individual variation in selection (Gillies et al. 2006). We selected priors to be uninformative: hierarchical $t(0, \sigma_\beta, 1)$ for μ_β and $\text{uniform}(0, 5)$ for all σ . We limited the analysis to 11 predictor variables to maintain a parameter:sample size ratio of approximately 1:20 ($n = 219$). We excluded rare variables and lumped some categories estimated independently in the field, such as different types of emergent vegetation (e.g., emergent aquatic clumped graminoids, emergent aquatic single-stemmed graminoids, and emergent aquatic forbs). Variables included in the model were distance from water and percent cover of open water, logs, litter, terrestrial clumped graminoids, terrestrial single-stemmed perennial graminoids, terrestrial forbs, terrestrial shrubs, terrestrial succulents, bare ground or sand, and emergent herbaceous vegetation. We also ran a separate model that examined selection of the two dominant non-native dune plants, Iceplant and European Beachgrass. To assess goodness-of-fit of each habitat selection model, we used the standardized Pearson χ^2 statistic (Hosmer et al. 2013) using the maximum

likelihood fit of each model with random individual slopes for each predictor variable.

We further used radiotelemetry data to estimate survival of California Red-legged Frogs in coastal dune habitat using time-to-event models. Because only two frogs were confirmed to have died during the study, we limited our analysis to have a constant hazard function, scaled to be the daily risk of mortality, and did not consider the effects of individual, temporal, or spatial variables on the risk of mortality. We based our model on material by Dennis Heisey (unpubl. report) and placed an uninformative $\text{uniform}(-20, 20)$ prior on γ , the log of the daily risk of mortality. For comparison and as a measure of fit, we visually compared the survival curve from the constant hazard model to a Kaplan-Meier curve (a hazard of zero when no mortalities occurred, and a hazard approximately equal to the proportion of the population dying during intervals when mortalities occurred; this results in a step-wise curve, where survival is constant during periods of no mortality, but falls rapidly during intervals when mortality occurs) to the event-time data, with the same prior for γ on intervals during which a mortality occurred, and γ fixed at -99.9 during all other intervals.

Bayesian analysis of models used Markov chain Monte Carlo (MCMC) sampling carried out in JAGS (Plummer, M. 2014. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Software version 3.4.0. <http://mcmc-jags.sourceforge.net/>. [Accessed 27 January 2017]). We selected model burn-in, sampling iterations, and thinning rates to ensure convergence was achieved and effective sample sizes were $> 5,000$ for all monitored parameters. For the Bernoulli and binomial models describing the probability of being in the terrestrial environment or away from the drainage bottoms, we based posterior inference on five chains of 100,000 iterations each, after a burn-in period of 10,000 iterations. We used five chains of 200,000 iterations each, after a burn-in period of 10,000 iterations, for posterior inference from the log-linear distance from water and movement distance and rate models. For the habitat selection models, we used five chains of 200,000 iterations each, following a burn-in period of 100,000 iterations, for posterior inference. We based posterior inference for the time-to-event model of California Red-legged Frog survival on five chains of 20,000 iterations each after a burn-in of 1,000 iterations. In all cases, we thinned the MCMC output so posterior inference was based upon 100,000 samples from the stationary posterior distribution (binomial model thinning rate = 5; log-linear and habitat selection model thinning rate = 10; survival model output was not thinned). We fit each model with JAGS 3.4.0 (Plummer 2014 *op. cit.*) called from R 3.2.1 (R Core Team 2015) using the packages `runjags` (Denwood 2016) or `jagsUI` (Kellner,

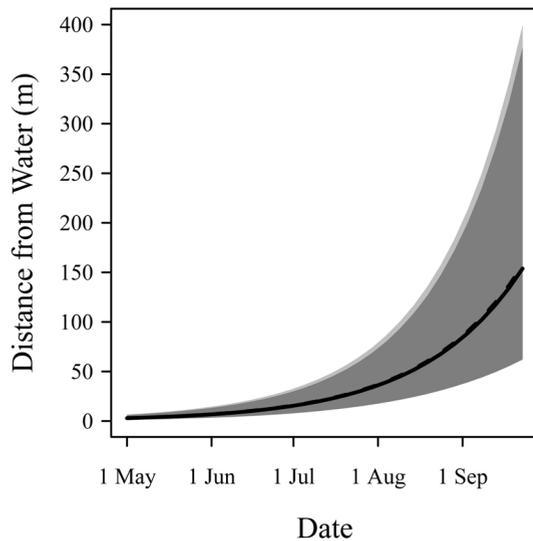


FIGURE 3. Model-based distance from surface water of radio-marked California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. The solid line and dark gray shaded area are for diurnal locations, the dashed line and light gray shaded area are for nocturnal observations. Bold lines represent posterior medians; shaded areas represent 95% credible intervals.

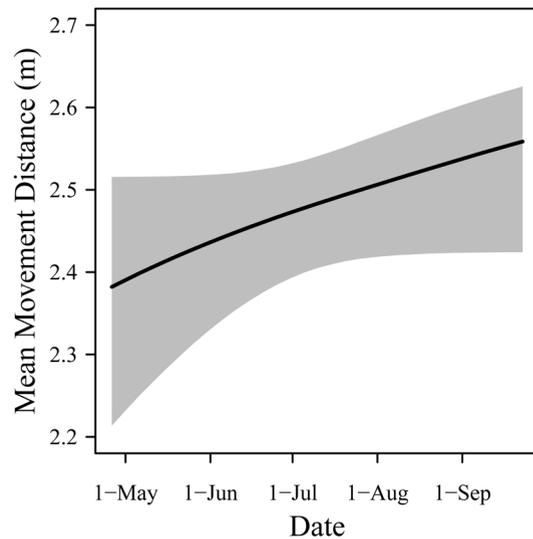


FIGURE 4. Model-based distance between successive observations of radio-marked California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. The bold line indicates the posterior median, gray shaded area indicates the 95% credible interval.

K. 2016. JagsUI: a wrapper around “rjags” to streamline “JAGS” analyses. R package version 1.4.2. <https://CRAN.R-project.org/package=jagsUI>. [Accessed 27 January 2017]. We diagnosed convergence with visual examination of history plots and with the Gelman-Rubin statistic (Gelman and Rubin 1992); no evidence for lack of convergence was observed ($\hat{r} < 1.01$ for all monitored parameters). Unless otherwise indicated, we report results as posterior median (95% credible interval).

RESULTS

Spatial ecology.—We radio-tracked 22 individual frogs, and observed frogs a mean of 9.9 ± 9.0 times (SD; range, 1–29 times) over a mean of 50.7 ± 43.9 d (range, 0–129 d). We made 26 of 218 (12%) frog observations at night. Individual frogs were in terrestrial habitats during 46% (95% CRI = 32–60%) of observations, and they were located in the bottoms of dune drainages during 66% (51–79%) of observations. The locations of frogs and probability of being in terrestrial habitats varied between night and day, with moderate evidence for lack of model fit for the probability of being in the terrestrial environment (Bayesian P -value = 0.07), but little evidence for lack of fit for the probability of being at the bottom of drainage (Bayesian P -value = 0.38). At night, frogs were 2.2 (1.5–4.1) times more likely to be in

terrestrial habitats and 0.28 (0.10–0.49) times as likely to be in the bottom of a drainage as during the day.

We found frogs up to 300 m from open surface water, but most individuals we observed were always within 10 m of aquatic environments (Table 1). The hierarchical linear regression model on log-transformed distance from water fit the data well (Bayesian P -value = 0.52), and the model including only the effect of date was strongly supported (posterior probability = 0.96). Distance from water increased later in the summer ($\beta_2 = 1.12$ [0.85–1.39]; Fig. 3), and much variation existed among individuals ($\sigma_{\text{ind}} = 1.18$ [0.66–1.84]; $\sigma = 1.24$ [1.09–1.41]). For each day later in the summer, the model-averaged mean distance from water increased by 1.012 (1.009–1.015) times (Fig. 3).

Movement patterns of individual frogs varied substantially (Table 1). The distances between successive locations and movement rates were well-described by the log-linear models (Bayesian P -value for movement distances = 0.51; Bayesian P -value for movement rates = 0.51). The mean distance between consecutive observations was affected by date (Table 2), with distances later in the year larger than those earlier in the year (Fig. 4). The model-averaged distance between observations was 1.005 (1.00–1.011) times greater for each day later in the year (Fig. 4). Movement rate also was affected by date and, to a much lesser extent, sex (Table 3). As for distance between locations, movement rates of California Red-legged Frogs were larger later

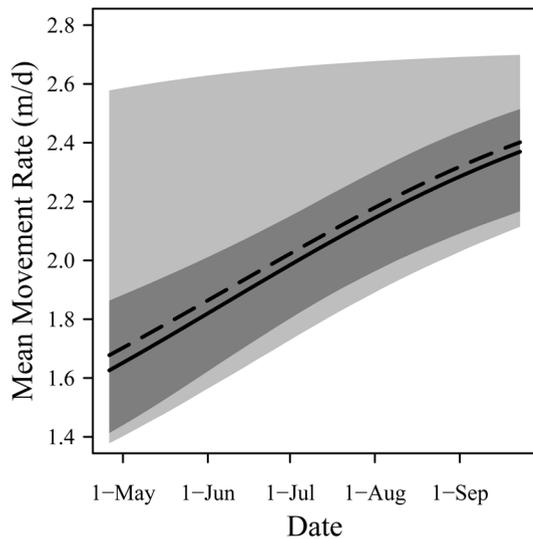


FIGURE 5. Model-based movement rate of female (dark gray shaded area and solid line) and male (light gray shaded area and dashed line) radio-marked California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. Bold lines indicate posterior medians, shaded areas indicate 95% credible intervals.

in the year (Fig. 5), with model-averaged movement rates increasing by 1.011 (1.007–1.017) times for each day later in the year. Although some evidence existed for males to move at greater rates than females, small sample size and model selection uncertainty obfuscated effect sizes (Fig. 5).

We were able to estimate home ranges for five individual frogs that we observed at least 20 times, but we could only estimate core areas for a single individual (Table 4). Frogs in dune drainages had a mean 100% α -LoCoH home range area of $4,480 \pm 8,350$ m² (range, 169–19,400 m²), and a mean MCP home range area of $11,700 \pm 20,100$ m² (range, 232–47,500 m²). All radio-marked frogs remained in the drainages in which they were marked (Fig. 6).

Habitat selection.—California Red-legged Frogs did not use habitat components of dune drainages at random. No evidence for lack of fit existed for the habitat selection model ($\chi^2 = -4.31 \times 10^{-15}$, $P = 0.500$), but the model for selection of invasive dune plants fitted poorly ($\chi^2 = -2.05$, $P = 0.020$). Despite the lack of fit of the invasive plants model, we describe the patterns in these data with the understanding that many other variables not included in the model affect selection of locations by California Red-legged Frogs. The omission of these variables likely caused the poor fit of the invasive plants model. At the population level, frogs selected areas near water with log cover (Fig. 7), but credible intervals of odds ratios for other habitat variables overlapped one. For every meter closer to surface water, a location was 1.70 (1.19–4.24) times more likely to be used by frogs, and a 10% increase in the percentage cover of logs increased the odds of use by frogs by 82.7 (2.03–17,200) times. Individuals varied most in their selection of open water and logs, and least in their selection of distance to water (Table 5). Both Iceplant and European Beachgrass were avoided by California Red-legged Frogs. Frogs were 0.68 (0.32–0.89) times as likely to use a location with a 10% increase in the percent cover of Iceplant, and 0.55 (0.24–0.75) times as likely to use a location with a 10% increase in European Beachgrass cover (Fig. 8). Frogs varied little in their avoidance of these species: logit-normal SD describing individual variation for selection of Iceplant = 0.429 (0.064–1.623); for selection of European Beachgrass = 0.411 (0.028–1.501).

Survival.—We confirmed only two individuals to have died during the study. Both confirmed mortalities were due to predation by California Red-sided Gartersnakes (*Thamnophis sirtalis infernalis*). The constant hazard model approximated the Kaplan-Meier curve well (Fig. 9). The daily risk of mortality was 8.2×10^{-4} (2.5×10^{-5} – 3.4×10^{-3}), resulting in an annual survival probability of 0.70 (0.27–0.96; Fig. 9).

TABLE 1. Movement metrics ($n = 18$) and distances from water ($n = 22$) of adult California Red-legged Frogs (*Rana draytonii*) radio-tracked in coastal dune drainages at Point Reyes National Seashore, California, USA, in 2015. Values are summary statistics across individual frogs. Frogs that were not observed to move were excluded from movement summary statistics.

Metric	Minimum	Median	Maximum	Mean	SD
Median distance (m) between successive observations	2.7	8.0	26	10	7.1
Maximum distance (m) between successive observations	5.0	28	320	77	94
Median rate of movement (m/d) between successive observations	0.2	1.6	7.7	2.4	2.0
Maximum rate of movement (m/d) between successive observations	0.2	14	260	38	61
Maximum displacement (m) from location of capture	0.0	32	780	100	180
Cumulative distance (m) moved	5.1	110	1,700	270	400
Median distance (m) from water	0.0	0.3	210	35	67
Maximum distance (m) from water	0.0	6.0	300	79	110

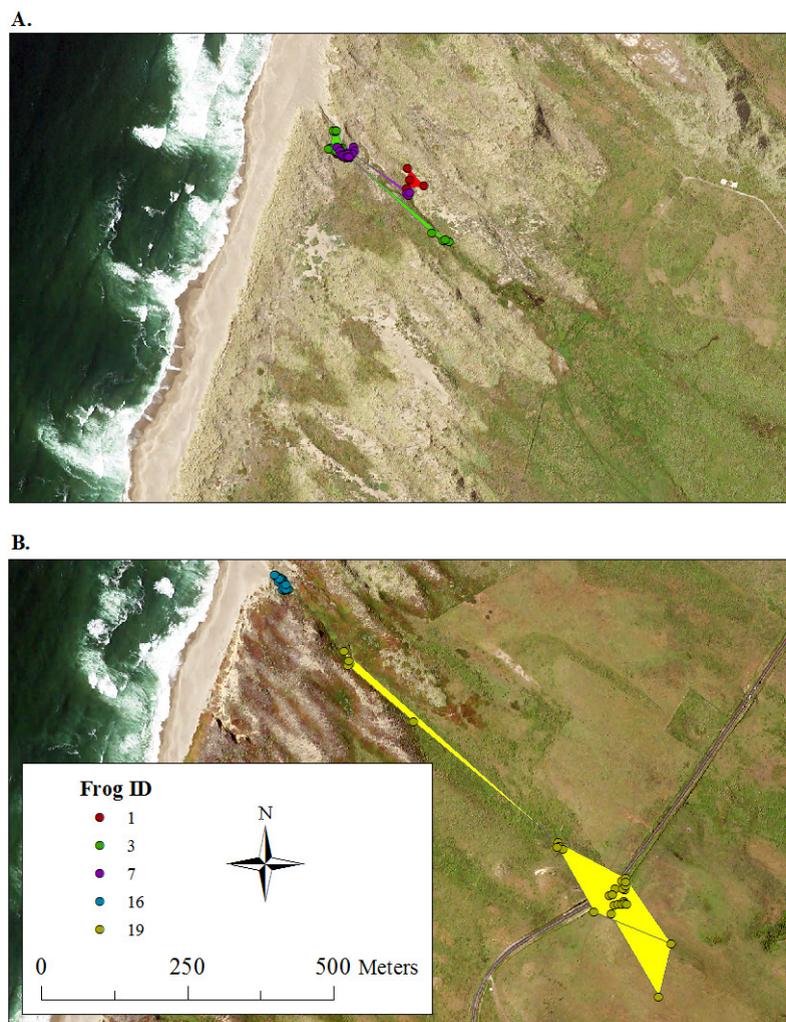


FIGURE 6. Observed locations (points) and Adaptive Local Convex Hull (*a*-LoCoH) utilization distributions (polygons) of five radio-marked California Red-legged Frogs (*Rana draytonii*) in the AT & T (A) and North Beach (B) coastal dune drainages at Point Reyes National Seashore, California, USA, in 2015. Different colors represent different frogs.

DISCUSSION

California Red-legged Frogs remained in their home drainages throughout the summer, generally staying close to water and taking advantage of the cover and environmental stability provided by logs and logjams. Dune drainages provided sufficient habitat quality to result in higher survival estimates of adult frogs than those estimated for a nearby California Red-legged Frog population (Gary Fellers et al., unpubl. report), indicating that the coastal dune ecosystem serves as quality habitat for California Red-legged Frogs. Even at the North Beach site, where water was seasonal and too shallow to support breeding, California Red-legged Frogs remained in the drainage throughout the driest portion of the year.

Although movement distances and rates were similar to those for California Red-legged Frogs in other habitats in northern California (Bulger et al. 2003; Fellers and Kleeman 2007; Tatarian 2008), frogs in dunes sheltered in terrestrial habitats nearly half the time, often far from surface water. This is in contrast to observations along a coastal stream, where observations of California Red-legged Frogs were predominantly associated with aquatic habitats and immediately adjacent cover (Keung 2015). Although 12 individuals in our study had a median distance to water < 1 m, five frogs had a median distance to water > 100 m. It was not uncommon for us to observe these frogs in moist microhabitats, such as seeps, or under log or vegetative cover in areas that provided humidity and shelter, but had no surface water. Increased movement rates and distances from

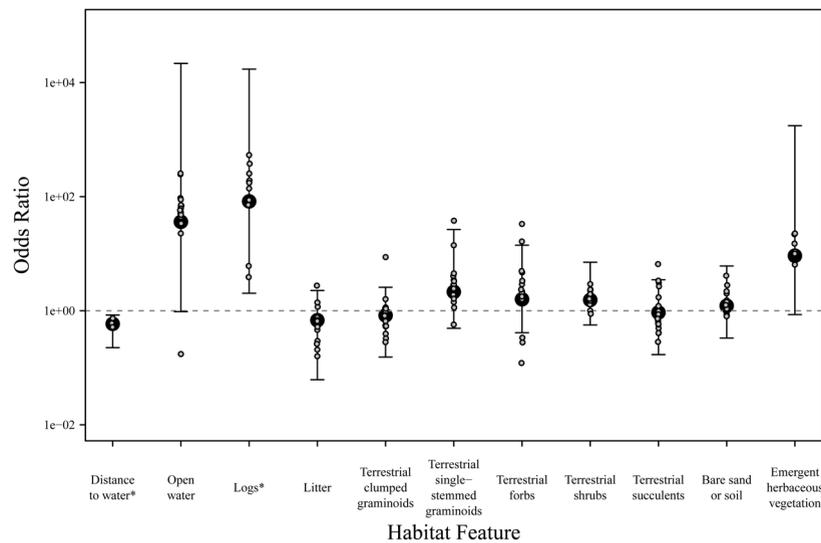


FIGURE 7. Odds ratios for the selection of different habitat variables and features by California Red-legged Frogs (*Rana draytonii*) in coastal dunes at Point Reyes National Seashore, California, USA, in 2015. Large black dots represent posterior medians of the population mean odds ratios; error bars represent 95% credible intervals of the population mean odds ratios; jittered gray dots represent posterior median odds ratios for individual frogs; the horizontal gray dashed line represents an odds ratio of one, at which habitat components are neither selected nor avoided. Variables with asterisks had 95% credible intervals that did not overlap one.

surface water were particularly pronounced later in the year as stream habitat dried and frogs sought moist microhabitats.

Affinity for water and the importance of cover and humid microhabitats also were well-supported in our analysis of habitat selection. Selection of locations near water was less variable among individuals in this analysis than would be expected by the degree of heterogeneity observed in distances to water. This difference is readily explained by the case-control design of our habitat selection study: regardless of how far frogs were from water, they were consistently closer to water than random points within 25 m of their location. The affinity of California Red-legged Frogs for water is well-known (Hayes and Jennings 1988; Bulger et al. 2003; Fellers and Kleeman 2007; Tatarian 2008; Keung 2015) and was an expected result.

TABLE 2. Model selection results for California Red-legged Frog (*Rana draytonii*) distances between consecutive observations in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability > 0.05 are included in the table. Models are listed in order of decreasing support.

Variable				
Date	Date ²	Sex	Snout-vent length	Posterior probability
1	0	0	0	0.37
1	0	1	0	0.18
0	0	0	0	0.18
1	0	0	1	0.07
0	0	1	0	0.05

In contrast to consistent affinity for water, we observed much heterogeneity among individuals for selection of logs; despite this heterogeneity, all individuals positively selected this habitat feature. Much of the variation among frogs in the strength of selection for logs was likely caused by differences in the availability of logs and their suitability as cover for different frogs. Logs likely provide thermally stable, moist microenvironments that protect frogs from many predators. These desirable characteristics were likely better provided by logs than other features in the coastal dune environment. The source of logjams in this coastal dune system is driftwood forced into the mouths of drainages during winter high tides and storm events, rather than the typical case of trees falling and being washed downstream. Because high tides and storm events both create and remove logjams, the logjams

TABLE 3. Model selection results for California Red-legged Frog (*Rana draytonii*) movement rates in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability > 0.05 and the null model are included in the table. Models are listed in order of decreasing support.

Variable				
Date	Date ²	Sex	Snout-vent length	Posterior probability
1	0	0	0	0.45
1	0	1	0	0.30
1	0	0	1	0.07
1	0	1	1	0.07
0	0	0	0	< 0.001

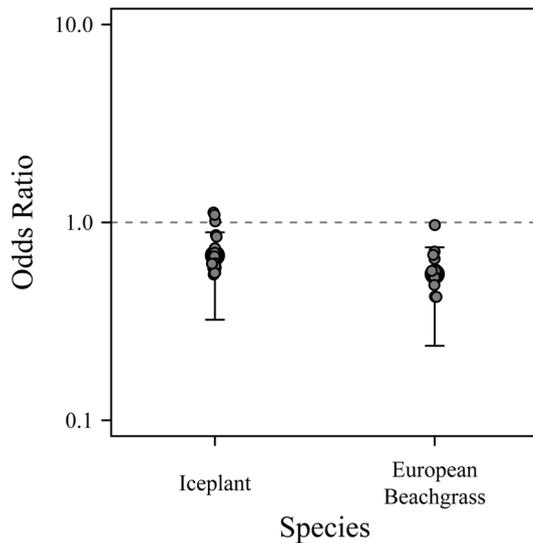


FIGURE 8. Odds ratios for the selection of exotic Iceplant (*Carpobrotus edulis*) and European Beachgrass (*Ammophila arenaria*) by California Red-legged Frogs (*Rana draytonii*) in coastal dunes at Point Reyes National Seashore, California, USA, in 2015. Large black dots represent posterior medians of the population mean odds ratios; error bars represent 95% credible intervals of the population mean odds ratios; jittered gray dots represent posterior median odds ratios for individual frogs; the horizontal gray dashed line represents an odds ratio of one, at which plants are neither selected nor avoided.

in this system are dynamic and often ephemeral. Regardless of their duration or source, the selection of logs is likely analogous to rock ledges (Tatarian 2008) and complex cover (Keung 2015) documented in other studies. Indeed, Keung (2015) noted that although logjams were rare at his coastal stream study site, they appeared important to many individual California Red-legged Frogs.

California Red-legged Frogs did not appear to select or avoid other habitat attributes. Adult California Red-legged Frogs might be rather indiscriminate about most features of the environment (Reis 1999; Bulger et al. 2003; Tatarian 2008), provided they have moisture, cover, and prey. Alternatively, sample sizes of our and other studies might be too small to detect selection at the population level, especially given the large degree of individual heterogeneity in selection. The latter hypothesis is supported by hints of positive selection of open water and emergent herbaceous vegetation in our study, despite population-level selection ratios overlapping one. Emergent or shoreline vegetation is an important correlate of California Red-legged Frog occurrence (Hayes and Jennings 1988); our results suggest that this might be the case for selection of sites within occupied areas as well. Positive selection of open

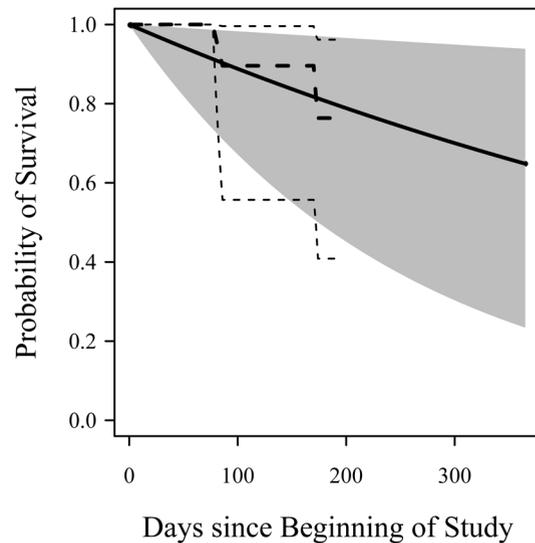


FIGURE 9. Survival curve for radio-marked California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, in 2015, based on a constant hazard (solid line, gray shaded area) and on a Kaplan-Meier model (dashed lines). The bold lines represent the posterior medians, the polygon and light lines represent 95% credible intervals.

water in the dune ecosystem is in contrast to avoidance of deep open water in a large seasonal marsh (Cook and Currylow 2014). We suspect that the relationship to open water in our study was because pools were small and generally $< 6 \text{ m}^2$, which is a very different situation from the 11 ha marsh studied by Cook and Currylow (2014). Some open water was usually associated with frog locations in aquatic habitats, but a smaller proportion of random points than frog locations were within pools.

California Red-legged Frogs appeared to avoid both invasive plant species, Iceplant and European Beachgrass. Avoidance of these plants could be caused by several mechanisms. High abundance of non-native plants might indicate avoidance or neutral selection, even if California Red-legged Frogs use this vegetation, because most random quadrats would have high cover of these plants. We suspect that this swamping effect is not an issue at our study site. More likely, the location of frogs in the bottom of drainages and the greater abundance of Iceplant and European Beachgrass on sand dunes resulted in frogs avoiding these plants by selecting microhabitats within drainages that provided access to moisture. Positive selection of Iceplant by three frogs was likely incidental to the selection of cover and moist microclimates provided by logs where Iceplant had overgrown a logjam. Regardless of the mechanisms underlying apparent avoidance of invasive Iceplant and European Beachgrass, reducing the prevalence and

TABLE 4. SCore (m²) and home range (m²) areas of California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, 2015. Abbreviations and definitions are n = number of locations; a = value of a for adaptive Local Convex Hull (a-LoCoH); Core area = 50% isopleth of the a-LoCoH; home range = 100% isopleth of the a-LoCoH; MCP = area of the 100% minimum convex polygon (MCP) home range (m²); NA indicates that the core area could not be estimated at the specified value of a.

Frog ID	n	a	Core area	Home range area	MCP
1	24	170	NA	656	3,340
3	22	280	NA	1,510	5,190
7	23	150	NA	652	2,040
16	23	30	24	169	232
19	29	800	NA	19,400	47,500

density of these species is unlikely to negatively affect California Red-legged Frogs.

One mechanism by which large California Red-legged Frogs might benefit indirectly from European Beachgrass is through alteration of prey communities. European Beachgrass stands have higher densities of North American Deermice than native dune communities (Boyd 1988), and we observed many mice during our study. Although high mouse densities increase seed predation on the endangered Tidestrom’s Lupine (Dangremond et al. 2010), mice could provide a prey source for large California Red-legged Frogs (Hayes and Tennant 1985). The 10 largest frogs in our study were females 85–104 mm snout-vent length, and although we captured all frogs large enough to carry a transmitter, our sample was biased toward females (19 females, 3 males). We suspect that the sex ratio we observed was the actual sex ratio in the coastal dune drainages, and not a sampling artifact. The possibility that large female California Red-legged Frogs are exploiting abundant

mice as a source of prey warrants further attention. If large females are exploiting mice as a food source in dune drainages, removal of European Beachgrass and reduced mouse density could alter the abundance, sex ratios, and size distributions of California Red-legged Frogs in this habitat. Such changes could be positive, as restoration could increase arthropod diversity (Slobodchikoff and Doyen 1977) that provides a larger prey base for small frogs, resulting in frog populations with typical size distributions and more equitable sex ratios.

The adult California Red-legged Frogs inhabiting coastal dunes at Point Reyes National Seashore had higher survival rates than a nearby population inhabiting a stock pond (Gary Fellers et al., unpubl. report). Our annualized estimate of survival, which assumes that the risk of mortality is constant throughout the year, was higher than estimates of apparent survival from a mark-recapture study at a stock pond in the Olema Valley approximately 18 km ESE of our study site (Gary Fellers et al., unpubl. report), although the credible and confidence intervals overlap. Whether the lower mark-recapture estimates are biased low by permanent emigration or survival in the coastal dune ecosystem is higher than in stock ponds is worthy of further study. In particular, males at breeding locations in the mark-recapture study of Gary Fellers et al. (unpubl. report) might be at greater risk of predation than the females at non-breeding locations in this study. Long-term mark-recapture or radiotelemetry studies would be particularly useful for evaluating this hypothesis.

In their current state, coastal dune drainages provide important habitat for California Red-legged Frogs. Restoration of the dune drainages will result in changes in vegetative cover, and possibly the dynamics of the system, because of the removal of the dune-stabilizing European Beachgrass and Iceplant (Mack

TABLE 5. Population mean log-odds ratios and logit-normal standard deviations describing individual variation in selection of habitat components by California Red-legged Frogs (*Rana draytonii*) in coastal dune drainages at Point Reyes National Seashore, California, USA, in spring and summer 2015. Values in the table are posterior medians (95% credible intervals).

Habitat variable	Log-odds ratio	Standard deviation
Distance to water	-0.530 (-1.487 to -0.176)	0.276 (0.013–1.264)
Percentage open water	3.589 (-0.035–9.984)	3.656 (0.656–4.940)
Percentage log	4.415 (0.707–9.752)	3.132 (0.630–4.899)
Percentage litter	-0.384 (-2.784–0.818)	1.851 (0.127–4.665)
Percentage terrestrial clumped graminoids	-0.188 (-1.868–0.948)	1.586 (0.417–4.001)
Percentage terrestrial single-stemmed perennial graminoids	0.762 (-0.709–3.277)	2.322 (0.241–4.782)
Percentage terrestrial forbs	0.462 (-0.887–2.646)	2.615 (0.423–4.804)
Percentage terrestrial shrubs	0.434 (-0.576–1.960)	0.924 (0.045–3.935)
Percentage terrestrial succulents	-0.070 (-1.769–1.251)	1.927 (0.151–4.634)
Percentage bare soil	0.201 (-1.104–1.807)	1.321 (0.070–4.451)
Percentage emergent herbaceous vegetation	2.220 (-0.156–7.470)	1.588 (0.079–4.687)

and D'Antonio 1998). In addition to reducing the cover of these invasive plants, restoration will destabilize the dunes and alter the dynamics of aquatic habitats. For example, destabilization of dunes could prevent succession of open water habitats in dune drainages and improve habitat for the frogs. Alternatively, shifting sands could reduce the occurrence and persistence of standing water. It will be interesting to observe the effects of dune restoration on the permanence of aquatic habitats in this ecosystem.

Regardless of long-term habitat changes, consideration of the spatial ecology and habitat selection of California Red-legged Frogs during dune restoration should allow for restoration activities to benefit dune specialist plants and animals, while not harming frog populations. This study showed that the frogs in these areas have an affinity for water and occur more frequently in the bottom of dune drainages than on the dunes themselves. For this reason, limiting disturbance of drainage bottoms during restoration activities will reduce the likelihood of direct mortality of California Red-legged Frogs. Given the sometimes large distances at which frogs were found from water, mortality of frogs would likely be reduced by having a trained biologist monitor major ground-disturbing activities. Frogs in dune drainages selected logs, so maintaining or enhancing logjams in drainages would likely benefit California Red-legged Frogs in the dunes as well. Dynamic restored coastal dune ecosystems dominated by native species that maintain the microhabitats and prey necessary to support California Red-legged Frogs will ensure that populations persist into the future.

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