SPATIAL ECOLOGY AND SITE OCCUPANCY OF THE NORTHERN RED-LEGGED FROG (*RANA AURORA*) IN A COASTAL DUNE ENVIRONMENT

By

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A Thesis
Presented to
The Faculty of Humboldt State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Arts
In Biology
May, 2008

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Masters of Arts.

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ABSTRACT

The southern distribution of the northern red-legged frog (*Rana aurora*) extends only into the three most northern coastal counties of California and seems to be restricted to the coastal belt. Because of recent declines in the population and destruction of its habitat, the California Department of Fish and Game has declared it a Species of Special Concern in California and it is also federally listed as a Sensitive Species by the US Forest Service. This study investigated the spatial distribution and habitat selection of the species on the North Spit of Humboldt Bay, CA in a locally isolated dune environment. The first part of this study concentrated on natural history facets of the species such as differences in relative abundance, movement, and breeding phenology between and among permanent and seasonal pond-breeding habitats in the study area. The second part of this study described the spatial distribution of the northern red-legged frog within seasonal wetlands of the dune swales using site occupancy models. It also gleaned knowledge on the species' habitat preferences during the breeding and post-breeding seasons and serves as a baseline experiment for future monitoring of this species distribution. Detection probability was also examined in the egg mass site occupancy models.

Frog abundance was greater in the smaller, permanent pond habitat. Movement towards the ponds was greatest during the breeding season in both habitats. Juveniles were most active prior to and during the breeding season, whereas adults were more active during and after the breeding season. Prior rainfall increased movements in both juveniles and adults, although adults were not as affected except prior to the breeding season. No differences in breeding chronology and physical characteristics were found between the habitats.

The egg mass occupancy models showed that gravid females preferred oviposition sites with deeper water and less than 50% emergent vegetation. Egg mass detection probabilities were affected by fluctuating water levels throughout the survey period. Egg mass occupancy rates were underestimated when detection was not incorporated into the models. Adult and juveniles in the post-breeding season selected sites with longer hydroperiods that were farther from sites which had contained egg masses.

Occupancy results indicate that water depth and hydroperiod length are important factors in determining the spatial distribution of *R. aurora* in palustrine wetlands, detection probability is an important parameter to include when surveying the species, and the adult and juveniles use more than just the breeding ponds in the wetland habitat. This is the first study to research *R. aurora* egg mass site occupancy incorporating detection probability. The top model can be used as a foundation to predict egg mass occurrence in palustrine wetlands and as a baseline for development of a larger monitoring program to research spatial dynamics and population fluctuations of the species.

ACKNOWLEDGEMENTS

I would like to thank Dr. John Reiss for his perfect mixture of guidance, support, encouragement, and freedom throughout my graduate experience. I could not have asked for a better advisor. I would also like to thank my committee members: Dr. Matthew Johnson for his close scrutiny of my occupancy models, Dr. Sharyn Marks for the use of her equipment and for her editorial expertise, and Dr. Jeffrey White for use of his lab and enthusiasm for integrating science and education.

I would like to thank my excellent field volunteers: Jen Cary, Karen Pope, Monty Larson, Cheryl Bondi, Ryan Bourque, Rebecca Degagne, and Laura Burkholder. Thanks also to Dr. Howard Stauffer for opening my eyes to a new world of statistics and his support that came along with it. Thanks to the HSU Biological Master's Grant and a RSCA grant from California State University for funding of this research.

A special thanks to Humboldt Bay National Wildlife Refuge, especially the Lanphere Dunes Unit for use of their property. The three years I spent as a caretaker at Lanphere Dunes inspired this thesis and my deep love for the dune environment. Also thanks to CJ and Carol Ralph who let me use their property and generously opened there home, storage space, and friendship to me.

Thanks to my parents for letting me explore 62 acres of Indiana deciduous forests as a child. This is where my love for nature began. Above all, thanks to my partner, Tara Zuroweste, whose love, support, friendship, kindness, and knowledge affects all aspects of who I am and will be.

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INTRODUCTION

Amphibian Decline

Amphibians are in decline on a global scale (Blaustein and Wake 1990, Bury 1999). Every continent has at least several species which are known to be decreasing at an alarming rate. Several factors have been found to contribute to amphibian declines: land use change, invasion of non-native species (Dodd and Smith 2003, Collins and Storfer 2003), global climate change, disease, and contaminants (Collins and Storfer 2003).

Land use changes such as urbanization have caused severe fragmentation of essential amphibian habitats, although declines are also prevalent in relatively pristine areas (Herrmann et al. 2005, Nelson and Graves 2004). Loss of wetlands, some 90% in California alone since 1700 (Allen and Feddema 1996), or modification of hydroperiod or water table has dramatically affected spatial patterns and distributions of many amphibians (Muths et al. 2006, Dodd and Smith 2003). The California red-legged frog (*Rana draytonii*) has declined extensively in several parts of California and its distribution, once widespread, is now geographically fragmented (Shaffer et al. 2004). Davidson et al. (2001) found that habitat destruction played a significant role in *R. draytonii* declines. Invasion of the bullfrog (*Rana catesbeiana*) to the Western United States has also been a contributing factor in *R. draytonii* declines in California (Semlitsch 2003) and reduced growth of northern red-legged frog (*Rana aurora*) larvae in Oregon (Kiesecker 2001).

Other emerging factors contributing to amphibian decline are climate change, disease, and pesticides (Collins and Storfer 2003, Daszak et al. 2003). A fungal disease called chytridiomycosis has been linked to declines of the Yosemite toad (*Bufo canorus*) and several amphibian populations in Australia and Panama (Daszak et al. 2003, Green and Kagarise-Sherman 2001, Berger et al. 1998). Another disease, saprolegniosis, has been reported as the cause of decline in boreal toads (*Bufo boreas*) and Cascade's frog (*Rana cascadae*) in the Pacific Northwest (Kiesecker et al. 2001). Climate change has been predicted to play a role not only in the spread of these diseases, but also in altering weather patterns, which can affect habitat quality throughout a species' distribution (Carey and Alexander 2003, Semlitsch 2003). Widely used herbicides such as atrazine and glyphosate (active ingredient in Round-Up) have detrimental effects on amphibians, including hermaphroditism in male leopard frogs (*Rana pipiens*) and 40-80% mortality of tadpoles and juvenile anurans exposed to commercial levels of Round-Up (Relyea 2005, Hayes et al. 2003).

Amphibian Ecology

Amphibians have been classified as indicator species for biodiversity due to their dual life stages associated with both aquatic and terrestrial habitats (Noss 1990, Blaustein et al. 1994). Amphibians tend to be locally abundant, and thus supply a significant amount of biomass to their environment (Gibbons 2006). Aquatic larvae tend to be herbivores, while terrestrial adults are carnivores. Thus, amphibians can have direct or indirect effects on many other species in the environment. Natural history characteristics such as poikilothermy, relatively small home ranges and dispersal capabilities, and the permeable nature of their eggs, gills, and skin make them good indicator species (deMaynadier and Hunter 1995). Their status can be used to represent overall environmental conditions and perturbations (Noss 1990).

Studies of pond breeding amphibian spatial dynamics have traditionally taken a "ponds-as-patches" view in which subpopulations exhibit extinction and colonization as functions of pond spatial arrangement (e.g., discrete subpopulations; Marsh and Trenham 2000). Recent studies have shown these subpopulations might actually be patchy populations due to frequent dispersal between ponds (e.g., habitat or breeding patches; Petranka and Holbrook 2006). However, disturbed upland surroundings could increase the likelihood of decline by creating dispersal barriers between these "patches," such as roads or urban development. Also, studies have shown that some amphibians use these upland habitats not only as dispersal routes, but also for foraging between the breeding seasons (Fellers and Kleeman 2007). Thus, conservation of pond-breeding amphibians depends partly on the terrestrial habitats adjacent to breeding ponds. The quality of these terrestrial habitats has gained recent importance in the conservation of pond-breeding amphibians (Vasconcelos and Calhoun 2004). Movement phenology (immigration and emigration from breeding habitats) of pond-breeding amphibians can vary depending on particular species' breeding seasons and climatic conditions. Quantifying these movements to and from breeding habitats can provide information on critical time requirements a species needs in a particular habitat. It is also important for successful implementation of pond-breeding amphibian conservation and monitoring studies

(Timm et al. 2007). Habitat selection within breeding habitats, along with successful dispersal or migration into and out of breeding habitats, could play vital roles in survival of these species.

Monitoring and Management of Amphibians

Several traditional methods of monitoring and measuring amphibian population status and spatial dynamics have been used in the last decade. One approach to measure anuran abundance is the use of call surveys (Pope et al. 2000). The North American Amphibian Monitoring Program (NAAMP), a collaborative between several federal, state, and nonprofit organizations, has established a protocol for estimating anuran abundance of vocal amphibians. For anurans with inaudible or erratic calls, Crouch and Paton (2000) proposed egg mass counts to estimate anuran abundance. Mark-recapture and radio telemetry techniques have been used to estimate parameters such as survival, home range, dispersal distance, and upland habitat selection (Watson et al. 2003, Birchfield and Deters 2005). Wildlife-habitat modeling has often been used to predict occurrence (presence) of an amphibian within its range (Welsh et al. 2006), and estimates of occupancy can be used to monitor changes in the distribution over time (Schmidt 2005). These latter models correlate the presence or absence of a species in a certain area with measured site-specific habitat characteristics.

Until recently, these amphibian studies assumed that the individuals were detected with 100% accuracy in each site or that detection was constant over all the sites. With the exception of radio telemetry, each monitoring approach previously listed is limited by the ability to detect the species. Biases in parameter estimates can occur if the probability of detection (*p*) is <1 (<100% chance to detect the species) and is not taken into account (MacKenzie et al. 2002, Gu and Swihart 2004, Mazerolle et al. 2005). This is especially important in dealing with rare and/or cryptic species. When estimating detection probability, studies must include a large sample size using count or mark-recapture data to estimate abundance or population size. If numbers are small, large variances in *p* result which greatly increase the variance of the parameter being estimated (MacKenzie et al. 2005). This makes accurate population or abundance estimates both time consuming and costly. Not incorporating detection probability into wildlife-habitat or occupancy modeling can also lead to erroneous results and inferences (Mazerolle et al. 2005). Issues occur when a site is only sampled once and the species is recorded "absent" at that site. False absences undoubtedly occur because most wildlife species do not have a detection probability of 1. Although the importance of estimating detection probability in wildlife studies was first described in the 1980's (Nichols 1986, Bean and Willig 1989), it was not until two decades later that it was first incorporated into an amphibian study (MacKenzie et al. 2002).

MacKenzie et al. 2002 developed a likelihood-based approach that accounted for detection probability <1 to estimate site occupancy rates of two anuran species. Because the cost and effort of abundance estimation that incorporates detection probability can be exponential, they suggested that the proportion of sites occupied could be used as an alternative monitoring approach for amphibian distributions (MacKenzie et al. 2002, Gu and Swihart 2004). These occupancy models applied over a single season can be used to:

(1) describe or predict a species occurrence throughout its distribution or certain habitat (e.g. wildlife-habitat modeling, Ball 2005), (2) estimate the proportion of sites occupied by a species within a given area (e.g., national park or wildlife refuge; Smith et al. 2006), and (3) develop future research and/or a large-scale monitoring program throughout a particular landscape (e.g., Humboldt Bay watershed) or the entire species' distribution (Bailey et al. 2007). This method could also be used over multiple seasons to estimate patch extinction and colonization probabilities which are important to our understanding of amphibian spatial dynamics (MacKenzie et al. 2002). Nichols et al. 2007 have recently used a multiple state (estimating occupancy with another parameter such as reproductive success) approach to this modeling method to determine possible mechanisms for changes in extinction and emigration rates over time.

One assumption of the occupancy approach is that occupancy remains constant over the survey period. However, occupancy estimates can be modeled as function of site-specific covariates that can vary spatially (MacKenzie et al. 2002, Bailey et al. 2004, Mazerolle et al. 2007). Detection estimates can be modeled as functions of both site-specific and survey-specific covariates, thus, accounting for both spatial and temporal variation (Bailey et al. 2004). The US Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) has adapted this occupancy approach and is currently using this method to research long-term changes in amphibian populations by examining the number of breeding sites occupied (Muths et al. 2006).

Northern Red-legged frog (Rana aurora) Status and Natural History

The northern red-legged frog (*Rana aurora)*, is listed as a Species of Special Concern by the California Department of Fish and Game and a Sensitive Species by the US Forest Service (DFG 2006). The species' southern range extends only into the three most northern coastal counties of California and forms several disjunct subpopulations (Blackburn et al. 2002). The frog's northern distribution extends to the southern coast of British Columbia (Stebbins 2003). The species' elevation range is 0-1427m in Oregon (Leonard et al. 2000) and 0-300m in California (Jennings and Hayes 1994). It is only found west of the Cascade-Sierra crest (Stebbins 2003, Dunlap 1955). Although noted as a species of concern, studies on the spatial ecology of northern red-legged frogs, especially within California, are lacking. Studying *R. aurora*'s spatial dynamics at the southern periphery of its range could pinpoint specific habitat components necessary to keep the population from further decline (Goldberg and Schwalbe 2004). Understanding the species' range structure is also an integral part of conservation management practices (Fortin 2005).

Recent developments in the classification of *R. aurora* have distinguished it as a separate species from *Rana draytonii*, the California red-legged frog (Frost et al. 2006), which was previously classified as a subspecies of *R. aurora*. *Rana draytonii* is a federally threatened species. It has been suggested that intergradations with *R. aurora* occur in Mendocino County, CA (Jennings and Hayes 1994). However, *R. aurora* seems to be more closely related to the Cascades frog (*Rana cascadae*) according to mtDNA studies (Shaffer et al. 2004). Several implications arise for *R. aurora* status as a separate species in California. Most studies in California have been concerned with *R. draytonii* and not *R. aurora*. Thus, little is known about *R. aurora*'s distribution and population status in northern California. Most knowledge of the species' natural history and ecology come from studies in Oregon and Washington where the distribution is more continuous (Jennings and Hayes 1994). Declines have been documented in the Williamette Valley area of Oregon (Blaustein and Wake 1990), though thorough investigations of declines are still lacking (Pearl 2005).

Rana aurora's breeding season typically runs between January and March; however, egg mass oviposition has been noted as early as late November and as late as April in some areas (Stebbins 2003). Males typically arrive at the breeding area first and usually call beneath the surface of the water. Their call is short and quiet and can only be heard from a short distance away (Leonard et al. 2000). Time of breeding is variable depending on locality and precipitation, but most northern red-legged females within subpopulations deposit their eggs within two to three weeks of each other (Leonard et al. 2000). Breeding habitat has been associated with relatively longer hydroperiods, little or no flow of water, and presence of some submerged or emergent vegetation (Storm 1960). Females can lay up to 1300 eggs per clutch and are assumed to lay only once per season. The egg mass is usually attached to vegetation either at the surface or submerged in the water (Jennings and Hayes 1994, Licht 1971). Total time from oviposition to metamorphosis varies with water temperature, but typically takes between four and six months (Leonard et al. 2000, Jennings and Hayes 1994). *Rana aurora* tadpoles have the lowest thermal maximum for any North American ranid species at 21° C (Licht 1971) and are algal-grazers throughout most of their larval stage (Jennings and Hayes 1994).

Male and female adult frogs typically disperse soon after breeding has occurred, usually during storm events, although they can remain at breeding areas until ponds completely dry. They have been found in a variety of upland habitats and a single female has been recorded as far as 2.4km from an initial capture site (Hayes et al. 2001). Although such movements have been recorded, the range of movement over multiple seasons for 3 different species of ranids (*Rana pretiosa*, *Rana sylvatica*, and *Rana draytonii*) with a sample size of 170 was 30-1400m (Watson et al. 2003, Baldwin et al. 2006, Fellers and Kleeman 2007). Larger movements might represent more of the species' maximum dispersal capabilities. Taking refuge in burrows and aestivation has also been noted in some anurans during the dry season to avoid desiccation (Semlitsch 2003, Lamoureux and Madison 1999).

Objectives

I examined the spatial distribution and habitat selection of *R. aurora* in an isolated, yet relatively undisturbed, coastal dune environment. Specifically, this study sought (1) to describe the physical and spatial habitat relationship of frogs using the permanent ponds and those using seasonal ponds for breeding, (2) to describe movement phenology within and among habitats before, during, and after the breeding season, (3) to model and describe the factors that influence oviposition selection and post-breeding juvenile and adult habitat selection in the seasonal wetlands of the dune swales, (4) to predict and map occupancy likelihood for egg masses, and juvenile and adults, within the seasonal wetlands of the dune swales, and (5) using the site occupancy models, to provide a foundation for a large-scale monitoring program in which *R. aurora*'s population status and spatial dynamics can be assessed over the long-term in palustrine wetlands.

I specifically chose to concentrate the research in ephemeral ponds due to the breeding nature of *R. aurora*. The frogs generally breed in permanent water due to a relatively long period to metamorphosis (4 to 6 months). Egg masses and tadpoles in temporary ponds can be more vulnerable to desiccation in any given year due to seasonal changes in hydrology and climate or other environmental stochasticity. Also, ephemeral ponds tend to lack non-native predators such as certain fishes and bullfrogs (*Rana catesbeiana*) because they need permanent waters for survival.

Although this is a highly localized study, implications for proper management of *R. aurora* in seasonal wetlands can be made due to the use of a deductive approach to the egg mass occupancy modeling and the generalized nature of the factors associated with all ephemeral wetland environments. This research is the first to examine movement patterns and habitat selection in a dune environment and to provide estimates of egg mass detection probability in seasonal wetlands for the northern red-legged frog.

MATERIALS AND METHODS

Study Area

All research was conducted in two adjacent properties on the North Spit of Humboldt Bay, CA (Figure 1). The larger property (approximately 263ha) is the Lanphere Dunes Unit of the Humboldt Bay National Wildlife Refuge. The Lanphere Dunes is unique in being a relatively pristine Pacific coastal dune and estuary habitat (Pickart 2002). Ephemeral dune swales, dune forest, deciduous swamp, and a small, slow-moving, perennial creek are all habitat types associated with the dune system in which the frog potentially occurs. Management in the dunes consists of exotic plant species removal, coastal dune habitat restoration, endangered and threatened plant species monitoring, and various research on coastal dune ecology. Public use of this area is monitored and limited to permit use only. A research permit (USFWS Special Use Permit #81590 – 07003) was obtained to conduct my study on this property.

The privately-owned adjacent land is approximately 16 hectares. Frog habitat consists of grazed pastureland, permanent ponds, and a channel which empties through floodgates into the Mad River Slough on both the north and south side of the study area. The permanent ponds were created in the past ten years and are under conservation easements from the USDA Farm Bill. Vegetation associated with the permanent ponds and channel ranges from sedges (*Carex*), rushes (*Juncus*), and bulrushes (*Scirpus*) to grasses (*Distichlis*) to floating herbaceous vegetation (*Hydrocotyle*). Other herbaceous genera represented include *Eleocharis*, *Glyceria*, and *Oenanthes.* This area was

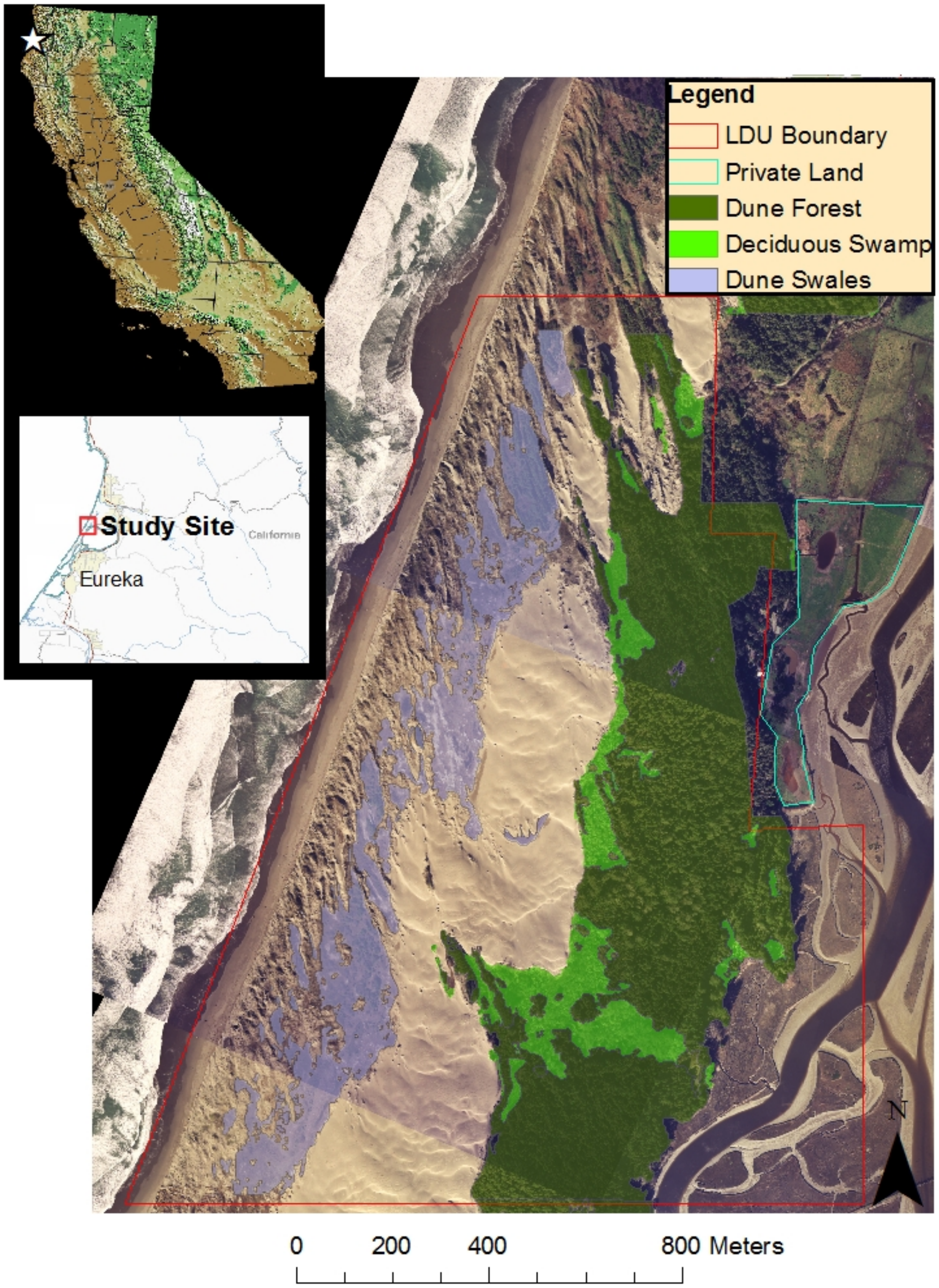

Figure 1. Study site and potential habitat for the northern red-legged frog (RAAU).

originally tidal-influenced wetlands, but was diked and converted to pastures over 100 years ago.

The dunes swales are home to several palustrine wetlands that lie in depressions behind dune ridges. During the rainy season (December to May), these depressions form a number of fluctuating, ephemeral ponds created by a rising water table that lies slightly above sea level. Most of these seasonal ponds are within 100 meters of the Pacific Ocean. Both herbaceous and woody hollows occupy the dune swale habitat. The herbaceous hollows predominately contain the ephemeral ponds and are associated with hydrophytic vegetation such as *Carex obnupta* and *Juncus breweri* (Pickart and Sawyer 1998).

The upland dune forest consists of older, stabilized dunes that are covered by a thin layer of soil which supports several coniferous and deciduous tree species, dense shrubbery, and thick ground cover. Some examples of more common vegetation species in the upland forest are beach pine (*Pinus contorta*), California huckleberry (*Vaccinium ovatum*), and salal (*Gaultheria shallon*). The dune forest also contains depression areas which become saturated swamps during the rainy season and are associated with thick canopies of Hooker willow (*Salix hookeriana*). Riparian areas along a small creek called Iron Creek are dominated by Red Alder (*Alnus rubra*) and also contain a dense canopy cover. This creek is the only known water source for those frogs breeding in the dunes swales during the summer.

The large tract of dense dune forest, predominately owned by the refuge, separates the two main frog breeding areas (permanent pasture ponds and temporary ponds in dune swales). Making dispersal between the two breeding habitats even more difficult is a large, barren tract of unvegetated, moving dunes that separates the east boundary of the dune forest from the dune swales. The entire study area is virtually isolated. It is separated from the inland farmlands by the Mad River Slough to the east and bordered by the Pacific Ocean to the west. It lies on the northern end of the spit which extends approximately 24km in length and is less than 1.5km in width (Pickart and Sawyer 1998).

Pilot Study

A pilot study was conducted between November 2005 and May 2006. All permanent and temporary ponds were mapped using a Global Positioning System (GPS) unit (Garmin GPSmap 76CS) with an accuracy of +/-3m, and entered into a Geographic Information System (ArcGIS, ESRI 2005). Seasonal ponds were measured at the peak of the rainy season (between January 15-20, 2006) to obtain maximum pond size. Presence/Absence surveys for egg masses were conducted in all ponds (permanent and temporary) from February through March of 2006. By using the proportion of egg masses found in these pond surveys, a naïve (without incorporating detection probability) estimate of egg mass occupancy for the breeding season was calculated in the ephemeral ponds and used in the design of the occupancy models (see Occupancy Surveys section below). An initial count of egg masses was also made in the permanent ponds.

Visual encounter surveys (VES) were also performed in permanent and seasonal pond habitats from February through April of 2006. Three VES's were conducted in the pastures on February 24 and 25 and April 1 of 2006. Only one VES was performed in the dune swales on April 18, 2006. All VES's were conducted in the afternoon with overcast skies. The perimeters of each pond in both habitats and the perimeter of the channel surrounding the pastures were surveyed. The perimeters were surveyed in a zigzag method no more than 2m from the water's edge. For each frog captured, I measured snout-vent length (SVL), weight, life history stage (adult or juvenile), and malformation presence. Frogs were recorded as adults if their SVL was greater than or equal to 40mm and juveniles if their SVL was less than 40mm. Adults were marked with Passive Integrated Transponder (PIT) tags (8.5mm x 2.02mm, BIOMARK 2005). The PIT tags were inserted underneath the skin of the frog through a minute V- shaped incision into the skin on the dorsum just above the sacral hump. All handling and marking of the frogs was approved by the Humboldt State Institutional Animal Care and Use Committee (protocol # 05/06.B.40.A) and carried out under a California Department of Fish and Game Scientific Collecting Permit (# SC – 008379).

Egg Mass Counts

In the pasture habitat, there were three conservation ponds and a permanent channel surrounding the property in which egg mass counts were made in the 2006, 2007, and 2008 breeding seasons. The perimeters of the permanent ponds were initially surveyed in February 2006 and egg masses were identified up to a meter in water depth. Flagged bamboo sticks were placed next to each egg mass so they would not be counted twice. In the dune swales, a single temporary pond was used to count egg masses during the 2007 and 2008 breeding seasons. This pond had contained the majority of egg masses previously observed in 2006. This temporary pond was surveyed to look at the variation in egg mass abundance per year and to compare relative abundance with the most populated permanent pond in the pastures. The ephemeral pond was surveyed in a zigzag, systematic manner throughout the entire area of the pond and the total number of egg masses detected within the pond was recorded.

Pitfall Traps

Movement between the two breeding habitats (permanent and seasonal ponds), breeding chronology, and relative abundance of the frogs within and between each habitat were examined using drift fences and pitfall traps. Each drift fence was 10 meters in length with 18.9 liter pitfall buckets placed on the ends of each side of the fence. A cover board with a hanging string was placed approximately 15cm above each bucket to allow other species such as small mammals and tree frogs to climb out (Karraker 2001) and protect captured animals from the elements. Each fence had 4 pitfall traps and was randomly placed along the ecotones of each breeding habitat next to the dune forest (Figure 2). Random sites were generated in ArcMap (ArcGIS 9.1, ESRI 2005) using X, Y spatial coordinates of the perimeter of the forest. A total of 10 fences (5 on each side of the forest) and 40 pitfall traps were set out and checked every few days for captures from November 10, 2006 to May 15, 2007. The fences and traps were strategically placed between the breeding ponds and the dune forest. They were placed on a North-South axis line which enabled movements to be determined as traveling either east or west. For example, a frog captured in a trap on the east side of a drift fence was assumed

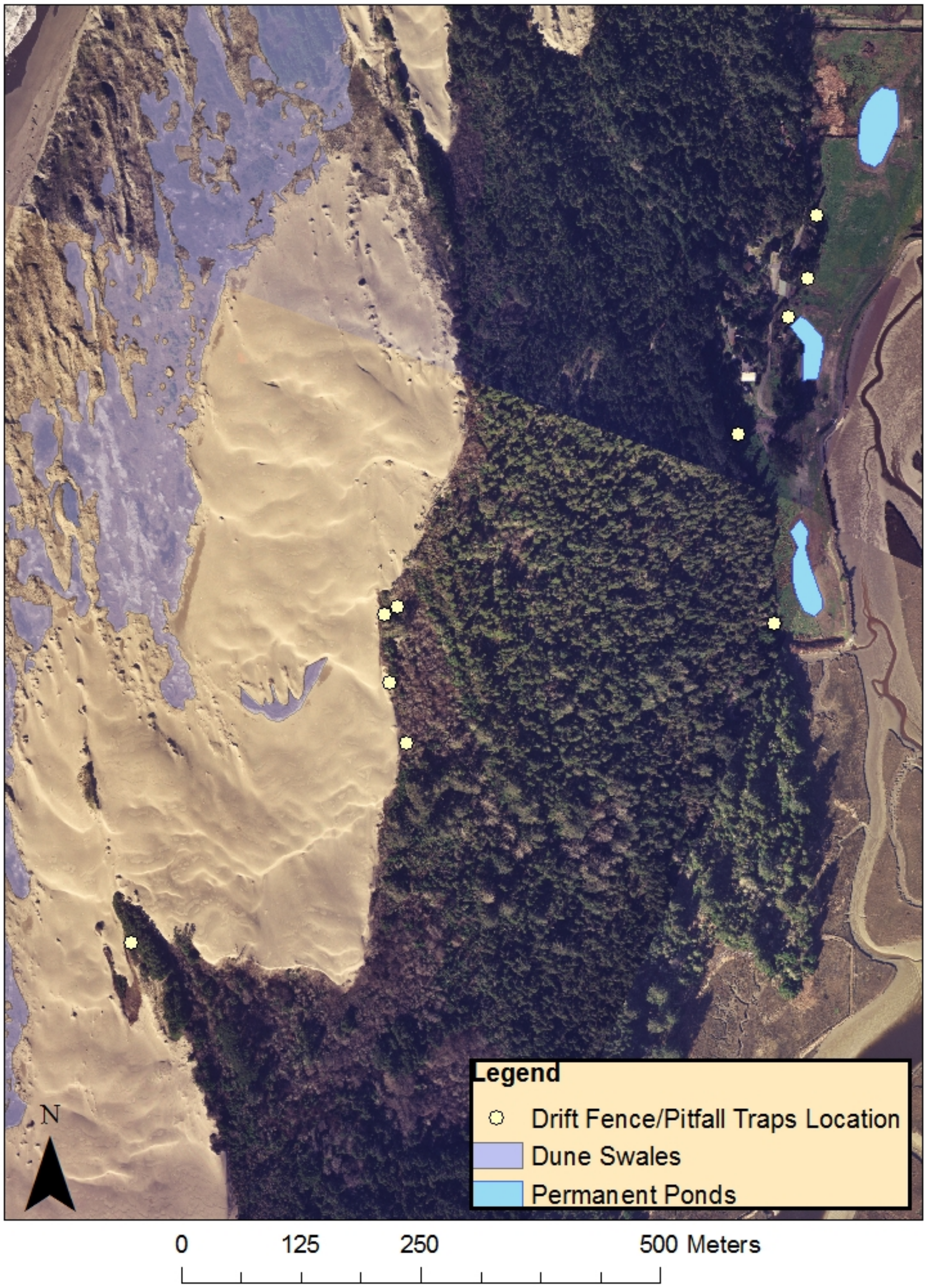

Figure 2. Locations of the ten drift fences on each side of the dune forest.

to be moving west. This directional movement was later recorded as the frog traveling to or from the pond habitat. The pitfall data were divided into three “seasons” depending on the date of capture: “pre-season” data consisted of frogs captured between November 10 and December 15, “breeding season” was between December 16 and March 16, and “post- season” was between March 17 and May 15. Physical measurements and marking of the red-legged frogs captured in the pitfall traps were as described in the Pilot Study section above. Any mortality in the traps was also noted. Other environmental variables recorded when the pitfall traps were checked were weather conditions, 24 hour rainfall, and temperature.

Occupancy Surveys

All surveys for egg mass occupancy (detection/nondetection) were conducted within the dune swale habitat. To determine the number of sites needed in the study, preliminary estimates of occupancy and detection, along with effort and precision were taken into consideration (MacKenzie et al. 2006). Data from the pilot study were used to calculate a naïve estimate of egg mass occupancy of 0.13 (i.e., 13% of the ponds contained egg masses that were detected in the initial survey). Research on detection probability of anuran egg masses is currently lacking, so a range of estimates from 0.5 to 1 were used to determine the proper allocation of sites. Using these estimates for occupancy and detection probability, the estimated minimum number of surveys needed at each site (MacKenzie et al. 2006) was 2 to 3. I chose to conduct three surveys at each site to maximize the probability of detecting an egg mass at least once within each site. Reasonable precision was set at standard error for occupancy estimate ≤ 0.05 and effort was set not to exceed 80 sites. With these conditions, 66 sites were determined necessary (MacKenzie et al. 2006). The number was raised to 76 to allow for possible exclusion of some sites that did not meet defined standards (e.g., sites with no water during the survey period).

The ephemeral ponds mapped in January of 2006 were used in a GIS (ArcGIS 9.1, ESRI 2005) to randomly generate 76 sites within the pond areas. Ponds less than 100m^2 were not used. Due to the particularly high precipitation during the rainy season in winter of 2005-2006, the ponds were larger than average. Thus, many areas that were inundated in 2006 were dry in 2007. The dune swales at the north boundary of the property were not used in generating the sites due to no frogs, egg masses, or water being sighted in the swales in previous years' observations.

A site was defined as a 10 x10m area within the seasonal ponds. Defined sites were used instead of individual ponds so the survey area would remain constant during the season. Seasonal ponds can vary in number and size throughout the rainy season due to variation in precipitation. This would cause added variables and unwanted noise in the occupancy models. Spatial coordinates were taken in a GIS of the dune swale habitat and used in the random generation of the site locations. Computer generated, random spatial (X,Y) coordinates which represented the SW corner of a site were mapped in GIS and all site locations not within the previously mapped ponds were disregarded. Coordinates were generated until a total of 76 site locations were established within the suitable ponds (Figure 3). All sites were then marked in the field with bamboo sticks representing the SW corner. When an individual site was surveyed, North and East compass bearings were taken from the bamboo stick and 10m was measured in each direction. The remaining site corner was established next by shooting the last cardinal bearing (either East or North) from one of the previously established corners.

Once the sites were established, visits were made every other day to ponds where the previous year's egg masses had been observed. Once an egg mass was discovered in a pond, detection/nondetection surveys of all the sites were begun within three weeks. *Rana aurora* breeding usually lasts only two to three weeks, so this lag time maximized the chance that the majority of breeding frogs had deposited their egg masses before the surveys had begun. Three separate surveys of all the sites were conducted. The first survey was conducted between January 19 and 24, the second survey between February 2 and 3, and the third survey between February 11 and 17 of 2007. To avoid observer bias, a different observer who had no prior knowledge of egg mass locations was used in each survey. Start sites were chosen at random by computer for each survey to minimize introduced heterogeneity of detection at certain time periods. All sites were surveyed using a zigzag, systematic, quadrat method (Heyer et. al. 1994). Each individual site was completely surveyed regardless of whether an egg mass was detected before that particular site's survey was complete. Besides northern red-legged frog egg masses, detection/nondetection was also noted for Pacific chorus frogs (*Pseudacris*

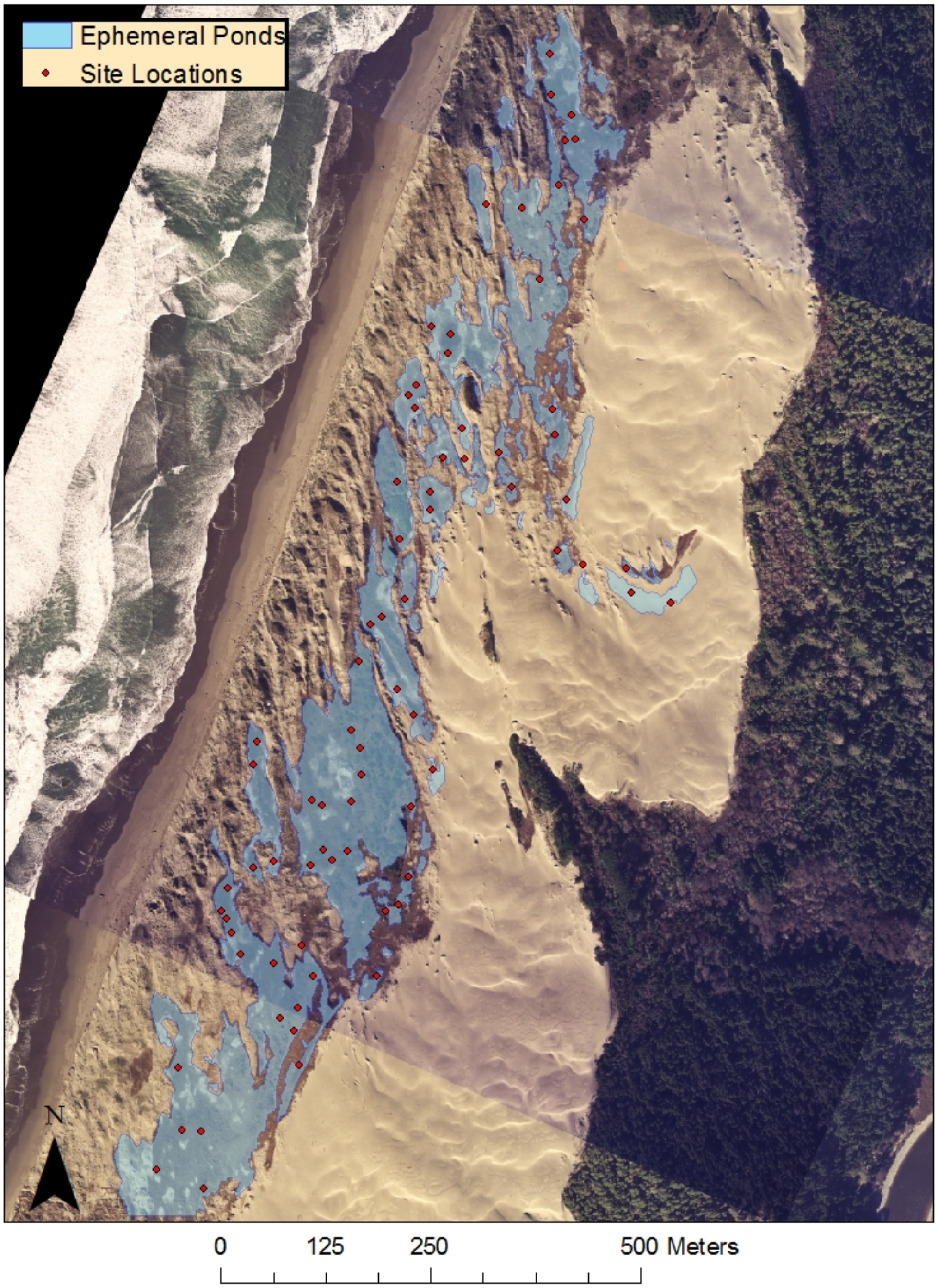

Figure 3. Site locations for the egg mass occupancy and terrestrial stage habitat selection surveys.

regilla). Detection/nondetection was also recorded for adult and juvenile *Rana aurora* and *Pseudacris regilla*.

Habitat and Vegetation Covariates

Water depth, water temperature, percent emergent vegetation, and percent of the site that contained standing water were recorded at each site during each occupancy survey. Water depth and water temperature measurements were taken in the deepest area of each site. Water temperature was recorded no deeper than 5 cm below the water surface. Percent emergent vegetation and percent of the site that contained standing water were measured using ocular estimates with ranges between 0-20, 21-40, 41-60, 61-80, 81-100. Weather conditions were also recorded for each survey and surveys did not take place during heavy rain or high winds. Salinity and pH measurements were taken for the first survey only.

Vegetation surveys were conducted in the 10 X 10m breeding units after the ephemeral ponds had dried to minimize impact on frog larval development. This survey took place between June 6 and 11, 2007. Vegetation covariates recorded were the percent of woody cover, *Carex obnupta* cover, *Scirpus* cover, other herbaceous vegetation cover, and total vegetation cover. Woody vegetation cover measurements were taken using ocular estimates with the ranges between 0-20, 21-40, 41-60, 61-80, 81-100 percentile ranges. All other vegetation measurements were recorded using ocular estimates of the Daubenmire percent classes: 0-5, 6-25, 26-50, 51-75, 76-95, and 96-100 (Daubenmire 1959).

Additional Surveys

A habitat selection survey was also performed on April 16, 2007, for adult and juvenile red-legged frogs. I define habitat selection in this study as the occupancy of at least one individual post-metamorphic (adult or juvenile) frog within a defined site during the particular survey. This detection/nondetection survey was conducted on all the previous sites to compare breeding site selection of adult females to post-breeding habitat selection by juveniles and adults. One assumption of occupancy surveys incorporating detection is that the species remains in the site for the entire survey period (i.e., "occupancy is closed," MacKenzie et al. 2002). Because the sites were only 100 m^2 and some were within several meters of each other, adult and juvenile frogs were assumed to be moving between the sites. Thus, all sites were surveyed only once. This did not allow detection probability to be estimated in the habitat selection models. Individual sites were surveyed in the same zigzag, systematic quadrat method (Heyer et. al. 1994) as used for egg masses for consistency. If a red-legged frog was detected, it was either captured or identified and the particular site was recorded as occupied. Adult and juvenile Pacific chorus frog presence was also noted.

Hydroperiod surveys at each site were continued monthly until all ponds had dried. The last hydroperiod survey was conducted on June 15, 2007. Water depth and percent of the site with standing water continued to be recorded for each site with any remaining water. Hydroperiod length, recorded in number of weeks with standing water, was then calculated for each site.

Statistical Analysis

One-way ANOVA’s were used to analyze differences in weight and length of the frogs in the two breeding habitats. Chi-square and Fisher’s exact tests were run in S-PLUS (Insightful 2000) to analyze all movement and breeding chronology data.

Occupancy models were developed and analyzed in program PRESENCE 2.0 (MacKenzie et al. 2003). MacKenzie et al. (2003) developed this program to incorporate detection probabilities into occupancy estimates when using a repeated survey design. The model accommodates variation in occupancy and detection probability as functions of site conditions (site covariates) and temporal variation (sample covariates). Site covariates used in the models were hydroperiod length (HYDRO), average water depth over the hydroperiod of the site (AWD), average percent of site with standing water (ASH), distance from the site to the dune forest (DIF), percent emergent vegetation (EMV), percent woody vegetation (WDY), and the percent of other herbaceous cover (OHB) for each site (Table 1). Water temperature was removed from the analysis due to very little variation between ponds. All ponds were greater than 6 degrees Celsius, which correlates with initiation of breeding (Storm 1960 and Licht 1971). Sample covariates used in the models were water depth (WD) and weather (WTH) during each survey, and percent woody vegetation (WDY) for each site. Occupancy (ψ) was estimated as a function of site covariates and detection (p) was estimated as a function of site and sample covariates. In order to reduce the number of covariates in the models, the percent

Table 1. Covariates used in egg mass occupancy models for probability of occupancy and probability of detection.

ψ[a]		
Type	**Covariate**	**Description**
Pond	AWD	Average water depth of the site (cm)
	HYDRO	Hydroperiod length (weeks)
	ASH	Average percent of the site with standing water
	EMV	Average percent emergent vegetation (*Carex obnupta*)
Spatial	DIF	Distance from the site to the dune forest (m)
Vegetation	WDY	Percent woody cover of the site
	OHB	Percent other herb cover of the site
p[b]		
Pond	WD	Water depth during each survey (cm)
Climatic	WTH	Weather during each survey
Vegetation	WDY	Percent woody cover of the site

[a] Probability of occupancy.
[b] Probability of detection.

woody vegetation and percent other herb covariates were reduced to two categorical variables: 0-40% and 41-100%. Percent emergent vegetation and average percent of site with standing water were treated as continuous variables and standardized by the estimated mode. All other continuous variables were standardized using the estimated mean. Five sites never produced standing water. These sites were eliminated because it was assumed the site must contain standing water during some period of the wet season in order for egg deposition to occur. This left a total of 71 sites.

Twenty-five *a priori* models were developed based on pond, spatial, and vegetation characteristics (Table 2). All covariates used in the models were assumed to have a linear relationship with egg mass occurrence and detection. Time of survey was also used as a sample covariate for detection probability. Thus, each survey period in some of the models has an estimate for detection probability of the egg masses. The pilot study observations, previous research, and collaboration with other wildlife biologists (L. Bailey, pers. comm., June 2006) were used in development of the *a priori* models. Due to the assumed significant multicollinearity between average water depth (AWD) and hydroperiod (HYDRO) of each site, these two covariates were modeled separately. The two global models (one which included hydroperiod and one which included average water depth) were run first in PRESENCE. A parametric bootstrap (n=10,000) was run with each model to assess Goodness-Of-Fit and adjust the variance inflation factor ($\hat{c}$) if the model was overdispersed (MacKenzie and Bailey 2004). The models were ranked according to lowest corrected AIC (AIC_c) values. The AIC_c adjusts models with smaller

Table 2. Models selected *a priori* to analysis of egg mass occupancy in program PRESENCE. Each model represents a LOGIT equation with and without covariates[a] for determining occupancy and detection estimates.

Egg Mass Occupancy Models
Null Model[b]
ψ (.),p(.)
Full Model
ψ (AWD+DIF+ASH+EMV+OHB+WDY)p(t+WD+WTH+WDY)
ψ (HYDRO+DIF+ASH+EMV+OHB+WDY)p(t+WD+WTH+WDY)
Pond Models
ψ (AWD),p(WD)
ψ (HYDRO),p(WD)
ψ (ASH),p(WD)
ψ (.),p(WD)
Pond + Environmental Models
ψ (AWD),p(WTH)
ψ (AWD+DIF),p(.)
ψ (HYDRO+DIF),p(WD)
ψ (DIF),p(WTH)
Pond + Environmental + Vegetation Models
ψ (AWD),p(WTH+WDY)
ψ (HYDRO+EMV),p(WD)
ψ (EMV+OHB),p(WD+WDY)
ψ (EMV),p(WD)
ψ (AWD+DIF+ EMV),p(WD+WDY)
ψ (HYDRO+DIF+EMV),p(WDY)
ψ (WDY+ASH),p(WD)
ψ (EMV),p(WTH+WDY)
ψ (EMV+WDY+OHB),p(WDY)
ψ (EMV+WDY),p(WTH)
ψ (AWD+WDY),p(.)
Temporal Models
ψ (AWD+EMV)p(t+WD)
ψ (HYDRO),p(t+WD)
ψ (HYDRO+EMV),p(t+WD)

[a] See Table 1 for the descriptions of the covariates used in egg mass site occupancy models.

[b] Null model was assumed occupancy and detection was constant across all sites (.).

sample sizes. Parametric bootstraps were also run on the top models. “Top models” were defined as those whose sums of their Akiake’s weights were ≥95%. Variables in these top models were averaged and ranked according to their relative strength of association with occupancy.

General Linear Models (GLMs) with a Logit-link function were performed in S-PLUS for the adult/juvenile, post-breeding, habitat selection models. Only a naïve estimate of occupancy was obtained for this survey. Detection probability could not be measured for these models because each site was only surveyed once. Thus, occupancy for the terrestrial stages might be underestimated. All site covariates in the occupancy models were also used in the habitat selection models with the exception of percent emergent vegetation. This variable was replaced with percent Carex obnupta (CAOB). Percent Carex obnupta was more relevant for adult or juvenile habitat selections because post-metamorphic stages of anurans are not always found in water. Distance from the nearest “detected” egg mass site (DEM) was also measured in a GIS and used as another covariate in these models (Table 3). It was not assumed that standing water must be present for terrestrial stage habitat selection so all 76 sites were used in these models. Fifteen a posteriori models were developed for this analysis (Table 4). Since detection probabilities were not included in these models, AIC values in these models cannot be directly compared with the egg mass occupancy AIC values. However, differences in factors associated with egg mass oviposition and terrestrial stage habitat selection for both modeling techniques can be compared. Differences in the performance of each

Table 3. Covariates used in juvenile/adult habitat selection models for probability of occupancy only.

ψ[a] Type	**Covariate**	**Description**
Pond	AWD	Average water depth of the site (cm)
	HYDRO	Hydroperiod length (weeks)
	ASH	Average percent of the site with standing water
Spatial	DIF	Distance from the site to the dune forest (m)
	DEM	Distance from the site to the nearest occupied egg mass site (m)
Vegetative	CAOB	Percent *Carex obnupta* foliar cover of the site
	WDY	Percent woody cover of the site
	OHB	Percent other herb cover of the site

[a] Probability of occupancy.

Table 4. Models selected *a posteriori* for terrestrial stage habitat selection models. Models represent LOGIT equations with covariates as functions of the occupancy parameter estimation. Probability of detection was not incorporated into these models.

Adult and Juvenile Site Occupancy Models
Full Models
Ψ^a (HYDRO + ASH + DIF + DEM + CAOB + WDY + OHB)
ψ (AWD + ASH + DIF + DEM + CAOB + WDY + OHB)
Pond Models
ψ (HYDRO)
ψ (AWD)
Pond +Spatial Models
ψ (DEM)
ψ (HYDRO + DEM)
Pond + Spatial + Vegetation Models
ψ (DIF + DEM)
ψ (HYDRO + ASH)
ψ (WDY + DIF)
ψ (CAOB + OHB)
ψ (AWD + DIF + DEM)
ψ (AWD + CAOB + DIF)
ψ (HYDRO + CAOB + WDY)
ψ (CAOB + DIF + DEM)
ψ (ASH + DIF + WDY)

[a] Naïve probability of occupancy (no detection probability)

occupancy modeling approach can also be compared. A bootstrap (n=10,000) was run on the full models and a ĉ value calculated using the deviance values. The models were ranked according to the lowest corrected Quasi-AIC ($QAIC_c$) values. Quasi-AIC inflates standard errors and provides rankings of more robust estimates when models are overdispersed. The top model was evaluated using a classification table and a receiver operating characteristic (ROC) report. Model averaging was also performed for the top habitat selection models. Variables were then ranked based on their relative strength of association with occupancy.

Occupancy Mapping

Using the top occupancy model and a GIS, a breeding suitability map of the ephemeral ponds in the dune swales was created. A probability of occupancy for each site location was calculated and added as a field to the attribute table of site locations in ArcMap 9.1 (ESRI 2005). Summary statistics of site locations in each pond were used in creating a mean probability of occupancy for each pond. If the pond only contained one site location, then that site's probability was used for the entire pond. Mapped ponds which did not contain at least one site location were not used in the creation of the suitability maps. A post-breeding, adult and juvenile habitat suitability map was also created using the top habitat selection model and a GIS. This map was created using the same techniques as the egg mass occupancy map, however, occupancy probabilities were replaced with habitat selection probabilities.

RESULTS

RAAU Abundance

At total of 217 adult and juvenile *R. aurora* were captured from February 2006 to May 2007. Of these, 125 were caught in the pastures and 92 in the dunes. Of the 125 caught in the pasture, 58 were classified as juveniles (<40 mm SVL) and 67 were classified as adults (≥40mm). Of the 92 caught in the dunes, 52 were juveniles and 40 were adults. Relative abundance for adults in each habitat was 3.52 frogs/acre in the pastures and 0.77 frogs/acre in the dune swales. Of the 104 PIT-tagged adult frogs, only three were recaptured during the sampling period (November 2006 - May 2007). All three were recaptured in the same habitat (pastures) and in the same drift fence traps in which they were first captured. Of all the frogs captured, 22 were caught from February 2006 to May 2006 during VES. Between November 2006 and May 2007, 148 RAAU were caught in the pitfall traps. All other frogs captured (n=47) were recorded as incidentals during other surveys. Using the pitfall traps, VES, and incidental data on captures of the adults, the pasture habitat had 4.5 times more frogs encountered than the dune swales. Six other species of herpetofauna were also captured in the pitfall traps (Table 5).

A total of 55, 82, and 119 egg masses were found in 2006, 2007, and 2008, respectively. Pond 2, nearest to the home site, contained the majority of the egg masses (Figure 4). The temporary swale pond surveyed contained 46 egg masses in 2007 and 36

Table 5. A list of the other herpetofauna captured in the pitfall traps.

Species	**No. Captured**	**Avg SVL (mm)**	**Avg Weight (g)**
Ambystoma gracile	6	62.3	7.3
Batrachoseps attenuatus	2	32.5	1.0
Elgaria coerulea	2	61.0	5.0
Ensatina eschscholtzii	2	41.0	2.5
Pseudacris regilla	5	25.5	2.2
Taricha granulosa	12	42.1	3.2

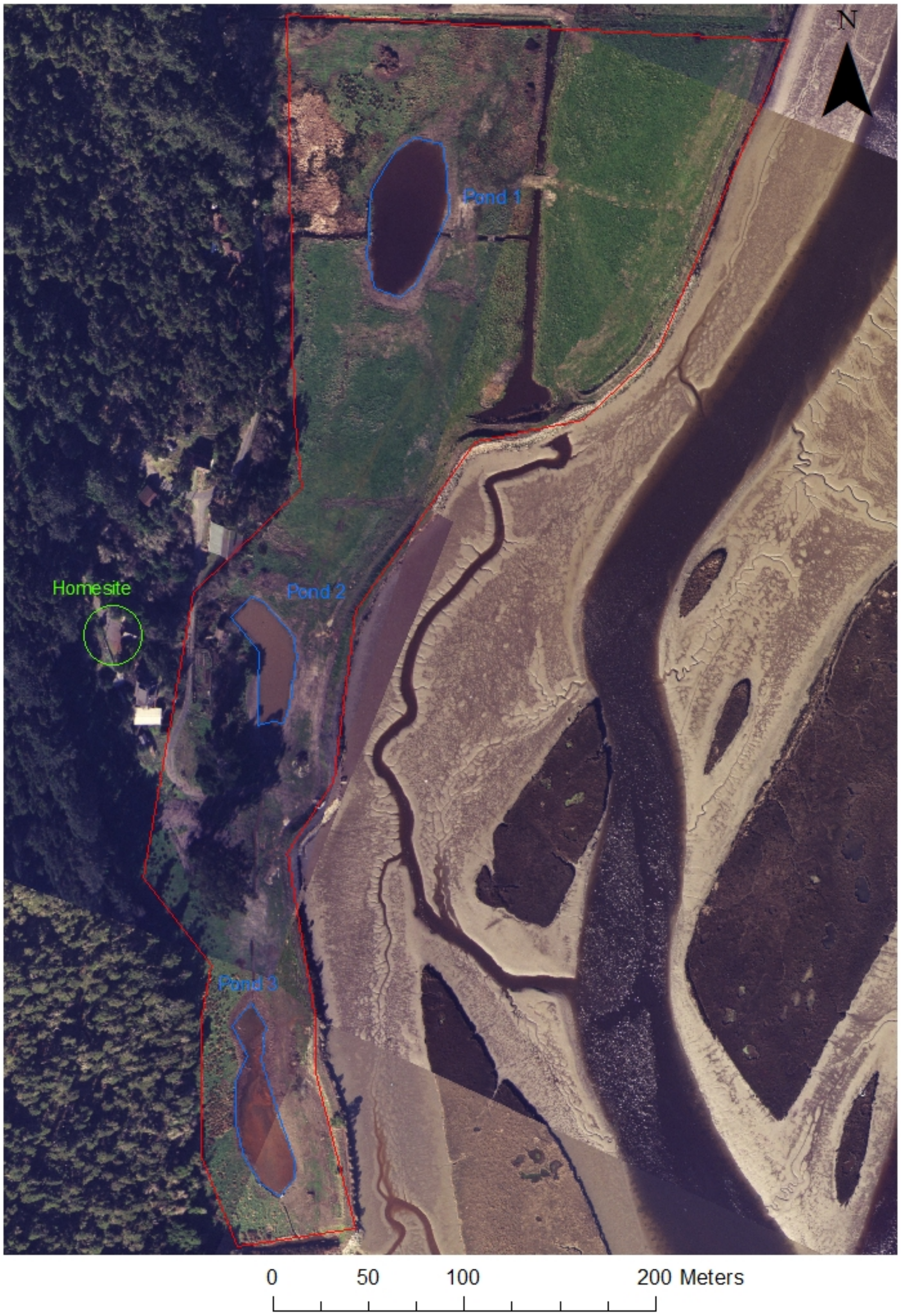

Figure 4. The three permanent ponds in the pasture habitat. The majority of egg masses each year were found in Pond 2.

in 2008. Based on the egg mass counts, relative abundance for breeding females was 4.31 females/acre in the pastures and 0.88 females/acre in the dune swales.

Physical Characteristics

Mean SVL and weight for the juveniles and adults in both habitats are summarized in Table 6. Neither weight nor SVL of the adults or juveniles varied significantly between habitats (Table 7). Although averages did not vary significantly between habitats, the largest frog was found in the pasture and the smallest was found in the dunes (Figure 5). Three frogs were recorded with abnormalities. All three were found in the pasture habitat and the abnormalities ranged from shortened to joined digits.

Movement Phenology

Frog movement to and from the ponds, as determined by the drift fence and pitfall traps, significantly varied by season, but not between habitats and life stages (Table 8). The greatest movement to the ponds occurred during the breeding season (Figure 6). When frogs were split into life stages (adults and juveniles), movement between the seasons did vary depending on life stage (Figure 7). Adult frogs were more active during the breeding and post-breeding seasons while juveniles were more active during the pre-breeding and breeding seasons. Movement also differed significantly depending on rainfall 24 hours prior to checking the pitfall traps (Table 8). Frogs were significantly more active when rain had fallen within 24 hours. When no rain had fallen in the past 24

Table 6. Summary statistics for adult and juvenile SVL (mm) and weight (g) in both breeding habitats.

	n	Habitat	Mean SVL	SE	Mean Weight	SE
Adults	39	Dunes	48.97	1.16	12.30	1.03
	67	Pasture	48.34	1.09	11.64	0.94
Juveniles	51	Dunes	33.35	0.49	3.38	0.13
	58	Pasture	34.09	0.45	3.64	0.17

Table 7. Results of ANOVA analyses of SVL (mm) and weight (g) between breeding habitats in both adults and juveniles.

	n	Variable	MS	F Value	p value
Adults	106	SVL	9.82	0.14	0.71
	104	Weight	10.24	0.2	0.66
Juveniles	109	SVL	14.59	1.22	0.27
	105	Weight	1.69	1.31	0.25

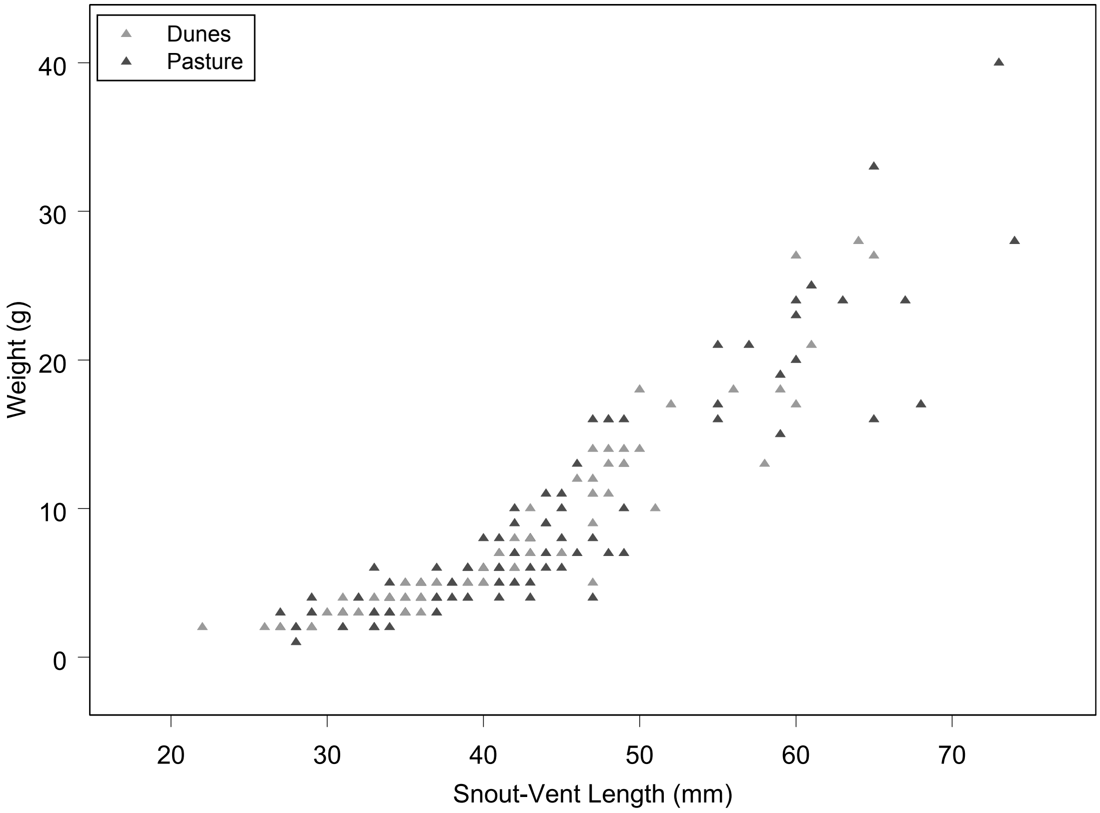

Figure 5. The relationship between weight and snout-vent length (SVL) of all frogs in each breeding habitat.

Table 8. Pearson's chi-square results when tested for differences with movement.

	χ^2	DF	p-value
Season	14.26	4	0.001
Habitats	3.59	2	0.17
Life stages	3.67	2	0.16
24HR Rain	7.93	2	0.02

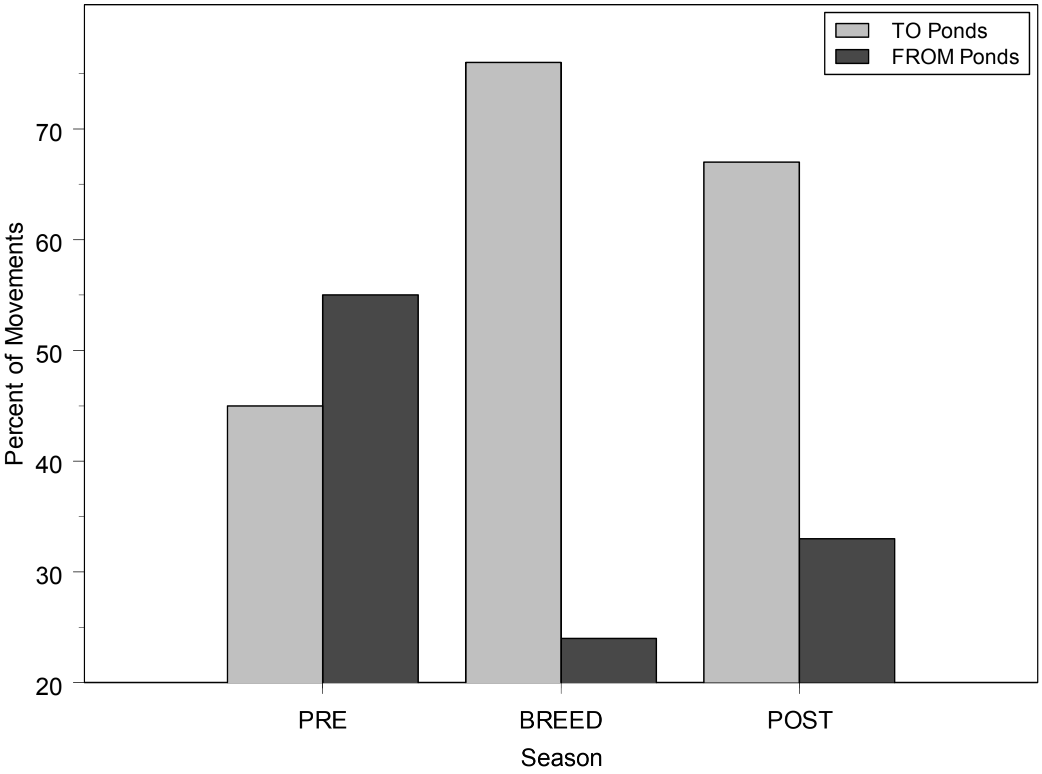

Figure 6. Differences in frog movement to and from the ponds during the pre-breeding, breeding, and post-breeding season.

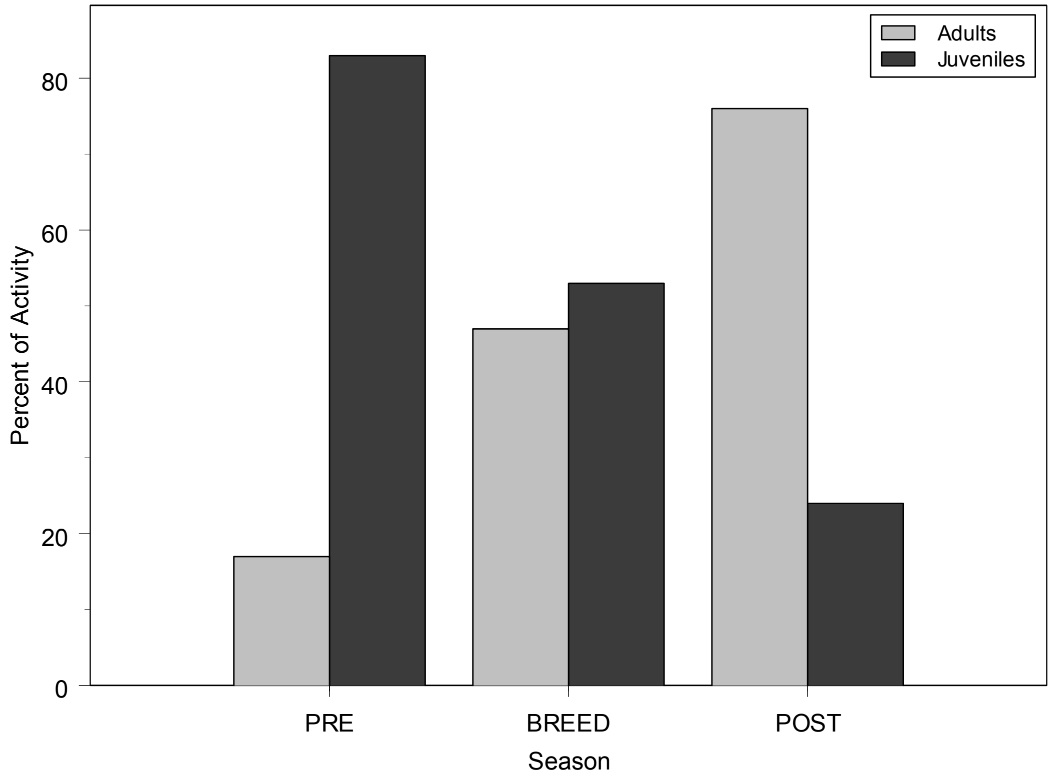

Figure 7. Differences in frog activity between adults and juveniles during the pre-breeding, breeding, and post-breeding seasons.

hours, frog movement was more likely to be towards the ponds. Juvenile frogs were 4.5 times more likely to be active after 24 hour rainfall then after no 24 hour rainfall. Adult movement activity did not vary whether it had previously rained or not. An exception to this occurred in the pre-breeding season when adults were 12 times more likely to be active after 24 hour rainfall. Two large movements of all frogs occurred in December and February, each during a week with a large amount of precipitation (Figure 8).

Egg Mass Occupancy and Oviposition Site Selection

Egg masses were found in 9 of the 71 sites surveyed, giving a naive estimate (assuming detection=1) of egg mass occupancy of 0.14 in the dune swale habitat. The parametric bootstrap for each global model showed no lack of fit or overdispersion (Table 9). Since the $\hat{c}$ value was less than 1, adjustments for QAIC were not necessary. All models were only adjusted for small samples sizes and were ranked according to AIC_c. Table 10 lists all models ranked according to the lowest AIC_c values. The best fitting model had occupancy as a function of average water depth (AWD) and percent emergent vegetation (EMV), and the probability of detection as a function of time plus the water depth (WD) during each survey (AIC_c=55.76, w_i=69%). For the top model, AWD for occupancy (ψ) was significant at the 95% confidence level and WD for detection (*p)* was significant at the 90% confidence level. AWD had a positive relationship, while EMV had a slightly negative relationship with ψ. The next closest fitting model included hydroperiod length (HYDRO) instead of AWD (AIC_c=58.01,

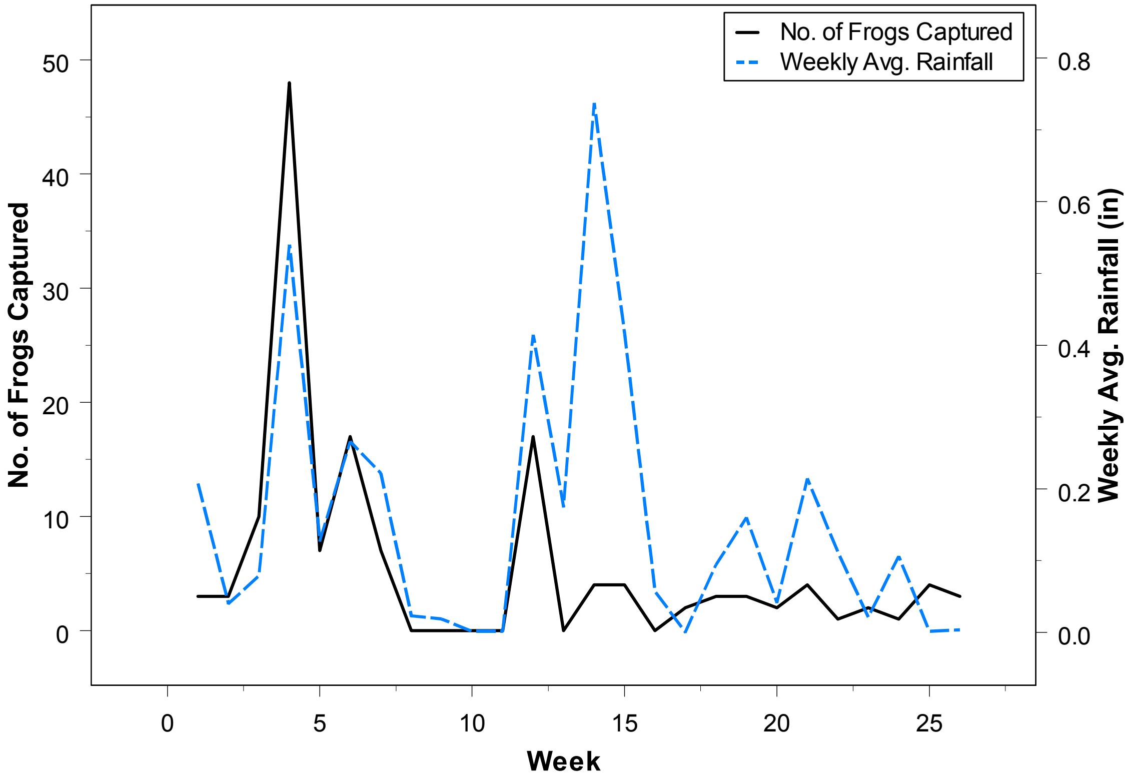

Figure 8. Number of frogs captured in the pitfall traps per week throughout the rainy season compared to the average weekly rainfall. The pitfall traps were run from November 10 (week 1) to May 15 (week 26), 2007.

Table 9. Goodness-of-Fit results for each full egg mass site occupancy model. A parametric bootstrap (n=10000) was run to check for any overdispersion (ĉ).

Model	**X^2**	**Bootstrap X^2**	**p-value**	**$\hat{c}$ [a]**
ψ (FULL-HYDRO), *p* (t+FULL)	1.5854	1.8103	0.4525	0.8758
ψ (FULL-AWD), *p* (t+FULL)	1.5737	1.8934	0.5196	0.8311

[a] $\hat{c} = X^2 /$ bootstrap X^2

Table 10. Ranking of egg mass site occupancy models according to the lowest AIC$_C$ values.

Model	AIC$_C$[a]	ΔAIC	(Log) Likelihood	w$_i$ [b]	Number of Parameters
ψ (AWD+EMV),*p*(t+WD)	55.76	0.00	1.00	0.69	7
ψ (HYDRO+EMV),*p*(t+WD)	58.01	2.25	0.32	0.22	7
ψ (HYDRO+EMV),*p*(WD)	61.89	6.14	0.05	0.03	5
ψ (HYDRO),*p*(t+WD)	62.38	6.62	0.04	0.03	6
ψ (FULL-HYDRO),*p*(t+FULL)	64.60	8.84	0.01	0.01	13
ψ (AWD),*p*(WD)	64.76	9.00	0.01	0.01	4
ψ (AWD),*p*(WTH)	65.35	9.59	0.01	0.01	4
ψ (AWD),*p*(WTH+WDY)	65.83	10.08	0.01	0.00	5
ψ (AWD+DIF+EMV),*p*(WD+WDY)	66.21	10.45	0.01	0.00	7
ψ (HYDRO),*p*(WD)	67.50	11.74	0.00	0.00	4
ψ (HYDRO+DIF),*p*(WD)	69.83	14.08	0.00	0.00	5
ψ (FULL-AWD),*p*(t+FULL)	70.31	14.55	0.00	0.00	13
ψ (EMV),*p*(WD)	77.36	21.60	0.00	0.00	4
ψ (AWD+DIF),*p*(.)	79.80	24.04	0.00	0.00	4
ψ (EMV+OHB),*p*(WD+WTH)	80.66	24.90	0.00	0.00	6
ψ *(.),p(WD)*	84.32	28.56	0.00	0.00	3
ψ (ASH),*p*(WD)	85.80	30.04	0.00	0.00	4
ψ (ASH+WDY),*p*(WD)	87.45	31.70	0.00	0.00	5
ψ (EMV),*p*(WTH+WDY)	96.16	40.41	0.00	0.00	5
ψ (EMV+OHB+WDY),*p*(WDY)	98.44	42.68	0.00	0.00	6
ψ (EMV+WDY),*p*(WTH)	98.61	42.86	0.00	0.00	5
ψ (.),*p*(.)	99.23	43.47	0.00	0.00	2
ψ (DIF),*p*(WTH)	102.49	46.73	0.00	0.00	4
ψ (AWD+WDY),*p*(.)	105.44	49.68	0.00	0.00	4
ψ (HYDRO+DIF+EMV),*p*(WDY)	106.80	51.04	0.00	0.00	6

[a] Corrected Akiake's Information Criterion

[b] Akiake's weight

w_i=22%). In this model, HYDRO and EMV for ψ were both significant at the 95% confidence level. HYDRO also had a positive relationship with ψ. Akiake weights for both models totaled 91%.

The estimate of occupancy from the top model after incorporating detection probability was 0.15 (SE=0.04). The probability of detection varied between each site and survey. The average detection probability of all sites in survey 1 was 0.42 (SE=0.03), in survey 2 was 0.67 (SE=0.01), and in survey 3 was 0.08 (SE=0.01). For the HYDRO and EMV model the estimate of occupancy after incorporating detection probability was 0.14 (SE=0.03). The average detection probability for this model in survey 1 was 0.46 (SE=0.03), in survey 2 was 0.71 (SE=0.01), and in survey 3 was 0.09 (SE=0.01). Probability estimates of occupancy produced by each of these two models are compared for each detected and selected non-detected sites in Figures 9-10. Some non-detected sites could have a high estimated probability of occupancy. They could be occupied, but went undetected in all three surveys. Thus, the issue concerning false absences predicted in traditional logistic regression analysis is eliminated.

The top four models, totaling 97% of the Akiake's weights, were used in the model averaging. Table 11 lists coefficient values and their corresponding significant confidence intervals for each of the four top models. It shows what type of relationship each variable had with occupancy and detection. These models were used to obtain a weighted average of the intercepts and the covariate coefficients contained in the models. Each coefficient was weighted according to each model's Akiake's weight in which the covariate was represented. Then each individual coefficient value was added to equal

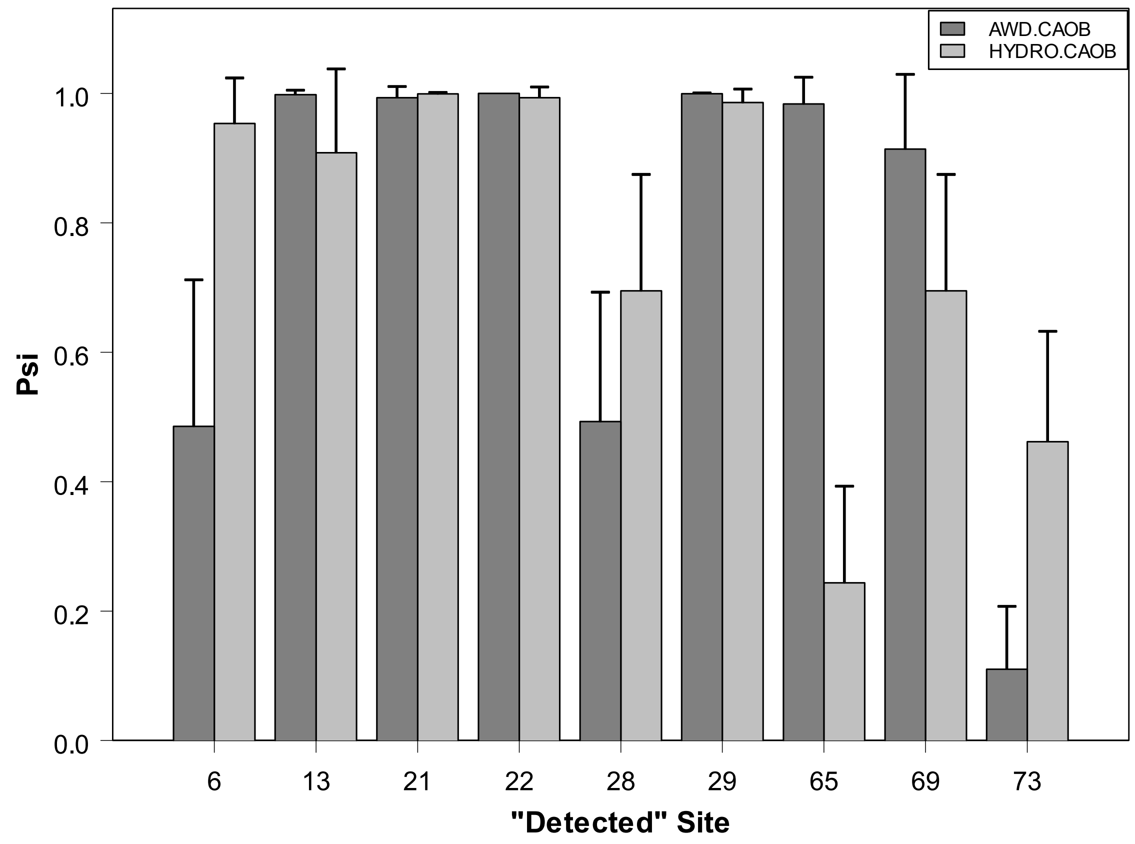

Figure 9. Top two models comparing psi (probability of occupancy) and the corresponding standard errors with the sites where at least one egg mass was detected. This represents how well the top two models predicted egg mass occupancy at these sites.

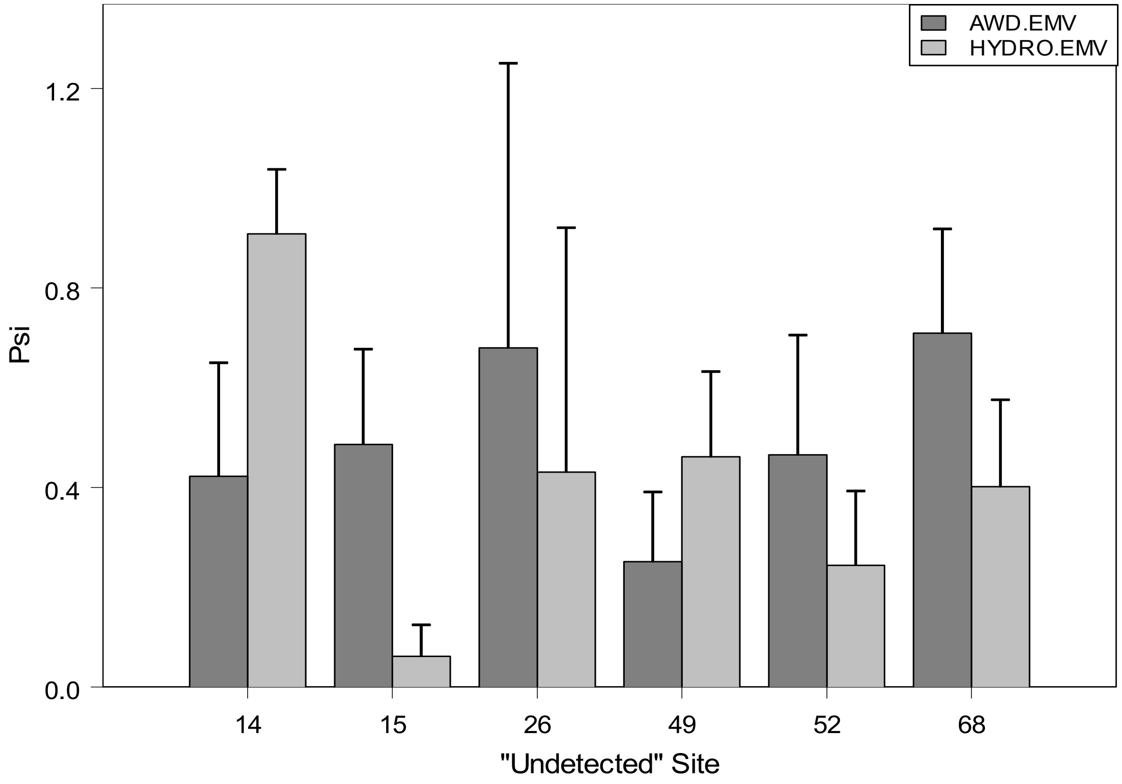

Figure 10. Top two best fitting models comparing psi and the corresponding standard errors with sites that went "undetected" for an egg mass. The non-detected sites selected had the highest estimated occupancy probabilities. Instead of absence at these sites, they have the strongest predictions that the site could be occupied, but an egg mass was not detected during any of the surveys.

Table 11. Top four occupancy model coefficients with the respective standard errors and confidence intervals. Significant confidence intervals are in bold.

	Coefficient	SE	95%CI		90%CI	
ψ =B0 + B1*AWD + B2*EMV; p = t1 +t2 +t3 + P4*WD						
int (B0)	-6.20	2.65	**-11.49**	**-0.91**	**-10.62**	**-1.78**
B1	0.63	0.30	**0.03**	**1.22**	**0.13**	**1.12**
B2	-0.24	0.16	-0.55	0.07	-0.50	0.02
t1	-0.31	1.18	-2.66	2.04	-2.27	1.65
t2	0.99	1.16	-1.33	3.31	-0.95	2.93
t3	-3.11	1.52	**-6.14**	**-0.09**	**-5.64**	**-0.59**
P4	0.15	0.08	-0.02	0.32	**0.01**	**0.29**
ψ =B0 + B1*HYDRO + B2*EMV, p = t1 + t2 + t3 + P4*WD						
int (B0)	-6.86	2.68	**-12.20**	**-1.51**	**-11.32**	**-2.39**
B1	0.62	0.26	**0.10**	**1.14**	**0.18**	**1.05**
B2	-0.34	0.16	-0.66	-0.02	**-0.60**	**-0.07**
t1	-0.13	1.13	-2.37	2.12	-2.01	1.75
t2	1.12	1.15	-1.18	3.42	-0.80	3.05
t3	-2.85	1.50	-5.84	0.14	**-5.35**	**-0.35**
P4	0.13	0.08	-0.04	0.30	-0.01	0.27
ψ =B0 + B1*HYDRO, p = t1 + t2 + t3 + P4*WD						
int (B0)	-5.14	1.90	**-8.93**	**-1.35**	**-8.31**	**-1.98**
B1	0.47	0.19	**0.10**	**0.85**	**0.16**	**0.79**
t1	-0.23	1.14	-2.50	2.05	-2.13	1.67
t2	1.00	1.17	-1.33	3.32	-0.95	2.94
t3	-2.93	1.52	-5.96	0.10	**-5.46**	**-0.40**
P4	0.14	0.09	-0.03	0.31	-0.01	0.28
ψ =B0 + B1*HYDRO + B2*EMV, p = P0 + P1*WD						
int (B0)	-19.26	9.65	**-38.49**	**-0.02**	**-35.34**	**-3.18**
B1	1.98	1.03	-0.06	4.03	**0.27**	**3.69**
B2	-0.88	0.49	-1.87	0.10	**-1.71**	**-0.06**
P0	-0.46	0.69	-1.83	0.90	-1.61	0.68
P1	0.06	0.04	-0.03	0.15	-0.01	0.13

the model averaged value. For example, HYDRO was represented in three of the four top models. The coefficient from each model was multiplied by the model's weight then added together to calculate the averaged coefficient value. The same method was used to obtain the particular coefficient's averaged standard error.

Average water depth had the strongest influence on egg mass occupancy at 0.43 (SE=0.20). Hydroperiod length had a coefficient value of 0.20 (SE 0.09). Emergent vegetation had a weak, but still significant, negative relationship with occupancy. For detection probability, water depth during each survey was the only variable in the top 4 four models that was used in the model averaging (Table 12).

Adult and Juvenile Habitat Selection

Frogs were found in 27 of the 76 sites surveyed, giving a naïve estimate for adult and juvenile occupancy in the dune swales of 0.36. The parametric bootstrap for the global model's deviance did show a slight overdispersion and the $\hat{c}$ was calculated at 1.10. Models were adjusted for the $\hat{c}$ and ranked according to their $QAIC_c$ values (Table 13). The best fitting model was a function of the hydroperiod (HYDRO) length and distance to nearest egg mass (DEM) covariates ($QAIC_c$=85.09, w_i=54%). Both the HYDRO and DEM coefficients had positive relationships with occupancy and were significant at the 95% confidence interval. The correct classification rate of the top model was 69.7% with a sensitivity of 0.67 and a specificity of 0.63. Area under the ROC curve was 0.72. The next closest model was a function of average water depth

Table 12. Weighted average coefficient values for intercepts and covariates in both the A) egg mass occupancy and B) habitat selection modeling.

A	**Avg Coefficient**	**SE**
intercept	-6.44	2.72
AWD	0.43	0.20
HYDRO	0.20	0.09
EMV	-0.26	0.15
WD	0.14	0.08
t1[a]	-0.26	1.11
t2[a]	0.95	1.11
t3[a]	-2.88	1.44

B	**Avg Coefficient**	**SE**
intercept	-0.58	0.25
AWD	0.02	0.01
HYDRO	0.06	0.02
DEM	0.06	0.02
DIF	0.02	0.02
CAOB	0.003	0.002
WDY	0.004	0.02
ASH	0.0002	0.001

[a] t1, t2, and t3 are coefficient estimates for time in each of the egg mass surveys

Table 13. Habitat selection models for adult and juvenile RAAU during the post-breeding season.

Model Name	**QAICc**[a]	**ΔQAICc**	**(Log) Likelihood**	**w_i** [b]	**Number of Parameters**
HYDRO, DEM	85.09	0.00	1.00	0.54	3
AWD, DIF, DEM	87.79	2.70	0.26	0.14	4
HYDRO	88.82	3.73	0.15	0.08	2
AWD	90.38	5.29	0.07	0.04	2
AWD, CAOB, DIF	90.50	5.42	0.07	0.04	3
HYDRO, ASH	90.75	5.66	0.06	0.03	3
HYDRO, CAOB, WDY	90.79	5.70	0.06	0.03	4
DEM	90.81	5.73	0.06	0.03	2
DIF, DEM	91.46	6.37	0.04	0.02	3
full.HYDRO	92.72	7.64	0.02	0.01	8
CAOB, DIF, DEM	93.17	8.08	0.02	0.01	4
WDY, DIF	94.01	8.92	0.01	0.01	3
full.AWD	94.83	9.74	0.01	0.00	8
CAOB, OHB	95.10	10.01	0.01	0.00	3
ASH, DIF, WDY	95.50	10.41	0.01	0.00	4

[a] Corrected Quasi-Akiake's Information Criterion

[b] Akiake's weight

(AWD), distance to forest (DIF), and DEM (QAIC$_c$=87.79, w$_i$=14%). The AWD and DEM coefficients were also positively related to occupancy and significant at the 95% confidence interval. Total Akiake's weight for these two models was 68%. Seven more models which had weights that ranged from 2% to 8% were included in the model averaging. These nine models totaled at least 95% of the total weights of all fifteen models used for habitat selection. It is important to note, however, that no other covariates except HYDRO, AWD, and DEM were significant at the 95 or 90% confidence level (Table 14).

The nine models were used to obtain weighted averages of the intercepts and covariates. Each coefficient was weighted and averaged as previously explained for the egg mass occupancy models. Hydroperiod and distance to nearest egg mass had the greatest influence on adult and juvenile habitat selection. Average water depth also played a significant role, though to a lesser degree. See Table 12 for the results of averaged variables in the habitat selection models.

Occupancy Maps

A total of 23 ponds had at least one site location and were used in creation of the suitability maps (Figures 11-12). Most of the ponds not used in map creation had an area less than 100m^2 and were not initially considered in the random placement of site locations. For egg mass oviposition, the predicted probability of occupancy in the ponds varied between 0 and 0.9967. The predicted probabilities for adult and juvenile habitat selection in the post-breeding season varied between 0.1097 and 0.6411.

Table 14. Top nine habitat selection model coefficients with the respective standard errors and confidence intervals. Significant confidence intervals are in bold.

	Coefficient	**SE**	**95%CI**		**90%CI**	
psi =B0 + B1*HYDRO + B2*DEM						
int(B0)	-0.60	0.26	**-1.12**	**-0.08**	**-1.03**	**-0.17**
B1	0.09	0.03	**0.02**	**0.16**	**0.04**	**0.14**
B2	0.08	0.03	**0.01**	**0.14**	**0.02**	**0.13**
psi =B0 + B1*AWD + B2*DEM +B3*DIF						
int(B0)	-0.60	0.26	**-1.12**	**-0.09**	**-1.03**	**-0.17**
B1	0.08	0.03	**0.01**	**0.14**	**0.02**	**0.13**
B2	0.08	0.03	**0.01**	**0.14**	**0.02**	**0.13**
B3	0.04	0.03	-0.02	0.10	-0.01	0.09
psi =B0 + B1*HYDRO						
int(B0)	-0.57	0.25	**-1.07**	**-0.08**	**-0.99**	**-0.16**
B1	0.06	0.03	0.00	0.12	**0.01**	**0.11**
psi =B0 + B1*AWD						
int(B0)	-0.58	0.24	**-1.07**	**-0.09**	**-0.99**	**-0.17**
B1	0.05	0.03	-0.01	0.11	0.00	0.10
psi =B0 + B1*AWD + B2*CAOB + B3*DIF						
int(B0)	-0.59	0.25	**-1.09**	**-0.09**	**-1.01**	**-0.18**
B1	0.06	0.03	0.00	0.12	**0.01**	**0.11**
B2	0.04	0.04	-0.03	0.11	-0.02	0.10
B3	0.02	0.60	-1.17	1.21	-0.97	1.01
psi =B0 + B1*HYDRO + B2*ASH						
int(B0)	-0.57	0.25	**-1.06**	**-0.07**	**-0.98**	**-0.15**
B1	0.01	0.03	-0.04	0.06	-0.04	0.05
B2	0.06	0.03	0.00	0.12	**0.01**	**0.11**
psi =B0 + B1*HYDRO + B2*CAOB + B3*WDY						
int(B0)	-0.69	0.51	-1.72	0.33	-1.55	0.17
B1	0.07	0.03	**0.01**	**0.13**	**0.02**	**0.12**
B2	0.05	0.03	-0.02	0.11	-0.01	0.10
B3	0.13	0.60	-1.05	1.32	-0.86	1.13
psi =B0 + B1*DEM						
int(B0)	-0.62	0.25	-1.11	-0.13	-1.03	-0.21
B1	0.05	0.03	-0.01	0.10	0.00	0.09
psi =B0 + B1*DEM + DIF						
int(B0)	-0.62	0.25	**-1.12**	**-0.13**	**-1.04**	**-0.21**
B1	0.05	0.03	-0.01	0.11	0.00	0.10
B2	0.04	0.03	-0.02	0.10	-0.01	0.09

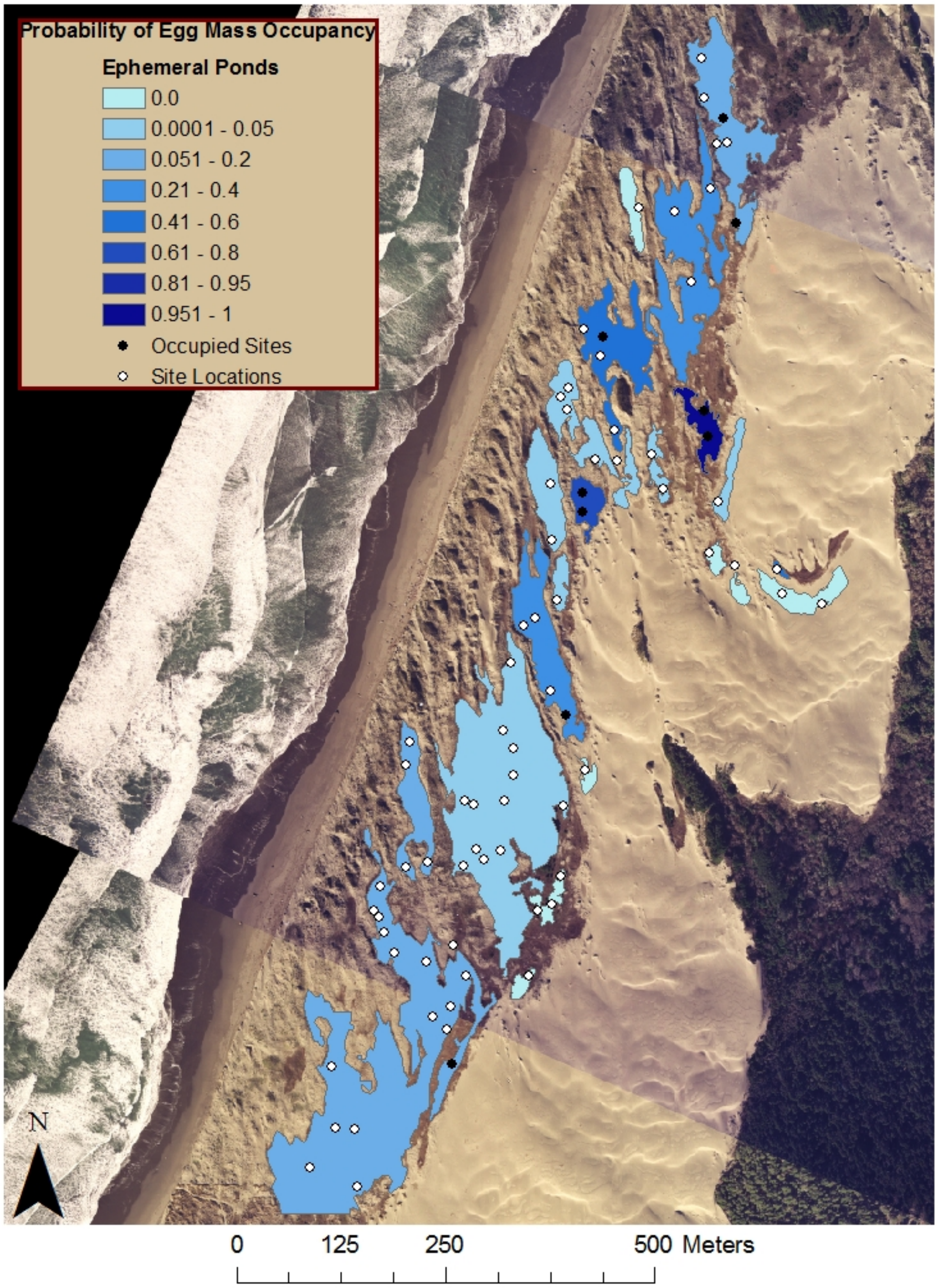

Figure 11. Predicted probability of egg mass occupancy of the ponds based on the average occupancy estimates from the site location/s within each pond.

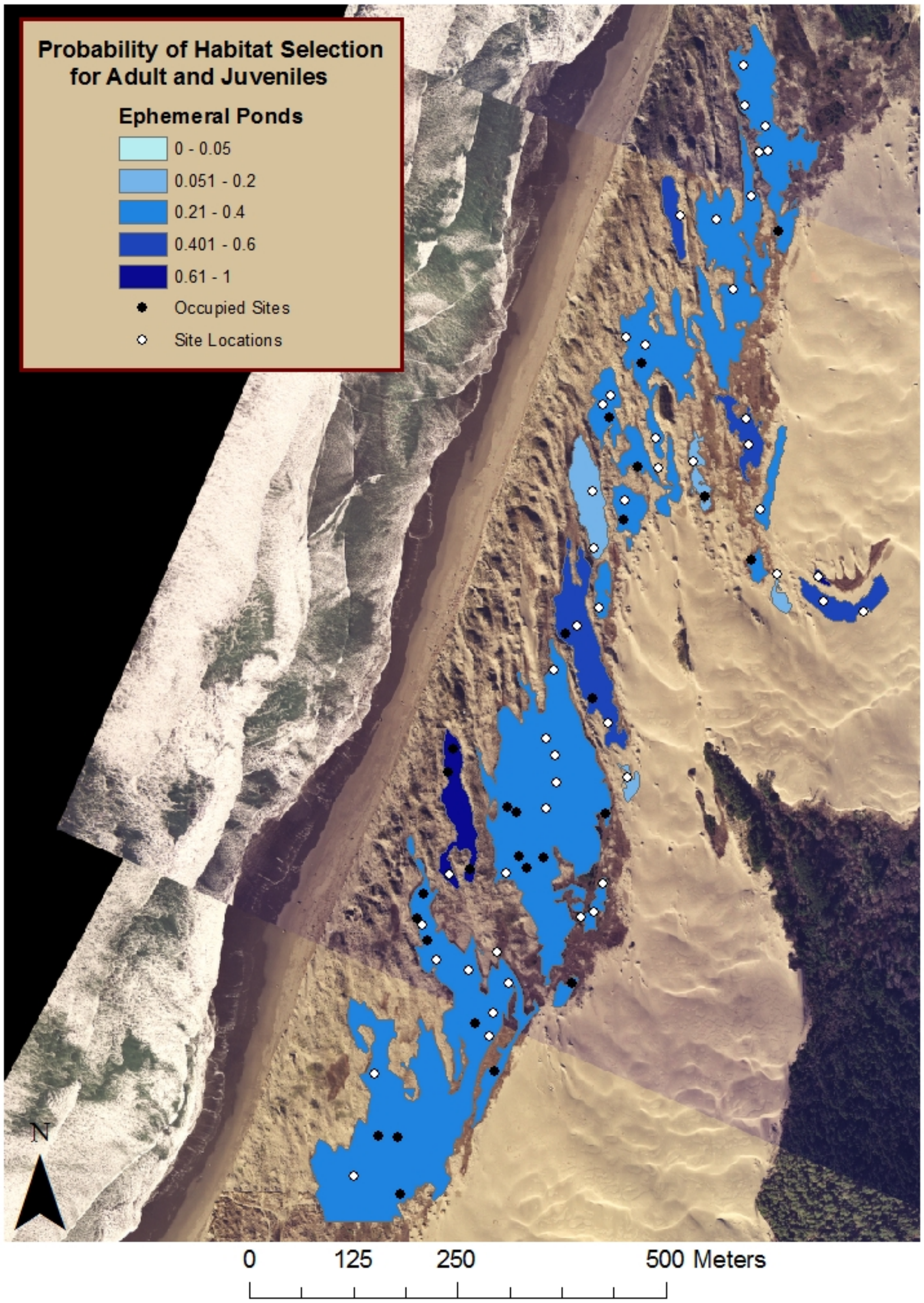

Figure 12. Predicted probability of habitat selection by terrestrial stage frogs of the ponds based on the average habitat selection probabilities from the site location/s within each pond.

DISCUSSION

Dispersal and Relative Abundance

The dune forest and moving dunes separate the two breeding habitats in this study. Surveying or tracking frogs is extremely difficult in the forest due to the dense shrub layer and thick groundcover. Due to the relatively small tract of forest, disturbance from drift fences, pitfall traps, and tracking of individuals might have negative effects on the vegetation (A. Pickart pers. comm., Jan 2006). Nevertheless, frogs are using the dune forest as a refuge or foraging habitat, as shown by captures within the forest outside of the breeding season, and the numerous captures in the ecotones where the drift fences and pitfall traps were placed.

I found no direct evidence of dispersal between breeding habitats, which was not surprising given the low recapture rate. There were no frogs captured in one habitat and later recaptured in the other habitat. *Rana aurora* has been observed moving at least 2.4km within a six month period (Hayes et al. 2001). Thus, the permanent and ephemeral ponds are a short enough distance apart (less than 600m) for frogs to migrate between them. However, the densely covered dune forest and extensive, unvegetated moving dunes that lie between these two breeding areas could limit dispersal. Dispersal or migration between these habitats would be better investigated over a multi-season study. A single *R. aurora* adult was spotted burrowing into the soil after the ephemeral ponds in the dune swales had dried (V. Metz pers. comm. June 2006). This suggests that some animals might not disperse to the dune forest, but instead remain burrowed in the swales throughout the dry season. Although burrowing and aestivation are common for some species of ranids, it has never been documented in *Rana aurora* (Pearl 2005). Whether this behavior is specific to the swales or occurs in other seasonal wetland habitats is unknown and warrants further investigation.

Although the permanent ponds on the adjacent property had less total area, the number of egg masses and post-metamorphic frogs recorded were greater than those for the ephemeral ponds in the dunes swales. Having a permanent water source near the dune forest could account for these apparent differences in abundance. The seasonal wetlands in the dune swales dry out completely during the summer and may pose a greater risk of desiccation to the frogs. The swales are also a greater distance away from the dune forest, meaning dispersal to and from the ephemeral ponds may be more risky than in the permanent pond habitat.

The drift fence arrays used in this study did not encircle entire breeding ponds because of time and cost constraints, so it is assumed that all frogs moving to and from ponds were not captured. This method would underestimate absolute abundance in each breeding habitat. However, the relative abundance between the two breeding habitats was comparable. The same number of pitfall traps and drift fences were placed along each habitat so a comparison of frogs captured between the two is appropriate. Egg mass counts were also used to estimate relative abundances and were similar to that of the pitfall estimates.

Egg mass counts have been highly correlated with the number of females and males found within breeding ponds (Crouch and Paton 2000). Egg mass counts require less labor and are more cost efficient than drift fence arrays with pitfall traps. Because estimates are also similar between the two methods, egg mass counts should be the preferred method for estimating ranid frog relative abundance under the assumption that each female lays one clutch per breeding season. However, due to climatic or hydrological variation in detection, accurate abundance estimates of egg masses over a period of time in any given area need to incorporate detection probabilities. Water depth levels rise and fall depending on precipitation in seasonal wetlands, and this affects the ability to detect the egg masses. If some egg masses go undetected in these types of surveys, abundance will be underestimated.

The drift fence techniques, accompanied by pitfall trapping, captured a large number of *R. aurora*. Design of the drift fence arrays and size of the pitfall traps are important considerations for successful capture of the species. Anurans, especially ranids and chorus frogs, have good jumping and climbing skills, so capture success from this technique has been mixed (Crosswhite et al. 1999, Jenkins et al. 2003). Large buckets (18.9L) were used as the pitfall traps so that escape was minimized. Very few other herpetofauna were captured during these surveys, which implies that they could be less abundant in the areas where the traps were placed. However, Pacific chorus frog abundance is relatively high within the dune system. Although no abundance estimates have been made in the area, several post-metamorphic frogs and egg masses were observed and numerous breeding calls were heard during this study. This suggests that chorus frogs were captured, but were able to escape the pitfall traps. Thus, this technique would not be useful to investigate this species.

Movement Phenology

The pitfall trap movement data revealed, unsurprisingly, that most migration towards the ponds from the dune forest took place during the breeding season (mid-Dec to mid-March). However, there was no significant migration of juvenile or adult frogs away from the ponds during the post-breeding season. Fellers and Kleeman (2007) found that adult California red-legged frogs often lingered at seasonal ponds until they almost completely dried. Their study was also in a coastal habitat, and they suggested that fog might allow the frogs to remain in these seasonal habitats without the risk of desiccation. They also found high variability in adult migration, with some frogs staying at breeding areas only a few days and others remaining all year. This would explain the lack of significant adult migration away from the ponds if *R. aurora* exhibits similar patterns to *R. draytonii*. Only five juveniles were captured during the post-breeding season, so they also may be remaining at the breeding sites, at least longer than the pitfall traps were run. The pitfall traps were only run for two months after the breeding season.

An unexpected result was the differences between the juvenile and adult activity levels during the pre-breeding, breeding, and post-breeding seasons. Although juvenile movement tends to be more sporadic than adults, why the juveniles were more active then the adults in the pre-breeding season remains speculative and warrants further investigation. One possible reason adults were more active in the post-breeding season is their decreased surface area to volume ratio. This allows them to retain moisture longer than the juveniles. When precipitation decreases, juveniles might be more prone to desiccation and thus move less frequently.

Associations between movements of frogs and rainfall events have been well documented (Greenberg 2001, Prado et al. 2005, Saenz et al. 2006, Fellers and Kleeman 2007). When adult and juvenile data were combined, this study showed more movement following or during rain events. While this also held true for the juveniles in all seasons, the adult movement was not associated with rainfall events in the breeding and post-breeding seasons. The adults' larger size gives them the ability to travel indiscriminately during drier times with less of a chance for desiccation. Only during the pre-breeding season were the adults several times more likely to be active directly after a rain event. This suggests that rainfall could be an environmental cue that results in adult movement toward the pond during the pre-breeding season.

Egg Mass and Post-Breeding Adult and Juvenile Frog Occupancy and Habitat Selection

Strategies of oviposition selection can affect egg mass location on several ecological scales (Marsh and Borrell 2001). At the site-specific scale, average water depth was the strongest factor associated with oviposition site selection, thus helping to predict spatial distribution of egg masses (though not larvae) at this scale. Hydroperiod length was also a contributing factor for predicting egg mass occurrence. The spatial distribution of egg masses in the swales at the pond scale could be associated with hydroperiod length. All nine sites in which egg masses were detected were aggregated into six ponds that had hydroperiods over 18 weeks. No egg masses were detected in sites with hydroperiods less than 18 weeks (n=57). The spatial distribution of egg masses and thus their larvae in the dune swale habitat should be predicted by a minimum hydroperiod length of the ephemeral ponds. Egg mass location within those ponds, on the other hand, is predicted by the average water depth. Other studies have shown that hydroperiod length of ephemeral ponds is associated with the breeding presence of several amphibian species (Skidds 2005, Snodgrass et al. 2000).

Whereas hydroperiod length at the pond scale is an important factor for tadpole fitness and survival (Richter et al. 2003), water depth is a more important factor for female oviposition site selection in the seasonal wetlands. Females tended to select oviposition sites with deeper average water depths over sites with longer hydroperiods. Because hydroperiod lengths were relatively short in the swale habitat (range = 4-24 weeks), females may be more apt to chose deeper sites as a reproductive strategy. They might associate deeper water as an environmental cue for increased offspring survival due to the strong relationship between water depth and hydroperiod length.

Many egg masses were located within the deepest area of the site. One reason for this might be that the deepest areas are the last to dry completely, thus giving the embryos more time to hatch in case variation in rainfall creates small periods of intermittent hydroperiods within the pond. Monthly rainfall in January of 2007 was unusually low. Water depth at several sites with egg masses receded to levels lower than where the egg mass was attached to the vegetation, or sites temporarily had no standing water at all. This only lasted one to two weeks in mid-February and metamorphosed juveniles were seen in these ponds in early June of the same year. New egg masses were not seen after water levels rose again so hatching of at least some of the eggs in a clutch must have occurred. This implies that egg masses can withstand an unknown length of time outside of water without complete desiccation and death of the embryo.

Percent emergent vegetation also seems to play a role in oviposition selection at both site-specific and pond scales. However, it could have different effects on occurrence at each scale. At the site-specific scale this study found a negative relationship with percent of emergent vegetation. Although egg masses are attached to either submerged or emergent vegetation (one plant could vary between the two conditions due to water depth fluctuations throughout the survey or season), most egg masses detected in this study were found attached to vegetation in relatively open areas of the pond. This indicates that emergent vegetation could have a negative relationship with oviposition at the site-specific scale, as in this study, but a positive relationship at the pond scale. Females prefer to deposit egg masses in the more open locations of the pond; however, they prefer ponds with more vegetation. Pearl et al. (2005) found that wetlands with a lower percentage of open water supported more red-legged frog breeding. If less open water means more submerged or emergent vegetation cover of the pond, then this relationship should be positive at the pond scale.

Oviposition site selection was treated as having a linear relationship with emergent vegetation in this study. After observations in the field and analyzing the covariate, however, the distribution might take a more quadratic relationship with oviposition selection. This would mean that females would tend to avoid depositing egg masses in areas with not enough and too much emergent vegetation. Their preference would lie somewhere in the middle. The time it takes for an egg mass to hatch has been closely associated with water temperature (Licht 1971). Although the temperature cannot exceed the thermal maximum of the species (21° C for *R. aurora*), faster hatch time is associated with warmer water temperatures (Licht 1971). Female frogs might select oviposition sites with more direct exposure to sunlight, resulting in higher water temperatures. If larvae were able to hatch quicker, they would have a better chance of metamorphosis before the ponds dry. However, if the pond had too little vegetation, the tadpoles could be exposed to increased predation, increased water temperatures, lower food resources, and a shorter hydroperiod than a pond with more vegetation. This quadratic relationship could be easily added to my original set of models. I chose not to, however, due to the *a priori* approach taken when developing this study. Also, even assuming the relationship was linear, emergent vegetation was an important factor for the estimation of occupancy.

Variation in water depth within the sites during the survey period played an important role in detection of the egg masses. The number of dry sites greatly increased from the first to second survey periods. A large storm event occurred between the second and third surveys, thus, all but five sites in the third survey contained standing water. As the water levels fluctuated in the sites, so did the probability of detecting the egg masses (Figure 13). The estimated average probability of detection across all the sites was 42% for the first survey. As the water depth decreased or the site dried up, the average

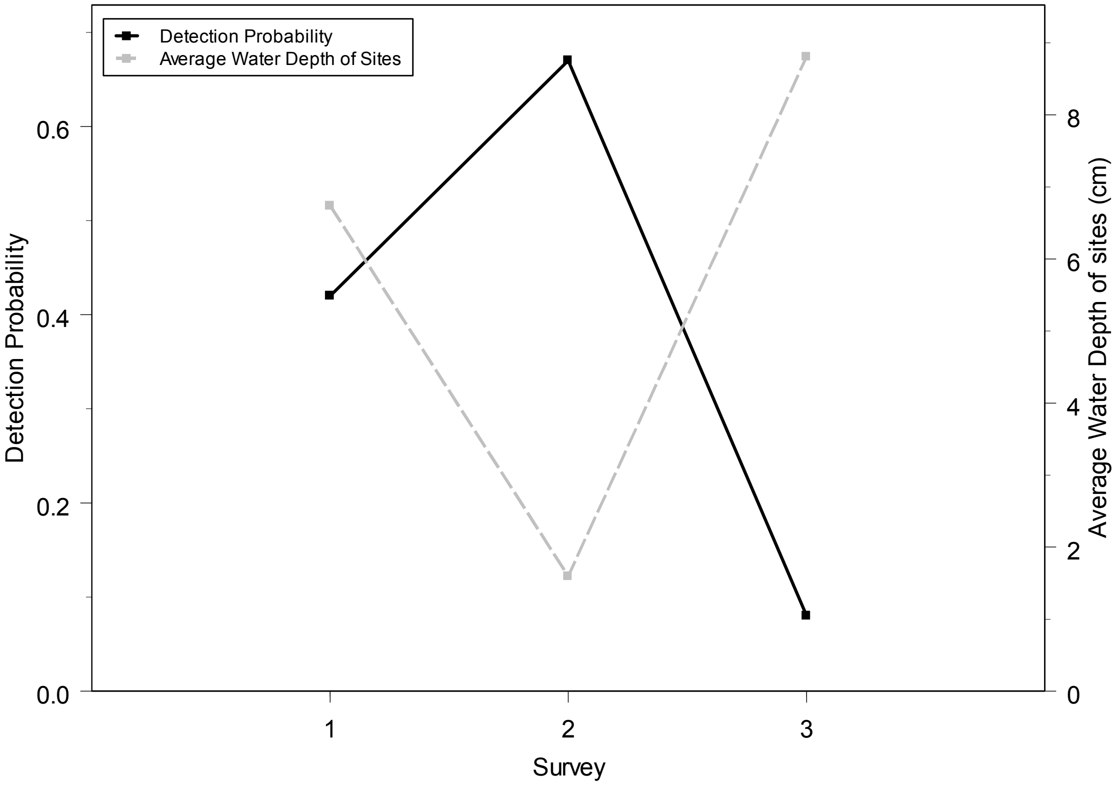

Figure 13. Average detection probability compared to average water depth across all the sites (n=71) for each survey. Detection probability was never equal to one or constant across all sites. Survey 1 was conducted between January 19 and 24, survey 2 between February 2 and 3, and survey 3 between February 11 and 17 of 2007.

probability of detection increased to 67% during the second survey. However, the opposite was seen from the second to the third survey. The average probability of detection across all the sites decreased to <8% in the third survey. As the water levels dropped in the ponds, the egg masses became more visible. They were found on the ground or hanging off vegetation. Once the water level rose, the egg masses were towards the bottom of the ponds or had been broken up and were no longer discernable. Precipitation (or lack thereof) indirectly affects detection of the egg masses by causing the water levels in the ponds to rise or fall.

Several other factors can also contribute to low detection probability of egg masses. Observer bias has been shown to affect detection of egg masses (Grant et al. 2005). When different observers with different levels of experience are used, detection probability can vary between them. If only one observer is used, biases can also occur. Once the single observer knows where the egg mass or masses are located in a site, she or he would then be more likely to detect the egg mass or masses in the subsequent surveys. Observer bias was assumed not to be a factor in this study. Different surveyors were used for each survey; however, levels of experience between the surveyors were similar.

Length of time from oviposition could also affect detection probability. As the egg mass gets older, it begins to deteriorate and algae begins to form around the gelatinous sacs that contain the developing larvae (Storm 1960). If the egg mass is submerged in the water, it might become better “camouflaged” when this occurs. Assuming this is true, the likelihood of detecting the egg mass would decrease each time a subsequent survey is conducted. Experienced surveyors and decreased amount of time between surveys can both reduce this likelihood. Again, this was assumed not to be a factor in the present study.

Without including detection probability, egg mass occupancy would have been underestimated. All models in which detection probability remained constant performed poorly relative to the top models according to AIC_c. This is in accordance with several other recent studies that have shown that occupancy rates can be underestimated when detection probability is not taken into account (Bailey et al. 2004, Gu and Swihart 2004). This is especially important when considering rare or cryptic species (Gu and Swihart 2004). Gu and Swihart (2004) showed that the direction of bias in wildlife-habitat models not accounting for detection probability (traditional logistic regression) can depend on how the site covariates are related to occupancy. This means that occupancy could be either under- or overestimated in certain situations. Detection probability in my study was affected on both a spatial and temporal scale. Models including detection probability as a function of time were ranked higher than those that only included a site-specific (spatial) covariate. The third best model, in which detection probability was constant but modeled only as a function of water depth, had a low Akiake's weight. It was also the only model in the top four that was overdispersed. This means there was more variation, with regards to detection of the egg masses, than was accounted for in the model.

Naïve occupancy rate for adult and juvenile frogs in the dunes swales was almost 2 ½ times greater than estimated egg mass occupancy. The occupancy map showed that habitat selection for adults and juveniles of this species includes more than just the breeding ponds in the dune swales. Because detection of the species for this habitat model was assumed to be = 1 (MacKenzie et al. 2002) and the hypotheses for frog presence were formed *a posteriori*, the best fitting models for the terrestrial stage habitat selection should be seen as exploratory only (Burnham and Anderson 2002). Adult and juvenile frogs move across the landscape and have different habitat needs than egg masses. Thus, the covariates used in these models might not have represented all the requirements that affected adult and juvenile selection. Other factors such as invertebrate abundance, if included, might have strengthened the models.

In the post-breeding habitat selection of adults and juveniles, the strongest factor associated with frog presence was hydroperiod length instead of average water depth. Adult and juvenile frogs need to stay moist, though they do not depend on standing water for survival as do the larval stages. Invertebrate abundance could also increase in areas associated with longer hydroperiods, though not necessarily with deeper water. Frogs also seemed to select the sites farther away from the ponds that contained egg masses. This behavior could be a survival strategy. A pond with a high density of tadpoles attracts predators such as birds and snakes. Adults and juveniles decrease the chance of being preyed upon if they are farther from the egg masses.

Habitat occupancy of the egg masses and frogs does not necessarily predict habitat quality throughout the dune swales. For example, some sites may contain egg masses, but may not produce metamorphic frogs. Habitat quality should be defined in terms of survival and production characteristics of the species (Van Horne 1983). By comparing, for example, metamorphic frog success between occupied egg mass ponds, one could provide more input on habitat quality of the ponds. The occupancy models in my study only show where and what associated habitat characteristics the frogs are selecting at a given time.

Model Performance

The information-theoretic approach, using AIC, is an alternative to the traditional approach using null hypothesis testing to address ecological questions. Ecological research very often involves observational studies where no manipulations to the environment have taken place. Researchers try to explain a pattern by relating a parameter estimate to several factors (e.g., habitat quality, resource availability, climatic conditions, etc.). Null hypothesis testing based on probability values (p values) has not performed well in these types of studies (Mazerolle 2006, Johnson 1999). AIC measures the strength of several working hypotheses based on the Kullback-Leibler distance (K-L distance, Kullback and Leibler 1951) each model (or the probability distribution of each model) is from the "true" probability distribution. Top models have the least K-L distance or divergence from the "true" probability distribution. A legitimate criticism of this technique lies in the set of working hypotheses where the top model is only the "best" model of the set and not necessarily the most accurate model for the parameter being estimated. Important biological and ecological considerations for the particular parameter estimate should go into the formation of these working hypotheses. A set of *a priori* candidate models are said to be predictive and any models formed *a posteriori* are said to be exploratory (Mazerolle 2007, Burnham and Anderson 2002).

I have used both predictive and exploratory methods in this study. The entire experimental design was developed only for the egg mass models. The egg mass occupancy model used an *a priori* approach in which the working hypotheses were created from previous knowledge of the species before the collection of the data (Burnham and Anderson 2002). After I began surveying for egg masses in the dune swales, I decided I could also examine similar factors to explore habitat selection in adult and juvenile frogs. Thus, all working hypotheses in this occupancy model were formed *a posteriori* and were based off observations in the field.

The top model for egg mass occupancy, which included detection probability, outperformed the habitat selection model for post-breeding adults and juveniles on both an ecological and a statistical level. After a parametric bootstrap was performed to obtain a Pearson chi-square statistic for the most global egg mass models (MacKenzie and Bailey 2004), the egg mass models were not found to be overdispersed so confidence intervals for individual site occupancy probabilities were smaller than for the terrestrial stage model. When a similar parametric bootstrap was performed on the adult and juvenile most global model (using the model's deviance as opposed to chi-square statistic), the model was found to be slightly overdispersed, which resulted in inflation of the confidence intervals when QAIC was used to rank these models. The egg mass model also predicted site occupancy better (higher probabilities of occupancy at sites which were truly occupied) than the terrestrial stage model. In the egg mass model, the top two models had a greater than 90% chance of being the most correct models out the 25 models used in the analysis. The adult and juvenile models had to include the top seven models before the weights reached 90%. In general, this shows more strength in the egg mass models.

However, both the naïve and unbiased egg mass occupancy rates were lower in the dune swales as compared to the occupancy rate of the adult and juvenile frogs. Barry and Elith (2006) suggest the minimum number of occupied sites needed for habitat selection modeling depends on the complexity of the pattern being modeled. My top egg mass models only used two covariates (both linear) to predict egg mass occupancy. Developed models were kept as parsimonious as possible to reduce the chance of overfitting and bias associated with small sample occurrences. Although the best method to test a model's strength is to evaluate its predictive power on a second dataset, the deductive approach taken with the formation of the top egg mass occupancy model should provide an effective starting point for monitoring of *R. aurora*'s breeding patch occupancy in palustrine wetlands.

Management Implications and Future Research

Finding more accurate ways to monitor northern red-legged frogs will help to distinguish between natural fluctuations and declines in the species' population. The single-site occupancy model used in this study could easily be incorporated into the design of a larger monitoring program (Bailey et al. 2007, Mazerolle et al. 2007) for Humboldt Bay. For palustrine wetlands, similar methods could be employed throughout the North and South Spits, the Salmon Creek and other plausible units of the Humboldt Bay National Wildlife Refuge, and any other appropriate habitats whether public or private. The dune swale system extends south into other public and private lands on the North Spit. Many ephemeral ponds within the dune swales are in close proximity to each other. Thus, they were not spatially discrete patches, but instead assumed to be one breeding cluster or patch. Other possible discrete breeding areas (permanent or ephemeral) could exist further south along the spit on private lands in Manila. More research is needed to include permanent and semi-permanent ponds on public lands into the model. This research could incorporate invasive and/or predator species into egg mass occurrence. Decline in occupancy rates throughout *R. aurora*'s distribution could be seen as a precursor to a possible population decline of the species. Long-term studies using occupancy as a monitoring approach could be more realistic and less costly than methods such as population estimates and abundance due to the decreased cost and labor associated with the field surveys.

Timing of the surveys was of critical importance for successfully detecting egg masses in my study. Rainfall events directly affect water levels in seasonal wetlands. If surveys are conducted after a significant rain event, detection probabilities will decrease and occupancy could be underestimated if oviposition has already begun. For species with detection probabilities < 0.15, the occupancy model does not perform as well and caution should be taken when inferences are made about parameter estimates (MacKenzie et al. 2002). The shortest possible intervals between surveys should reduce variation in detection probabilities. Independent double-observer surveys could eliminate temporal variation altogether. Using this approach, each surveyor could independently survey a site one after another without discussing detection or nondetection of each site. Thus, repeat surveys can take place without having to take time between them.

Breeding chronology is also an important factor to consider when surveying for egg masses. In the study area, *R. aurora* egg masses were not observed before January. However, egg masses have been observed as early as December 17 in other permanent ponds around Humboldt Bay (J. Bettaso, pers comm., January 2007). After initial oviposition has begun, it averages an additional two to three weeks for most breeding to occur (Jennings and Hayes 1994). Egg mass surveys should be conducted after most breeding has occurred to maximize the probability of occupancy in any given season. Once an initial survey has been completed, any new egg masses in the sites found in the subsequent surveys cannot be included. This would violate the closure assumption of the occupancy model and can bias detection and occupancy probabilities. Newer egg masses are easily identified by larval Gosner stage (Gosner 1960) and the compact gelatinous matter surrounding the larva.

Monitoring of the northern red-legged frog in California is important to be able to accurately assess changes in the population. The species is fragmented and much of its habitat has been reduced in California. Proactive management can help to conserve this species before they become rare or threatened and cost more to protect.

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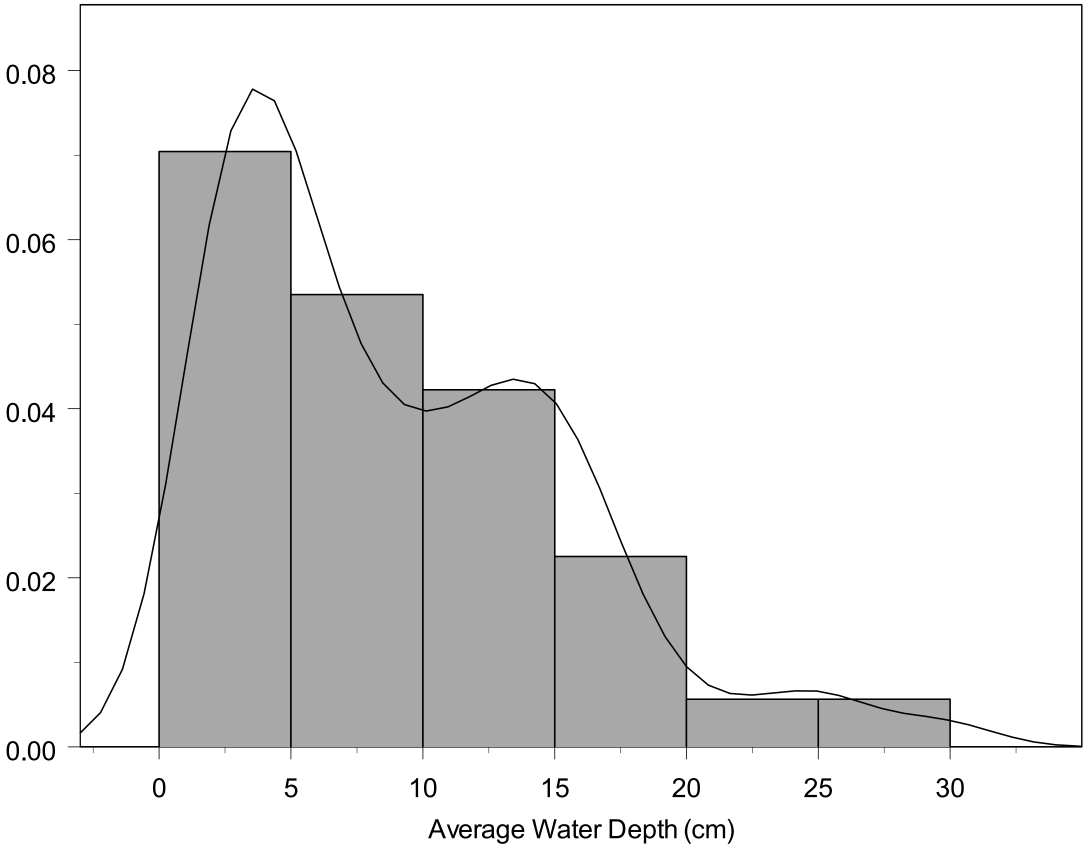
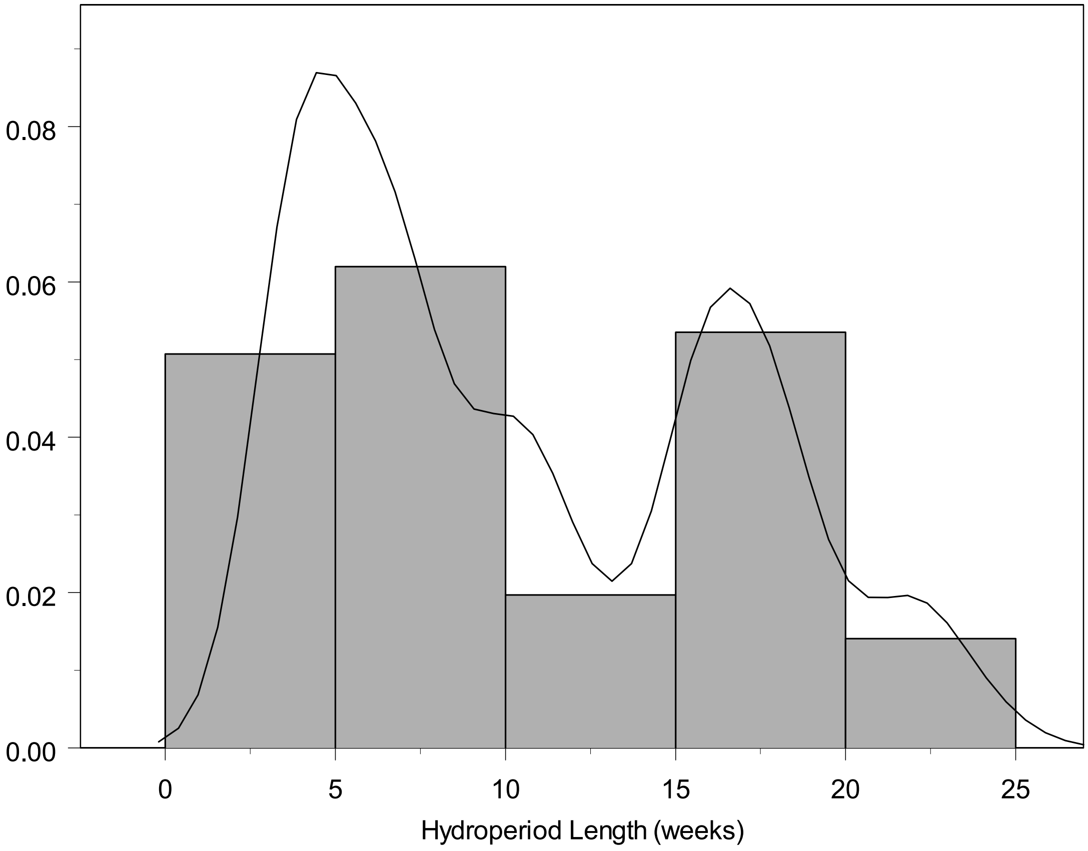
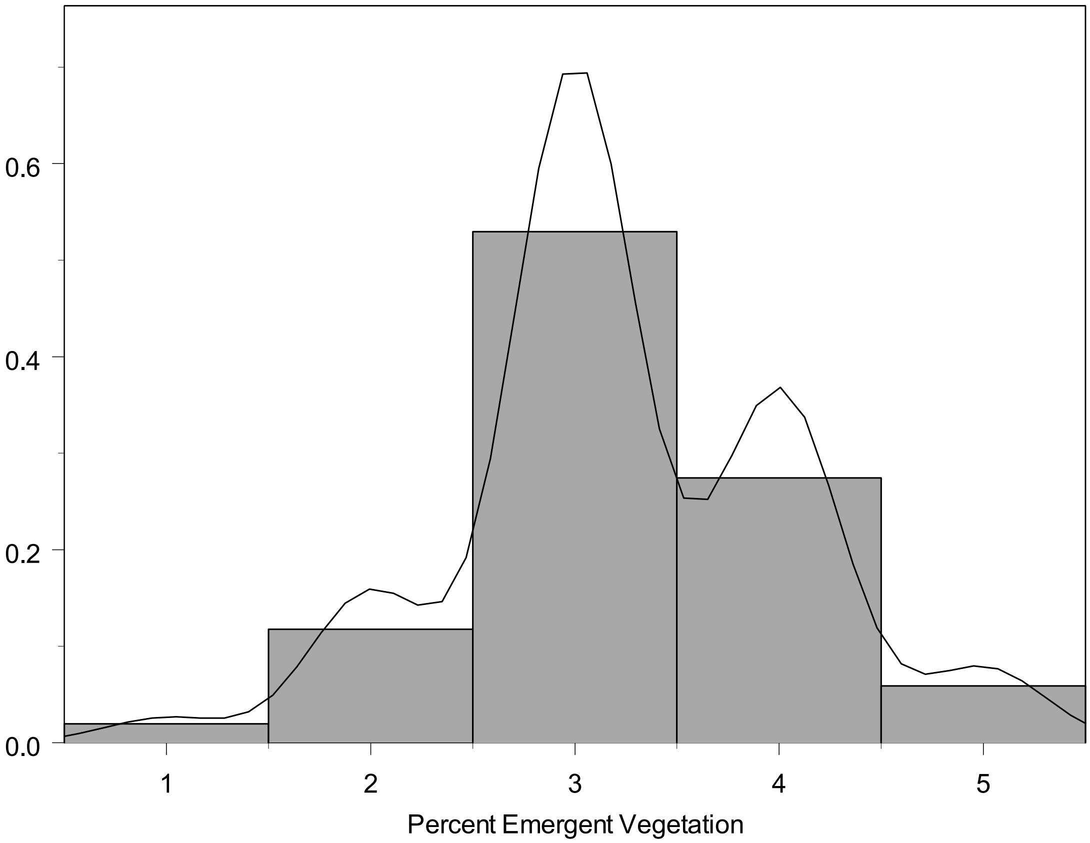
APPENDIX A

Histograms of the frequency distribution across all the sites of the three covariates (Average Water Depth, Hydroperiod, and Emergent Vegetation) which were found to significantly influence occupancy.

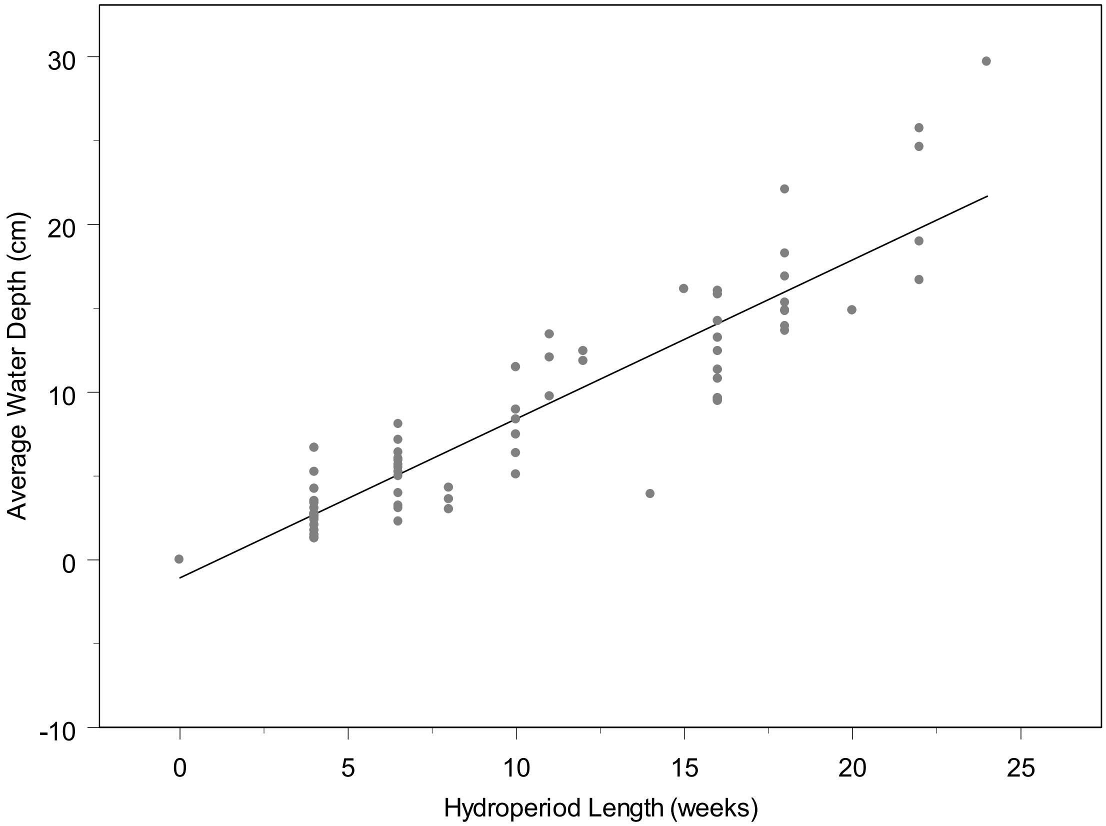



0.08
0.06
0.04
0.02
0.00
0
5
10
15
20
25
Hydroperiod Length (weeks)


0.0
0.2
0.4
0.6
1
2
3
4
5
Percent Emergent Vegetation

APPENDIX B

The relationship between average water depth and hydroperiod in the seasonal wetlands of the dune swales.



APPENDIX C

Descriptive statistics of all variables[a] used in the egg mass and adult/juvenile occupancy models.

	AWD	HYDRO	EMV	DIF	ASH	CAOB[b]	WDY	OHB	DEM[b]
Mean	9.04	10.74	3.17	293.08	3.17	3.27	1.89	2.12	109.80
SE	0.77	0.72	0.12	11.18	0.10	0.10	0.12	0.16	8.37
SD	6.48	6.07	0.80	94.20	0.84	0.84	1.05	0.97	73.98
Mode	14.9	4	3	146.8	3	4	1	2	0
Range	28	20	4	388	4	3	3	4	243
Minimum	1	4	1	93	1	1	1	1	0
Maximum	29	24	5	481	5	4	4	5	243
Count	71	71	51	71	71	71	71	71	76

	WD1	WD2	WD3
Mean	6.74	1.59	8.96
SE	1.06	0.46	1.02
SD	8.93	3.90	8.60
Range	29	18	34
Minimum	0	0	0
Maximum	29	18	34
Count	71	71	71

[a] See Table 1 and Table 3 for description of covariates.

[b] Only used in habitat selection model.