Patterns of dispersal and short-term survivorship in post-metamorphic California Red-legged frogs (*Rana draytonii*)

By
Hale V. Garcia-Dean
a thesis submitted to
Sonoma State University
in partial fulfilment of the requirements
for the degree of
MASTER OF SCIENCE
in
Biology

Biology Committee Members:
Dr. Derek Girman, Chair
Dr. Daniel Crocker
Mr. Jeffery Wilcox

Date: 08/05/2025

Authorization for Reproduction of Master's Thesis

I grant permission for the print or digital reproduction of this thesis without further authorization from me, on the condition that the person or agency requesting reproduction absorb the cost and provide proper acknowledgement of authorship.

Date: 08/05/2025

Name: Hale V. Garcia-Dean

Patterns of dispersal and short-term survivorship in post-metamorphic California Red-legged frogs (*Rana draytonii*)

By
Hale V. Garcia-Dean

Abstract

Populations of animals can often be spatially distributed across the landscape to avoid the effects of competition and overcrowding at centralized sites. Species of amphibian often reflect this established concept, and adults may engage with seasonal migration movements, moving from these spatially distributed aquatic habitats to centralized breeding habitats to complete their life cycles. However, due to low parental investment, newly metamorphosed juveniles are often naive to surrounding landscape features and the location of secondary aquatic sites on the landscape. These species may be of particular concern because not only are amphibians declining globally, but they occupy aquatic and terrestrial environments, requiring connectivity between these habitat types. We examined patterns of dispersal undergone by recently metamorphosed California Red-legged frogs (*Rana draytonii*), a federally threatened species. We used radio telemetry techniques to track the dispersal strategies, movement patterns, orientation, and short-term survivorship of metamorphs leaving an established perennial breeding pond in an oak-savanna habitat in Sonoma County, CA. We investigated the dispersal strategies associated with partial migration (dispersing in favor of a secondary residence site or remaining a resident of the breeding pond) related to sex, the state variable growth rate, and found that mean growth rate influenced whether metamorphs remained resident or engaged in dispersal. Despite their naivety, dispersing metamorphs demonstrated a non-random orientation away from the pond, suggesting a preference for specific landscape features. We investigated what effect sex and the state variable size (snout-to-urostyle length) had on short-term survivorship in these dispersing metamorphs and found that both sex and dispersal size affected survival. By sampling multiple times in a 24-hour period, we were also able to evaluate the effects of weather (daily precipitation accumulation, daily relative humidity, daily mean wind speed, daily mean temperature), time outside natal pond, and time of day on movement rates and distances moved demonstrated by dispersing metamorphs. We found that movement patterns changed with respect to time of day, sex, the state variables size and mean growth rate, and moisture-related weather patterns.

MS Program: Biology
Sonoma State University
Date: 08/05/2025

Acknowledgements

It’s with much pleasure and gratitude that I dedicate this thesis to Jeffery Wilcox, whom I consider a great mentor, and a dear friend. It was Jeff who imparted upon me a fraction of his wealth of knowledge of this incredible species, who taught me the skills necessary to answer the questions I asked, and who encouraged me to challenge myself, and always ask why? Your unwavering dedication to scientific research, and reassuring support have continuously inspired me to be the best researcher I can be.

Thank you to the Sonoma Mountain Ranch Preservation Foundation for graciously hosting my research at the gorgeous and magical Mitsui Ranch Preserve, as well as providing supplies and materials for the project. I will forever cherish my time living on the mountain, foraging Chanterelles, catching frogs, and seeing some of the most beautiful sunrises and sunsets of my life so far.

Thank you so much to the Sonoma WATERS collaborative for providing funding for our project. It's often that we have the drive but not the means to pursue our endeavors, and this collaboration between Sonoma State’s Center for Environmental Inquiry and Sonoma Water has helped to provide those means of seeing the project through. Water is the lifeblood of all organisms on Earth, yet amphibians hold a particularly special relationship with water, even within the terrestrially adapted life stage. Water is, and will always be, our most precious resource, and fostering a better understanding, appreciation and respect for the waters of this planet will be key to our continued persistence on this planet.

I am extremely grateful to my advisor, Dr. Derek Girman, who has guided me through the tumultuous journey of discovery and research with seemingly endless patience and understanding. I am eternally grateful for this opportunity; these are memories I will cherish for a lifetime. It was an honor to be a member of his research lab, through which I have possibly made lifelong friends and connections.

To my lab mates, Jesse Schmieg, Kate Fox, Victoria Brunal-Byrd, Bella Boggio, Beth Sabo and Sydni Wong, thank you not only for your support, but for your friendship. It’s often through the most difficult circumstances and situations that the strongest friendships are forged, and so far, I have experienced few challenges greater than those of graduate school. You have all inspired me to demonstrate continuous curiosity, to trust myself, and to always strive to be a better researcher and individual. I will cherish the memories of cold, wet night surveys, hot, dry desert adventures, as well as the smiles, the laughs, and the tears that we shared throughout this incredible journey.

To my parents, Julie Garcia and Matt Dean, thank you for your unwavering support, constant encouragement to strive to meet my goals, and to reach for the stars. You both have always supported my academic endeavors and pushed me to pursue what makes me happy. I am honored to have had this opportunity, but I would not have gotten here if not for the explicit and undying love and support from both of you. I hope that I’ve made you as proud as I am of this project.

To my best friend and partner, Anthony Amari, thank you endlessly for your unwavering support, and dedication to us, even throughout the hardest academic years of both of our lives. Thank you for coming out with me on more surveys than anyone else through the length of the project, and for spending two anniversaries with me at one of my favorite places on Earth, Mitsui Ranch. The deep, loving bond we share has helped me through some of the darkest moments in my life, and in this project. Your steadfast, grounded nature has helped quell much anxiety and doubt throughout this journey, and even just a hug from you feels like home.

To Beth Day, Monica Mendia, Ben Murray, Joe Currie, Lily Cella, Kaylie Richards, Emily Hascall, Audrey Gironda, Alex Berryman, Michele Conrad, T Wagner, Ben DeDominic, Connor Murphy, Emily Garcia-Hernandez, Pedro Garcia, Lily Sells, Mira Falicki, Luc Meyers, Ryan Anderson, Jess Torres, Brian Tauzer, Jennaca Hajek, Lisa Surber-Cunningham, Kyle Surber-Cunningham, and everyone else who volunteered on this project, I express my deepest gratitude. This project simply would not have been possible without the tireless efforts of so many volunteers, and each and every one of you helped to make this dream a reality. You joined me in less-than-favorable conditions more often than not, pulling all-nighters from sunset to sunrise on some of the coldest, wettest, and windiest conditions I have ever lived through. It was an honor to have you by my side during these surveys, and I hope you are as proud as I am to see this project through.

To *Rana draytonii*, thank you for your continued persistence and perseverance in the face of decline, both anthropogenic and natural. You’ve taught me much about resilience, survival and navigating a world which is both alien and, at times, unforgiving. May you flourish despite adversity, continue to play a vital role in the ecosystems in which you are found, and recolonize locations where extirpation has previously occurred.

Table of Contents

List of Figures

Introduction

Migratory behavior has been documented widely across animal taxa, in groups including birds, mammals, fish, reptiles, insects, and amphibians (Dingle & Drake 2007, Davis et al. 2024). The reasons for migration can vary depending on ecological requirements, seasonal timing, climate, individual variation, and life history, but are often mechanisms for acquiring greater resources or more suitable breeding opportunities and/or exploiting resources on a seasonal basis (Outlaw et al. 2003, Alerstam & Bäckman 2018). Additionally, migration can be a response to competition among species or individuals which occupy similar niches; those that cannot efficiently compete engage in travel to attain resources elsewhere (Outlaw et al. 2003, Hedh et al. 2024). Typically, migration movements are responses to seasonal changes which generate competition under limited availability of resources in the home range and provide an alternative strategy for survival for those individuals that are unable to remain as residents (Grayson et al. 2011, Winger et al. 2019).

Migratory patterns are not uniform, even within a species. Intraspecific variation may occur leading to partial migration, where some individuals migrate and other individuals in the same population remain resident at the breeding site (Chapman et al. 2011). What determines which individuals are likely to migrate each year can be dependent on the species' life history and individual condition (Dingle & Drake 2007, Grayson et al. 2011). Of those species that employ partial migration behavior, many are in decline and vulnerable to extinction due to requiring multiple habitat types throughout their lives, and this is particularly true for amphibian species (Luedtke et al. 2023, Davis et al. 2024). Moreover, among age classes, juvenile animals across taxa typically encounter the greatest likelihood of mortality, and the energetic costs associated with migration or dispersal movements may exacerbate this risk (Pianka 1970, Rothermel 2004).

Dispersal movements are one-way migration events from birth sites to new residential or breeding locations among populations. These dispersal movements are thought to be important in colonization of unoccupied sites or sites where extirpation has previously occurred, and local population persistence, dispersal is thought to be more common among juvenile amphibians than adults (Berven & Grudzien 1990, Harper & Semlitsch 2007, Semlitsch 2008). State variables (e.g. mean growth rate and body size), as well as environmental effects such as relative humidity, temperature, and precipitation, have been demonstrated to affect the movement patterns of various amphibian species, both anuran and caudate (Sinsch 1997, Chan-McLeod 2003, Roe & Grayson 2008, Dervo et al. 2016, Dalpasso et al. 2023). Despite most species having a terrestrially adapted life stage, amphibians are heavily tied to the presence of moisture in their environments due to the high permeability of their cuticle, which loses moisture evaporatively, leading to the potential for desiccation (Sprenger et al. 2024). Amphibians hydroregulate behaviorally to maintain a careful water balance, including by foregoing movements in favor of remaining moist in appropriate microhabitats (Mitchell & Bergmann 2015). Therefore, the quality of the habitat through which individual anurans migrate, and the available microhabitats for stopover refuge, may be critical for survival of individuals undergoing migration (Seebacher & Alford 2002). Thus, juvenile amphibians, who are naive to the terrestrial landscape, may engage with partial migration and/or display migratory behaviors differently from adult individuals who have used migratory routes experienced from prior migrations, and are thus acquainted with the landscape (Sinsch 1997, Grayson et al., 2011).

Juvenile anurans are thought to be at higher risk of desiccation compared to adults, whose larger body sizes facilitate water conservation due to advantageous differences in surface area to volume ratio (Shoop 1974). It has been suggested that, in amphibians, initial orientation behavior is critical for the survival and fitness of an individual but may be limited by their sensory capabilities (Pittman et al. 2014). These studies have explored the role of both direct cues such as visual landscape features and olfactory cues, as well as the use of indirect cues like celestial patterns or geomagnetic fields for orientation and dispersal in pond-breeding amphibians and suggest that a mix of cues may be employed (Sinsch 1990, Patrick et al. 2007, Popescu et al. 2012).

Confronting the choice of partial migration, some juvenile individuals may forgo dispersal movements in favor of remaining at or near the breeding site, until reaching sexual maturity (Semlitsch 2008). Migration is energetically costly, increases the risk of desiccation, and exposes individuals to predation (Shoop 1974, Semlitsch 2008). In addition, secondary sites and appropriate habitat may not be intercepted during dispersal movements (Pittman et al. 2014). Larger size at metamorphosis, as a result of increased growth rates, can be associated with fitness advantages such as higher fecundity and earlier age of first reproduction (Smith 1987, Berven 1990). Thus, some post-metamorphic individuals may reach sexual maturity sooner and forgo dispersal to maximize their fitness (Berven 1990).

The California Red-Legged Frog *Rana draytonii* is the largest member of the Ranid family native to the Western U.S. and has been extirpated from approximately 70% of its former range (Jennings & Hayes 1988). Historic overexploitation by people, habitat destruction, introduction of non-native species, and disease are just a few of the pressures that have been implicated in contributing to its decline (Jennings & Hayes 1985). Today, they are federally protected under the US Endangered Species Act and listed as threatened (USFWS 1996). *Rana draytonii*, provides an excellent model for studying how patterns of partial migration among various age classes may occur in an amphibian species.

During the breeding season (November-April), adult *R. draytonii* not already living at the breeding site migrate from their upland and residential aquatic habitats to breeding habitats including ponds, seasonal marshes, creeks, and channels, with breeding itself lasting about 2-3 weeks. Females deposit their egg masses and attach them to emergent vegetation which are externally fertilized by the males (Alvarez et al. 2013). Larvae emerge after 1-8 weeks, and transition to a more terrestrially adapted stage through metamorphosis 3-7 months later, depending on factors such as water temperature (Jennings & Hayes 1994). By mid-summer, most *R. draytonii* larvae have transitioned from the larval form, through metamorphosis, into a small version of the terrestrial adult form known as metamorphs or froglets (henceforth froglet). Froglets then may disperse from their natal pond into the surrounding habitats or remain in the natal pond until achieving reproductive age following the arrival of seasonal rainfall, which marks the end of the hot, dry Mediterranean summer, transforms the landscape into a more suitable environment for amphibian movement by reducing the risk of desiccation (Stebbins 2003, Allaback 2010).

The lack of information on the dispersal habits of recently metamorphosed California Red-legged frogs is a critical missing piece of our understanding of their movement ecology. Previous studies have addressed adult *R. draytonii* landscape movement patterns through the implementation of radio telemetry in both the pre-, and post-breeding seasons, (Bulger et al. 2003, Fellers & Kleeman 2007, Tartarian 2008). Necessarily, these studies targeted adult frogs, and did not address the drivers of partial migration strategies. In addition, they did not examine fine-scale movement patterns of the individuals monitored, as the frequency of tracking sessions was approximately 2-3 times per week. Critically, while these studies improved understanding of the movement ecology of adult *R. draytonii* in relation to both their seasonal breeding migrations and non-breeding movements, they did not address how post-metamorphic juveniles interact with environmental conditions and landscape factors during initial naive dispersal movements, or the proportion and characteristics of juveniles who may forgo dispersal in favor for remaining at the natal site as residents.

In this study, we used radio telemetry to track the terrestrial movements of *R. draytonii* froglets during the dispersal from a natal pond. We investigated the drivers of partial migration strategies exhibited by froglets tracked in the study (remaining resident in the breeding pond or dispersing), as related to sex and individual state variables (size, mean growth rate). For individuals that did disperse from their natal pond, we investigated whether initial travel direction was random, or whether they demonstrated evidence of orientation. Further, we examined the patterns of movement (whether frogs moved from their previously occupied microhabitat and rate of movement) with respect to time of day, and climatic factors such as precipitation, temperature, wind speed, and relative humidity. Finally, we examined whether sex, state variables (size, mean growth rate), mean movement rate, or climatic factors impacted likelihood of survival through the period of monitoring.

Methods

Study Site

The study took place at the Mitsui Ranch Preserve (**Figure 1**), a 632-acre cattle ranch located 8 kilometers East of Petaluma in Sonoma County, CA, near the summit of Sonoma Mountain. Parts of Sonoma Mountain are currently listed as a critical designated habitat for *R. draytonii,* with approximately 60% of the property itself falling under the SON-2 unit of designated critical habitat for the species. The property consists of patchy oak savanna as well as more than 80% open rangeland used for seasonal cattle grazing. Plant species which make up these features include Coast Live Oak (*Quercus agrifolia*), Oregon White Oak (*Quercus garryana*), Black Oak (*Quercus kelloggii*), California Bay Laurel (*Umbellularia californica*), as well as native and invasive grasses. Located on the property are two ponds consistently used by *R. draytonii* for breeding (Wilcox et al. 2017). This study was centered around Bonnie's Pond, the smaller of the two ponds, which consistently produces egg masses each year (Wilcox et al. 2017). Directly North of the pond, there is a small, forested area, whereas directly South of the pond, there is mostly open grassland. Further Northwards from the pond, there are other additional property features known to support *R. draytonii* including Copeland Creek, a non-breeding perennial pond, and springs. Approximately 600 meters south of Bonnie's Pond is Leaky Lake, a larger ephemeral pond that also serves as a breeding site for *R. draytonii* on the property.

Marking Individuals

Following metamorphosis, individual froglets were hand-captured after dark, weighed to the nearest 0.1 gram using a Pesola spring scale, and snout-to-urostyle length (SUL) and gape were measured to the nearest millimeter using a ruler. Individuals who met the minimum length of 35 mm SUL were selected to have a Passive Integrated Transponder (PIT-tag) installed subdurally using sterile forceps and scissors in the upper back. After insertion, the PIT-tag was coaxed gently down the length of the back and over the sacral hump using a finger. Each PIT-tag (Biomark MiniHPT8) contains a unique alphanumeric code that can be used to identify the individual using a hand-held scanning device in the field (Biomark HPR Lite Reader). Although these tags weren't the primary method for tracking individuals, they proved helpful in identifying individuals that had shed their transmitters, so another could be attached and data collection could continue, and for reidentifying individuals in the subsequent years to sex them.

Transmitter Attachment and Tracking

Prior to the onset of seasonal rains in fall 2022 and 2023, froglets were collected from the pond edge, and were determined to be eligible to carry a transmitter (BD-2 Transmitter, Holohil Systems Ltd.) based on individual mass. In accordance with the 10% rule, the transmitter package did not surpass 10% of the frog's total body mass to minimize any burden during movement (Richards et al. 1994). With this limit, frogs weighing 8 grams or more were eligible to wear a transmitter. Transmitters were attached to the frogs using <1 mm outer diameter polyethylene microcatheter surgical tubing as a belt around the waist, or the narrowest portion of the frog just forward of the hind legs (**Figure 2**; World Precision Instruments LLC). The two ends of the tubing were secured with cotton thread and tied together using a square knot. Cotton thread ensured that the belt would remain on the froglet for the life of the transmitter battery, but not long enough for the growing froglet to be constrained or injured by the belt. Cotton would eventually rot and break in the event of premature battery failure, or in our inability to relocate the froglet for manual removal at the end of the field season (Bartlet & Peterson 2000). Once outfitted with a transmitter package, the froglets were released back into the pond. Froglets were located using a three-element Yagi antenna and receiver (R-1000, Communication Specialists Inc.), and their locations recorded using a GPS unit (Garmin GPSMAP 64sc). A flag was placed near the located froglet to better assess whether it had moved from its previous position. Efforts were made to confirm froglet position visually while not disturbing them physically. A new GPS location was only taken if the froglet had moved more than 1 meter from its previous location. Prior to transmitter expiration, efforts were made to locate the froglet to replace its transmitter with a new one to extend tracking periods, as each transmitter had a guaranteed battery life of 21 days. During these transmitter replacement periods, the demographic information of each froglet (SUL, gape and mass) were updated.

Frequency of telemetry tracking sessions varied between the two years. During year one, to try and capture fine-scale movement patterns on rainy nights, surveys were conducted every two hours from sunset to sunrise, with two checks during the day, one at noon and one at 14:00, as we assumed that froglets may move more during the night (Fellers & Kleeman 2007). However, this frequency of sampling was unnecessary as frogs did not move as far or as quickly as anticipated, so checks were reduced to two daily surveys during the second year, one at sunset, and one at sunrise. If a froglet died during the tracking period, their body was recovered, and necropsies were performed in order to try and identify the cause of death and assess final body condition.

Weather Data

To evaluate the effects that weather variation had on dispersing froglets' movement patterns, we retrieved daily weather information of mean daily relative humidity (%), mean daily temperature (°C), mean daily wind speed (km/h), and precipitation accumulation (mm). The data were collected approximately 3 kilometers Southwest of the study site at Chateau weather station (KCAPETAL214) near Petaluma, CA, and was accessed via Weather (wunderground.org).

Statistical Analyses

Statistical analyses were performed in JMP 17 (SAS Institute), and R (R Studios). To assess which factors influenced whether froglets moved either at least 1 meter or 5 meters from their last known positions, generalized linear mixed models with a binomial distribution were used for each of these response variables. Daily mean relative humidity, daily mean wind speed, daily mean temperature, daily precipitation accumulation, number of days since the froglet was seen in the pond, and whether the time of day leading up to the survey was daytime or nighttime, and initial SUL, were included as explanatory variables in the model. Because the data were not independent, PIT-tag number was included as a random variable.

To investigate the orientation abilities of dispersing froglets, ArcGIS Pro was used to calculate froglet position angles relative to North. To do this, a reference angle placed in the center of the pond was created and using the Measure Tool and the angles of the positions relative to North (designated as 0°) were calculated. These angles were split into two categories: Initial Foray, and Initial Dispersal. A Watson Two-Sample Test was used to evaluate whether there were differences in movement patterns between the two cohorts, allowing us to pool the data from both field seasons (2022-3 and 2023-4) if there were not. The generated angles were then used in two analyses, using the R Circular package. The first was a Rayleigh's Test to assess whether froglet initial foray positions (forays are temporary terrestrial movements that ultimately end up with the frog back in the pond) were randomly distributed or whether froglets demonstrate pre-dispersal orientation, investigating the quality of habitat and habitat type surrounding the pond prior to dispersal. The second was another Rayleigh's Test assessing whether froglet initial dispersal movements were randomly distributed, or if they showed significant directionality.

Movement distance was calculated as a straight-line distance between recorded GPS locations in ArcGIS Pro using the Measure tool. These were divided by the number of hours between surveys in order to generate a movement rate of meters per hour (m/h). To evaluate the effects that time of day (day/night), daily mean temperature, daily mean relative humidity, daily precipitation accumulation and number of days since the froglet was seen in the pond had on the movement rate of dispersing froglets, a generalized linear mixed model with a Poisson distribution was employed. Because the data were not independent, PIT-tag number was again included as a random effect. Temperature, relative humidity and precipitation accumulation were all checked for multicollinearity. Instances in which we could not confidently say whether day or night had exclusively passed between surveys were excluded from the data sets analyzed where time of day was investigated as an explanatory factor. For all analyses, instances where frogs were in the pond were excluded as they didn't qualify as dispersal movements. Nominal logistic regression analyses with a logit function were performed to evaluate the effects of dispersal size (SUL) and mean movement rate (m/h) had on whether or not (Y/N) a frog reached a secondary aquatic site (used as a proxy for surviving dispersal), and whether sex and mean growth rate (mm/day) affected froglet movement strategy (dispersing away from the pond or foregoing dispersal to remain a resident). Dispersal SUL was used rather than initial SUL as not all individuals dispersed at the beginning of the tracking period, giving froglets the opportunity to continue foraging and growing in the pond. Dispersal SUL was the size recorded during transmitter replacement and demographic updates closest to the date of dispersal. Sex was determined from surviving frogs recaptured in subsequent years during weekly demographic surveys (Wilcox, J. unpub. data). Using PIT-tag numbers to identify individuals, we determined sex once they had reached sizes associated with sexual maturity and the exhibited secondary sexual characteristics indicating male (presence of nuptial pads and paired vocal sacs), or female (presence of amplexal scars, lack of male characters, and loss of 15–20% of body weight after the breeding season). Mean growth rate (mm/day) was determined by calculating the difference between their final SUL and initial SUL divided by the number of days the frog was in the study.

Results

A total of 39 froglets were tracked over two seasons; 19 froglets were tracked in the first season, and 20 in the second season. The first cohort of froglets was tracked from October 31, 2022, until January 12, 2023, and the second cohort from October 26, 2023, until May 6, 2024. The data show how the state variable growth rate influences dispersal strategy, with froglets demonstrating higher mean growth rates (mm/day) being more likely to become residents of the pond, as opposed to dispersing ($X^2 = 10.55$, $p = 0.012$; **Figure 3**). Males were less inclined to disperse away from the natal pond than females ($X^2 = 35.40$, $p < 0.0001$).

The Watson Two-Sample Tests showed no difference among cohort foray, and dispersal positions ($p = 0.10$), allowing us to pool the two cohorts together for the orientation analyses. The Rayleigh's test investigating froglet initial foray orientations demonstrated significant directionality, and froglets were distributed in a fan-like arrangement around the Northern shore of the pond, with some individuals having explored the Southwest shore ($R = 0.44$, $p = 0.0023$; **Figure 4**). Similarly, the initial dispersal movements of froglets were significantly directional ($R = 0.54$, $p = 0.0002$, **Figure 4**) and demonstrated that froglets primarily dispersed Northwards of the pond, in that similar fan-like arrangement. The mean direction of travel was 15.7 degrees East of true North.

Of the explanatory factors investigated for their influence over whether or not a froglet moved more than 1 m from their last known location, daily mean temperature ($F_{1,106} = 8.5628$, $p = 0.0042$, $R^2=0.003$), daily mean relative humidity ($F_{1,388} = 17.0152$, $p < 0.0001$; **Figure 5**), and number of days since being in the pond ($F_{1,388} = 7.6473$, $p = 0.0060$) were all found to be influential. Frogs moved more than 1 m from their last known positions at daily mean relative humidity rates of 67% or higher, with no movements at relative humidities under 67%. Froglets also moved more than 1 m from their last known positions more often the more recently they were seen in the pond, so as time since being in the pond increased, their movements decreased. For longer distance movements of greater than 5 m, daily mean relative humidity ($F_{1,342}$ = 15.1873, p = 0.0001), number of days since the froglet was seen in the pond ($F_{1,342}$ = 7.6993, p = 0.00058), and day/night ($F_{1,342}$ = 7.0245, p = 0.0084) were found to be influential. Size (initial SUL), temperature, wind speed, and precipitation accumulation were not significant and removed from the model. A minimum daily mean relative humidity of 67% threshold also applied for 5 m movement distances. While froglets moved 5 m or more both diurnally and nocturnally, they tended to favor nocturnal movements for these longer movements.

Froglets' dispersal movement rates increased as daily mean relative humidity increased ($F_{1,521}$ = 55.0975, p < 0.0001; **Figure 6**) and daily precipitation accumulation increased ($F_{1,521}$ = 5.3598, p = 0.0210). Additionally, they showed movements between 5°C and 16 °C, but the highest rates of movement between 9°C and 14 °C ($F_{1,521}$ = 5.8749, p = 0.0157; **Figure 7**). Dispersing froglets moved both during the day and at night, however their movement rates were significantly higher at night ($F_{1, 521}$ = 48.9482, p < 0.0001; **Figure 8**). Wind speed was not found to significantly affect movement rate.

Both larger size at dispersal (dispersal SUL) (X^2 = 6.14, p = 0.013) (**Figure 9**) and higher mean dispersal movement rate (m/h) (X^2 = 8.30, p = 0.004) increased the likelihood of a froglet surviving dispersal, by reaching a secondary aquatic site. Many of the frogs tracked died during their dispersal movements without having made it to a secondary aquatic site. Over the course of both field seasons, when excluding transmitter failures and slipped belts, approximately 45% of froglets tracked died without having made it to a secondary site. 36% of the froglets tracked became pond residents, never having dispersed away, and the remaining 18% successfully dispersed to a secondary aquatic site, all of which were located North of the breeding pond. Ten froglets had necropsies performed on them, two froglets died of puncture wounds that might have indicated predation attempts, three were severely dessicated at the time of recovery, and the rest had no obvious causes of death.

Discussion

Partial Migration

This study is the first to address how some post-metamorphic froglets interact with environmental conditions and landscape features during naive dispersal movements, and we also address the question of which froglets forgo dispersal in favor of remaining at the natal site as residents. We confirmed a pattern of partial migration for the metamorph life stage at this site where frogs with higher mean growth rates tended to become resident at natal ponds whereas those with smaller mean growth rates dispersed. Dispersing from the natal pond is not only dangerous due to the risk of desiccation, but energetically costly as well (Shoop 1974, Semlitsch 2008). However, due to density limitations and competition with conspecifics for resources, not all frogs remain at the breeding site (Wilbur 1980, Semlitsch 2008). Resident frogs exhibited higher mean growth rates (mm/day). Anurans are gape-limited predators, and larger body size as a froglet may confer competitive foraging advantages through impacts on gape-size (Szekely et al. 2020). Other studies found that larger individuals generally tend to remain residents as opposed to dispersing, so having increased growth rates can help frogs reach a larger size faster (Grayson et al. 2011). Since adult frogs are cannibalistic, individuals who grow quicker and larger than other members of the cohort may attain a body size large enough to avoid cannibalism by resident adult frogs, conferring a greater chance of survival in the pond environment (Dickerson 1906). Faster growing, larger, frogs may also reach sexual maturity quicker than those who grow more slowly (Smith 1987).

Males are thought to be more likely to remain at the breeding site to maximize their breeding opportunities, whereas females often disperse away from the pond in favor of secondary sites in order to garner greater resources for provisioning their egg production, and for avoiding harassment by males near the breeding season (Fellers & Kleeman 2007, Bloch & Grayson 2010). Larger size at metamorphosis has been implicated in other studies to lead to higher juvenile survival rates, earlier reproductive age, and larger adult size (Smith 1987, Berven 1990, Szekely et al. 2020). In the second field season, two non-dispersing, large-bodied froglets remained in a wetland adjacent to the natal pond from late December 2023 until early May of 2024, moving minimally between surveys, before ultimately returning to the natal pond. The timing of their return to the pond coincided with the end of the breeding season, as adult males had ceased calling. This avoidance behavior may be an evolutionary strategy employed by developing frogs who remain residents of the pond area, but avoid cannibalism by larger adults who are present in higher numbers during the breeding period (Fellers & Kleeman 2007).

Dispersing froglets seek a secondary aquatic residential site or appropriate upland habitat where they can forage and grow until reaching maturity, thereby avoiding competition for food at the natal site (Semlitsch 2008). However, dispersal across unknown landscapes is fraught with danger, especially in the form of desiccation (Shoop 1974). For this reason, *R. draytonii* froglets dispersed during the seasonal rain events, and not earlier (Semlitsch 2008, Allaback 2010). The arrival of seasonal rainfall doesn’t only facilitate juvenile movement, it is also the same environmental trigger which urges adult non-resident frogs to make their journey back to the breeding pond to complete their life cycles, due to seasonal rainfall providing much-needed moisture which reduces the risk of desiccation in the terrestrial environment (Bulger et al. 2003, Stebbins 2003). Although the juvenile class is thought to be responsible for among-population dispersal and the maintenance of metapopulations through gene flow, we did not document any movement between the two breeding sites over the course of the study (Berven & Grudzien 1990, Semlitsch 2008).

Orientation of Dispersing Metamorphs

For dispersing froglets, their ability to orient from the pond edge and respond to environmental cues while traversing through their dispersal corridors may be critical to minimizing their likelihood of desiccation and maximizing their chance of survival (Pittman et al. 2014). While some studies suggest that frogs move randomly from the pond edge (Semlitsch 2008), other studies on Ranid frogs, including this study, demonstrate the opposite (Vasconcelos & Calhoun 2004, Patrick et al. 2007). However, prior to engaging in dispersal movements, *R. draytonii* froglets seemingly engaged in short–distance foray behavior. Forays resulted in the froglet returning to the pond and were not considered dispersal movements. Froglets participated in an average of 1.6 forays before either permanently dispersing away from the pond or eventually returning to the natal pond without dispersing. Forays may serve as a mechanism of making temporary exploratory movements to assess the qualities of the terrestrial environment surrounding the pond prior to dispersal, and/or for foraging purposes, as *R. draytonii* largely rely on terrestrial prey (Bishop et al. 2014). The distribution of the forays closely resembled those of their dispersal movements (**Figure 4**), which indicates that frogs may have been assessing cues they intended to use to disperse prior to ultimately dispersing.

Direct cues such as olfactory cues or visual cues (e.g. landscape features) may serve to aid in orientation for dispersal (Rothermel & Semlitsch 2002). The result of the Rayleigh's test on the distribution of initial dispersal orientations identified the Northern direction as favorable to the majority of froglets in the study. Two distinct habitat types are found adjacent to the natal pond: canopy and forested area to the North, and open grassland to the South. Some froglets dispersed Southwest, but there were very few, and none that continued dispersal in that direction survived until the end of the study. Canopied edge found proximal to the Northern edge of the pond had a mean distance from pond edge to canopy of around 12 m and may have served as a landscape feature acting as a visual cue. Canopy is known to reduce solar radiance and higher levels of relative humidity are generally found below the canopy, both of which can reduce desiccation threats and serve as favorable dispersal corridors (Spranger et al. 2024). Canopied areas also provide a greater diversity of microhabitats for frogs to occupy between dispersal movements (Rothermel & Semlistch 2002, Puay et al. 2018). It appears that in this population, forest canopied areas may be the preferred migratory pathway for dispersing *R. draytonii* froglets. Whether or not visual cues such as canopied forest are driving orientation preferences by dispersing froglets requires further investigation.

Indirect cues (celestial, magnetic etc.), not measured in this study, may be influencing the initial orientation and movement patterns of froglets. The heritability dispersal direction has been investigated in other species and suggests that the ability to follow environmental cues may be genetically passed onto offspring by adults as a mechanism of species survival and persistence (Miaud et al. 2005). In this population, the majority of breeding adult frogs are not residents, and live part of the year at secondary aquatic sites spatially distributed across the landscape, mostly North of the breeding pond (**Figure 1**). Most adults annually return to the breeding pond, ostensibly passing on their genetic predisposition for detecting indirect cues related to orientation by their offspring. Individuals who travel South into the grassland environment may not survive to pass on their alleles and perpetuate their preferred dispersal direction.

Body Size Impacts On Movements And Survivorship

Among dispersers, those that survived were generally of larger body size and exhibited higher mean movement rates compared to non-surviving dispersers. Larger body sizes are known to reduce the rate of evaporative loss, compared to smaller body size due to differences in surface area to volume ratio, allowing larger frogs longer periods of time outside of moist and/or humid environments, or better able to resist periods of dry conditions (Bulger et al. 2003, Fellers & Kleeman 2007, Sheridan et al. 2022). In addition to the advantages that larger body size brings to surviving under desiccation stress, larger body size is correlated with larger gape. Larger frogs can therefore consume larger prey, and can grow more quickly as a result, since they efficiently convert prey biomass into body biomass (Grayson et al. 2005). Larger frogs also have the capacity for greater movement rates due to their larger body sizes which may allow larger frogs to have a greater chance at reaching secondary aquatic sites, and surviving their first-year migration (Bredeweg et al. 2019, Murphy and Boone 2022).

Impacts of Environmental Moisture

With the arrival of moist seasonal conditions from precipitation, an otherwise dry environment is transformed into a more favorable landscape for frog movement, by reducing the risk of desiccation in the terrestrial landscape (Allaback 2010, Todd et al. 2011). Thus, in response to moisture-related conditions, such as higher relative humidity and precipitation, froglets moved greater distances between surveys, resulting in higher movement rates. Additionally, moist conditions also impacted whether frogs moved at least 1 m and 5 m from their last known positions, with a general requirement of a mean daily RH of approximately 67% for movement. Due to their highly permeable cuticle, frogs can absorb water easily through the skin, but lose water evaporatively under drier conditions (Sprenger et al. 2024). Burrow et al. 2023 suggested that even relatively modest changes in rainfall and humidity could have drastic impacts on metamorph survival which can be compounded for froglets by the differences in surface area to volume ratio between juveniles and adults (Bulger et al. 2003, Fellers & Kleeman 2007).

Migration Movements Over Time

Metamorph frogs were also more likely to move earlier in their individual migration journeys with movement rates decreasing as more time passed since they left the pond. As individuals disperse, and encounter moist microhabitats such as leaf litter, canopied forest, or other refugia, their movements may decrease or cease altogether, as they encounter appropriate microhabitats to occupy (Roznik & Johnson 2009). Additionally, the timing of moist conditions can vary significantly, with long periods of dry weather between sporadic seasonal rainfall, meaning that frogs who disperse early on may encounter an appropriate microhabitat to temporarily settle in, only to find that the conditions which enable movement do not return for long periods, discouraging continued dispersal (Burrow et al. 2023). Furthermore, the energetic influences of size at metamorphosis and dispersal can influence the movement patterns of dispersing individuals, with the compounding effects of desiccation avoidance, thermoregulation, and predator avoidance depleting the energy stores of dispersing froglets who have finite energy reserves at the time of leaving the pond, leading to a decrease in movement and activity (Bredeweg et al. 2019).

Temperature Effects on Movement

Froglets moved between 5 °C and 16 °C, and there was a slightly higher probability of movement when it was warmer. As ectotherms, frogs may attempt to balance higher temperatures for functional performance, including jumping performance, and lower temperatures for reduction in desiccation effects (Kohler et al. 2011). In red-legged frog metamorphs, which show a lower high end temperature for movement than some other frog species (Renauld & Stevens 1983, Crespo-Martinez et al. 2025), it appears that desiccation may be the key driving factor for movement activities within the range of functional temperatures and that, despite the statistical significance of the temperature variable being identified, it is likely that the biological significance of any exact temperature between the 5 °C and 16 °C on movement is minor given the R^2 of 0.003.

Movement Timing

Unlike adult frogs who tend to exclusively engage in nocturnal terrestrial activities (Hayes & Tenant 1985), froglets make both diurnal and nocturnal terrestrial movements, although they were more likely to complete longer distance (>5 m) movements after dark and demonstrated higher movement rates during the night period. The lack of time preference for shorter distance movements (<5 m) in froglets may be associated with exploratory behavior and foraging activities in alignment with their terrestrial orientation and dispersal strategies (Rothermel & Semlitsch 2002, Joly 2019, Burrow et al., 2023). Short-distance movements may also occur during the day to adjust microhabitat cover as this can have important effects on desiccation avoidance (Kohler et al., 2011). Nocturnal movements are thought to be beneficial for longer movements as they would reduce the effect of solar radiance on dispersing froglets, and generally have higher rates of relative humidity, which further provide conditions more favorable for froglet movement (Todd & Winne 2006).

Ecological Importance of Froglet Survivorship

Because the juvenile life stage is thought to be a critical life stage in colonizing habitats where extirpation has occurred, recruiting into neighboring populations, maintaining the local adult population, and playing an essential role in gene flow through among-population movement, their survivorship is essential to species persistence on the landscape (Semlitsch 2008). Additionally, the juvenile life stage faces higher selection pressures compared to the adult life stage, and successes in their survival into adulthood can support future generations through passing down of genetic predisposition for survival strategies such as direction of travel, habitat selection, and/or dispersal strategy (Pianka 1970, Miaud et al. 2003). In an era of anthropogenic disturbances, habitat fragmentation, and changes in moisture-based weather patterns due to climate change, creating a better understanding of their population dynamics, movement strategies, and general survivorship in the juvenile life stage are critical in supporting the vulnerable populations of *R. draytonii* and other species of amphibian which persist, even in the face of decline (Landler 2022). Further studies are needed to explore the survivorship rates of dispersers and residents in their first and second juvenile years prior to reaching adulthood.

Conclusions

We observed two movement strategies in red-legged froglets associated with partial migration strategy for the species, to remain resident at the breeding site, or disperse in hopes of reaching a secondary aquatic site. Higher mean daily growth rates appeared to be a key factor in avoiding the rigors of dispersal in favor of remaining residents of the pond and facing the associated competitive environment. For those froglets that dispersed, they were more likely to survive dispersal (reach a secondary aquatic site) if they were larger-bodied at dispersal, and/or exhibited a higher mean movement rate. These results reflect established concepts in evolutionary biology that partial migration behavior is a response to sex and state variables of mean growth rate and dispersal size. Those who cannot compete adequately venture away from the site to access necessary resources for survival, and to maximize their fitness (Grayson et al. 2011, Winger et al., 2019). Frogs who dispersed largely engaged in orientation and moved in a Northward direction, seemingly towards canopy, however, investigations into the role of both direct and indirect cues on the orientation abilities of recently-metamorphosed *Rana draytonii* are needed to more confidently identify what factors influence their dispersal direction preferences. Froglet movement followed common patterns in amphibian migration being largely tied to desiccation avoidance behaviors with larger frogs moving at higher rates and generating higher rates of survival. This study highlights the differences in dispersal strategies undertaken by emerging froglets, which have implications for the spatial population structure of the species, as well as the importance of moisture-related weather patterns, and protective habitat types (such as canopy and secondary aquatic sites) in this critical life stage of *R. draytonii*. By better understanding the dispersal habits, movement patterns, and survival strategies of this vulnerable species of anuran during this key life stage, that potentially impacts both persistence of this breeding population and dispersal among populations, we can potentially take actions to impact their survival in a time when anthropogenic and climatological changes threaten the persistence of this species.

Figures

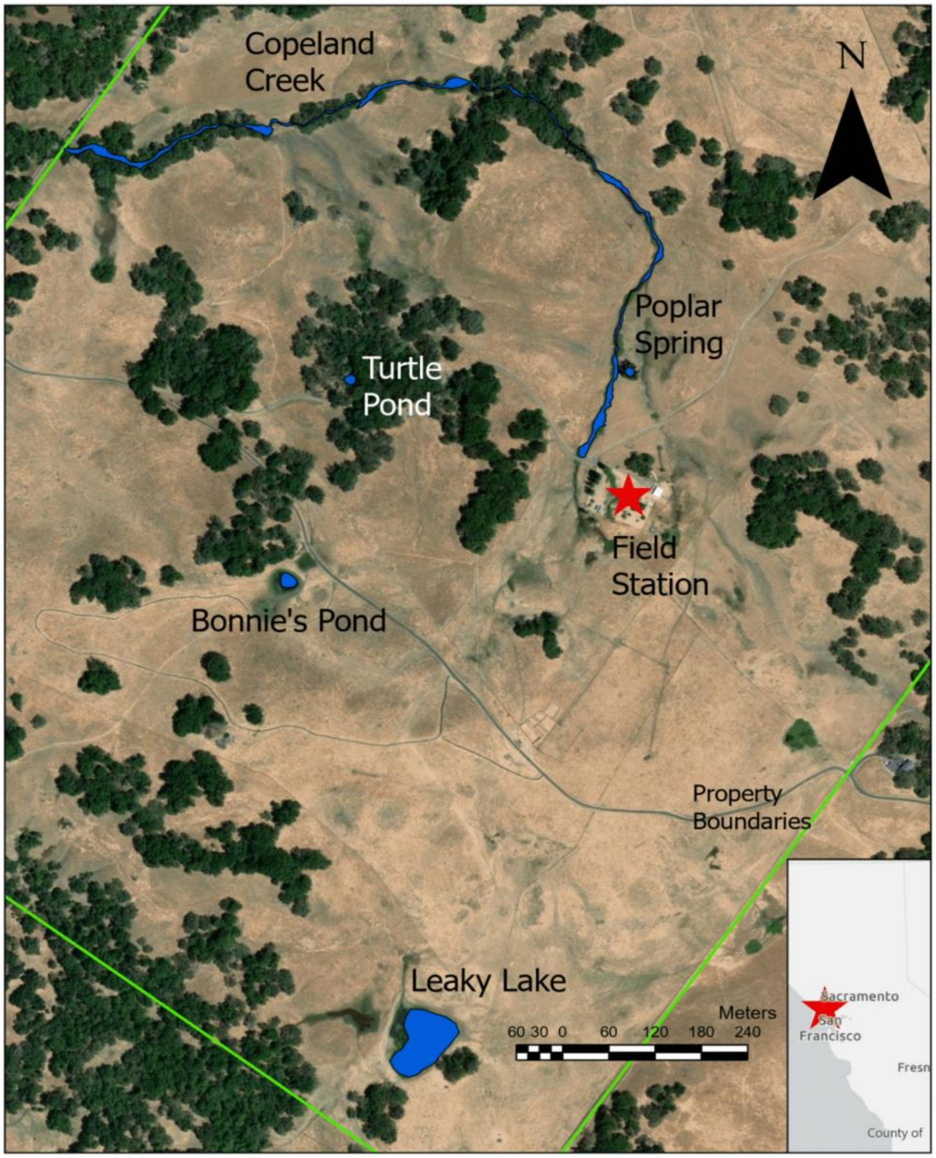


Figure 1. Map of Mitsui Ranch Preserve. A map of the Mitsui Ranch Preserve featuring the two breeding stock ponds (Bonnie's and Leaky Lake), as well as perennial aquatic residence sites (Copeland Creek, Poplar Spring, and Turtle Pond), and the Mitsui Ranch field station.

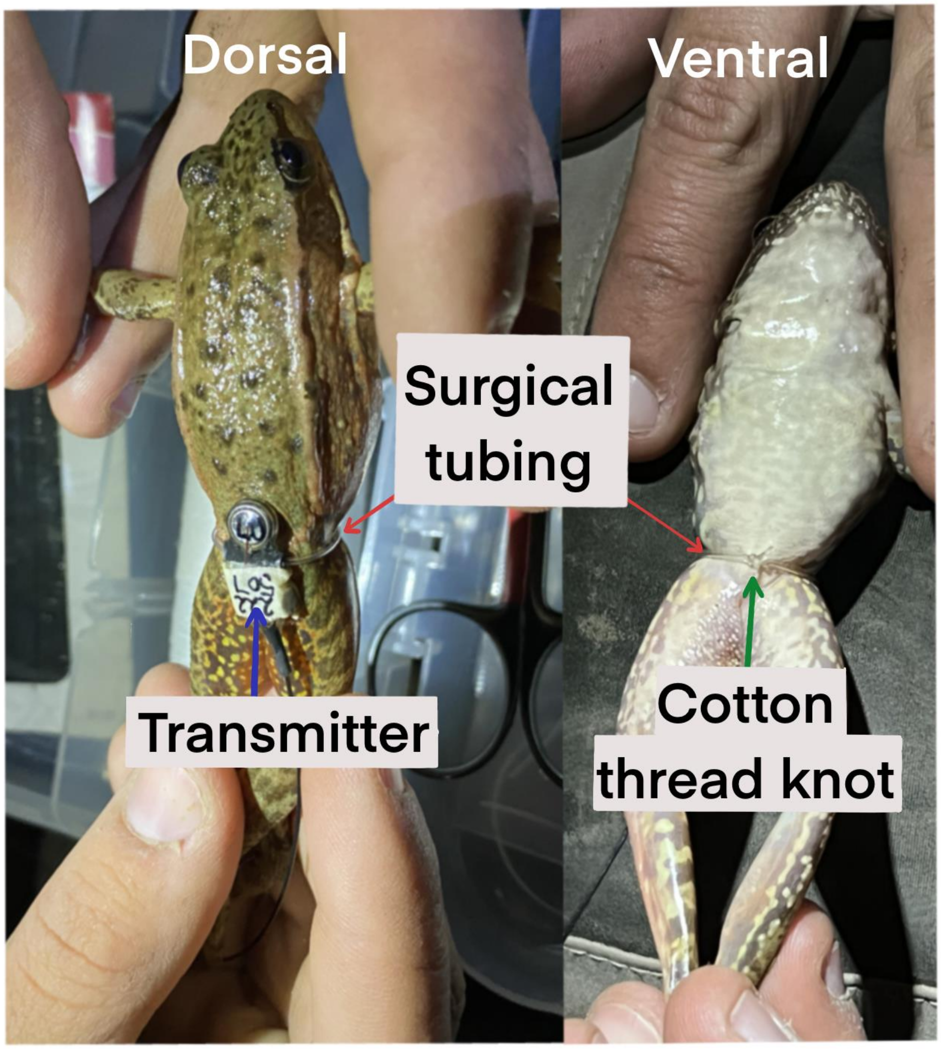


Figure 2. Transmitter attachment method. An image depicting the novel transmitter attachment method for each froglet. A custom length of surgical tubing was cut to fit each froglet, looped through the transmitter's hole, the two ends of tubing were stitched together using cotton thread, and tied off with a square knot.

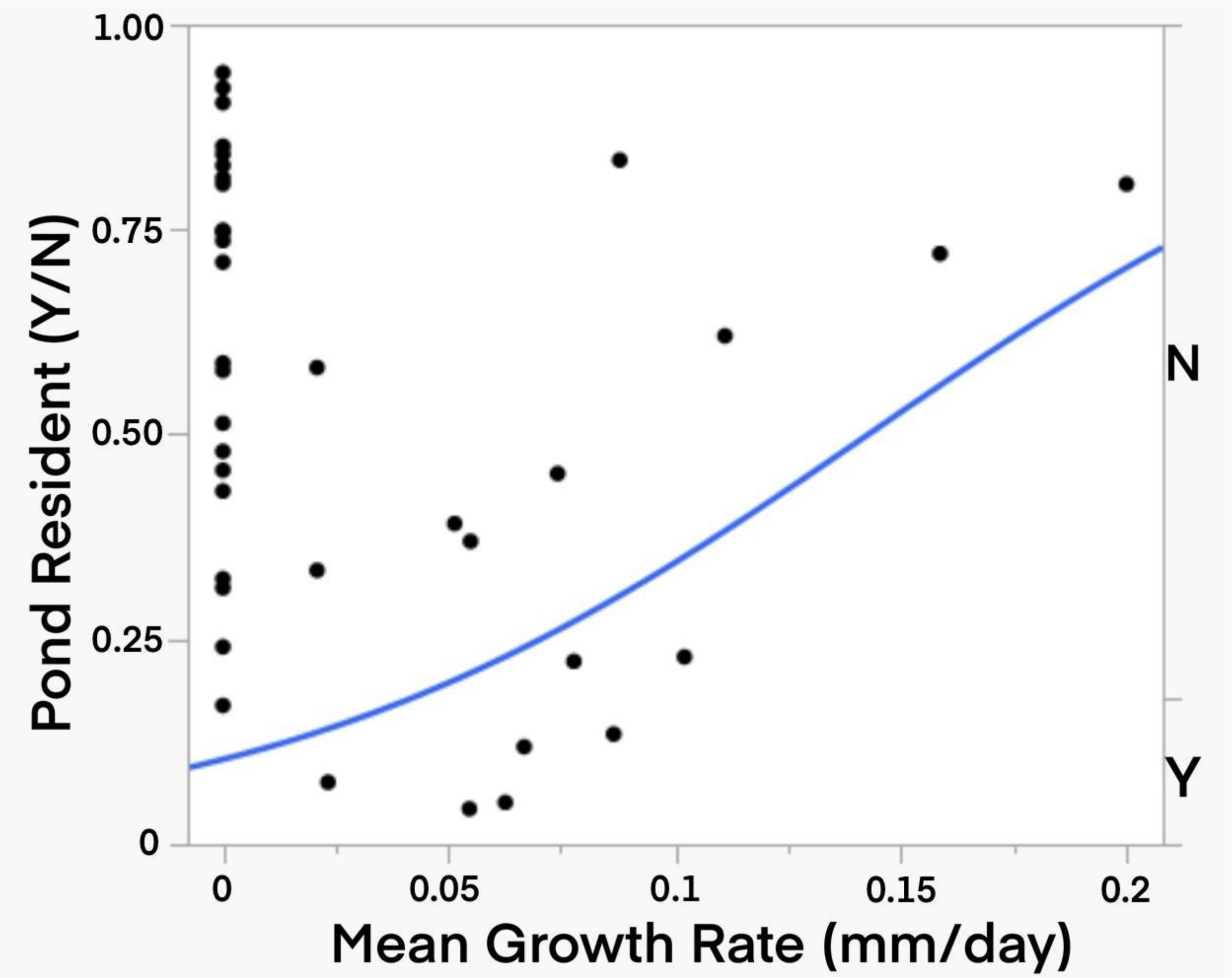
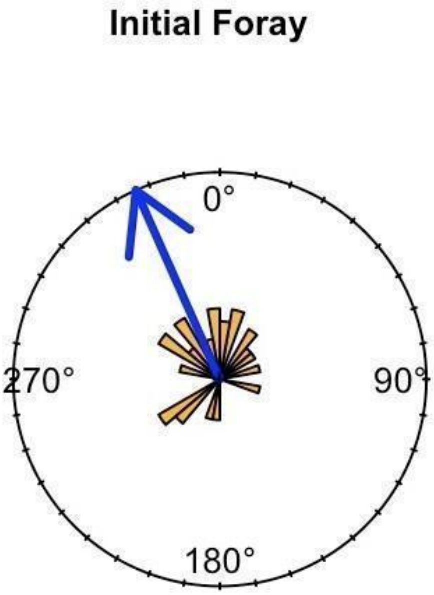


Figure 3. . Dispersal strategy as a response to mean growth rate. Graph demonstrating the differences in mean growth rate by dispersal strategy, identifying pond residents as having some of the highest daily mean growth rates ($X^2 = 10.55$, $p = 0.012$).



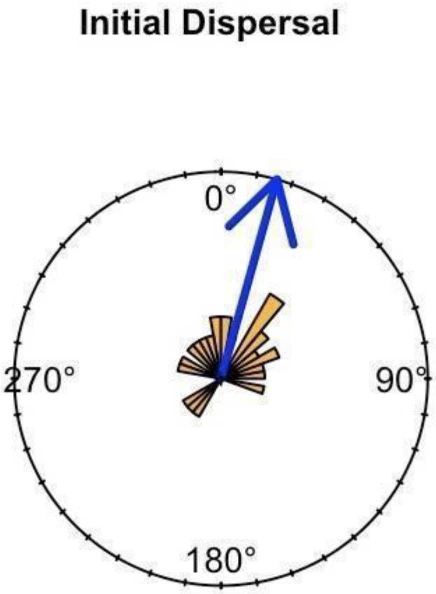


Figure 4. Froglet foray and dispersal orientation rosettes. Rosette diagrams demonstrating the arrangement of foray and dispersal patterns of froglets leaving the breeding pond, relative to North (0°). The blue arrows indicate the mean travel direction, and the length of the arms indicate more individuals moving in those directions.

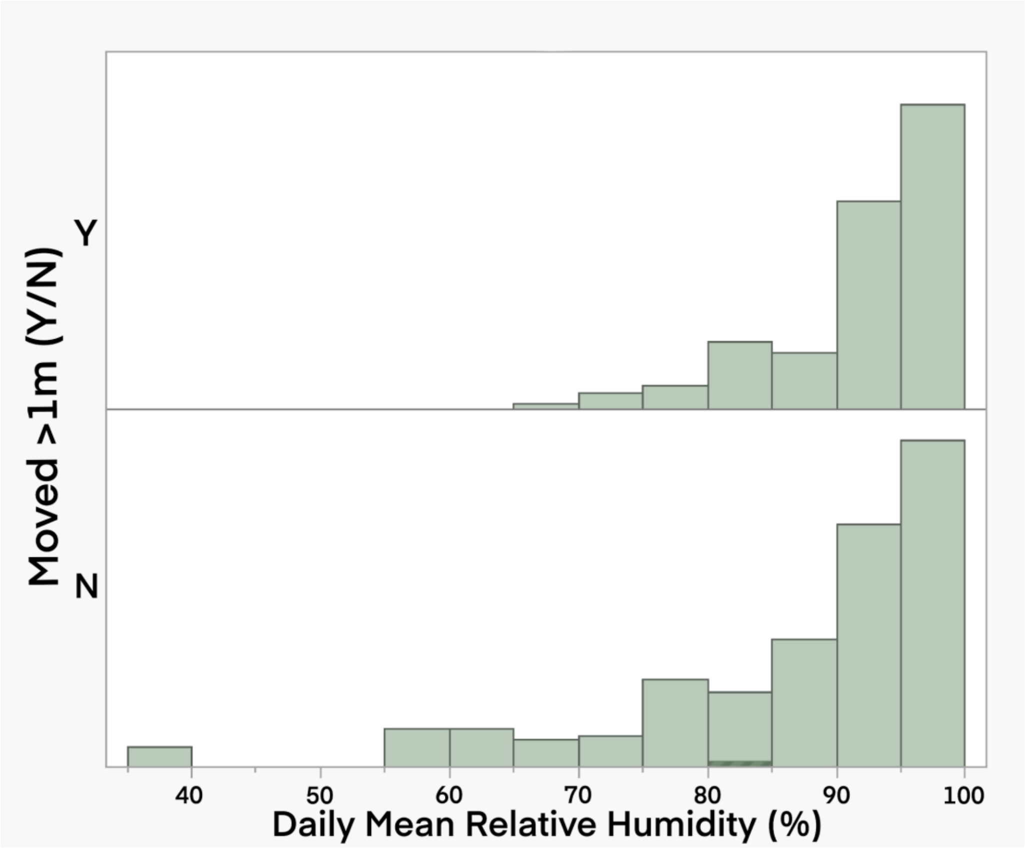


Figure 5. Distance moved (>1 m) as a response to daily mean relative humidity. Graph demonstrating the range of relative humidity (%) relative to whether or not a froglet moved at least 1 m from last known position ($F_{1,388} = 17.0152$, $p < 0.0001$).

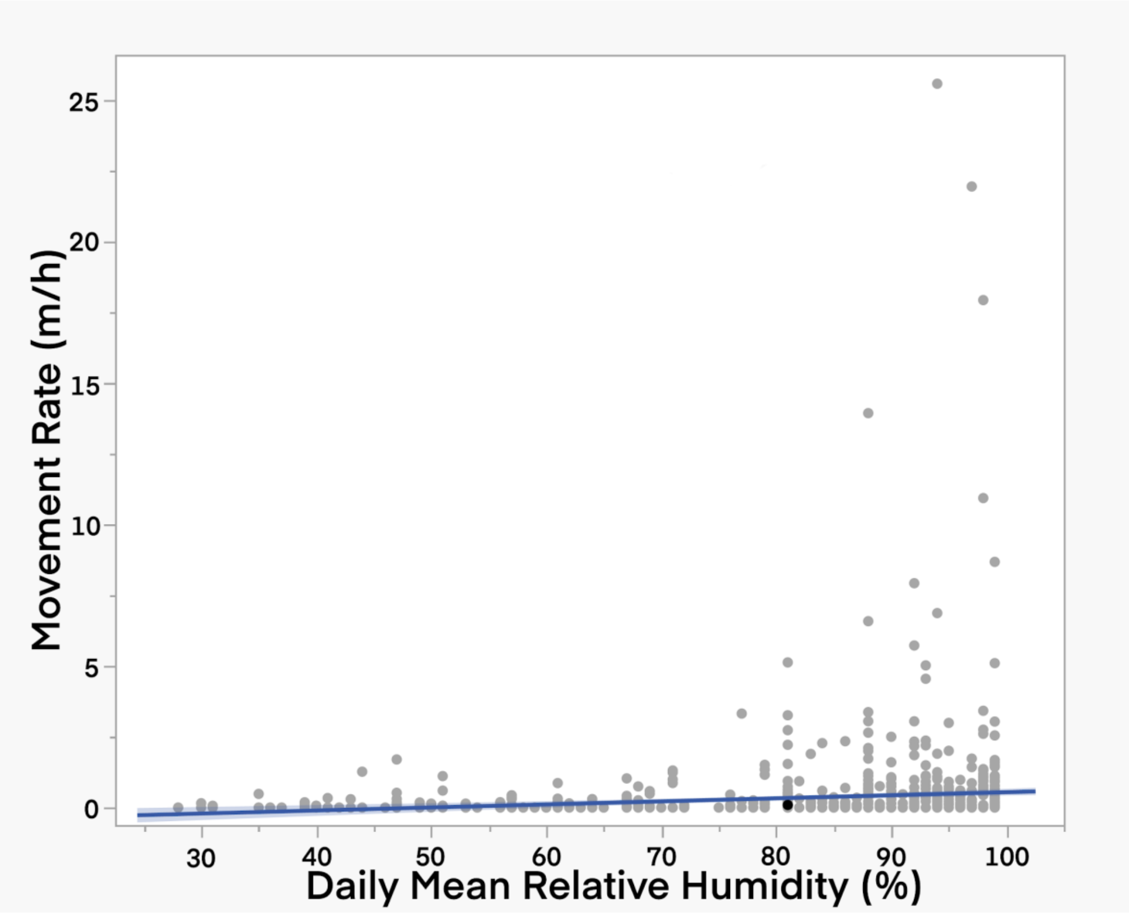


Figure 6. Movement rate as a response to daily mean relative humidity. Graph depicting froglets' increase in dispersal movement rate (m/h) as daily mean relative humidity (%) increases ($F_{1,521} = 55.0975$, $p < 0.0001$).

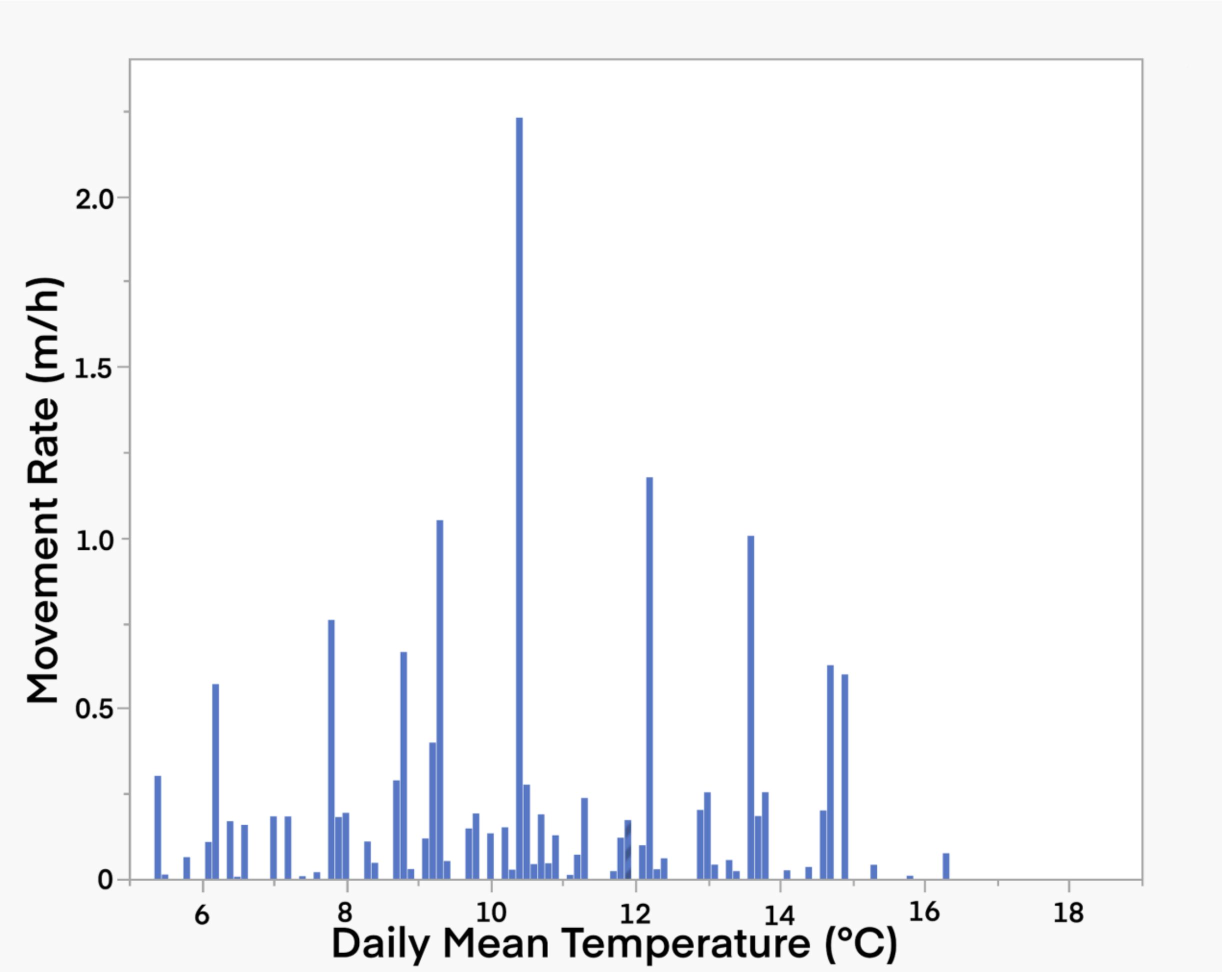


Figure 7. Movement rate as a response to daily mean temperature. Graph demonstrating generalized linear mixed model results investigating dispersing froglet movement rates (m/h) as a response to daily mean temperature (°C) ($F_{1,521} = 5.8749$, $p = 0.0157$).

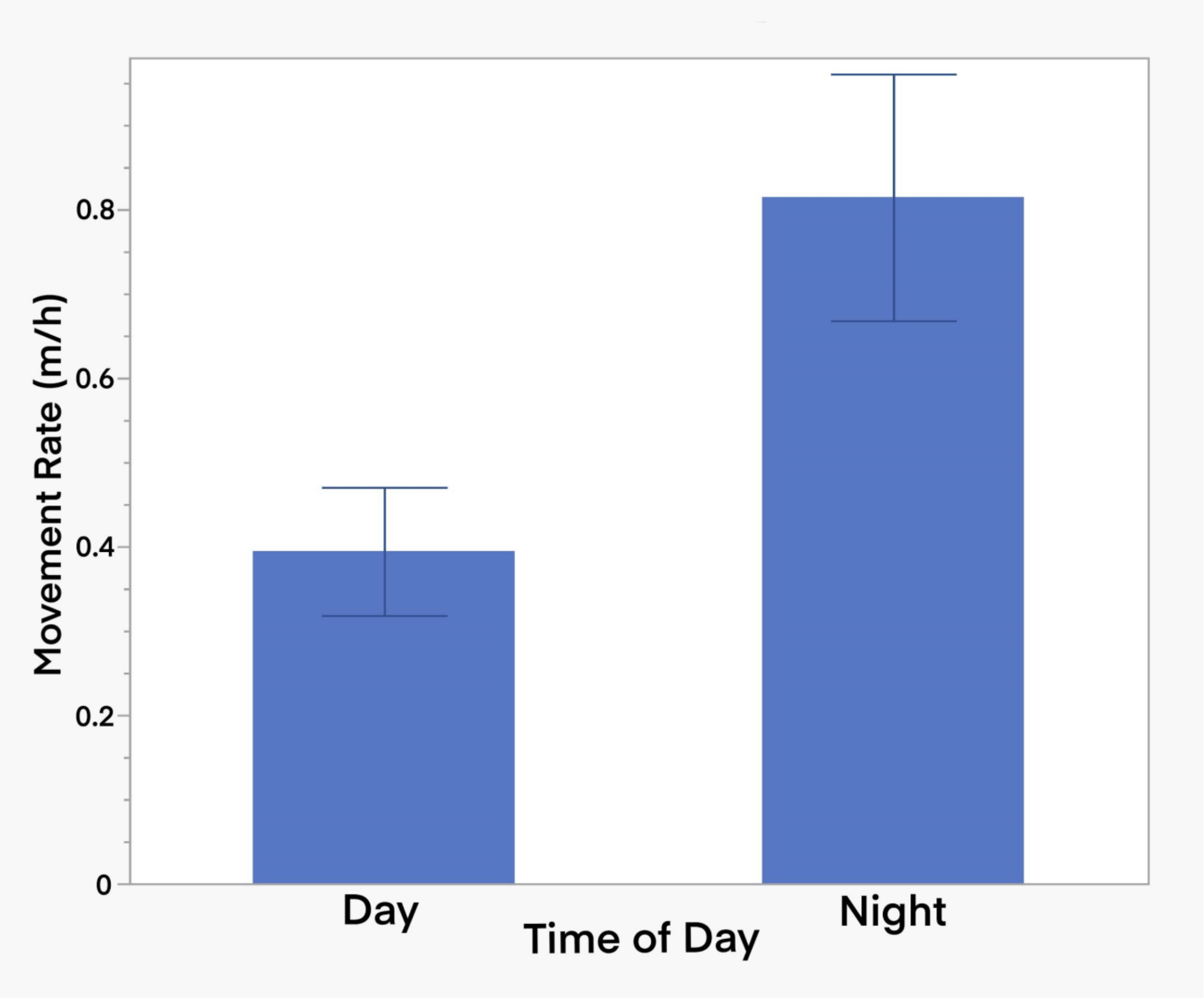


Figure 8. Movement rate as a response to time of day. Results of generalized linear mixed model demonstrating variation in nocturnal and diurnal movement rates ($F_{1, 521} = 48.9482$, $p < 0.0001$).

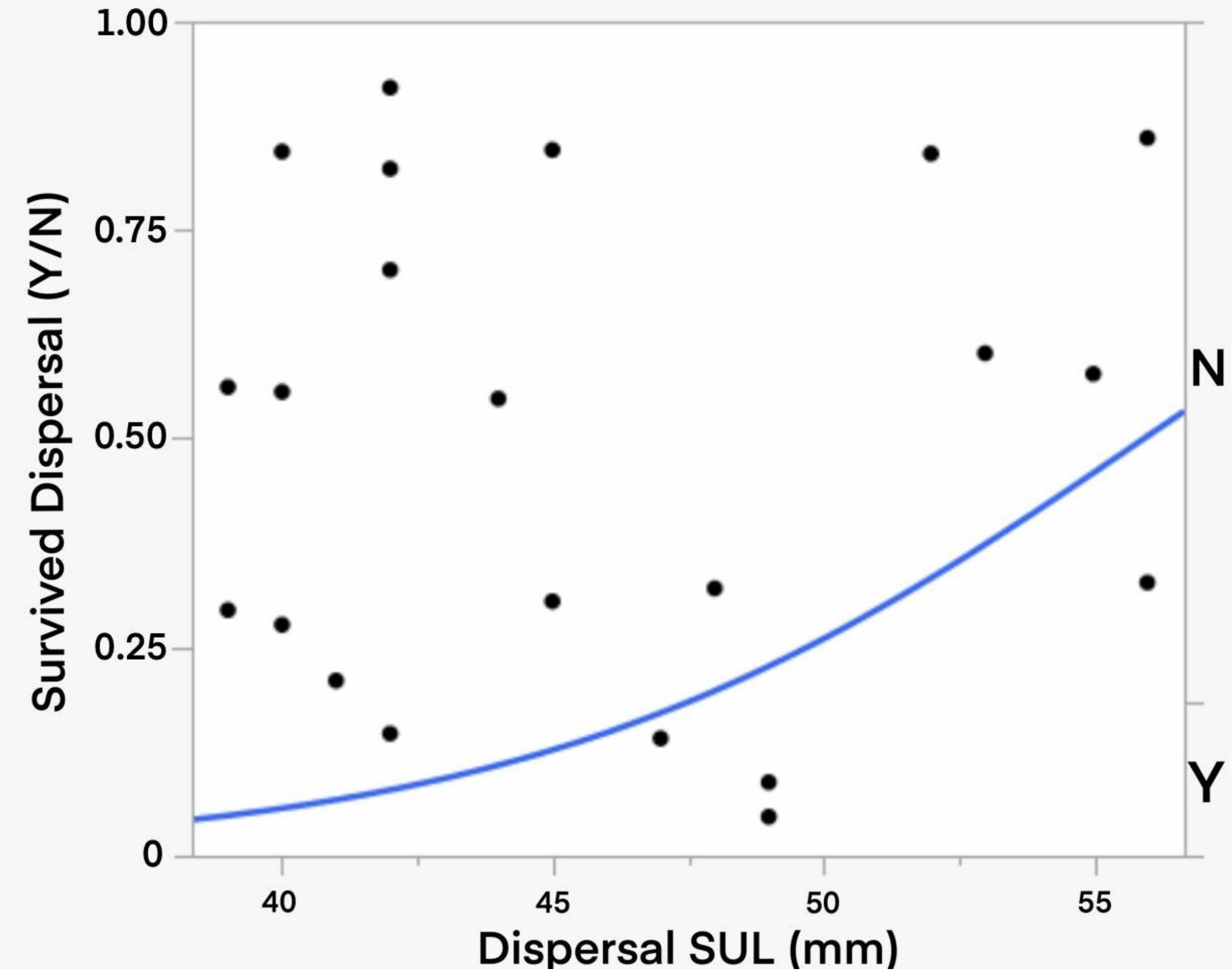


Figure 9. Survivorship as a response to dispersal size (SUL). Results of Nominal Logistic regression analysis demonstrating that froglets with higher dispersal size (SUL) were more likely to survive their dispersal movements by reaching a secondary aquatic residence site ($X^2 = 6.14$, $p = 0.013$).

Literature Cited

Alerstam, T. & Bäckman, J., 2018. Ecology of animal migration. *Current Biology*, 28(17), pp.R968–R972.

Allaback, M., Keegan, D. & Harwayne, J., 2010. *Rana draytonii* (California Red-legged Frog) dispersal. *Herpetological Review*, 40(1), pp.204–206.

Alvarez, J.A. et al., 2013. Comparative microhabitat characteristics at oviposition sites of the California red-legged frog (*Rana draytonii*). *Herpetological Conservation and Biology*, 8(3), pp.539–551.

Bartelt, P.E. & Peterson, C.R., 2000. A description and evaluation of a plastic belt for attaching radio transmitters to Western Toads (*Bufo boreas*). *Northwestern Naturalist*, 81(3), p.122.

Berven, K.A., 1990. Factors affecting population fluctuations in the larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, 71, pp.1599–1608.

Berven, K.A. & Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution*, 44(8), pp.2047–2056.

Bishop, M., Drewes, R. & Vredenburg, V., 2014. Food web linkages demonstrate importance of terrestrial prey for the threatened California red-legged frog. *Journal of Herpetology*, 48, pp.137–143.

Bloch, A.M. & Grayson, K.L., 2010. Reproductive costs of migration for males in a partially migrating, pond-breeding amphibian. *Canadian Journal of Zoology*, 88(11), pp.1113–1120.

Bredeweg, E.M., Urbina, J., Morzillo, A.T. and Garcia, T.S. 2019. Starting on the Right Foot: Carryover Effects of Larval Hydroperiod and Terrain Moisture on Post-metamorphic Frog Movement Behavior. *Frontiers in Ecology and Evolution*, 7.

Bulger, J.B., Scott, N.J. & Seymour, R.B., 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. *Biological Conservation*, 110(1), pp.85–95.

Burrow, A.K., McEntire, K.D. and Maerz, J.C., 2023. Estimating the potential drivers of dispersal outcomes for juvenile gopher frogs (*Rana capito*) using agent-based models. Frontiers in Ecology and Evolution, 11, p.1026541.

Chapman, B.B. et al., 2011. The ecology and evolution of partial migration. *Oikos*, 120(12), pp.1764–1775.

Chan-McLeod, A.C.A., 2003. Factors affecting the permeability of clearcuts to red-legged frogs. *The Journal of Wildlife Management*, 67(4), pp.663–671.

Crespo-Martínez, G.M., Ríos-López, N., Tremblay, R. and Sabat, A., 2025. The jumping performance of two Eleutherodactylus frogs: the effect of temperature. Journal of Thermal Biology, p.104113.

Dalpasso, A. et al., 2023. Effects of temperature and precipitation changes on shifts in breeding phenology of an endangered toad. *Scientific Reports*, 13, 14573.

Davis, F., Szopa-Comley, A., Rouse, S., Caromel, A., Arnell, A., Basrur, S., Bhola, N., Brooks, H., Costa-Domingo, G., Cunningham, C., Hunter, K., Kaplan, M., Sheppard, A., and Malsch, K., UNEP-WCMC, 2024. *State of the world's migratory species*. Cambridge, UK: UNEP-WCMC.

Dervo, B.K. et al., 2016. Effects of temperature and precipitation on breeding migrations of amphibian species in southeastern Norway. *Scientifica*, 2016, Article ID 3174316.

Dickerson, M.C., 1906. *The frog book; North American toads and frogs, with a study of the habits and life histories of those of the northeastern states*. New York: Doubleday, Page.

Dingle, H. & Drake, V.A., 2007. What is migration? *Bioscience*, 57(2), pp.113–121.

Fellers, G.M. & Kleeman, P.M., 2007. California red-legged frog (*Rana draytonii*) movement and habitat use: Implications for conservation. *Journal of Herpetology*, 41(2), pp.276–286.

Grayson, K.L. et al., 2005. Effects of prey type on specific dynamic action, growth, and mass conversion efficiencies in the horned frog, *Ceratophrys cranwelli*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 141(3), pp.298–304.

Grayson, K.L., Bailey, L.L. & Wilbur, H.M., 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology*, 92(6), pp.1236–1246.

Harper, E.B. & Semlitsch, R.D., 2007. Density dependence in the terrestrial life history stage of two anurans. *Oecologia*, 153(4), pp.879–889.

Hayes, M.P. & Tennant, M.R., 1985. Diet and feeding behavior of the California red-legged frog, *Rana aurora draytonii* (Ranidae). *The Southwestern Naturalist*, 30(4), pp.601–605.

Hayes, M. & Jennings, M., 1988. Habitat correlates of distribution of the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylii*): Implications for management. *Unpublished report*.

Hedh, L., Dänhardt, J. and Anders Hedenström (2024). Evolution of leapfrog migration: A test of competition-based hypotheses. *Ecology*.

Hu, J. et al., 2019. Genetic diversity in frogs linked to past and future climate changes on the roof of the world. *Journal of Animal Ecology*, 88, pp.953–963.

Jennings, M.R. & Hayes, M.P., 1985. Pre-1900 overharvest of California red-legged frogs (*Rana aurora draytonii*): The inducement for bullfrog (*Rana catesbeiana*) introduction. *Herpetologica*, 41(1), pp.94–103.

Jennings, M.R. & Hayes, M.P., 1994. *Amphibian and reptile species of special concern in California*. California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, CA.

Joly, P., 2019. Behavior in a changing landscape: using movement ecology to inform the conservation of pond-breeding amphibians. Frontiers in Ecology and Evolution, 7, p.155.

Köhler, A., Sadowska, J., Olszewska, J., Trzeciak, P., Berger-Tal, O. and Tracy, C.R., 2011. Staying warm or moist? Operative temperature and thermal preferences of common frogs (*Rana temporaria*), and effects on locomotion. The Herpetological Journal, 21(1), pp.17-26.

Landler, L., 2022. Orientation and emigration of larval and juvenile amphibians: selected topics and hypotheses. *Amphibia-Reptilia*, 43(1), pp.1–11.

Luedtke, J.A. et al., 2023. Ongoing declines for the world's amphibians in the face of emerging threats. *Nature*, 622(7982), pp.308–314.

Miaud, C. et al., 2003. Preliminary results on the genetic control of dispersal in common frog *Rana temporaria* froglets. *Herpetologia Petropolitana*, pp.193.

Mitchell, A. and Bergmann, P.J. 2015. Thermal and moisture habitat preferences do not maximize jumping performance in frogs. *Functional Ecology*, 30(5), pp.733–742.

Murphy, M. & Boone, M., 2022. Evaluating the role of body size and habitat type in movement behavior in human-dominated systems: A frog's eye view. *Ecology and Evolution*, 12(6), e9022.

Patrick, D., Calhoun, A. & Hunter, M., 2007. Orientation of juvenile wood frogs, *Rana sylvatica*, leaving experimental ponds. *Journal of Herpetology*, 41(1), pp.158–163.

Pianka, E.R., 1970. On r- and K-selection. *The American Naturalist*, 104(940), pp.592–597.

Pittman, S.E., Osbourn, M.S. & Semlitsch, R.D., 2014. Movement ecology of amphibians: A missing component for understanding population declines. *Biological Conservation*, 169, pp.44–53.

Popescu, V.D., Brodie, B.S., Hunter, M.L. and Zydlewski, J.D., 2012. Use of olfactory cues by newly metamorphosed wood frogs (*Lithobates sylvaticus*) during emigration. *Copeia*, *2012*(3), pp.424-431.

Puay Yok, T. et al., 2018. A method to partition the relative effects of evaporative cooling and shading on air temperature within vegetation canopy. *Journal of Urban Ecology*, 4.

Renaud, J.M. and Stevens, E.D., 1983. The extent of long-term temperature compensation for jumping distance in the frog, *Rana pipiens*, and the toad, *Bufo americanus*. Canadian Journal of Zoology, 61(6), pp.1284-1287.

Richards, S.J., Sinsch, U. & Alford, R.A., 1994. Radio tracking. In: Heyer, W.R. et al. eds. *Measuring and monitoring biological diversity: standard methods for amphibians*. Washington D.C.: Smithsonian Institution Press, pp.155–158.

Roe, A.W. & Grayson, K.L., 2008. Terrestrial movements and habitat use of juvenile and emigrating adult eastern red-spotted newts, *Notophthalmus viridescens*. *Journal of Herpetology*, 42(1), pp.22–30.

Rothermel, B.B. & Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology*, 16(5), pp.1324–1332.

Rothermel, B.B. (2004). Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications*, 14(5), pp.1535–1546.

Roznik, E.A. and Johnson, S.A. 2009. Canopy closure and emigration by juvenile gopher frogs. *Journal of Wildlife Management*, 73(2), pp.260–268.

Seebacher, F. & Alford, R.A., 2002. Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of Herpetology*, 36(1), pp.69–75.

Semlitsch, R., 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. *The Journal of Wildlife Management*, 72, pp.260–267.

Shakhparonov, V.V., Bolshakova, A.A., Koblikova, E.O. & Tsoi, J.A., 2024. European common frogs determine migratory direction by inclination magnetic compass and show diurnal variation in orientation. *Journal of Experimental Biology*, 227(4), jeb246150.

Sheridan, J.A., Mendenhall, C.D. & Yambun, P., 2022. Frog body size responses to precipitation shift from resource-driven to desiccation-resistant as temperatures warm. *Ecology and Evolution*, 12, e9589.

Shoop, C.R., 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology*, 55(2), pp.440–444.

Sinsch, U., 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. *Oecologia*, 112(1), pp.42–47.

Smith, D.C., 1987. Adult recruitment in chorus frogs: Effects of size and date at metamorphosis. *Ecology*, 68(2), pp.344–350.

Spranger, R.R., Raffel, T.R. and Sinervo, B.R. (2024). Canopy coverage, light, and moisture affect thermoregulatory trade-offs in an amphibian breeding habitat. *Journal of Thermal Biology*, [online] 122, pp.103864–103864.

Stebbins, R.C., 2003. *A field guide to western reptiles and amphibians*. 3rd ed. Boston: Houghton Mifflin.

Székely, D. et al., 2020. How to recover from a bad start: Size at metamorphosis affects growth and survival in a tropical amphibian. *BMC Ecology*, 20, 24.

Tatarian, P., 2008. Movement patterns of California red-legged frog (*Rana draytonii*) in an inland California environment. *Herpetological Conservation and Biology*, 3(2), pp.155–169.

Todd, B.D., Scott, D.E., Pechmann, J.H.K. & Gibbons, J.W., 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proceedings of the Royal Society B: Biological Sciences*, 278, pp.2191–2197.

Todd, B.D. and Winne, C.T., 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. Canadian Journal of Zoology, 84(5), pp.715-722.

U.S. Fish and Wildlife Service (USFWS), 1996. Determination of threatened status for the California red-legged frog. *Federal Register*, 6(101), pp.25813–25833.

Vasconcelos, D., 2009. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *Journal of Herpetology*, 38, pp.551–561.

Wilbur, H.M., 1980. Complex life cycles. *Annual Review of Ecology and Systematics*, 11, pp.67–93.

Wilcox, J.T., Davies, M.L., Wellstone, K.D. & Keller, M.F., 2017. Traditional surveys may underestimate *Rana draytonii* egg-mass counts in perennial stock ponds. *California Fish and Game*, 103(2), pp.66–71.

Winger, B.M., Auteri, G.G., Pegan, T.M. and Weeks, B.C. (2019). A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*, 94(3), pp.737–752.