A Telemetric Study of Migration and Habitat Use of the Post-breeding California Red-Legged Frog (*Rana draytonii*)

by

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ABSTRACT

As species across the globe encounter increased rates of decline, knowledge of movement ecology is critical for the conservation of migrating species. The California Red-legged frog *(Rana draytonii*) is a federally threatened species that exhibits seasonal migration between breeding and non-breeding habitat. The goal of this study was to examine the behavior and habitat use of post-breeding adult *R. draytonii* in a grassland and oak-savannah habitat. I used radio telemetry to track the movement of 40 adult *R. draytonii* in Sonoma County, California from January to May of 2022, one to three times per 24-hour period, during a drought year. I evaluated the effects of weather, canopy cover, ground moisture, and time of day on migration, forays, and rate of movement. Only 33% of frogs migrated away from the breeding pond, 77% of which were female. Frogs were more likely to migrate during the night, within 48 hours of major rain events, although they were found to be generally active during the day, during drier periods when they were not actively moving toward their destination non-breeding aquatic sites. Precipitation, wind, canopy cover and known moisture corridors (known waterways and wetlands), were found to have a significant effect on movement rate. Non-migrating frogs were observed making frequent forays between the pond and adjacent wetlands during humid conditions. The results of this study show the importance of habitat moisture levels and forest canopy connectivity for *R. draytonii* migration, as well as the use of adjacent wetlands by non-migrating frogs. *R. draytonii* appear to adjust their migratory behavior in response to seasonal climactic patterns and habitat features that impact desiccation avoidance, so understanding their movement ecology at a site-specific level may contribute to more effective conservation and restoration efforts.

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All frogs were captured and handled under US Fish and Wildlife Service federal recovery permit number TE-068745-5 issued to Jeff Wilcox and California Department of Fish and Game Scientific Collectors Permit SC-211560001.

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Introduction

Knowledge of movement ecology is critical for the conservation of migrating species as animals across the globe face increased rates of extinction (Russel et al. 2005). Research suggests a sixth mass extinction may already be under way (Ceballos et al. 2017). As species continue to decline, effective conservation strategies require an in-depth understanding of species' ecology. Many species exhibit facultative seasonal migration, in which individuals may migrate some years and not others. (Newton 2012). This is typically driven by adaptive associations with separate breeding and feeding sites, depending on the conditions and environmental stressors (Fudickar et al. 2021). Studies suggest that populations of vertebrates that undergo facultative seasonal migration are under pressure worldwide (Both et al. 2010, Piersma 2007).

Migratory vertebrates, in particular, may face unique challenges as they require access to multiple environments throughout their life cycle (Law and Dickman 1998). As such, these organisms need to respond not only to their resident habitats and resource requirements, but also to those associated with their migratory pathways. Thus, vertebrates using facultative migration typically adjust their movement patterns to environmental conditions, often using specific seasonal climate and habitat cues to determine the timing and patterns of seasonal migration activities (Winkler et al. 2014). For example, an individual may choose to move in search of more optimal conditions, to increase foraging success, or to avoid predation and competition. Movement away from a familiar area is often associated with an increased risk of mortality due to predation, desiccation, and starvation, however, the benefits often outweigh the costs (Fudickar et al. 2021). For most amphibian species, which often have extremely strict requirements related to desiccation avoidance, the role of seasonal migration may be just as critical to survival as the use of resident ponds and streams used for breeding and/or feeding (Erway 2022). Thus, understanding the associated habitat requirements for migration would allow for development of more effective management strategies for species preservation as climate shifts occur in existing habitats (Shuter et al. 2011).

Amphibians are one of many groups of organisms that undergo facultative migration, often relying on movements between breeding and non-breeding habitat. Unfortunately, amphibians are experiencing global decline with at least 32.5% of all amphibian species at risk of extinction (Adams et al. 2013). Many of these species have the potential to be legally protected and may eventually be listed as “threatened” or “endangered” (USFWS 2021). One species that uses seasonal migration and is a species of concern is the California Red-legged Frog (*Rana draytonii*) which was listed as federally threatened in 1996 and is currently protected under the US Endangered Species Act (USFWS 1996). Its current range extends from Mendocino County and the Sierra Nevada Foothills to Baja California, although it has been extirpated from 70% of its former range (Fellers 2005). Potential threats and causes of decline include elimination and alteration of habitat resulting from development and land use activities, as well as habitat invasion by non-native species (USFWS 2002).

Rana draytonii is the largest ranid native to the western United States. Their large size allows for easier observation and tracking, making them an ideal study species for understanding amphibian movement ecology. Like most amphibians, *R. draytonii* has a biphasic life cycle. During the breeding season, adults will migrate to localities where they lay eggs in still or slow-moving bodies of water such as ponds, channels, creeks, or seasonal marshes that are surrounded by littoral vegetation on which they deposit their egg masses (Wilcox et al. 2017). This typically occurs November through April depending on location and seasonal climactic patterns and lasts approximately 2-3 weeks (USFWS 2010). Embryos will hatch in 2-3 weeks and the resulting larvae will attain metamorphosis in 3.5 to 7 months depending on water temperatures (Storer 1925, Stebbins and McGinnis 2012, Alvarez et al. 2013). The post-metamorphic juveniles will then migrate to a mix of riparian and upland habitats where they will spend much of their adult lives before returning to breeding sites after reaching sexual maturity at 2-3 years of age (Storer 1925, Stebbins and McGinnis 2012, Jennings and Hayes 1985, Garcia-Dean, unpubl. data).

Of particular concern is how *R, draytonii* avoid desiccation during seasonal migration. Water balance is critical for species survival and impacts dispersal capabilities as water loss can vary in time and space across the landscape used by amphibians (Peterman et al. 2013). Since active and mobile amphibians are at greater risk of water loss than those that are inactive, migration can be a particularly risky endeavor with respect to water balance (Feder and Landos 1984). Threat of desiccation can be mitigated by several factors including: larger body size, skin resistant to water loss, selecting moist microhabitats, and nocturnality (Tracy et al. 2010). Thus, red-legged frogs can potentially adjust their facultative migratory behaviors in response to microhabitat conditions and to timing of migratory activity.

While studies have shown biphasic amphibian juvenile dispersal from natal sites to be random, adults typically migrate to and from breeding sites in a non-random manner (Semlitsch 2008, Wilson 2001, Sinsch 1990). Breeding and non-breeding sites are often spatially separated by abrupt transitions in habitat type. This can include a variety of habitat types including grasslands, riparian forests, marshes, and coastal dunes ranging from zero to 1500 meters in elevation (USFWS 2002). While little is known about *R. draytonii* use of upland terrain, studies suggest *R. draytonii* move in straight line distances across terrain instead of using corridors. In a telemetric study of terrestrial activity of adult *R. draytonii*, non-migrating adults were found to stay close to aquatic sites, whereas migrating adults moved overland up to 2,800 m, in a seemingly straight line to target sites without apparent regard to vegetation, topography or riparian corridors (Bulger et al. 2003). Fellers and Kleeman (2007) found most *R. draytonii* moved the seemingly shortest route across grazed pastures to the nearest riparian zone. These studies relied on radio telemetry but employed radio tracking sessions no more than two to three times per week, and distances between observations were presumed to be navigated in a straight line. However, due to the long intervals between tracking sessions during these long-term studies, the rate and pattern of movements of individuals between observations is not precisely understood. Studies with more frequent sampling of individual locations could allow for a more fine-scaled understanding of how *R. draytonii* move through and use their environment. Moreover, a fine-scaled investigation of microhabitat use during migration with respect to factors that may reduce threat of desiccation, such as canopy cover, ground moisture, or subterranean cover, could reveal factors that are critical to survival during seasonal migration (Surber 2019). Nocturnality, may also be a key factor in successful seasonal migration. Studies focusing on presence/absence surveys have found *R. draytonii* to be detected significantly more during the night than during the day (Fellers and Kleeman 2006, Surber 2019). Similarly, when observing feeding behavior, Hayes and Tennant (1985) found adult *R. draytonii* to be largely nocturnal and generally inactive during the day, while juveniles were found to be both diurnally and nocturnally active. This suggests adult *R. draytonii* likely forage primarily at night while staying hidden under refugia during the day presumably to avoid predation and desiccation. However, these studies are based strictly on visual observations and may not represent active periods of migration or foraging. Confirmation of diurnal versus nocturnal migratory activity would require more frequent sampling and be enhanced by the use of a tracking device.

To examine factors such as movement patterns, microhabitat use, and daily activities, remote tracking is often necessary. As has been demonstrated from many studies (McClintock et al. 2012, Thomas 1982, Wilson et al. 2009, Weber et al. 2013), radio telemetry is one such technique that has be used to track movements of many different groups of wildlife, including amphibians. It is a non-invasive method that allows for continuous monitoring, while minimizing the need for physical handling or recapturing of animals, likely reducing stress and potential impacts on behavior and physiology.

The objective of this study was to examine the biotic and abiotic factors that influence seasonal migration of post-breeding adult *R. draytonii*. I used radio telemetry to map the movement patterns of *Rana draytonii* as they navigated their native grassland and oak savannah habit for either migration or local forays in Sonoma County, California, USA. I analyzed the effects of weather, canopy cover, ground moisture, and time of day on migration, forays, and rate of movement. In addition, I used the resulting understanding of *R. draytonii* migration behavior and habitat use to make recommendations related to habitat restoration and land management practices as well as policies pertaining to the recovery and conservation of this species.

Methods

Study Area

The study was conducted on the Mitsui Ranch, a 632-acre property owned by the Sonoma Mountain Ranch Preservation Foundation, 8 km east of Petaluma in Sonoma County, California. It is located at the top of Sonoma Mountain at an elevation ranging from 611 to 730 meters. It has a Mediterranean climate consisting of cool, wet winters and hot, dry summers. Fog is common throughout the year as well as an occasional occurrence of snow during winter months. The ranch consists of both oak woodland and more than 80% open rangelands that are used primarily for cattle grazing (Fig. 1). It contains two perennial stock ponds that have been shown to consistently serve as successful breeding ponds for *R. draytonii* (Wilcox et al. 2017). One of these breeding ponds, Bonnie's Pond, has a surface area of 0.15 ha, with patches of littoral vegetation where *R. draytonii* have been known to attach and deposit egg masses. The pond and two adjacent wetlands are fed by a spring. The two wetlands extend approximately 25 meters to the north, and approximately 50 meters to the south of the pond respectively. Grasslands surround most of the pond, with dense oak woodland and Copeland Creek extending to the north. There are a variety of other creeks and ponds of varying depths in the nearby area to which *R. draytonii* have been known to disperse and inhabit. Two low traffic roads, one dirt and one paved, extend through the property, separating the breeding pond from other aquatic sites used by this population.

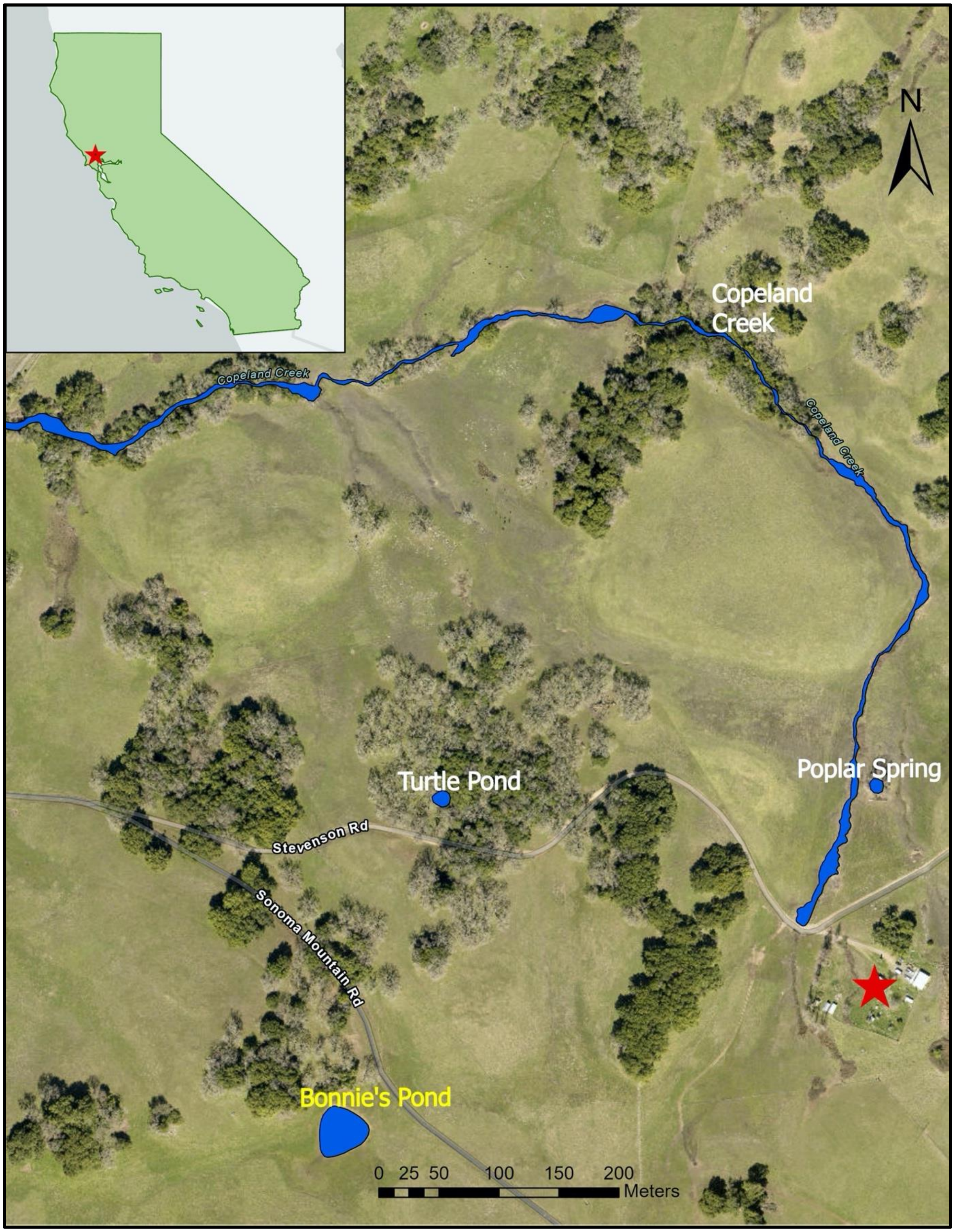

Figure 1. Map of Mitsui Ranch study area showing breeding site (Bonnie's Pond) and known aquatic sites including Turtle Pond, Poplar Spring, and Copeland Creek indicated in dark blue.

Field Methods

Bonnie's Pond was visually surveyed for egg masses leading up to the known breeding season. Following the sighting of the first egg mass on January 17th, 2022, adult *R. draytonii* were captured by hand. Mass was obtained using a Pesola scale to the nearest 0.5 grams. Snout-urostyle length (SUL) was measured using a ruler to the nearest millimeter. Sex was determined through physical examination of presence/absence of nuptial excrescence (present for males, absent for females). After morphological data was obtained, each frog was tagged with a passive integrated transponder (PIT) if it did not contain one already. PIT tags are permanent, internal, electronic microchips containing an alphanumeric code that is unique to each individual. The tags (Biomark MiniHPT8, Boise, ID) are 8mm long and 1.2mm in diameter. They are surgically inserted under the dermis of the upper back using sterile scissors first to make a small incision, and then cannulated forceps to insert the tag, which is gently pushed with a finger down over the sacral hump away from the incision area. While PIT tags were not the primary method of tracking frog movements, they allowed for unique identification in the event that transmitters failed, were removed, or were lost during the study. A unique advantage to working on the Mitsui Ranch is that most of the frogs were previously captured and fitted with PIT tags. Thus, basic measurements and individual location histories were already known for many of those captured for this study.

Only males with an SUL above 65mm (to ensure they are of breeding age) (J. Wilcox, pers. comm) and post-gravid females were used in the study. In addition to an SUL >65mm, females showing signs of having recently deposited eggs (lean with loose skin, and a recent loss of 15–20% of body weight) were fitted with radios. Transmitters (1 set each of Holohil BD-2; 1.7g, 11-week battery and 2.8g, 24-week battery; 150–151 MHz) were attached to frogs via an aluminum beaded waistband, custom fit to each frog (Fellers and Kleeman 2007). Per the 10% rule, transmitter weight was no more than 10% of the animal's body mass (Richards et al. 1994) to minimize hindrance of frog movement and minimize energy costs to the individual. Due to frog inactivity at the start of the field season, the geolocation of frogs was determined once per day until the first rain event, and then twice per day (once in the morning and once at night) until hot, dry conditions once again resulted in inactivity. An additional tracking session was completed at midnight during heavy rain events. Observations collected during midnight and morning sessions were considered night movements and observations collected during evening sessions were considered day movements. Frogs were tracked for a total of five months, using a three-element Yagi antenna and a receiver (R-1000; Communication Specialists). Frogs were visually checked every two to three weeks for abrasions or injury from the tracking belts and removed as needed. Frog locations were recorded (WGS-1984) using a handheld GPS unit (Garmin 64st) with an error of up to 3.65m. The accuracy of observed locations was corrected in ArcGIS Pro with the knowledge of the landscape and visual observations. For the purpose of this study, locations were only taken if they were greater than one meter from the prior observation. Belts were removed before the end of the study if they reached a non-breeding aquatic site and ceased to move for 2-3 weeks to prevent injury from the tracking belts. The study was concluded when high temperatures and dry conditions resulted in little to no movement for 30 days.

Spatial Analysis

Coordinates of individual frog positions were uploaded to a computer using Garmin Basecamp and transferred to a geographic information system (ArcGIS Pro 3.0.2, Esri Inc. 2022). A detailed pathway of dispersal and movement from Bonnie's Pond was mapped by connecting positions in order of date observed to obtain a movement pathway for each individual frog. The Add Surface Information (3D Analyst) tool was used to calculate the 3D distance for each movement vector. This required the input of the movement vector layer and a lidar-based, bare earth Digital Elevation Model (DEM) with a 1-meter accuracy (sonomavegmap.org). The coordinate system for all coordinates and tools used in this analysis were converted to the NAD-1983 UTM Zone 10 coordinate system for accuracy.

To analyze *R. draytonii* use of moisture corridors, a “moisture zone” polygon layer was mapped to represent all areas of the study site that are known to become inundated during the winter months. This includes perennial, intermittent, ephemeral, and annual water features such as streams, creeks, ponds, wetlands, and wet meadows. This layer was created using a handheld GPS, visual observations of surface moisture, and knowledge of the study site. The Near tool was used to calculate the distance in meters from each frog position to the nearest moisture zone polygon.

To evaluate the effects of canopy on migration, two LiDAR-based intensity rasters were used for both canopy density and canopy height (sonomavegmap.org). The density raster is depicted by a ratio of the aboveground LiDAR return to total count LiDAR return. The output is a raster data set ranging from 0.0 (no canopy) to 1.0 (very dense canopy). The canopy height raster is a digital elevation model represented by the highest hit, including man-made structures and vegetation, and lowest hit bare earth. The output is a raster data set ranging from 0.0m to 23.1m. The coordinate systems for both rasters were converted from California State Plane Zone II (FIPS 0402), NAD83 (2011) to NAD-1983 UTM Zone 10. Each pixel was three feet wide and captured the average intensity and average tree height for canopy density and canopy height respectively. All horizontal and vertical units were converted from US Survey feet to meters.

Weather Data

To study the effects of weather, average temperature (Cº), average wind speed (mph), average humidity (%) and precipitation accumulation (cm) were obtained for each day for the duration of the study. Weather data was collected approximately 3 kilometers southwest of the study site at the Chateau weather station (KCAPETAL214) in Petaluma and retrieved from Weather Underground (wunderground.com). Because frogs had greater movements in the days immediately following rain events, each frog movement was evaluated for whether there was precipitation in the 48-hours prior to the movement.

Movement Classification

In order to determine whether *R. draytonii* completed a migration movement or a round trip foray, a “foray” was defined as a movement or series of movements that begins and ends at the same body of water. “Migration” was defined as any movement that starts at Bonnie’s Pond and ends in a different non-breeding aquatic habitat. Each observed frog position was further categorized as a “movement” or “non-movement” relative to the previous observed position.

Statistical Analysis

All analyses were performed using JMP Pro v17.0.0 (SAS Institute Inc., Cary, NC, USA). Statistical significance was assessed at $p < 0.05$. To test the effects of sex and size on whether or not frogs migrated, I used a Likelihood Ratio chi-square test. To determine the effects of sex, size, weather, canopy, distance from water, and time of day on migration, I used a generalized linear mixed model with a binomial nominal response variable and a logit linking function. Migration movement was designated at two different levels: movement to a different location relative to the previous observation (Y) and non-movement relative to the previous observation (N). The model included sex, SUL, precipitation accumulation, temperature, humidity, wind speed, within 48 hours of precipitation, canopy density, canopy height, in or out of water, and day or night as the fixed effects. PIT tag was included as a random effect to account for repeated sampling of individuals. This same model was run separately for non-migrating frogs to account for any differences between landscape conditions and behavioral differences that may be associated with the two different movement types. To assess the potential for multicollinearity, correlations between fixed effects were evaluated at 0.5.

Once frogs started migrating, factors affecting movement rate (meters per minute) were analyzed using a general linear mixed model, using only movement positions at which frogs had moved relative the previous observation. The model included sex, SUL, precipitation accumulation, temperature, humidity, wind speed, within 48 hours of precipitation, canopy density, canopy height, in or out of water, and day or night as the fixed effects, and PIT tag as a random effect. I ran two different models – a reduced model with a smaller sample size that included day/night, and a larger model with more data that did not include day/night as an explanatory factor. This same model was run with the smaller data set, eliminating all movements under 10 meters to account for any differences in behavior during dry versus humid conditions. Movement rate was log transformed for all models to allow for a normal distribution of data. Fixed effects were evaluated for collinearity and model residuals were checked for approximate visual normality and homoscedasticity.

To examine the use of moisture zones by both migrating and non-migrating frogs, I used a Likelihood Ratio chi-square test for both movement types separately. The expected frequencies for frog positions, assuming that there is no preference for moisture zone or dry area, were 50/50. To test the effects of site conditions on migrating frogs when they were not observed in a moisture zone, I used a generalized linear mixed model with a binomial nominal response and a logit linking function. Frog positions were designated at two levels: observed within a moisture area (in) or observed outside of a moisture area (out). Correlations between fixed effects were evaluated at 0.5. To test the effects of site conditions as frog position distance from moisture zone increased, I used a general linear mixed model with the log transformed distance from moisture zone (in meters) as the response variable. Fixed affects were evaluated for collinearity and model residuals were visually assessed for approximate normality and homoscedasticity. Both models included sex, SUL, precipitation accumulation, temperature, humidity, wind speed, canopy density, within 48 hours of precipitation, canopy height, and day or night as the fixed effects, and PIT tag as a random effect.

Results

Movement Behaviors

Migrating frogs. Of the 40 frogs that were tracked during this study, 13 out 40 (33%) migrated away from Bonnie's Pond to a historically non-breeding aquatic site. Migration away from the pond began with the first post-breeding major rain event on March 3rd. The last frog to reach a non-breeding aquatic site did so on April 19th. There were 999 total observations for migrating frogs, 163 of which were movements relative to the previous observation (Fig. 2). There were 836 observations categorized as non-movements, in which the frog was observed either in the exact same spot or within one meter of the previous location. The average distance travelled between two points was 51meters with the longest being 562 meters. Total duration of migration from the breeding pond to the end point non-breeding aquatic sites ranged from less than 24 hours to 50 days (Table 1) with an average of 18 days. Ten of the 13 migrating frogs ended at known non-breeding aquatic sites including Copeland Creek, Turtle Pond, and Poplar Spring at which *R. draytonii* have been found to regularly inhabit during visual surveys. The three remaining frogs ended in a large riparian spring, a brush dam along a creek under canopy, and a head cut extending from Copeland Creek. The study concluded on May 27th, when conditions were hot and dry, and movement was minimal.

Figure 2. Map of Mitsui Ranch study area with GPS locations of the thirteen migrating *R. draytonii*. Each color/pattern represents a different individual frog. The mapped moisture zone layer represents known inundated terrestrial habitats and is indicated by the light blue polygon layer.

Table 1. Summary of individual migrating frogs including sex, migration duration, and distance to end-point aquatic sites. PIT tags with asterisks represent frogs that returned to non-breeding aquatic cites they had been observed at during previous years.

PIT	Sex	Start Date	End Date	Distance to End Point (m)	Migration Duration (days)	End Point
3C7FC19	F	3/3/22	3/13/22	343	10	Bonnie's Drainage
3C7E304*	F	3/3/22	3/15/22	630	12	Copeland Creek
93DE187*	F	3/3/22	3/28/22	640	25	Copeland Creek
93DE153	F	3/12/22	5/1/22	535	50	Head Cut
3C821F9*	F	3/13/22	3/28/22	268	13	Turtle Pond
3C7F501	F	3/13/22	3/13/22	183	<1	Turtle Pond
3C7D620	F	3/14/22	4/16/22	496	33	Big Spring
3C6E634	F	3/14/22	3/15/22	578	1	Copeland Creek
93DE1E4	F	3/14/22	3/23/22	506	9	Poplar Spring
3C81B63	M	3/14/22	3/23/22	491	9	Poplar Spring
3C7F126*	F	3/14/22	4/14/22	495	31	Poplar Spring
3C7F393*	M	3/28/22	4/14/22	580	17	Copeland Creek
93DE156*	M	4/14/22	4/19/22	182	5	Turtle Pond

Within the mixed model analyzing conditions affecting migration, SUL, used as a proxy for body size, had no effect on whether or not frogs migrated. The likelihood of migration was significantly higher in females than males (LRX^2=13.005, p=0.0003). Of the 13 frogs that migrated, 10 were female (77%) whereas only 3 were male (33%). Most major movements occurred around four main rain events (Fig. 3). Frogs were more likely to migrate during the night than during the day ($F_{1,781}$=31.7, p<0.0001) and during time periods with higher levels of precipitation ($F_{1,781}$=39.3, p<0.0001). Frogs migrated at higher rates if it rained within 48 hours ($F_{1,152.8}$=27.3, p<0.0001) and if they were outside of a moisture zone ($F_{1,149.8}$=21.2, p<0.0001), and at slower rates as wind speed increased ($F_{1,150.6}$=5.9, p=0.0166) (Fig. 4). Using the smaller data set to analyze movement rate, which included day/night, frogs migrated at higher rates as they were further away from moisture zones ($F_{1,108}$=13.1, p=0.0004) (Fig. 5) and if it had rained in the past 48 hours ($F_{1,109.7}$=36.9, p<0.001). When eliminating all movements under ten meters, movement rate increased if it had rained in the last 48 hours ($F_{53.66}$=9.3, p=0.0036) and if it was night ($F_{52.88}$=4.7, p=0.0344).

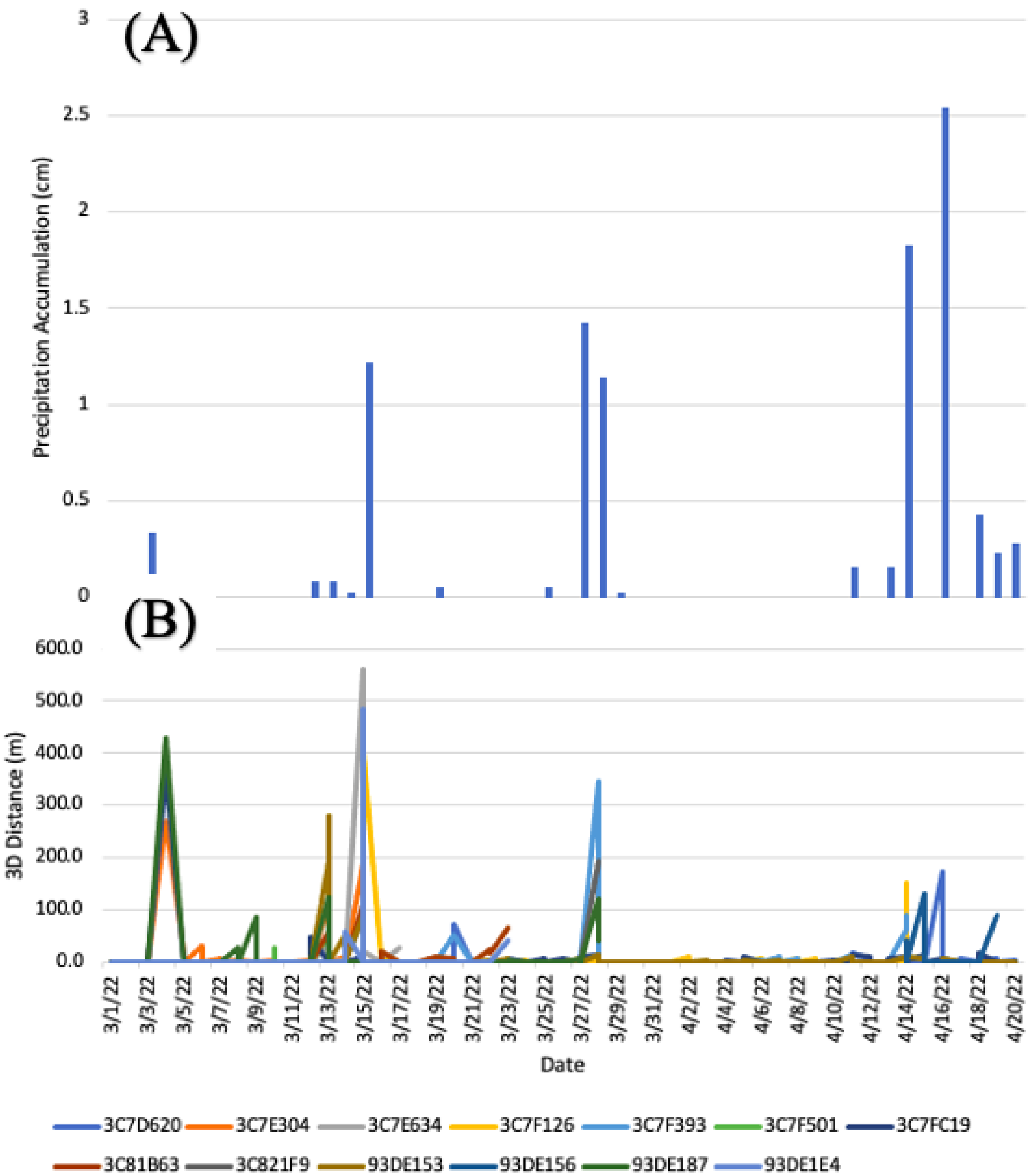

Figure 3. Time series graph showing precipitation accumulation (A) and distance travelled (B) during the period containing the four major rain events when most long-distance movement took place. Most movement occurred during major rain events. Each color-PIT tag represents a different frog.

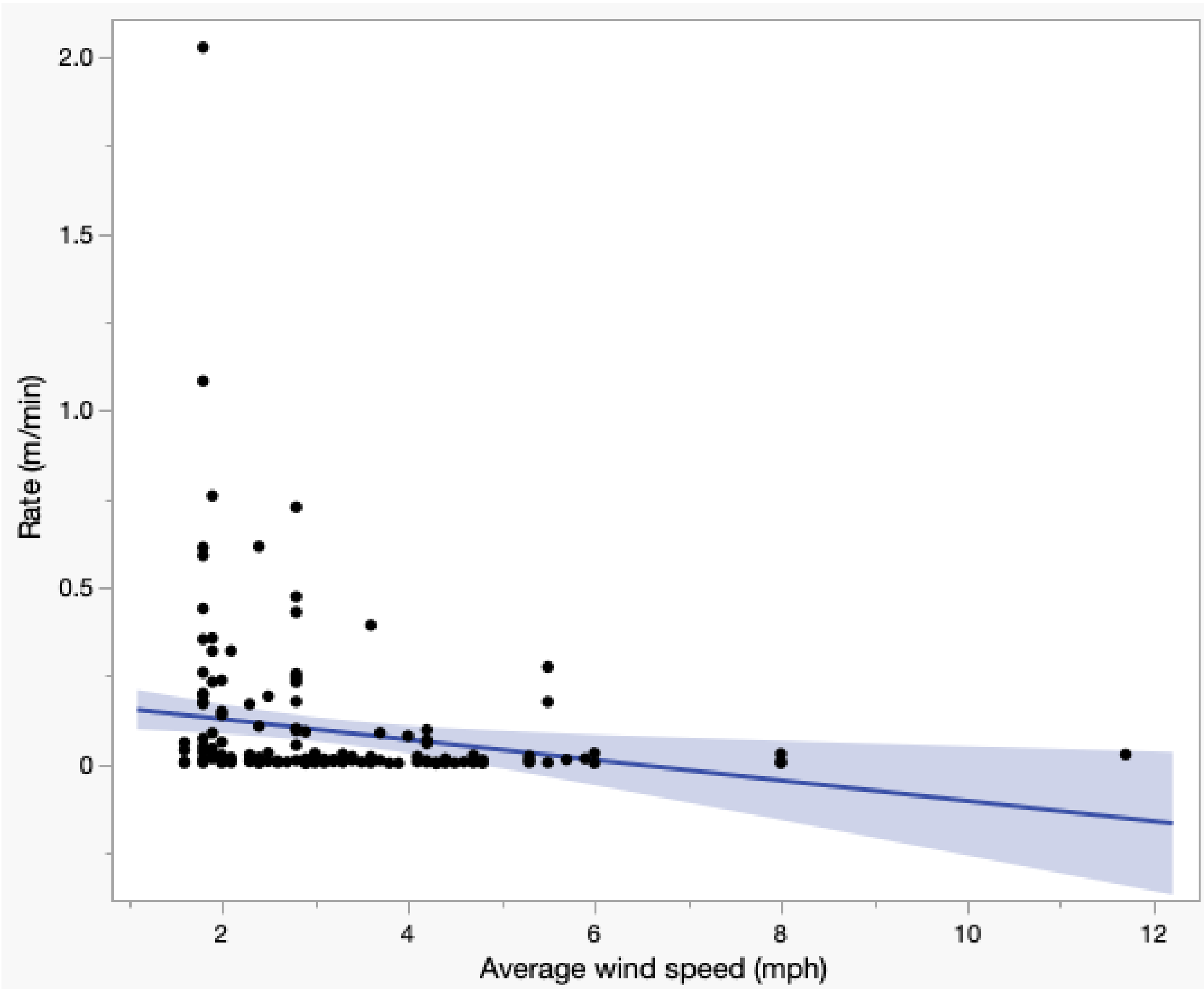

Figure 4. Regression of movement rate for migrating *R. draytonii* associated with a significant effect of average wind speed ($F_{1,150.6}$=5.9, p=0.0166).

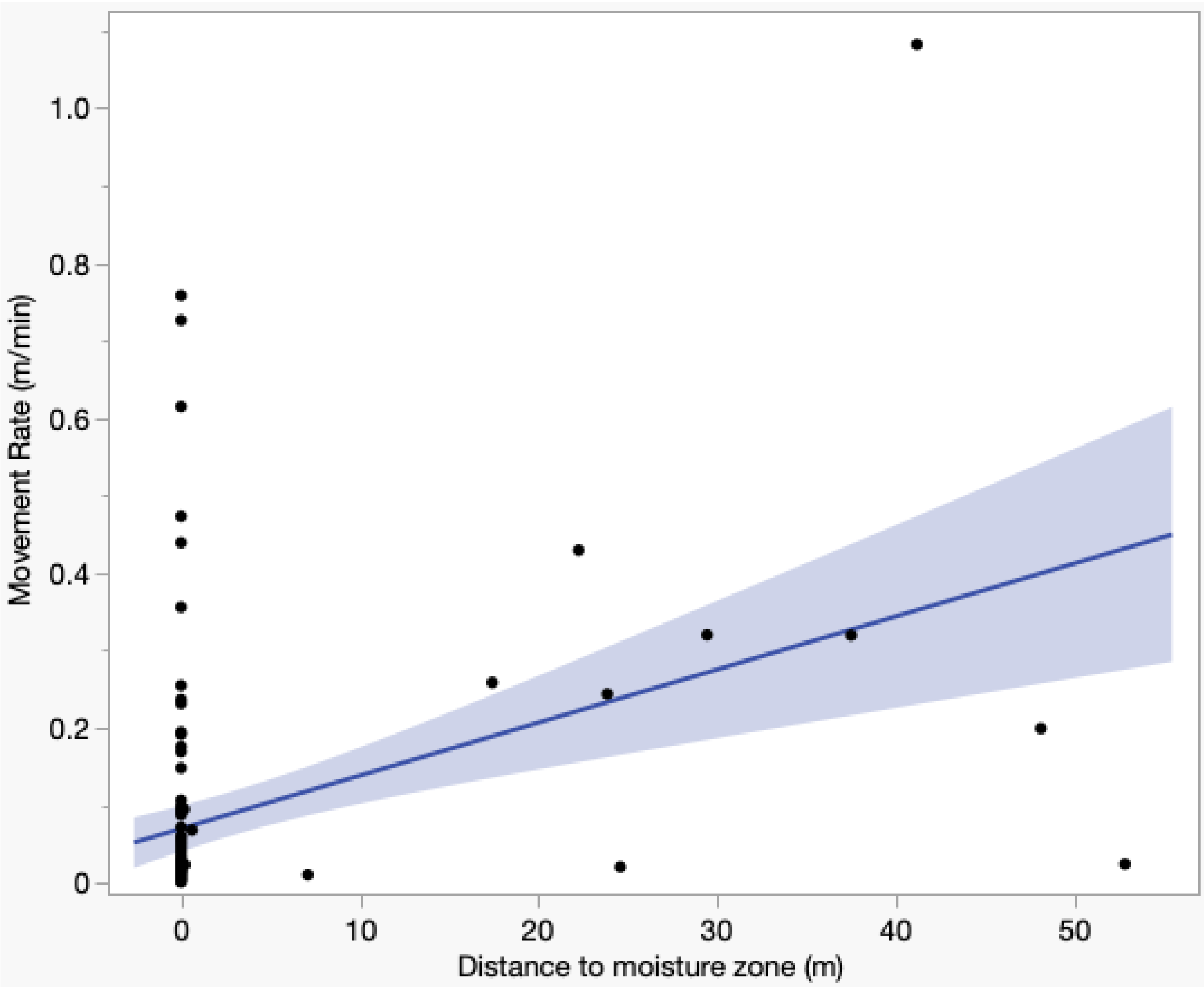

Figure 5. Regression of movement rate for migrating *R. draytonii* associated with a significant effect of distance from moisture zone ($F_{1,108}$=13.1, p=0.0004).

Non-migrating frogs. Of the 40 frogs that were tracked, 27 (77%) remained at Bonnie's Pond for the duration of the study. Of those non-migrating frogs, 5 of 27 (19%) were female, and 22 of 27 (81%) were male. Throughout the study, 17 of 27 (63%) of the non-migrating frogs were observed making forays between the pond and adjacent wetlands, while 10 of 27 (37%) were never observed outside of the pond (Fig. 6). The average distance vector travelled between the wetlands and the pond was 35 meters. The longest distance vector was 107 meters; however, this vector was from one wetland to the other, transecting through the middle of the pond over a 24 period. Only two terrestrial forays outside of the wetlands were observed, in which two frogs each made one foray from the breeding pond to land, at distances of 23 and 30 meters, and then back, both of which were under the nearest canopy. When analyzing factors affecting foray movements, frogs were more likely to move in conditions with higher levels of humidity ($F_{1,417}$=12.5, $p>0.0005$). On average humidity during forays was 82% with a minimum threshold of 67%.

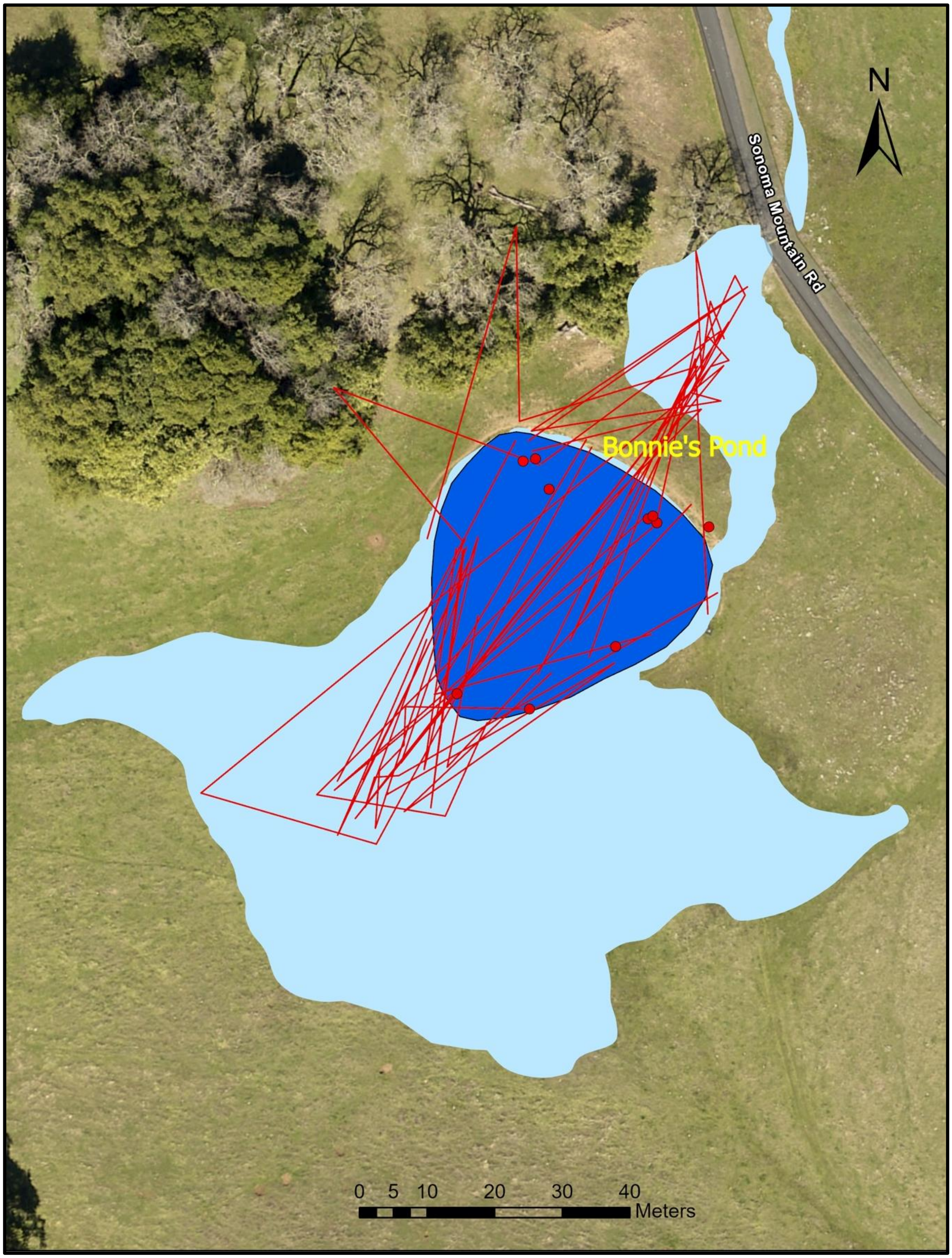

Figure 6. Map of Bonnie’s Pond (dark blue), including the two adjacent wetlands to the northwest and southeast ends of the pond. Seventeen frogs were observed making forays between the pond and the wetlands (red vectors). Ten frogs were only observed in the pond for the duration of the study (red points).

Influence of Moisture Corridors

When analyzing the use of moisture corridors, both migrating and non-migrating frogs were more likely to be found in a moisture zone than out (LRX^2=770.8, p<0.0001 and LRX^2=294.7, p<0.0001 respectively) (Fig.7). Migrating frogs were more likely to be found outside of a moisture zone if canopy density was higher ($F_{1,781}$=15.1, p=0.0001). Females were more likely to be found in a moisture zone (F=$_{1,9.2}$=5.9, p=0.0377), although males were more likely to be further from a moisture zone ($F_{1,10.4}$=7.1, p=0.023). Frog distance from moisture zones increased as canopy height increased ($F_{1,767.1}$=53.3, p<0.0001) (Fig. 8) and as temperature decreased ($F_{1,771}$=4.9, p=0.0266) (Fig. 9). The farthest distance from moisture zones during migration was 66 meters.

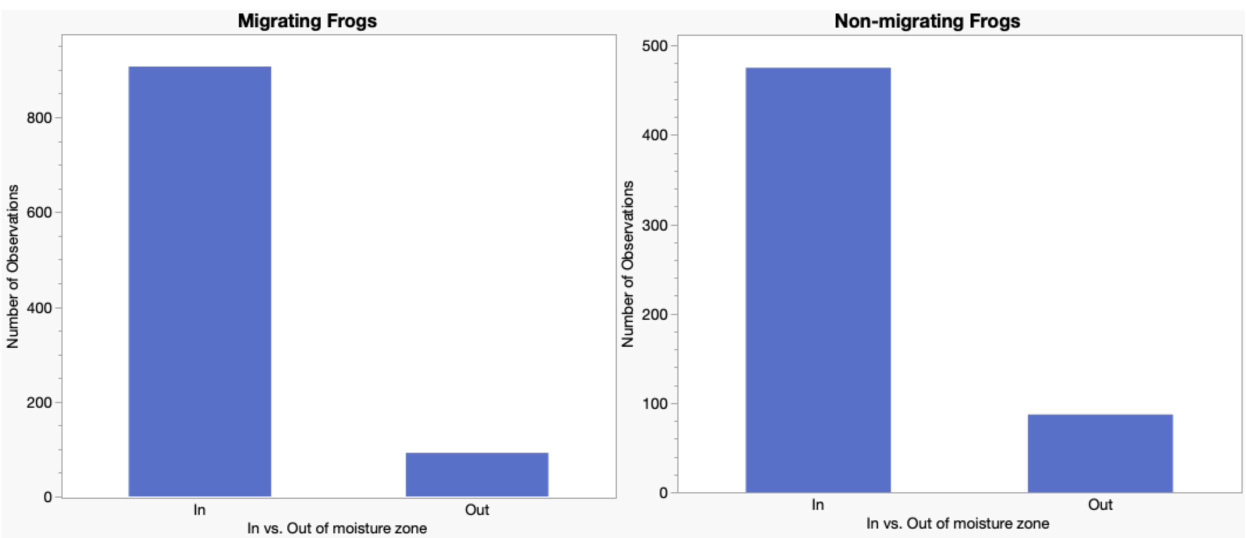

Figure 7. *R. draytonii* were more likely to be found within a moisture zone than out for both migrating (LRX^2=770.8, p<0.0001) and non-migrating frogs (LRX^2=294.7, p<0.0001).

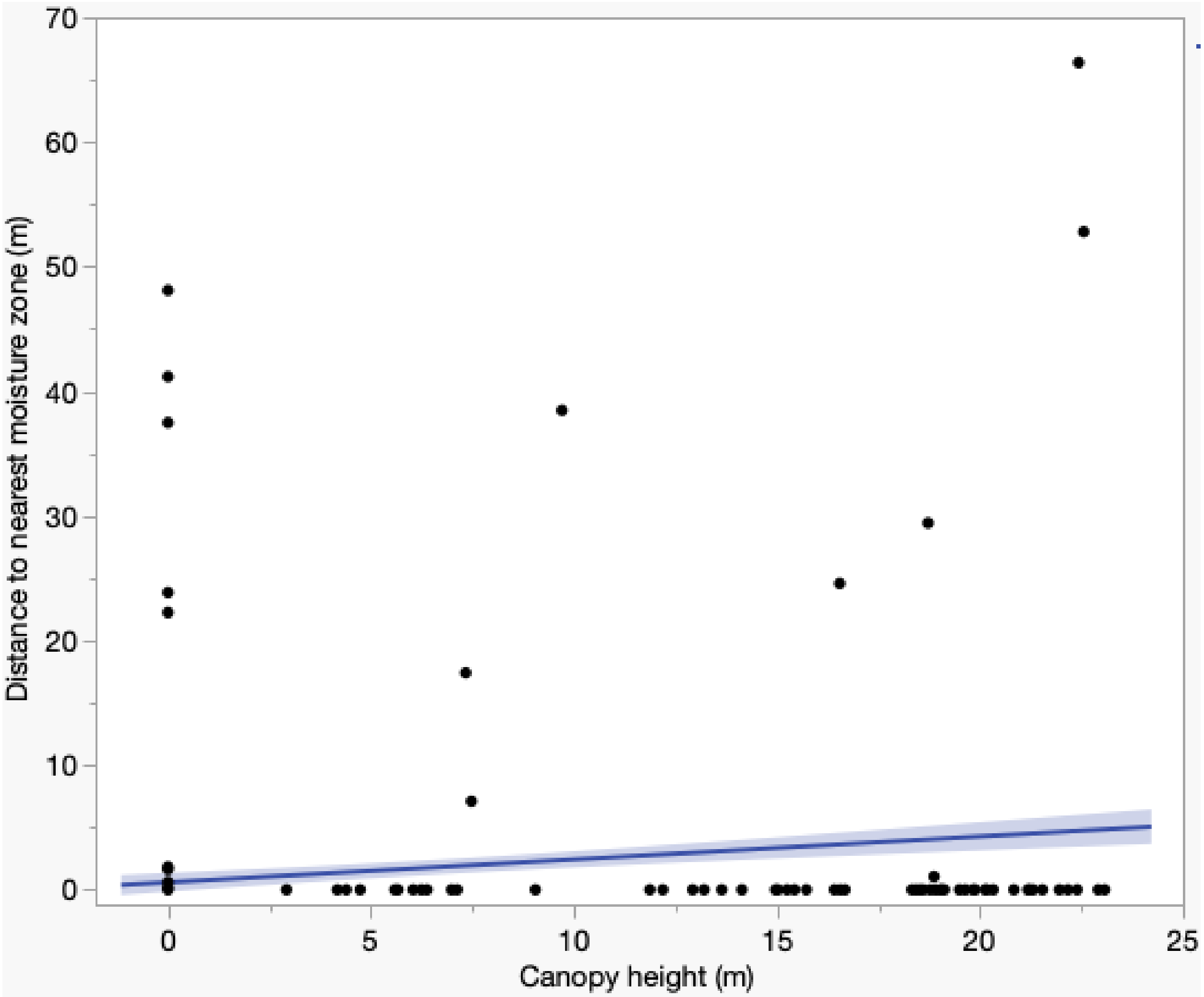

Figure 8. Regression of distance from moisture zones of migrating *R. draytonii* associated with a significant effect of canopy height ($F_{1,767.1}$=53.3, p<0.0001).

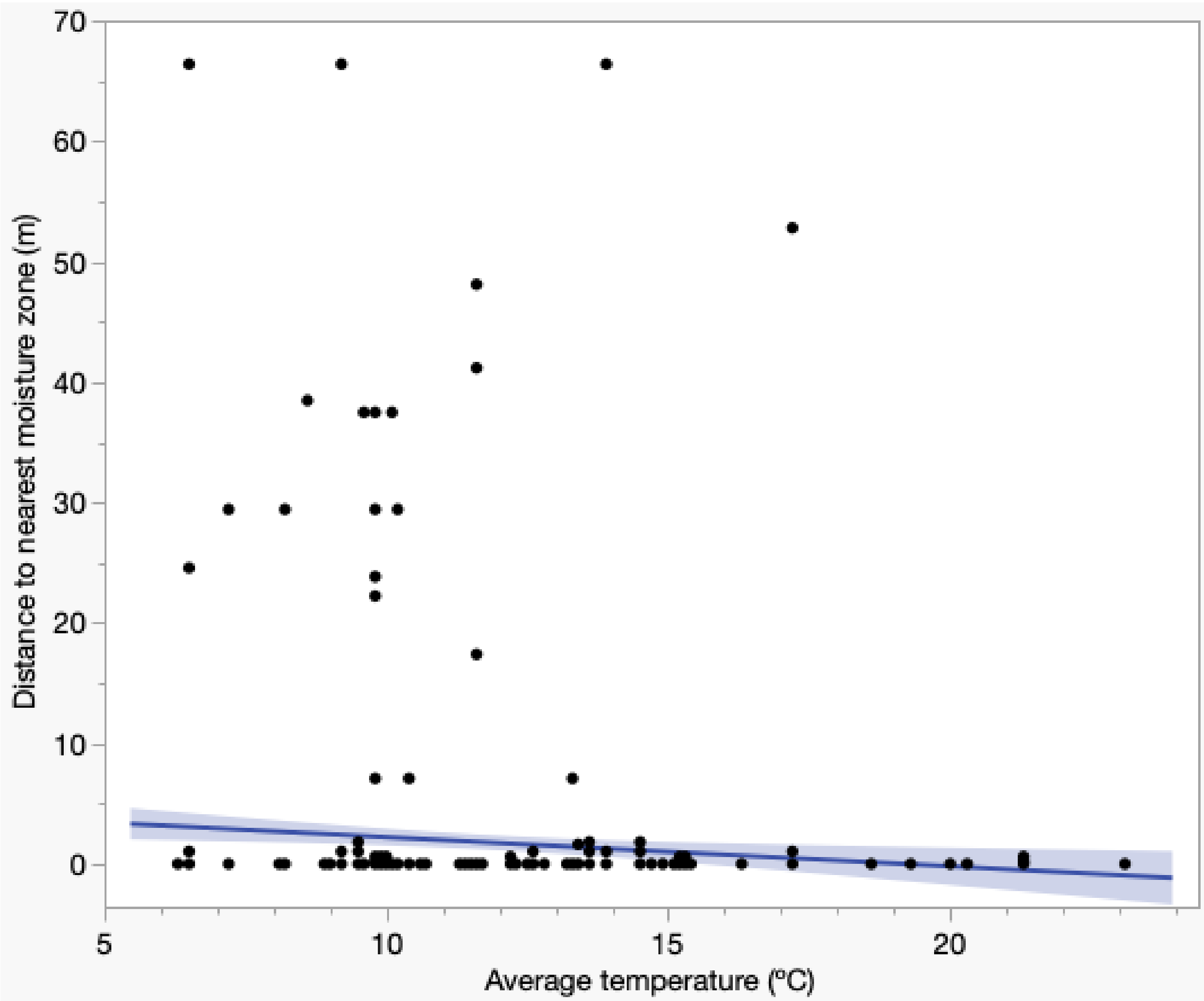

Figure 9. Regression of distance from moisture zones of migrating *R. draytonii* associated with a significant effect of average temperature ($F_{1,771}$=4.9, p=0.0266).

Injuries and Mortalities

Frogs were checked for abrasions or belt injuries approximately every 2-3 weeks. Several frogs developed mild abrasions as a result of the belts. Two frogs had severe abrasions in which case the belts were removed. These frogs were subsequently caught several times throughout the study, and although the abrasions healed quickly, these frogs were not included in the study. One frog was found in the wetland adjacent to Bonnie’s Pond with a broken leg halfway through the study and the belt was removed. This frog was caught several times in the pond throughout the study following the removal of the transmitter. Its leg has since been observed fully healed (J. Wilcox, pers. comm).

Four incidents of mortality occurred. A small male that had remained at the pond for the duration of the study, was preyed upon by a garter snake on May 25th and the transmitter was retrieved following defecation by the snake. A female was found decapitated in a head cut connected to Copeland creek on May 23rd which it had inhabited for several weeks. An autopsy revealed the cause of death was likely a result of a vole it had consumed, resulting in a blockage of matted fur in the bowels and was later scavenged by another animal. Another female was found in a woodpile in the wetland to the northwest of Bonnie's Pond, eight weeks into the study on March 18th. The cause of death was unknown, but attempted predation or trauma is suspected. After the study had concluded, a fourth frog was found in the pond after drying conditions had caused the water line to recede. Only the rear end of the frog was found under a large rock.

Discussion

Environmental factors and timing of activities are important drivers of the facultative seasonal migration of *R. draytonii*. Driven by the strong influence of water balance, typical of most amphibians, *R. draytonii* adjust their migratory behavior in response to climate, microhabitat, and daily rhythms to maximize their likelihood of survival and minimize their chance of succumbing to desiccation.

Migration, Precipitation, and Moisture Zones

The data confirm established paradigms about amphibians migrating in association with rain events. Once migration began, *R. draytonii* continued to move at higher rates in the first 48 hours following rain events before settling down and remaining in the same general area until the next rain event. In addition to precipitation, *R. draytonii* showed a strong preference for moisture zones while migrating from the breeding pond to non-breeding aquatic sites. During drier periods when *R. draytonii* were not actively moving toward their end point aquatic site, they were found within a moisture zone where they stayed for several weeks until the next rain event. These areas included a variety of drainages, springs, and wet meadows. During these drier periods, individuals were frequently observed moving around within an average of one to three meters of the same small area around an inundated habitat patch. There were three instances of individuals that remained outside of moisture zones for longer than 48 hours following rain events, all of which occurred under forest canopy. One individual was tracked to a debris pile 66 meters from the nearest moisture zone while heading north in the direction of Copeland Creek where it ultimately ended its migration 290 meters away; however, from the debris pile it redirected west to the nearest drainage within four days, along which it continued a much longer and more sinuous journey to its end site in Copeland Creek. Two other individuals were observed in the same dry portion of a drainage at different times. While these areas of the creek were within the mapped moisture zone, they did not contain standing water during these times. These frogs were buried deep in the duff layer along the creek for five and eight days, where they remained in the same location and position, and appeared increasingly emaciated, lethargic, and unresponsive to our presence. This apparent state of brumation was a notable difference in behavior when compared to frogs that stopped in inundated areas.

Canopy Cover

Both canopy density and height had significant effects on *R. draytonii* migration. While canopy density was a driving factor for frogs found outside of moisture zones, distance from moisture zones increased as canopy height increased and temperature decreased, and movement rate increased as distance from water increased. Areas near water had higher canopy density and thicker understory with low lying vegetation, leaf litter, and organic debris. As distance from water increased, canopy height increased with the presence of larger, more mature trees, while the thicker riparian understory transitioned to grassland. Studies have shown that open habitats such as croplands or pastures, which often dominate the landscape matrix between forest patches, may be inhospitable for migrating amphibians due to higher temperatures and lower soil moisture, making amphibians more vulnerable to desiccation (Rothermel and Semlitch 2002). Thus, canopy provides a cooler and more humid environment during migration, in addition to providing covered protection from predators. Grassland habitats have also been known to act as barriers for some amphibian species and been found to have lower capture rates possibly from poor survival (Rittenhouse and Semlitch 2006). This supports several studies that have found preferred use of closed canopy by many species of emigrating amphibians (Demaynadier and Hunter 1999, Vasconcelos and Calhoun 2004). The use of open grassland terrain primarily occurred during heavy rain events, during the night, when they were observed actively moving across the terrain, taking the seemingly shortest route to the nearest riparian zone. There was only one occurrence of a frog found far from a moisture zone during the day and without canopy. This individual was observed in a small mammal burrow after a major rain event for 48 hours, after which it moved to the nearest moisture zone, 25 meters away. Wind speed also had a negative effect on movement rate, further supporting the beneficial role of canopy in protecting against environmental conditions. Wind speed has been found to limit activity and increase rates of desiccation by increasing evaporative water loss (Muller et al. 2018). This is consistent with observations during regular surveys at the Mitsui Ranch, where frogs are rarely observed outside of water on windy nights.

Migration Timing

As expected, *R. draytonii* were found to migrate significantly more during the night than during the day. However, time of day was not found to have a significant effect on movement rate. This was likely due to the micro-movements that occurred during drier periods when frogs remained in the same small area around an inundated habitat patch until the next rain event. When movements under ten meters were removed from the data analysis, which was more than 30% of their movements, time of day had a significant effect on movement rate. This does not include the numerous movements under one meter that were not included in the data collection. Similar behavior was observed for non-migrating frogs that remained at the breeding pond for the duration of the study. Wetland forays consisted of short distances in humid conditions, unrelated to time of day and precipitation. These results indicate that while *R. draytonii* move long distances during the night, if some variations of moist conditions are available, they are often active during the day, likely foraging or exploring their immediate surroundings. Although frogs were often found in different positions during the day, they would have been difficult to locate without the use of a tracking device due to their cryptic coloration and limited movement. These fine-scale observations reveal a higher level of localized activity during daylight hours than previously assumed for adult *R. draytonii*.

Sex Biased Migration

Most frogs that migrated away from the pond were female. While a significant majority of frogs that remained at the breeding pond were male, it is unclear what percentage were yearlong residents of the pond or whether they waited until later in the year after most females had left to migrate. These results are similar to those of other amphibian studies in which a higher percentage of females migrated from breeding sites (Fellers andKleeman 2007, Palo et al. 2004, Austin et al. 2003). By remaining at the pond, or arriving first and leaving last, males may optimize access to females arriving at the pond, likely increasing reproductive success (Greenwood 1980).

Females were more likely to be found in a moisture zone than out, while males were found farther from moisture zones if they left them. Of the three males that migrated, only two were found significantly further from moisture zones than females. One of these cases consisted of a small male that stopped in a small mammal burrow on a grassy hillside for two days before finishing the trek to the nearest inundated habitat patch. The other occurrence was a male that stopped on a steep hillside under thick canopy where it stayed under a fallen tree for four days before concluding its migration at Turtle Pond 60 meters away. The two females that also migrated to Turtle Pond did so in such a short amount of time (roughly 140 meters in several hours) that we were not able to observe their pathway between tracking sessions. However, the disproportionate number of frogs observed under closed-canopy conditions suggests these females likely took a similar route as the male via the route with the most canopy availability, since there was no riparian connectivity between the two sites.

Climate Effects on Facultative Seasonal Migration

Sixty-seven percent of the frogs in this study did not migrate in the five months following breeding. This facultative seasonal migration behavior has been shown to be highly variable in other studies focusing on *R. draytonii* breeding migration. Bulger et. al (2003) found that 78-89% of the adult population remained at the breeding site while only a small percentage emigrated. Conversely, Fellers and Kleeman (2007) found most frogs migrated away from breeding sites, but few moved farther than the nearest non-breeding aquatic site. Both studies were within six kilometers of the ocean, at lower elevations, with varying distances between aquatic sites. This suggests that the decision to migrate is dependent on site and environmental conditions as supported for other species rather than species-specific behavior (Fudickar et al. 2021).

This study occurred during the last of several consecutive drought years, during which portions of Copeland Creek, a popular year-round aquatic habitat for *R. draytonii,* had reached historically low levels, including some portions that had completely dried out. Many cattle ponds at which *R. draytonii* have been known to breed are designed to retain water throughout the year. Many of these ponds have reached extremely low levels in recent drought years, sometimes drying out completely. These conditions have been known to drive migration away from ponds, potentially during the hottest and driest times of the year (Fellers and Kleeman 2007). Bonnie's Pond feeds into ephemeral wetlands that extend to the northeast and southwest in which *R. draytonii* were frequently observed making forays or inhabiting for extended periods of time. Only two forays among the non-migrating frogs occurred outside moisture zones during two separate rain events for short periods of time, both of which were under canopy. The presence of wetlands surrounding the breeding pond may have influenced the behavior of *R. draytonii*, reducing the need to migrate by providing additional space and resources in areas that allow reduced desiccation. The availability of wetlands may also alleviate competition for limited resources and reduce overcrowding at the pond. More research would be needed over several consecutive years to give better insight into the effects of drought, landscape composition, and density.

Limitations on Dispersal

Beyond the use of the wetlands, both migrating and non-migrating frogs did not exhibit migration or foraging behavior in the southern direction. Although the other of the two breeding ponds, Leaky Lake, is located approximately 580 meters south, the land in between these two ponds consists of cattle-grazed grasslands with little habitat associated with moisture zones or forest canopy between. Due to physiological restraints, amphibians are often regarded as poor dispersers with a tendency for high site fidelity (Blaustein et al 1994, Smith and Green 2005). An ongoing, long-term demographic study at the ranch has found only one occurrence of crossover between the two ponds over the course of several years (J. Wilcox, pers. comm). While *R. draytonii* has been known to travel much longer distances (Scott and Rathbun in litt. 1998, Bulger et al. 2003), the absence of suitable moist habitat and forest canopy emphasizes the importance of these elements in metapopulation dynamics. The population associated with Bonnie's Pond, including several of the migrators and non-migrators in this study, have indeed exhibited high site fidelity over the years, where they have often been observed returning to the same non-breeding aquatic site at which they had been observed in previous years, or suspected to be year-round residents of the breeding pond. Frogs that migrated to these sites did so in a highly oriented manner while sticking to drainages and canopy wherever possible unless during rain events. While site fidelity may be partially responsible for the lack of interaction between the breeding populations at Bonnie's Pond and Leaky Lake, a telemetric study on juvenile dispersal from Bonnie's Pond and Leaky Lake could provide insights on whether naive juveniles might move in a more random manner, and whether those travelling in the areas between the breeding ponds during the winter rainy season, away from moisture zones and forest canopy may achieve successful dispersal or be subject to high mortality rates.

Management Implications

The frogs in this study showed a high preference for moisture zones during migration and forays and for forest canopy if not in a moisture zone, particularly during dry periods and daylight hours. This suggests *R. draytonii* and other migrating amphibians are likely to benefit from efforts to maintain forest canopy connectivity between aquatic sites. Additionally, creation or restoration of wetlands near breeding ponds will likely benefit non-migrating frogs, which may potentially include high percentages of breeding populations. Telemetric studies on *R. draytonii* have differed considerably in landscape as well as quantity, hydrology, and distance between aquatic sites, and therefore differed in their results. Due to the diversity of ecosystems throughout California and the ability of *R. draytonii* to exist in a variety of mesic, xeric, and coastal habitats, conservation of regional or local populations may ultimately require the knowledge of the local landscape and population. *R. draytonii* appear to adjust their behavior and rate of travel in response to habitat features, so understanding amphibian movement ecology at a species and site-specific level, will contribute to more effective conservation and restoration efforts. Applying these efforts beyond the land between breeding and non-breeding sites to include land between breeding populations will likely contribute to recruitment, gene flow, and regional persistence in areas with unstable populations.

The U.S. Fish and Wildlife Service California Red-Legged Frog Recovery Plan (2002) recognizes the importance of adjacent upland and outlines the necessary actions needed for the recovery of *R. draytonii*. This includes conducting research to better understand the dispersal habits and overland movements in order to establish appropriate buffers, best management practices, and optimal restoration strategies (USFWS, 2002). Determination of habitat protection will likely include both breeding and non-breeding aquatic habitat, as well as adjacent upland migration corridors. Continued amphibian decline will likely result in a loss of biodiversity and associated ecosystem services. The recovery plan takes an ecosystem approach that, if successful, will not only benefit *R. draytonii* but many other co-occurring endangered and non-endangered animals and plants that share and depend on riparian and nearby moisture zones.

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