BEHAVIOR AND ECOLOGY OF THE RIPARIAN BRUSH RABBIT AT THE SAN JOAQUIN RIVER NATIONAL WILDLIFE REFUGE AS DETERMINED BY CAMERA TRAPS

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By
Celia M. Tarcha
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CERTIFICATION OF APPROVAL

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Dr. Patrick A. Kelly Professor of Zoology	Date
Dr. Michael P. Fleming Associate Professor of Biology Education	Date
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DEDICATION

For my family, living and departed, who first introduced me to wildlife and appreciating inconspicuous beauty.

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ABSTRACT

The riparian brush rabbit (*Sylvilagus bachmani riparius*; RBR) is a state- and federally-listed species only found in a few areas of the northern San Joaquin Valley of central California. It requires the dense brush associated with riparian areas for food and for protection from predators. This project studied RBR on San Joaquin River National Wildlife Refuge (SJRNWR) from February to August 2017 using camera traps. The primary objectives were to study the activity patterns and behavior of RBR as well as their usage of different resources on SJRNWR, specifically, plant communities restored in the early 2000s and artificial feed sites deployed to sustain levee-stranded RBR during major flooding in spring 2017. Riparian brush rabbits did not have a distinctive crepuscular, diurnal, or nocturnal activity pattern. Riparian brush rabbits engaged in consumptive, territorial, and reproductive behaviors with exotic plant species and artificial feed sites as well as native plants. A majority of behaviors recorded were individual behaviors followed by intraspecific with few interspecific interactions, suggesting a solitary lifestyle. Interspecific interactions were primarily with competitor species, specifically desert cottontails (*Sylvilagus audononii*). Few aggressive or territorial behaviors were recorded, suggesting a passive nature. Although a variety of behaviors were recorded during the study, vigilance and foraging behaviors were the most prominent across sites.

CHAPTER I

INTRODUCTION

In recent years, there has been a growing appreciation of the importance of behavioral research in animal conservation and recovery planning (Caro 1998, Blumstein and Fernández-Juricic 2004, Berger-Tal et al. 2011, Greggor et al. 2019). Behavior can serve as an indicator of individual and population health from the status of social and reproductive dynamics to activity patterns and habitat interactions. Understanding a species' behavior can potentially provide a way to predict their response to habitat disturbance as well as measure impact of habitat disturbance (Caro 1998). Further, knowing how animals use habitat daily, seasonally, and annually provides a better understanding of how they may contend with environmental change, perhaps even climate change. Behavior and activity can influence response to climate change because mammals with flexible activity periods may do better than obligate diurnal or nocturnal species (McCain and King 2014). Consequently, it is important for recovery and management purposes to have a better understanding of animal behavior, in particular, to predict how species are likely to respond to future changes.

One mammalian order that seems particularly vulnerable to climate change is the Lagomorpha, the rabbits, hares, and pikas. Although native to all continents except Australia and Antarctica, there are a little over 90 named species of lagomorphs, a very small number in comparison with the over 2,000 species of Rodentia with which they share the Glires clade (Lacher, Jr et al. 2016). Further, although there are many studies on rodent behavior, there are relatively few behavioral studies on members of the Order Lagomorpha, especially for the Leporidae, the rabbits and hares (Smith et al. 2018). Leporid behavioral studies have primarily focused on the European rabbit (*Oryctolagus cuniculus*), a widespread species that is declining in its native range, but paradoxically is an invasive species in many parts of its current range (Chapman and Flux 2008, Delibes-Mateos et al. 2011). Many of the least known and most imperiled leporids are habitat specialists. These include the Sumatran rabbit (*Nesolagus netscheri*), the Tehuantepec jackrabbit (*Lepus flavigularis*), the volcano rabbit (*Romerolagus diazi*), and the riverine rabbit (*Bunolagus monticularis*) (Chapman et al. 1990, Smith et al. 2018). Habitat specialists are important indicators of habitat quality. Given that most lagomorphs are important prey species, their presence or absence reflects the health of the biological community as a whole (Delibes-Mateos et al. 2011). Additionally, they provide vital ecosystem services such as seed and nutrient cycling, sometimes with large effect due to their population dynamics (Delibes-Mateos et l. 2011). Globally, habitats and the specialists that depend on them are in decline, often due to human activities, resulting in endangered status for multiple lagomorph species (Smith et al. 2018).

The riparian brush rabbit (*Sylvilagus bachmani riparius*; RBR), which is only found in the northern San Joaquin Valley and is the focus of my research, is such a taxon. It is a habitat specialist and is endangered primarily as a result of habitat loss (USFWS 1998, 2000). Brush rabbits are distributed along the Pacific coast of North America from the Columbia River in the Pacific Northwest to the southern tip of Baja

California, extending inland to the Cascade-Sierra Nevada Range. In the Central Valley of California they are only found at a few locations along the San Joaquin and Stanislaus rivers in San Joaquin and Stanislaus counties (Orr 1940, Chapman 1974). It is differentiated from other subspecies based on the convex shape of its skull (Orr 1940).

Unlike desert cottontails (*Sylvilagus audubonii*), which can be found in a variety of habitat types and land use conditions, RBR live in dense brush or densely vegetated riparian habitat where the thick cover provides protection for foraging and movement (Phillips et al. 2005). Further, Kelt et al. (2014) demonstrated that riparian brush rabbits on the San Joaquin River National Wildlife Refuge (RBR reintroduced there from 2002 to 2013) prefer habitats with willow and a few other shrub species, especially California rose (*Rosa californica*) and blackberry (*Rubus ursinus*). Despite the ecological research of Chapman (1971) and others, there are few specific details on the daily lives of brush rabbits: e.g., activity cycle, key foraging plants, and interactions with other species. Given that the riparian brush rabbit is an especially cryptic species, the scarcity of behavioral information is not that surprising. However, a better understanding of RBR life history, ecology, and behavior is important in developing effective conservation and management strategies.

By virtue of their habitat requirements, riparian brush rabbit populations are under continual threat from flooding, but they are also under threat from wildfire, and both remnant and reestablished RBR populations have experienced major fires and floods in recent decades, the most recent of which was in winter/spring of 2017. The

San Joaquin River National Wildlife Refuge (SJRNWR), the primary location of RBR interagency recovery efforts from 2002 to 2013, has experienced major disturbance events in recent years, including a wildfire (2004) and flooding (2006, 2011, 2017) (Kelly 2018).

There are no studies on the consequences of environmental disturbance on riparian brush rabbit behavior. The 2017 flood offered an opportunity to study RBR behavior in the context of significant environmental disturbance. In particular, this study was designed to gather information on behavior and flood impacts to better understand RBR ecology to benefit recovery management prescriptions. As such, this project focused on collecting data on three primary areas of RBR ecology: activity, behavior, and interactions. I set out to answer three questions: 1) Do riparian brush rabbits have a defined activity period? 2) What typical activities are representative of the riparian brush rabbit behavioral repertoire? 3) How do riparian brush rabbits interact with other species? To answer these questions, I primarily used camera traps to address my working hypotheses: 1) RBR would predominantly show a crepuscular activity pattern; 2) given the secretive nature of RBR, their behavioral repertoire would be defined primarily by solitary behaviors, and 3) RBR would interact amicably and/or cooperatively with species that potentially benefit them (e.g., quail) but aggressively towards potential competitors (e.g. ground squirrels).

CHAPTER II

BACKGROUND

Ecology and Conservation

The brush rabbit lives up to its name through its distinct preference for habitat that is characterized by brush or dense cover vegetation. The riparian brush rabbit is an endangered subspecies that is only found in a few small areas of the northern San Joaquin Valley (Orr 1940), typically in dense riparian vegetation. This subspecies was listed as endangered by the California Department of Fish and Wildlife in 1994 and by the U.S. Fish and Wildlife Service in 2000 (USFWS 2000). Understanding this specialist brush rabbit may help understand the threats facing other brush rabbit species, many of which are popular game animals. Rabbits in general provide good models for researching ecology, especially home range and predation, and a riparian specialist may reveal more information on riparian communities (Chapman and Flux 1990). Additionally, protecting the habitats of the riparian brush rabbit benefits other species, including the endangered riparian woodrat (*Neotoma fuscipes riparia*, Larsen 1993). Unknown ecological details such as the RBR activity cycle, the key plants they forage on, and how they interact with other species would better inform management decisions (Williams et al. 2008; Hamilton et al. 2010; Kelt et al. 2014). We cannot just rely on what we know from related species. Even somewhat comparable species, such as desert cottontails, do not necessarily have similar behaviors and may not respond to environmental cues in the same way. Thus, the behavior of species of management concern, such as the endangered riparian brush rabbit, require study to develop a specialized conservation plan.

The primary factor in the listing of the riparian brush rabbit as an endangered species was the loss of riparian habitat, primarily to agriculture, in the northern San Joaquin Valley (USFWS 2000). Habitat loss occurred when rivers were restructured from meandering woodlands into more linear and less vegetated channels. In areas where the river was left intact, surrounding uplands were converted to agricultural fields removing habitat that served as refuge from seasonal flooding. Additionally, agricultural lands provide little food or cover for brush rabbits, further restricting the remaining populations from dispersing to other areas. Loss of connecting habitats has also isolated populations putting them at greater risk of extinction. While agricultural lands are used to some extent by desert cottontails, brush rabbits are restricted to upland habitat remnants, often along rivers and channels (USFWS 1998).

Habitat alteration possibly further endangered RBR by facilitating competition from desert cottontails. Desert cottontails utilize some of the same habitats as riparian brush rabbits, but unlike brush rabbits, desert cottontails also use more open habitat (Williams and Basey 1986). In addition, desert cottontails are thought to mature faster than brush rabbits and breed year-round, also resulting in competition pressure for the brush rabbit (Williams and Basey 1986, Larsen 1993). Habitat alteration may have caused the desert cottontail to expand its range to areas that were historically exclusive to riparian brush rabbits (Williams 1988). Increased overlap of the two lagomorph species in small areas could pose a risk of disease or parasite transmission to the riparian brush rabbit, further illustrating the importance of understanding species interactions for the recovery of RBR (Williams et al. 2002).

Not all riparian habitat is suitable for riparian brush rabbits. They demonstrate a strong preference for willow-shrub habitats and have varying sizes of home ranges and core areas within these habitats (Kelt et al. 2014). The home ranges and core areas of RBR are larger in the breeding season, with increased overlap in the nonbreeding season, suggesting that there may be territoriality during the breeding season (Kelt et al. 2014). This suggests that RBR activity and behavior influence habitat use and that this usage may shift seasonally. Additionally, it highlights the need to understand RBR habitat use from a behavioral context as well as a survival one to understand the ecological value of restored sites.

Geographic and Regulatory Setting

The most significant of the remaining riparian habitat remnants for RBR is Caswell Memorial State Park (Caswell MSP) on the Stanislaus River (Williams and Basey 1986). However, management activities for mosquito and fire control at the park removed protective cover for rabbits, and caused a decline in this population in the 1980s (Williams 1988); the population in the park has remained low (ESRP unpublished data). In 2000, the riparian brush rabbit was listed as federally endangered following being listed as a candidate species in 1996. At that time there were only two known wild populations remaining, one at Caswell MSP and the other in the South Delta, mostly on private property (Figure 1). In an effort to recover this endangered species, an interagency controlled propagation and reintroduction program was initiated in 2001 with the San Joaquin River National Wildlife Refuge (SJRNWR) in Stanislaus County chosen as the site for the new population (Kelly 2018). Since their release, the growing population has faced a variety of obstacles, the largest being a fire in 2004 followed by floods in 2005 and 2011, that resulted in significant loss of individuals and habitat (Phillips et al. 2005; Kelt et. al 2014; Kelly 2018). Despite these setbacks, recent genetic research on this population documented high genetic diversity and a unique genetic composition (Rippert et al. 2017).

San Joaquin River National Wildlife Refuge was selected for this study due to its low visitor traffic and human impact, limited to a single trail, compared to Caswell MSP, a multi-recreational park. The managers at SJRNWR have also made large-scale efforts to restore habitat, creating a number of distinct plant communities to be evaluated. The initial plan for this thesis involved camera surveys in these different plant communities. However, the focus was changed when there was a very large flood event during the 2017 data collection year where there was opportunity to evaluate RBR behavior during a time of flood as well as their utilization of the restored habitat. This was a significant opportunity to study RBR behavior as riparian brush rabbits are associated with not only their namesake riparian forests but also their adaptation to floods.

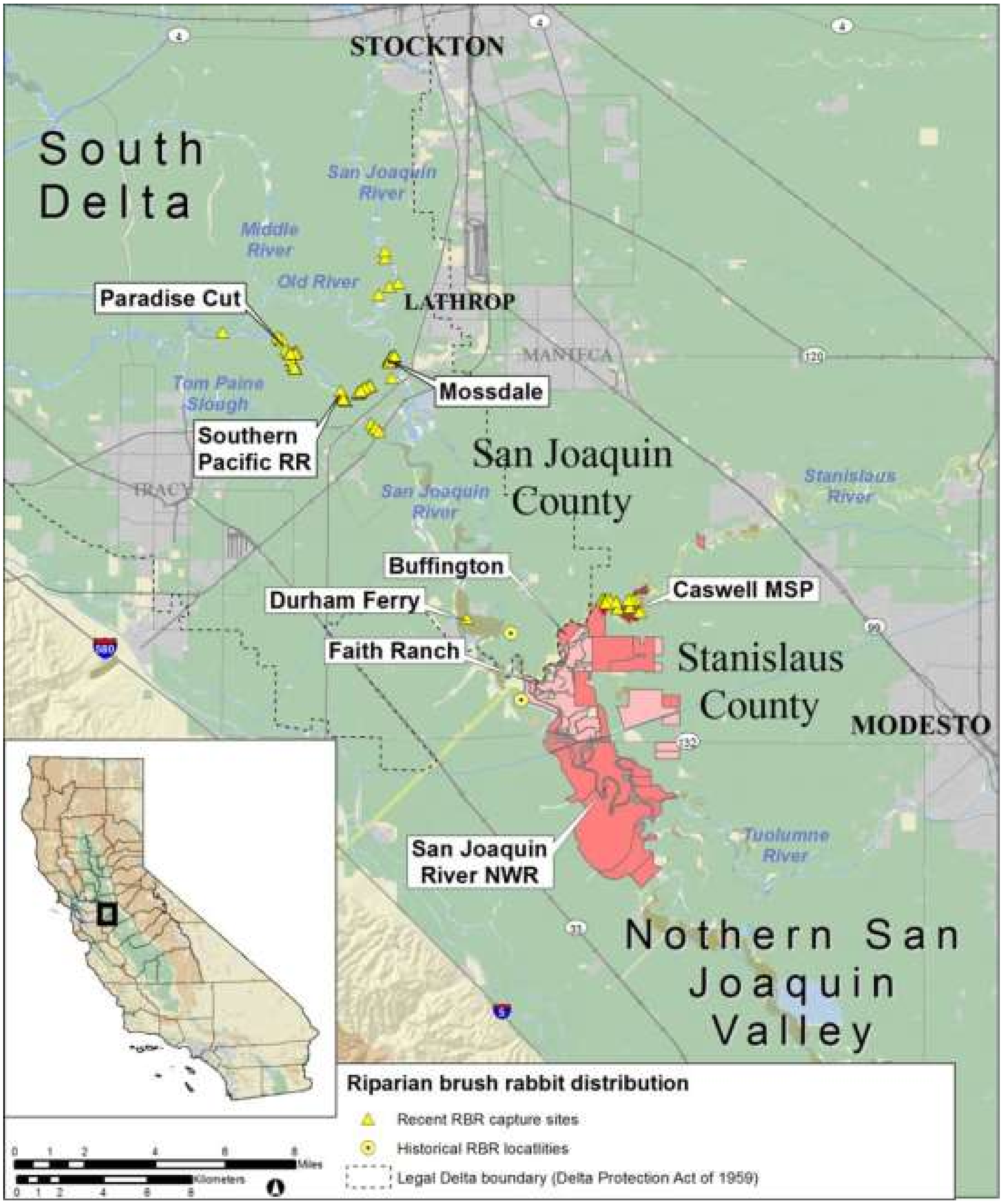

Figure 1. Distribution of the riparian brush rabbit with the San Joaquin River National Wildlife Refuge (highlighted in red). Map created by Scott Phillips, California State University Stanislaus/ Endangered Species Recovery Program.

Previous Riparian Brush Rabbit Research and Emerging Technologies

Different techniques have been employed to study riparian brush rabbits. Williams and Basey (1986) used live-trapping to look at habitat use and sympatry of riparian brush rabbits and cottontails. Williams (1988) was able to determine areas of increased densities of rabbits at Caswell MSP based on numbers of animals captured by live-trapping in different habitats. Williams (1988) also used fecal pellet surveys to evaluate rabbit presence and the degree of usage of different habitat types. Surveying for pellets and vegetation clippings can indicate habitat utilization, but it does not provide information on usage at a specific time period. Plant assemblages where RBR were captured have been compared to non-capture sites and expected captured sites to characterize preferred habitat (Basey 1990). Elsholz (2010) conducted presence surveys using baited aluminum track plates, also at Caswell MSP, but did not detect any rabbits, suggesting that they may avoid conspicuous objects or alterations to the ground, even when bait is provided.

Since the riparian brush rabbit is an especially cryptic species, and therefore difficult to observe even under ideal conditions, marking rabbits with colored tags to observe them during the day is generally not feasible. Williams (1993) tried reflective tape tags for spotlight surveys to census rabbits at night. This census technique was ineffective, because reflections from the tape were not visible through the dense brush (Williams 1993). As a result of the difficulty in observing riparian brush rabbits, any studies on RBR sociality have been limited to data collected from live-trapping.

Basey (1990) also used trapping data to ascertain home range sizes and intraspecific spatial relationships of RBR, finding increased territoriality in females based on the size of home range overlaps. Reproductive periods were determined by collecting reproductive status data from trapped rabbits (Basey 1990). However, as noted by Basey, females were not reproductive throughout the purported reproductive season and males were found reproductive outside of the female reproductive season suggesting that trapping data is limited to reproductive potential (Basey 1990). Unless pregnant or lactating females are captured, live-trapping cannot document the proportion of the population engaging in reproductive activities, only how many RBR have the potential for these behaviors.

Radiotelemetry has been the most effective technique to date for quantifying riparian brush rabbit activity. It has allowed researchers to examine rabbit survival and space use, by sex and over time (Hamilton et al. 2010; Kelt et al. 2014; Williams et al. 2002; Williams et al. 2008). All of these studies were able to quantify habitat use at a finer scale than previous work. However, there are limitations to radiotelemetry. In addition to the intensive labor and material cost of radiotelemetry, at SJRNWR, data collection was restricted to around sunset due to radio interference during the day (Kelt et al. 2014). This limited the efficacy of this technology to collect data as it only yields a small sample of daily activity. Additionally, each triangulation (telemetry location) can only bring researchers within a few meters of the rabbit, limiting behavioral observation.

The use of remote cameras, or camera traps, offers many advantages over alternative methods. Cameras can be operated in a wide range of temporal, light, and weather conditions, recording data otherwise unattainable by human observation. Less obtrusive than human observers, camera traps can be an alternative for studying behaviors of sensitive species. Camera traps have been used successfully with a variety of lagomorph species, including species that are hard to observe. For example, camera traps have been used in research on pygmy rabbits (*Brachylagus idahoensis*), a tiny lagomorph that lives in dense sagebrush habitat, and have been shown to not disturb rabbit activities (Larrucea and Brussard 2008; Larrucea and Brussard 2009; Lee et al. 2010; Pierce et al. 2011; Hickman 2016).

An important advantage of camera traps is their ability to gather continuous activity data. Camera traps were used to gather detailed data (24 hr/day) on daily and seasonal activity of pygmy rabbits (Larrucea and Brussard 2009; Lee et al. 2010). Pierce et al. (2011) used cameras to study the activity of pygmy rabbits and their predators in sagebrush habitat. From cameras deployed in habitat edges, they were able to gather much more data to characterize the influence of edge effects on pygmy rabbits than they would have from trapping, as the cameras collected data on the predators as well as the focal species.

Identification of individual lagomorphs by observation in the field is difficult because they are usually moving, often very quickly. However, camera traps can provide the opportunity for precise identification of species and individual marks with multiple photographs and thus, the potential to identify a particular rabbit (Larrucea and Brussard 2008a). Elsholz (2010) used camera traps at Caswell MSP, and although only a few photos were taken, he did get photographs where riparian brush rabbits could be distinguished from desert cottontails. Further, in an undergraduate project on riparian woodrats (*Neotoma fucipes riparius*) conducted on the SJRNWR, brush rabbits were readily recognizable in a number of photographs recorded by camera traps (Parks, Isley, and Kelly – unpublished data).

Environmental Threats to Riparian Brush Rabbit Recovery

In June 2004, a large fire, named the Pelican Fire, swept across most of the SJRNWR. The Pelican Fire burned 53% of the high quality and 44% of the moderate quality RBR habitat areas of the Refuge (Phillips et al. 2005). Despite the sizable amount of damage, a monitoring program during 2002 to 2005 found higher RBR mortality to floods in March, May, and June 2005 than the Pelican Fire (Hamilton et al. 2010).There have been a number of smaller fires since 2004, but a more serious and regular threat is large scale flooding (Hamilton et al. 2010, Wittmer et al. 2016, P. Kelly pers.comm.).

In January of 2017 multiple storms in the Central Valley flooded the San Joaquin River National Wildlife Refuge. The high flows inundated floodplain areas of the refuge while the southern portion was flooded from a broken levee, breached intentionally to relieve pressure from the swollen river (E. Hopson pers. comm.). The broken levee restricted land access, leaving the southern portion of the SJRNWR only accessible by boat. By early February an estimated 90% of the riparian brush rabbit habitat was flooded and those areas were still flooded after April (Takahashi 2017).

The surviving wildlife moved to higher ground resulting in high concentrations of herbivorous mammals. These herbivores at high density quickly exhausted the available resources resulting in forage lines above RBR standing height and the only widespread, easily accessible vegetation available was toxic poison hemlock (*Conium maculatum*).

Apart from the outright mortality of RBR from floodwaters, the other major problems resulting from the flood were the stranding of RBR and the food shortage from high concentrations of RBR and other herbivores exhausting resources. Raised berms created during the restoration of the Refuge had been planted with upland brush species to act as upland flood refugia in response to a massive flood in March 2005 (Hamilton et al. 2010). During the 2017 flood these berms acted as islands and initially saved RBR; however, the ability of the berms to sustain the stranded wildlife during the months of flooding was limited. San Joaquin River National Wildlife Refuge personnel responded by capturing RBR stranded on smaller islands and moving them to more optimal areas. Between January and March, the worst of the flood period, SJRNWR staff captured and relocated 158 riparian brush rabbits (Heffernan and Takahashi 2017, Takahashi 2017). In the last week of February 2017, the USFWS began weekly distributions of dried alfalfa (*Medicago sativa*) and rabbit pellets (AG Farmers Best Feed Rabbit Pellets) on levees and large berms to supplement for exhausted vegetation. On the research levee the food was typically thrown from a moving truck two to three times a week: scoops of pellets were thrown from the cab and employees would throw slabs of alfalfa from the back, aiming towards the underbrush. The pellets were noticeably depleted faster than the alfalfa with piles of alfalfa often remaining into the next distribution. Supplemental feeding was continued until August 2017 (Heffernan and Takahashi 2017, E. Hopson pers. comm.).

The food shortage for the surviving RBR had two major effects that shaped USFWS response to the flood events. The first effect was the increased concentration of herbivores such as RBR, desert cottontail, and California ground squirrel (*Otospermophilus beecheyi*) on small areas of upland habitats. As a result, herbaceous ground plants were quickly overgrazed and shrub species were overbrowsed, forming distinctive browse lines that were challenging for RBR to reach without climbing into the brush. Although the only ground plants that remained were moss and toxic poison hemlock, multiple poison hemlock plants were clipped and consumed, presumably by rabbits, demonstrating the second outcome of the food shortage: the dominance of toxic plants that threatened RBR with poisoning. A member of the public mentioned seeing a rabbit, either a RBR or desert cottontail, walking in tight circles, a symptom of neurological damage from nutritional deficiencies (Fisher and Carpenter 2012), illustrating the extreme food shortage and supporting the possibility of RBR feeding on hemlock out of starvation. With the signs of RBR possibly feeding on poison hemlock and dead RBR found without signs of predation, thirteen RBR carcasses were exported for necropsies to determine if cause of death was poison hemlock ingestion. One carcass had the toxin coniine in its system, a result of poison hemlock ingestion; however, the level was not high enough to have been the cause of death.

Other complications from the flood events were the increased visitor presence and increased dog presence. More than half of the nature trail was closed due to damage or flooding. The portion of the trail available was on the same levee as this project, concentrating the visitor presence to a smaller area. Problems with dogs (*Canis familiaris*) included feral and off-leash pets brought by visitors wandering off-trail, potentially threatening the already stressed wildlife. Refuge staff trapped feral dogs and increased signage prohibiting off-leash dogs in response.

The variety of issues affecting RBR during the 2017 flood illustrate the multifaceted impacts of floods on the recovery of this specialist species and the need for more knowledge of RBR ecology. Understanding RBR behavior and ecology can better inform management for not only species recovery but also rapid response to mitigate the effects of environmental disasters such as fires and floods.

CHAPTER III

METHODS

The main method of data collection in this study was motion-activated camera trap. Camera traps were set in sites with specific environmental characteristics and would take photos when triggered by movement in the camera's field of view. These photos were examined on a photo-processing program where they were assigned additional metadata. The metadata were then exported to a spreadsheet program for analysis. Vegetation data were also collected in the field and by examining the camera trap photographs.

Because of major levee breaches and flooding in the months of January through June 2017 restricting access, the scope of the intended fieldwork had to be changed considerably. Initially the scope of this project was to include the entire San Joaquin River National Wildlife Refuge but the 2017 flood inundated 45 of the 48 stations initially chosen for cameras. The flood restricted the project to the two connected levees north of Hospital Creek. The three remaining sites (Run7, RunB1, and RunB2) were surveyed and set as a group that would be part of a new set of camera sites (PH1, PH2, PH3, PH4, and PH5) set on the levee available (Figure 2). Cameras collected data from February 24 to August 16, 2017 (Table 1,Table 2).

Table 1. *Camera sessions and dates during the flood of 2017.*

	February		March (1)		April (1)		April (2)		May (1)	
Site	Start	End	Start	End	Start	End	Start	End	Start	End
Run7	2/24	3/3	3/3	3/10	-	-	4/2	4/21	4/25	5/8
RunB1	2/24	3/3	3/3	3/10	-	-	3/31	4/25	4/25	5/8
RunB2	2/24	3/3	3/3	3/10	-	-	3/31	4/25	4/25	5/8
PH1	-	-	3/3	3/10	-	-	3/31	4/25	4/25	5/8
PH2	-	-	3/3	3/10	-	-	4/9	4/21	4/25	5/8
PH3	-	-	3/3	3/10	3/31	4/9	4/9	4/21	4/25	5/8
PH4	-	-	3/3	3/10	3/31	4/9	4/9	4/21	4/25	5/8
PH5	-	-	3/10	3/17	3/31	4/9	4/9	4/21	4/25	5/8

Table 2. *Camera sessions and dates after 2017 floodwaters began to recede.*

	May (3)		June		July		August	
Site	Start	End	Start	End	Start	End	Start	End
Run7	5/19	6/1	6/14	6/21	7/19	8/3	8/4	8/16
RunB1	5/19	6/1	6/14	6/21	7/19	8/3	-	-
RunB2	5/19	6/1	6/14	6/21	7/19	8/3	8/4	8/16
PH1	5/19	6/1	6/14	6/21	-	-	-	-
PH2	5/19	6/1	6/14	6/21	7/19	8/3	-	-
PH3	5/19	6/1	6/14	6/21	7/19	8/3	-	-
PH4	5/19	6/1	6/14	6/21	7/19	8/3	-	-
PH5	5/19	6/1	6/14	6/21	7/19	8/3	-	-

Camera Survey

Equipment

Cuddeback Black Flash E3 Model 1231 remote cameras were used in the study. This passive infrared (PIR) camera model uses twenty 940 nanometer LED bulbs for no-glow infrared photos and has a trigger speed of ¼ second. It is a discreet camera trap: apart from a barely audible click when it transitions to a different flash mode, the camera is otherwise silent. Throughout the study, lithium batteries and 8GB Sandisk Class 4 memory cards were used.

Camera Placement

In March 2017, five new camera sites (PH1-PH5) were established in addition to the remnant sites (Run7, RunB1, RunB2) along the levee near available food sources, poison hemlock and alfalfa piles (Figure 2). Stations were chosen based on the availability of one or both of these food sources and visibility to the general public on the levee trail (Table 3). Because of greater public use of the area, more caution had to be taken for camera placement making concealment an important factor. For instance, shrubs with extreme browsing could not properly hide cameras, and similar to areas with sparse vegetation, could not be utilized. Likewise, areas where plants were extremely dense and impassable without alteration could not be used as resulting pathways would be more apparent to visitors, increasing risk of camera disturbance. Environmental differences such as these determined camera distribution, resulting in the distribution of the camera stations not being equidistant (Figure 2).

When placing cameras under normal circumstances, they would be pointed to the north or northeast, away from the sun; however, in this study cameras were often placed facing in directions other than to the north because of vegetation characteristics and visibility concerns. Sometimes a camera had to be moved within the site due to vegetation changes such as growth impeding the camera or defoliation exposing it (Table 4). Characteristics of the individual sites including photographs are detailed in Appendix A.

The cameras were typically placed on a stem or stake approximately 10-30 cm above the ground, positioned for the best frontal view of RBR at a resource within the field of view (Table 3). The camera detection zone was set to narrow view, which better served the relatively confined field of view within the brush. The cameras were set to take 5 photos per trigger (Burst Mode) on Fast-as-Possible (FAP) mode, with approximately 1 second delay between shots. These settings were essential to capture fast behaviors that can happen within 60 seconds. The flash settings were no flash in the day and no-glow Black Flash in darkness to reduce disturbance. Cameras were activated in sets to capture at least a week's worth of photos per month. The dates cameras were active are detailed in Table 1, Table 2, and Table 41.

Figure 2. Levee camera sites and live observation meadow locations on SJRNWR. Map created with Google Earth Pro. Imagery date 5/17/2017.

Table 3. *Habitat resources present at each site.*

Habitat Resource	PH1	PH2	PH3	PH4	PH5	Run7	Run B1	Run B2
Runways	X	X	X	X	X	X	X	X
Poison Hemlock, *Conium maculatum*	X	X	X	X				
Alfalfa (Dried), *Medicago sativa*			X	X	X			

Table 4. *Orientations and alterations to camera sites.*

Site	Camera Orientation	Notes
PH1	232°	-
PH1a	-	Permanently removed in July due to dried trail reopening.
PH2	250°	-
PH3	268°	-
PH4	346°	-
PH5	152°	-
PH5a	105°	Moved for May Session 3 due to sprouting elderberry.
Run7	168°	-
Run7a	80°	Position on runway flipped in July when canopy defoliated.
RunB1	28°	-
RunB1a	72°	Shifted orientation in July due to lower trail reopening.
RunB2	58°	-

Vegetation Surveys

For this study there were two types of vegetation surveys performed: one based on the camera trap photos and one done in field by transect. The plant community composition survey was based on camera trap photos, where I identified the natural resources in the photos for each month to characterize changes in composition within the site. The in-field transect surveys were done at the end of the study to characterize the larger community of each camera site by evaluating density and dominance.

Plant Community Composition

Plant species recorded in photographs were identified to species when possible or functional group (i.e. moss, ground forb). Other environmental parameters, presence of water and alfalfa replenishment, were recorded as well.

Plant Density and Dominance

Vegetation surveys were postponed until after the camera data collection was completely finished. These surveys risked damaging the limited sources of food and protection available to the rabbits during the flooding. Environmental damage in the focal area risked altering animal behavior as well as adding additional stress to the animals. Furthermore, cameras recorded RBR collecting sticks, suggesting that rabbits were nesting nearby despite the flooding, and vegetation surveys risked disturbing them.

Plant density was measured to account for community variation of sites. For understory plants, the point-intercept method was used where 5 meter tape was extended from the camera in each cardinal direction (Higgins et al. 2012). Each 5 meters was broken into 50 evenly spaced points where a 0.48x121.92 cm (3/16x48 inch) poplar dowel was vertically placed every 0.1 meter, any plant species touching the rod was recorded for that point. Any plant too high to come into contact with the dowel was recorded as canopy. If there was only bare ground at the point it was recorded as bare ground and similarly if there was only litter at the point if would be recorded as litter. The dowel was marked for the maximum height a rabbit can reach to forage, approximately 35 cm based on observations of RBR and the forage lines on plants during the flood. Vegetation that touched the dowel above this measurement was considered canopy, anything below it was considered in the forage area. Resources are considered accessible and in the foraging area if they are within a brush rabbits reach when standing (on their hind feet) or on the ground (on all fours). In the transect surveys each species touching the dowel was recorded into one of three classes: canopy, forage area, and ground. Each was treated as a separate data point, if a species intersected at both the forage area and the canopy it would be recorded present in both categories, not one.

Photo Processing

After photos were collected they were directly transferred onto a computer for processing. Photos were tagged using Photo Mechanic 5 (2016) by Camera Bits, Inc. for faster processing of the large numbers of images recorded. Tags are descriptors of what was recorded in a given photograph, not only the type of animal in the photo (e.g., mammal, bird, riparian brush rabbit, coyote, etc.), but also the behavior displayed if the animal was an RBR. The tags used for riparian brush rabbits were based on an ethogram (Table 38, Appendix B) created from research (Lehner 1979, Chapman and Flux 1990, Chapman and Ceballos 1990) and direct observation. The live observation was conducted in a refuge meadow bordered by dense brush at the corner of Dairy and Pelican Road with the purpose of directly viewing and photographing RBR behaviors to understand how they translated into static photos (Figure 2). Camera trap photos that did not record an animal were not tagged. In Photo Mechanic, tags were separated by commas so that they could be easily processed using Microsoft Excel (2013). If an animal was present, the photo would first be tagged with its Class: *Mammal*, *bird*, or *herp*. These different tags were used for easier visual interpretation as mammals were of greatest interest to this study. The tag *herp* was used to represent amphibians and reptiles collectively as both are unreliably captured by PIR camera traps (Hobbs and Brehme 2017). If an animal was identifiable to species, the species name was also included (Table 39, Appendix C).

Descriptive photo tags were only used for riparian brush rabbits and included tags for number of individuals present, their behavior, and what they were interacting with. For example, if an RBR was alone and vigilant the tags on the photo would be '*Mammal, Lagomorph, Riparian Brush Rabbit, vigilant*' and if the photo had two RBR feeding on the same alfalfa pile the photo would be tagged '*Mammal, Lagomorph, Riparian Brush Rabbit, 2, intra, feed, Alfalfa*'. This could expand if species in addition to RBR were present, for example, if a coyote caught a riparian brush rabbit while 2 others escaped the tags would be '*Mammal, Lagomorph, Riparian Brush Rabbit, 3, multiple, Predator, Coyote, inter, predation, flight*'. All photos with an RBR and another species present were tagged as *multiple*. Such detail was not collected for other species. The number of individuals of other species was excluded from the tags as well as behaviors of other species that were not direct interactions with RBR. When an RBR and another species were present in the same photo, they would be tagged as interacting if there were specific behavioral interactions; simply being present at the same time was not considered an interspecific interaction (Table 39, Appendix C). Multiple RBR present were considered interacting if the RBR were within 2 meters of each other, photos with RBR further away from each other were not tagged as intraspecific interactions. Behaviors were further classified with regard to specific activity (grooming, dust-bathing, feeding, etc.). In addition to behaviors, if an RBR interacted with a particular vegetation types, the species, if known, or the vegetation type was included as tags as well (Table 40).

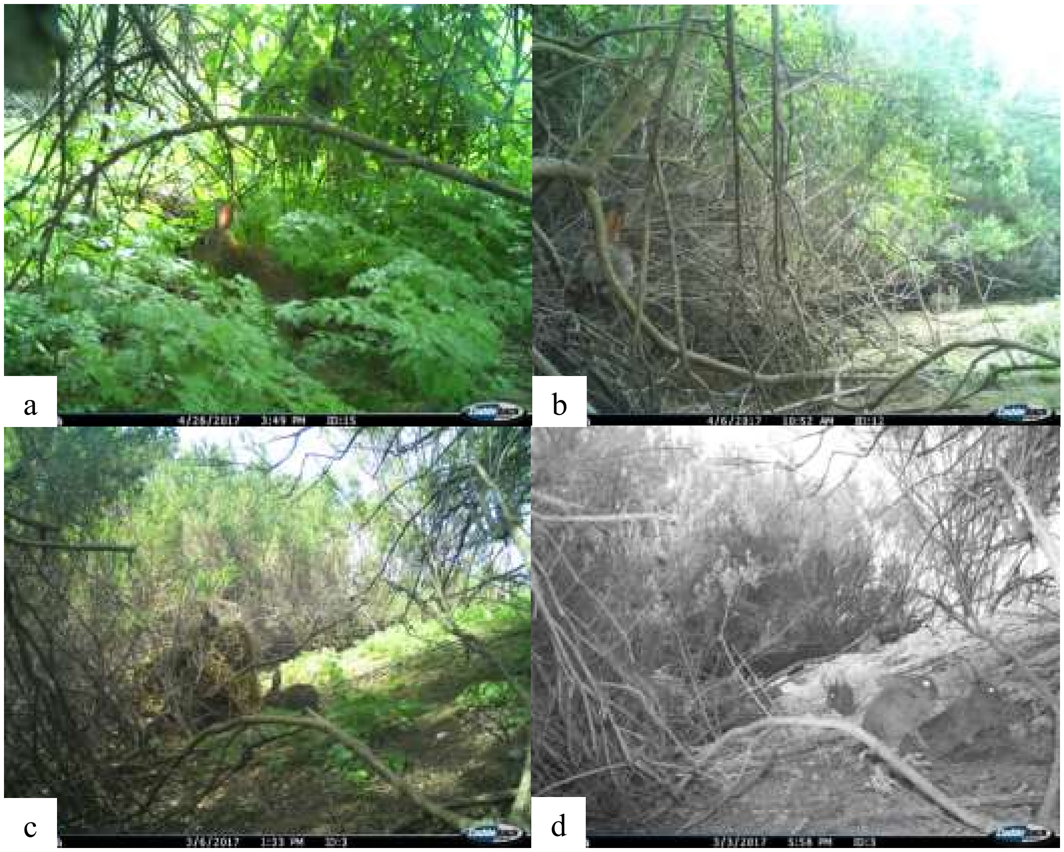

Figure 3. Examples of riparian brush rabbit photos: an individual is vigilant (a.), a vigilant riparian brush rabbit co-occurred with another vigilant individual that climbed into a coyote brush (b.), an intraspecific photo of a vigilant riparian brush rabbit near a feeding conspecific that climbed on an alfalfa bale (c.), an intraspecific photo with intraspecific behaviors (mating) and individual behaviors (vigilant and feeding) (d.).

Data Analysis

The metadata (date, time, and tags) for the photos were exported from Photo Mechanic 5 (Camera Bits, Inc. 2016) as text files and imported into Microsoft Excel. Data clean-up consisted of deleting photos without tags and checking tags for completeness. This was accelerated by first using the sort function to review the data ordered by first tag (*Mammal*, *bird*, or *herp*) instead of picture number, separating the data and causing inaccuracies to become more visible. Afterwards, the data were reviewed a second time in sequential order of picture number. The add-on Kutools (Addin Technology Inc. 2018) was used to isolate photo data with RBR and extract them to separate files. Microsoft Excel was used for all calculations and analysis except for the Tukey's honest significant difference (HSD) tests which were calculated with the VassarStats: Website for Statistical Computation online tool (Lowry 2020).

Photo Data Analysis

Species presence. For total species the COUNT function was used to sum the number of each species tag. The percentage of each species out of the total number of species tags was also calculated. For the number of RBR present in photos, the COUNT function was used for each number tag (1-10; 10 was the greatest number recorded in a single photo) for each site as well as to sum the total number of RBR photos.

Riparian brush rabbit activity. In this study, riparian brush rabbit activity was defined as times RBR were photographed and not engaged in resting behaviors. Activity was calculated in two different sets: a set that included all photos and a set broken into five minute periods. The data for RBR activity was evaluated by isolating metadata of photos with RBR tags from all other data. After isolation, the data were combined by camera station. Photos with RBR were isolated in their own file using Kutools (Addin Technology Inc. 2018). There were separate sets of calculations due to the photo burst mode the cameras used to maximize RBR capture. Since there were five photos taken per trigger but not all of the photos would necessarily have the same behavior, all photos had to be included in calculations for behavior, especially since some behaviors were rarely captured. However, for calculating activity, if each photo containing RBR was considered a datapoint, this could skew the activity times for sites where RBR would be in the photo area for extended periods of time and continuously triggering the cameras. Additionally, as there were five photos per single trigger, those five photos would not be independent of each other. Thus, a second set of data was created to evaluate activity patterns with more statistical independence whereas the first set conserved all photos to mirror the behavior calculations.

For the first set, each time was grouped into the nearest hour with the MROUND function (=MROUND(time,1/24)). The Excel COUNT function summed the number of photos for each hour and the number of rest photos for each hour were subtracted for RBR activity. For the combined station graphs the total activity for each site was summed. The average number of photos for each time interval was calculated with standard error to evaluate the variance of photo amounts between sites within each hour (STDEV function, n=8).

For the second set, all times recorded for all sites were listed together with their dates and converted into standard time. They were then grouped into five minute interval bins, hereby referred to as grouped events, reducing the excess data from burst mode. This reduced the data to a binary format of present/absent where if there were any RBR photos within the 5 minute time span, the bin would be a single data point of present. For time intervals with RBR the bin would be labeled as active or inactive depending on the behavior. In a separate spreadsheet with the dates, the time intervals were assigned as night, dawn, day, or dusk, based on the calculation of the time of day and sunrise/sunset of the date (State of Washington 2005, S. Phillips pers. comm.). This was to further reduce the data to represent one of four values (night, dawn, day, dusk) rather than hours, allowing activity to be analyzed as the amount of instances RBR were active during a specific period of day. The variance between time intervals was calculated by single factor analysis of variance (ANOVA) between the four time periods separately and between night, day, and the combined numbers of dawn and dusk.

The similarity between the two sets, total photos combined and grouped events was compared with analysis of variance. The difference between the amount of RBR rest and activity was calculated with a paired two-sample Student's t-Test.

Riparian brush rabbit behavior. The total number of behaviors was compiled in a similar fashion to the species totals by using the COUNT function to sum the number of each behavior tag. The percentage of the number of photos of each behavior was calculated out of the summed number of all behavior tags.

Riparian brush rabbit interactions. To further examine RBR interactions, data was separated into four behavior types: intraspecific and interspecific interactions, individual behaviors, and allospecific. Allospecific refers to photos with a RBR and another species co-occurring but not interacting. The number of intraspecific and interspecific interactions was determined using the COUNT function to count the number of *intra* and *inter* tags. The number of individual behaviors, behaviors that did not involve interaction with another individual, was calculated from these numbers. After analyzing the variance between individual, intraspecific, and interspecific interactions, a paired two-sample Student's t-Test was performed to evaluate the difference between the interactions in pairs. A Tukey’s honest significant difference (HSD) test was performed for all three interaction types to evaluate the difference between their means using the VassarStats online calculator (Lowry 2020).

Brush rabbits were often photographed with other species, referred to as co-occurrence, but this did not always involve an observable interspecific interaction. The number of allospecific photos, was calculated by using the COUNT function to sum the number of photos with the *multiple* tag, a tag used when an RBR and another species were present, followed by subtracting the number of interspecific interactions recorded. A paired two-sample Student's t-Test was also performed to investigate the difference between the number of allospecific and interspecific photos.

Interspecific behaviors were further examined by type, negative or amicable, and the species type (beneficial, competitor, or predator) that RBR were interacting with. Interactions with beneficial species were interactions with California quails and competitor species interactions were with desert cottontails and California ground squirrels. For this analysis, all predatory species RBR interacted with were included. Species that were not in any of these categories were not included. An analysis of variance was performed to compare the relationship of negative and amicable interactions. In addition, another ANOVA was implemented for the three species types to determine if there was a difference in the number of RBR interactions with these different types. Further, a Tukey's HSD test was performed to determine the significance of the difference between the means of the three species types (Lowry 2020).

Vegetation Data Analysis

There were two foliage categories calculated in this study: canopy, foliage above RBR forage height and forage area, all foliage within RBR forage height. The percentage of each plant species was calculated within individual categories; for instance, if coyote brush was recorded in both the canopy and forage area the percentage of coyote brush canopy was calculated based on the counts of other canopy species. Both coyote brush counts were not combined.

Percentages of cover derived from these surveys were used to classify a site's vegetation alliance with the Manual of California Vegetation Online (CNPS, 2019). The species with the highest percentage in the canopy was considered dominant. If there was not a species with a percentage at or above 50% in the canopy then the forage area species with the highest percentage would be considered dominant. The co-dominant for a site was a species with the closest percentage to the dominant within 30%. If there was not a species with a percentage within this 30% threshold there was no species recorded as co-dominant.

CHAPTER IV

RESULTS

Between February and August 2017, over a combined time of 639 camera days, 105,777 photos were collected at the 8 camera stations distributed along the Hospital Creek and Vierra levees (Table 5, Table 6). Photos were successfully collected during every active camera session and at all times of the day and night. A total of 38 species was recorded, including riparian brush rabbits. Riparian brush rabbits were photographed at all hours, but at different frequencies. Cameras also successfully captured 24 RBR behaviors, including both intraspecific and interspecific interactions. Due to the restrictions caused by the 2017 flood, vegetation surveys were limited to photographs and post-flood transects.

Table 5. *Number of photos collected at each site by month.*

Site	Feb	Mar	Apr (1)	Apr (2)	May (1)	May (3)	June	July	Aug
Run7	415	600	-	80	95	1,495	15	124	205
RunB1	1,830	2,500	-	3,680	3,250	800	120	1,290	-
RunB2	1,815	1,030	-	2,850	185	95	5	20	465
PH1	-	235	-	2,485	425	2,170	565	-	-
PH2	-	770	-	1,825	2,695	2,965	40	830	-
PH3	-	8,464	6,334	6,465	5,095	5,380	4,250	1,165	-
PH4	-	6,430	315	210	75	60	20	105	-
PH5	-	4,965	7,165	1,955	7,075	1,315	230	735	-

Table 6. *Number of days cameras were active at each site.*

Site	Feb	Mar	Apr (1)	Apr (2)	May (1)	May (3)	June	July	Aug	Total
Run7	7	7	-	19	13	13	7	15	12	93
RunB1	7	7	-	25	13	13	7	15	-	87
RunB2	7	7	-	25	13	13	7	15	12	99
PH1	-	7	-	25	13	13	7	-	-	65
PH2	-	7	-	12	13	13	7	15	-	67
PH3	-	7	9	12	13	13	7	15	-	76
PH4	-	7	9	12	13	13	7	15	-	76
PH5	-	7	9	12	13	13	7	15	-	76

Riparian Brush Rabbit Activity

Activity by Total Photos

The number of photos recorded at each time period varied; there was never a time period with zero photos. For all 8 sites combined, the greatest number of photos was taken between 09:00 and 11:00 with the peak at 10:00 (Figure 4). The 10:00 peak was followed by peaks at 20:00 and 03:00, which had a similar distribution: the preceding two hours low followed by a spike in the last hour. The lowest numbers of photos recorded were at 00:00, 07:00, and 13:00 through 14:00. Of these low points, 00:00 (midnight) was the lowest.

The activity of RBR varied between sites (Figure 6) resulting in an average activity distribution with heterogeneous variance (Figure 5). Site PH3 had the most photos followed by PH5, with an activity distribution closest to the total (Figure 4, Figure 6). However, none of the sites had a distribution that completely matched the distribution of the total (Figure 6) a result of the variance of photo numbers taken during each time interval between sites (Figure 5). However, while RBR seemed to be more active between 02:00 through 05:00 and 09:00 through 11:00, variance was higher during those periods than when they appeared to be least active, 00:00 and 13:00 through 17:00 (Figure 5).

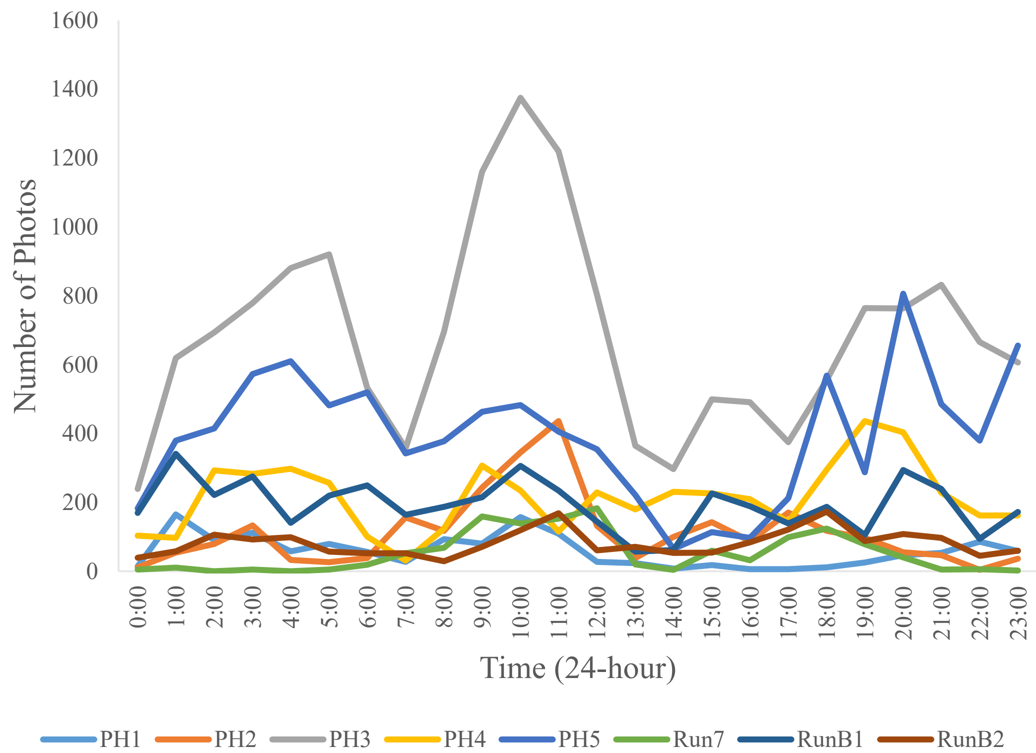

Figure 4. Riparian brush rabbit activity as measured by number of photos.

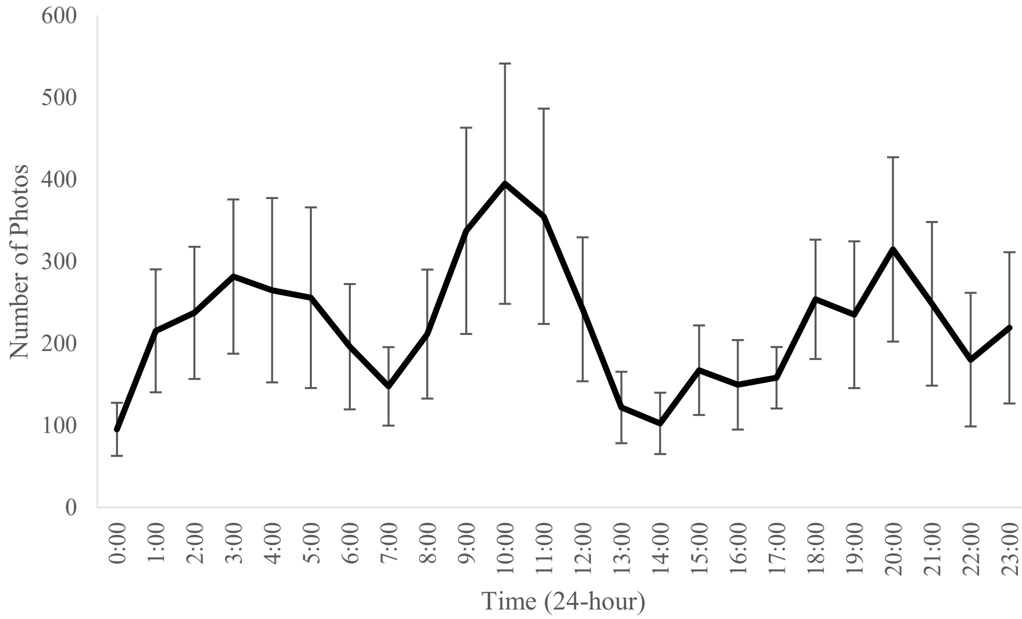

Figure 5. Combined average number of RBR photos per hour (±1 SE).

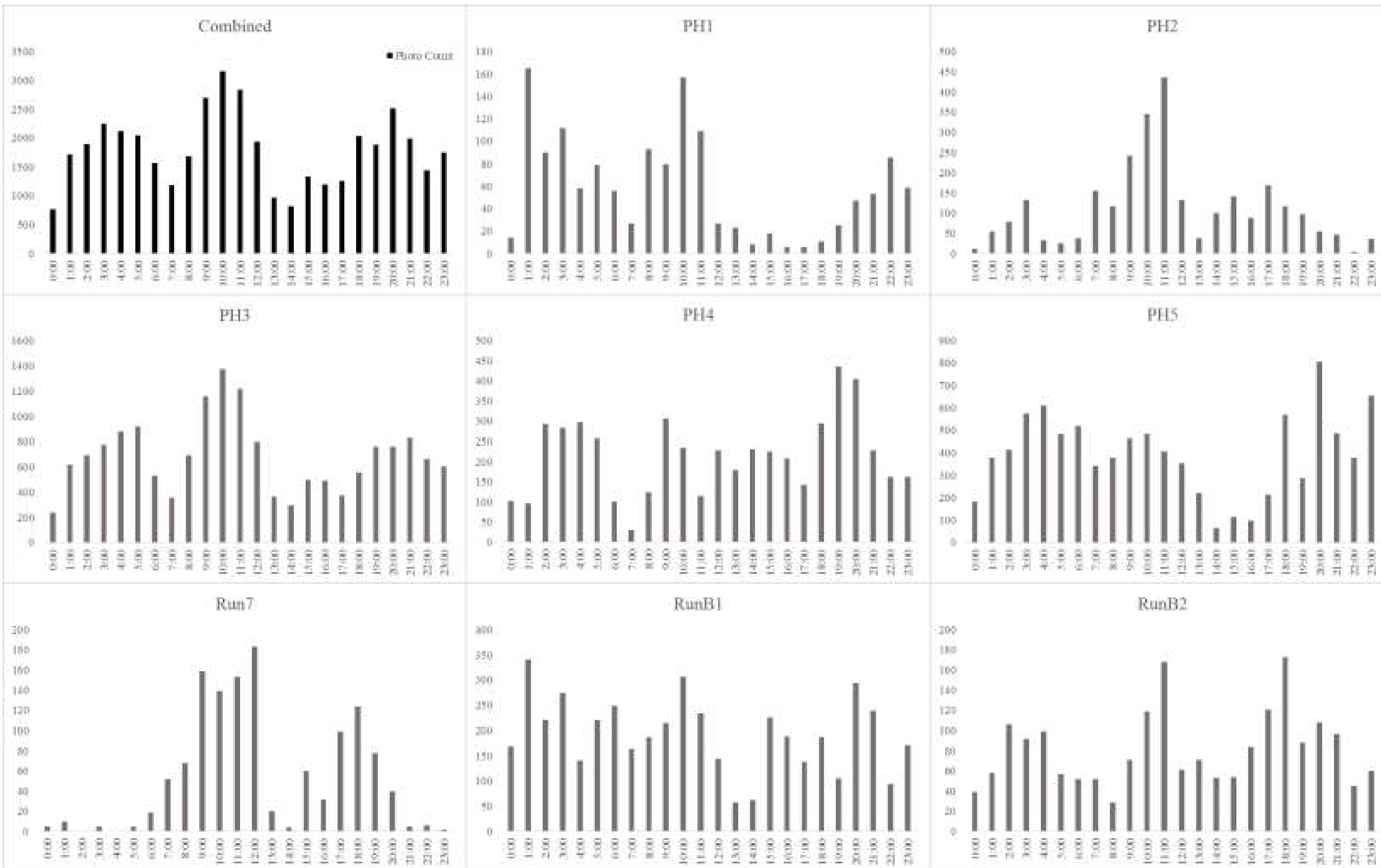

Figure 6. Riparian brush rabbit activity at individual stations based on the total number of RBR photos taken each hour.

Activity by Events

When photos were broken into events and compared with the combined photos there was a significant difference in time ($F_{1,46}$= 124.55, p < 0.05, Figure 7). After completing an ANOVA of the number of events occurring day, night, dawn, and dusk separately there was no difference between time periods ($F_{3,4}$= 0.44, p = 0.74, Figure 8, Table 7) and running the test with dawn and dusk combined had similar results ($F_{2,3}$= 0.19, p = 0.83, Table 8). The number of events recorded per hour varied between time periods with less recorded at dawn (78 e/hr) compared to day (172.5 e/hr), night (164.3 e/hr), and dusk (123.8 e/hr) (Figure 8).

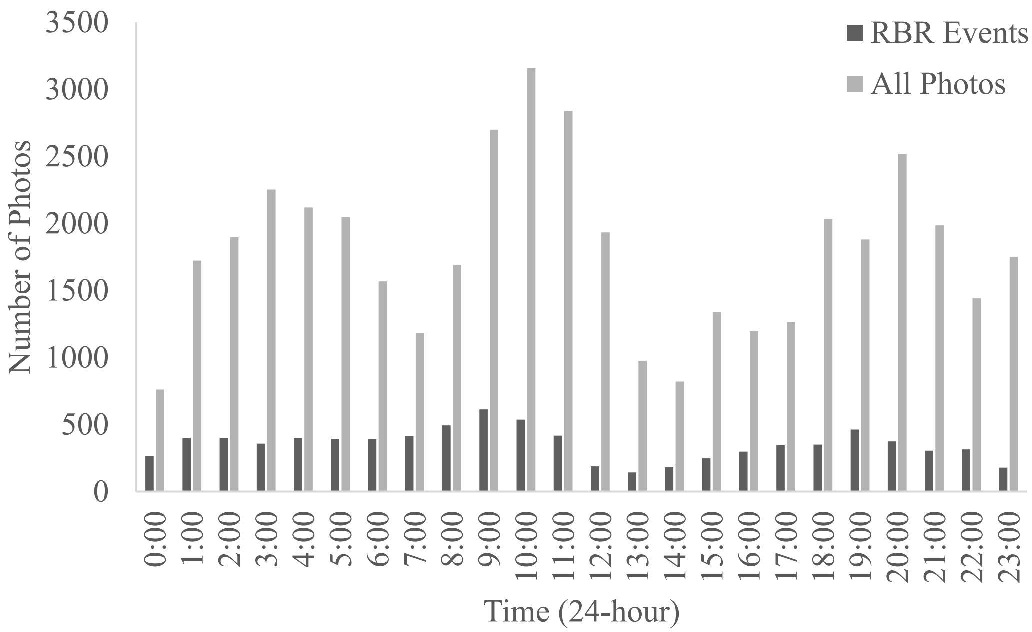

Figure 7. Difference in time distribution between events and all photos.

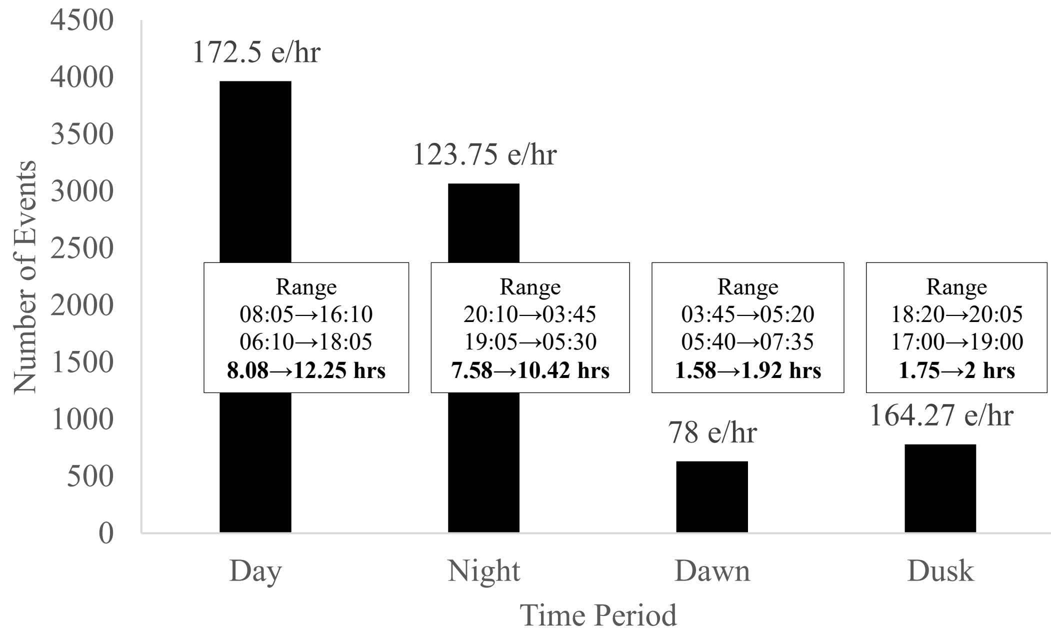

Figure 8. Riparian brush rabbit activity at different time periods with the number of events recorded per hour (e/hr).

Table 7. Results of single factor analysis of variance (ANOVA) for all time periods separately.

Summary

Groups	Count	Sum	Average	Variance
day	2	4,000	2,000	7,714,592
night	2	3,082	1,541	4,657,352
dawn	2	632	316	197,192
dusk	2	785	392.50	300,312.50

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	4,228,061.37	3	1,409,353.79	0.44	0.74	6.59
Within Groups	12,869,448.50	4	3,217,362.12	-	-	-
Total	17,097,509.88	7	-	-	-	-

Table 8. Results of single factor analysis of variance (ANOVA) between time periods with dawn and dusk combined into one group, crepuscular.

Summary

Groups	Count	Sum	Average	Variance
crepuscular	2	1,417	708.50	984,204.50
day	2	4,000	2,000	7,714,592
night	2	3,082	1,541	4,657,352

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	1,714,473	2	857,236.50	0.19	0.83	9.55
Within Groups	13,356,149	3	4,452,050	-	-	-
Total	15,070,622	5	-	-	-	-

Rest

Riparian brush rabbits were also photographed at rest in two different rest postures: sitting and lying down (Figure 9). Similar to what was seen for the total activity peaks at 10:00 and 20:00 (Figure 6), the RBR rest distribution had peaks at 11:00 and 20:00 (Figure 9). This similarity was also shared with PH2 and RunB2 (Figure 6). However, there were peaks for rest activity at other times as well, some of which correspond with the activity peaks in the elevated total activity (Figure 6, Figure 9). There was also similar trend between the activity and rest histograms at 7:00 and 13:00 where the number of photos was low. The rest and activity did differ significantly ($t(3) = -2.54$, $p = 0.045$) (Table 9, Table 10) yet the time similarity between rest and activity times was also present when rest was distributed across the four time periods: day, night, dawn, and dusk (Figure 10).

The two rest activities were not equally distributed; sitting was much more commonly recorded than lying down (238:61 photos) (Figure 9). Sitting had multiple peaks, the greatest at 11:00 and 14:00 followed by 20:00. Lying down was mostly recorded during day time periods, with the greatest number of occurrences between 10:00 and 12:00 and between 15:00 and 18:00.

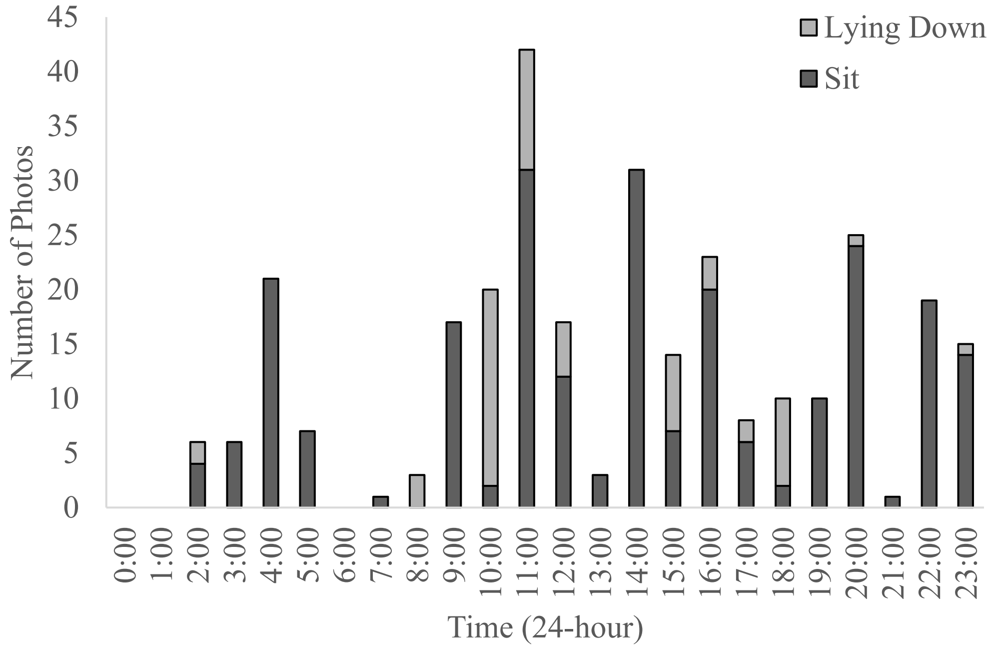

Figure 9. Distribution of the number of photographs with riparian brush rabbits at rest (rest and vigilance/rest tags) with proportions of rest positions (lie down, sit) of riparian brush rabbits recorded.

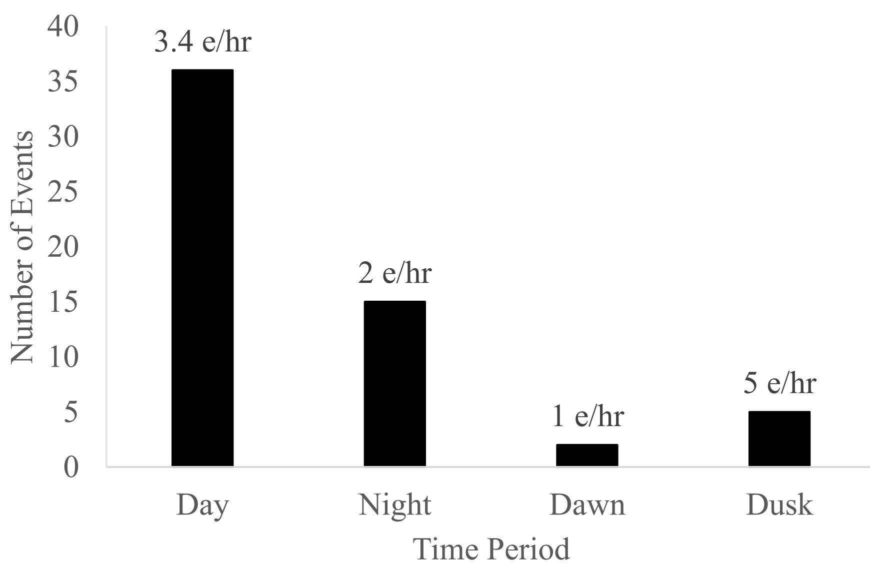

Figure 10. Riparian brush rabbit rest at different time periods with the average number of events recorded per hour (e/hr).

Table 9. *Results of single factor analysis of variance (ANOVA) between the number of times riparian brush rabbits were at rest and active in the grouped data.*

Summary

Groups	Count	Sum	Average	Variance
rest	4	58	14.5	236.33
active	4	8,441	2,110.25	2,770,821.58

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	8,784,336.13	1	8,784,336.13	6.34	0.045	5.99
Within Groups	8,313,173.75	6	1,385,528.96	-	-	-
Total	17,097,509.9	7	-	-	-	-

Table 10. *Results of t-Test of riparian brush rabbit rest and activity.*

t-Test: Paired Two Sample for Means

	rest	active
Mean	14.5	2,110
Variance	236.33	2,770,821.58
Observations	4	4
Pearson Correlation	0.93	-
Hypothesized Mean Difference	0	-
df	3	-
t Stat	-2.54	-
P(T<=t) one-tail	0.04	-
t Critical one-tail	2.35	-
P(T<=t) two-tail	0.08	-
t Critical two-tail	3.18	-

Vigilance

A concern with this project was whether the behavior vigilance would be better categorized as inactive like *rest*, rather than be included with activity calculations. To first examine this possibility the second dataset was reconfigured to remove times where RBR were recorded *vigilant* (Table 11). This new dataset was compared with the original with an ANOVA and found that there was no difference in variance whether vigilance was included or not ($F_{1,6}$ = 0.65, p = 0.45).

To explore the categorization of vigilance, the second dataset was re-categorized with vigilance and rest times binned together as 'inactive' and the other times were classified as 'active'. The number of events at each time period (day, night, dusk, and dawn) were added and compared. When compared with an ANOVA there was no difference between the inactive and active ($F_{1,6}$ = 0.73, p = 0.43, Table 12).

Table 11. Analysis of variance (ANOVA) between activity with and without the tag *vigilant*.

Summary

Groups	Count	Sum	Average	Variance
Activity w/o vigilant	4	5,289	1,322.25	1,064,030.25
Activity w/ vigilant	4	8,441	2,110.25	2,770,821.583

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	1,241,888	1	1,241,888	0.647684997	0.451644614	5.987377607
Within Groups	11,504,555.5	6	1,917,425.917	-	-	-
Total	12,746,443.5	7	-	-	-	-

Table 12. *Analysis of variance (ANOVA) between times RBR were inactive, resting or vigilant, and active.*

Summary

Groups	Count	Sum	Average	Variance
inactive	4	3,210	802.5	424,504.333
active	4	5,289	1,322.25	1,064,030.25

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	540,280.125	1	540,280.125	0.72592217	0.42690136	5.98737761
Within Groups	4,465,603.75	6	744,267.292	-	-	-
Total	5,005,883.88	7	-	-	-	-

Activity by Behavior Type

Riparian brush rabbit activity was also isolated by behavior type: inactive, consumptive, and reproductive. The behavior type 'inactive' includes conservative behaviors vigilant, rest, and vigilance/rest where RBR are expending less energy than other behaviors (Figure 11). Consumptive activity included photos of RBR feeding and foraging, expending energy to gain nutrients (Figure 12). Reproductive activity only included recordings of *mating* behaviors and not *nesting* due to the low recorded incidence of the behavior and its related behavior *carry* (Figure 13). When graphed, the inactive and consumptive behaviors reflected the trends of the total behavior of all photos (Figure 7), however, reproductive activity did not reflect other activity trends and was primarily captured at night.

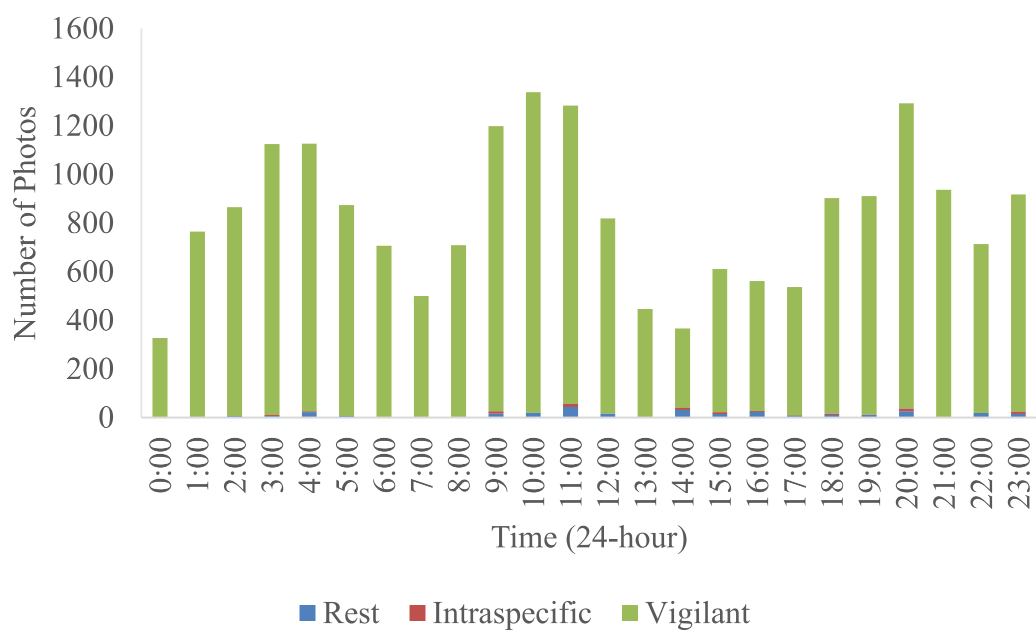

Figure 11. Number of photos of inactive behaviors taken each hour including *rest*, *vigilant*, and the intraspecific interaction *vigilance/rest*.

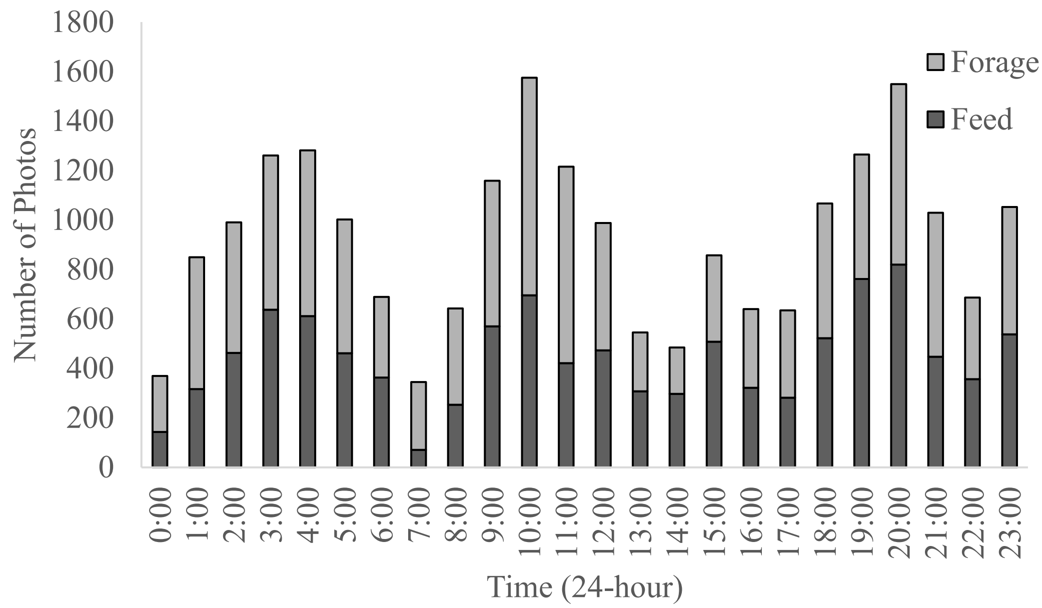

Figure 12. Number of photos of consumptive behaviors (*feed* and *forage*) collected distributed over 24 hours.

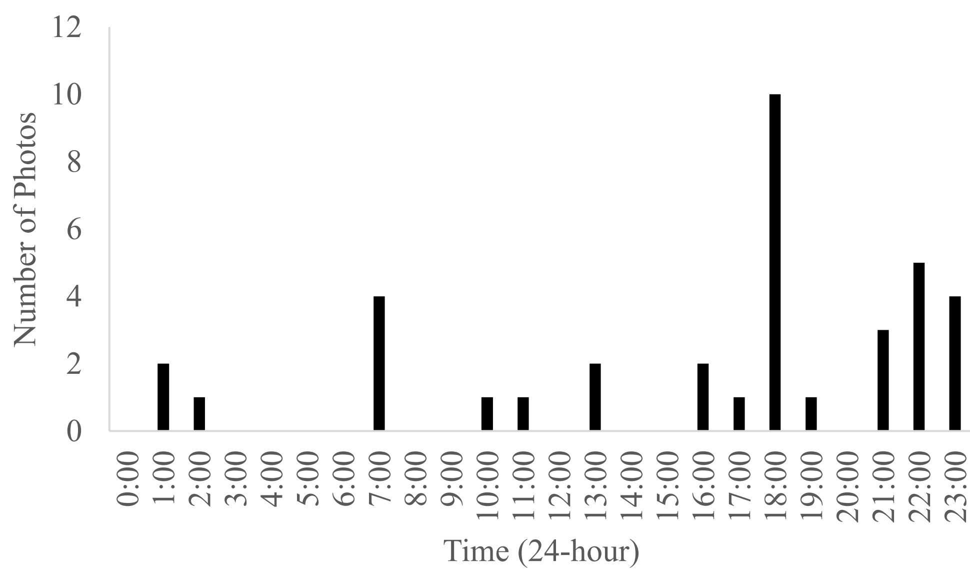

Figure 13. Number of photos of riparian brush rabbit *mating* behaviors distributed over 24 hours. Nesting behaviors were not included due to the low number of captures.

Riparian Brush Rabbit Activity by Site

Of the three site conditions (alfalfa, poison hemlock, runway), far more photos were recorded at the sites with alfalfa (72.34%) than the poison hemlock (9.51%) and runway (18.15%) sites (Figure 14). Sites with alfalfa (PH3, PH4, and PH5) had higher totals over all other types when combined with peaks that closely mirror total activity (Figure 6, Figure 14). Sites with poison hemlock (PH1 and PH2) and runways only (Run7, RunB1, and RunB2) had more similar numbers but slightly different peaks (Figure 14, Figure 15). When sites were separated by type, the runway sites show higher variance compared to the other site types (Figure 15, Figure 16).

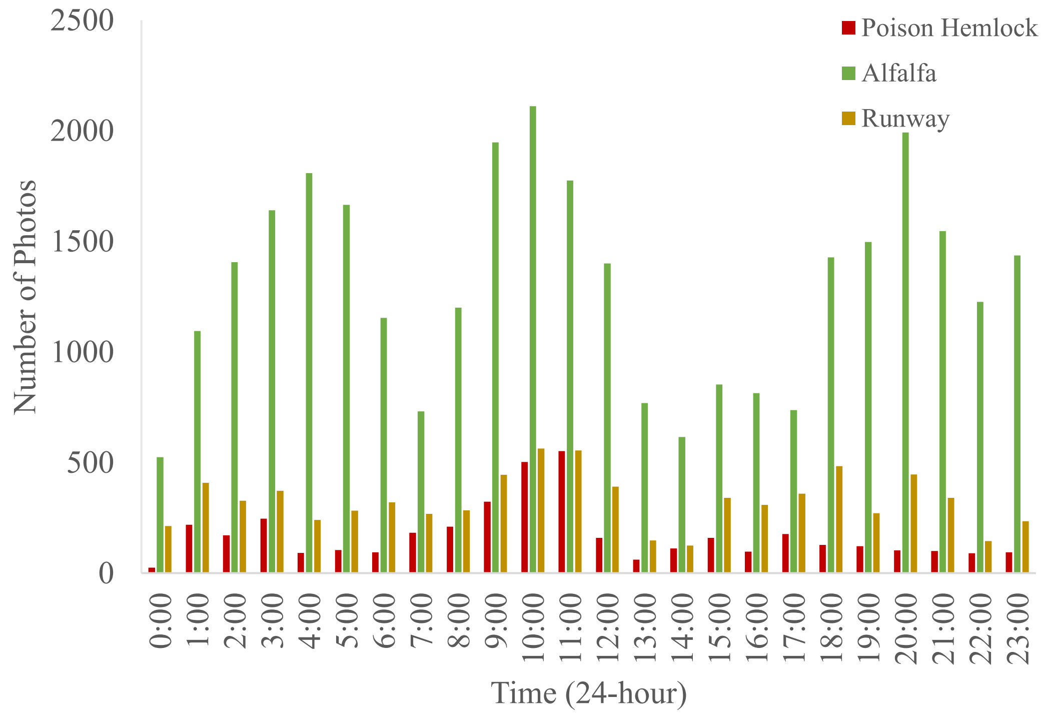

Figure 14. Riparian brush rabbit activity as measured by number of photos separated by hour and station type.

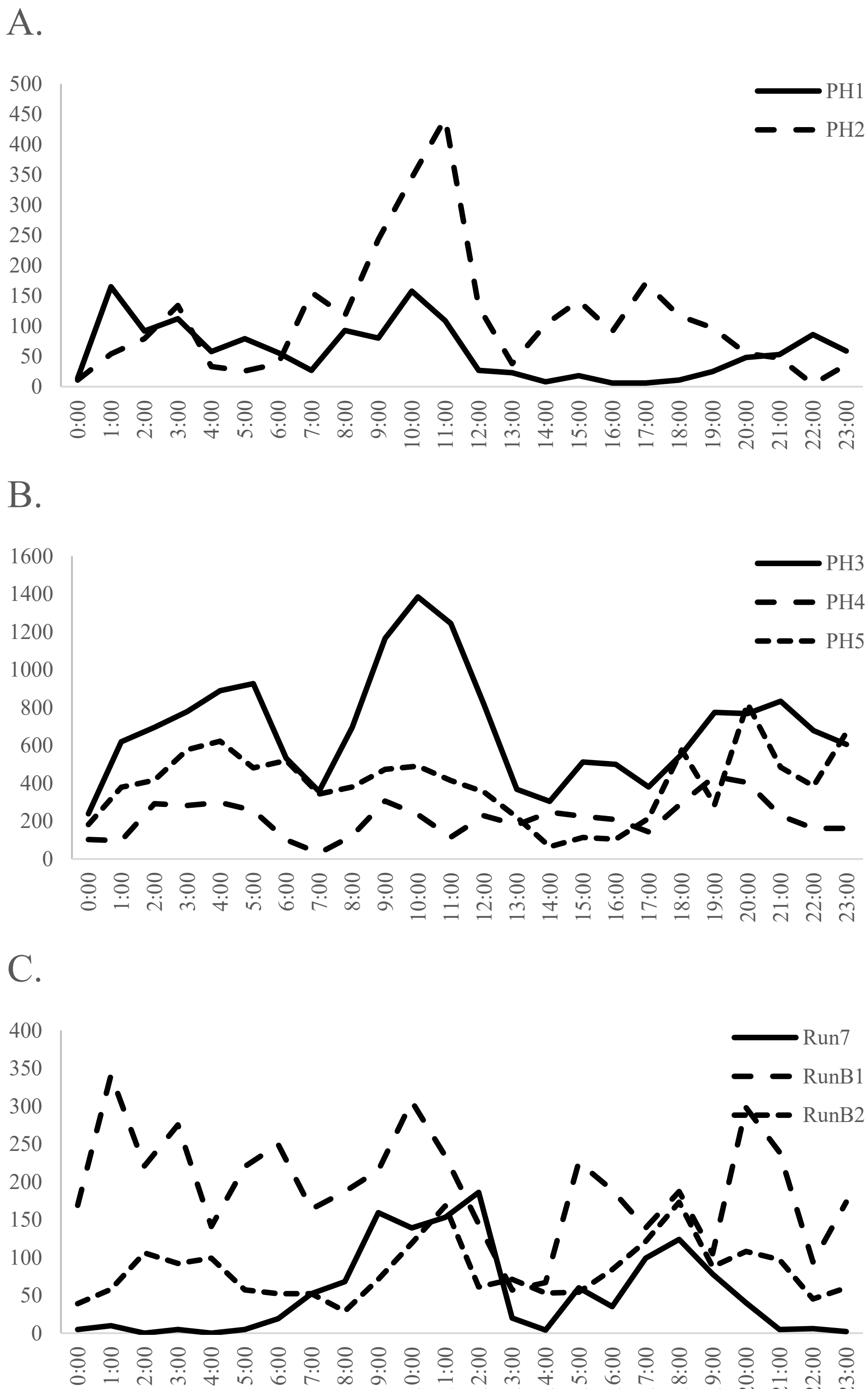

Figure 15. Riparian brush rabbit activity at different *s*ite types: poison hemlock (A), alfalfa (B), and runways (C).

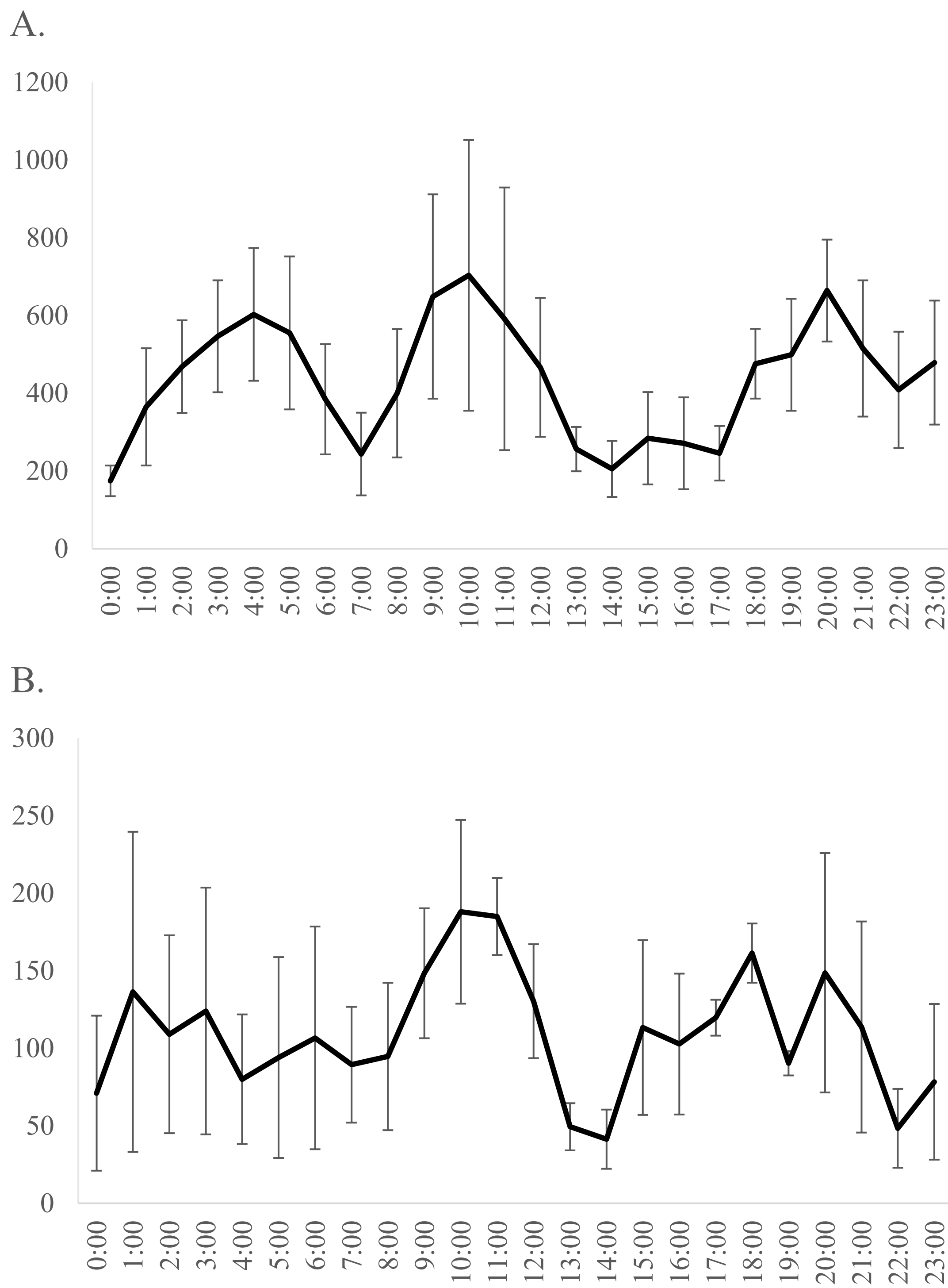

Figure 16. Average activity and standard error of different site types: alfalfa (A) and runways (B).

Riparian Brush Rabbit Community Ecology

Of the 105,777 photos collected, 68,909 photos recorded at least one animal present, a 65% capture success. Five functional groups were represented: lagomorphs, rodents, predators, birds, and reptiles (Table 13).

Table 13. *Number of photos recorded per species and proportion of tagged photos.*

Group	Species	Common Name	Photos	Percent
lagomorph	*Sylvilagus bachmani riparius*	Riparian Brush Rabbit	44,053	60.06%
	Sylvilagus audobonii	Desert Cottontail	14,946	20.38%
rodent	*Otospermophilus beecheyi*	California Ground Squirrel	2,042	2.78%
	Neotoma fuscipes riparia	Riparian Woodrat	345	0.47%
		Rodent sp.	252	0.34%
	Rattus rattus	Black Rat	243	0.33%
	Sciurus niger	Fox Squirrel	20	0.03%
predator	*Procyon lotor*	Raccoon	2,837	3.87%
	Canis latrans	Coyote	1,521	2.07%
	Didelphis virginiana	Opossum	324	0.44%
	Mephitis mephitis	Striped Skunk	163	0.22%
	Felis catus	Domestic Cat	66	0.09%
	Mustela frenata	Long-tailed Weasel	27	0.04%
	Homo sapien	Human	20	0.03%
	Neovison vison	American Mink	14	0.02%
	Canis familiaris	Domestic Dog	5	0.01%
	Tyto alba	Barn Owl	2	0.00%
	Pituophis catenifer	Gopher Snake	19	0.03%
bird	*Callipepla californica*	California Quail	2,775	3.78%
	Pipilo maculatus	Spotted Towhee	949	1.29%
		Unknown Sparrow	718	0.98%
	Toxostoma redivivum	California Thrasher	419	0.57%
		Unknown Thrush	275	0.37%
	Passerella iliaca	Fox Sparrow	270	0.37%
	Catharus guttatus	Hermit Thrush	269	0.37%
	Zonotrichia atricapilla	Golden-crowned Sparrow	230	0.31%
	Melozone crissalis	California Towhee	161	0.22%
	Zonotrichia leucophrys	White-crowned Sparrow	97	0.13%
	Fulica americana	American Coot	88	0.12%
	Aphelocoma californica	Scrub Jay	49	0.07%
	Nycticorax nycticorax	Black-crowned Night-Heron	35	0.05%
	Turdus migratorius	American Robin	29	0.04%
		Unknown Wren	20	0.03%
	Baeolophus inornatus	Oak Titmouse	15	0.02%
	Chamaea fasciata	Wrentit	10	0.01%

	Sayornis saya	Say's Phoebe	9	0.01%
	Passerculus sandwichensis	Savannah Sparrow	6	0.01%
	Geothlypis trichas	Common Yellowthroat	5	0.01%
	Zenaida macroura	Mourning Dove	5	0.01%
	Thryomanes bewickii	Bewick's Wren	4	0.01%
	Cistothorus palustris	Marsh Wren	1	0.00%
reptile	*Sceloporus occidentalis*	Western Fence Lizard	10	0.01%

Riparian Brush Rabbit Presence

Of the 68,909 tagged photos, 44,053 photos included RBR (63.93%). Most of the RBR photos (69.58%) contained only one RBR present followed by photos with two RBR (14.41%). Photos with more than three RBR present were all collected at alfalfa sites PH3, PH4, and PH5 (Table 14).

Table 14. *Number of photos with different numbers of riparian brush rabbit co-occurring per site.*

# RBR	Total	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2
1	30,654	1,363	2,579	11,190	1,424	6,380	1,254	4,548	1,916
2	6,347	83	132	2,671	1,661	1,517	35	177	71
3	3,647	0	7	1,680	1,197	763	0	0	0
4	1,915	0	0	857	585	473	0	0	0
5	937	0	0	359	251	327	0	0	0
6	387	0	0	97	91	199	0	0	0
7	124	0	0	2	18	104	0	0	0
8	35	0	0	0	4	31	0	0	0
9	6	0	0	0	2	4	0	0	0
10	1	0	0	0	0	1	0	0	0
Total	44,053	1,446	2,718	16,856	5,233	9,799	1,289	4,725	1,987

Riparian Brush Rabbit Utilization of Habitat

Riparian brush rabbits were recorded interacting with seven different plant species and four different plant material types (Table 15, Table 40).

Native Plant Interactions

Riparian brush rabbits interacted with five native plant species (black willow, blue elderberry, California blackberry, California rose, and coyote brush) in PH2, PH3, PH4, Run7, RunB1, and RunB2 (Table 15). Direct interactions included feeding, carrying, smelling, marking, and climbing. Feeding interactions included browsing live vegetation and eating fallen leaves including California rose and black willow, *Salix gooddingii*. In 73 photos, RBR were documented carrying bundles of fallen sticks from coyote brush (*Baccharis pilularis*) and California rose. Also, RBR were photographed chin-marking low branches of coyote brush at PH3 and of blue elderberry (*Sambucus nigra caerulea*) at PH2. Additionally, RBR were photographed climbing coyote brush on two separate occasions at PH3, once at PH4, and on two separate occasions at RunB2; this was also directly observed for quail bush (*Atriplex lentiformis*) during live observation. Riparian brush rabbits were also photographed climbing low growing California rose and blackberry in single events at RunB1 and PH2.

Alfalfa Interactions

Riparian brush rabbits were primarily recorded feeding on alfalfa during the study (Table 15). However, despite the high usage, not all alfalfa was consumed as some remained at sites PH4 and PH5 after June when RBR visitation declined.

Riparian brush rabbits were documented in 413 photos climbing alfalfa bales to feed from the top of the pile, at times staying on the top of the bale to feed instead of feeding from the sides. An RBR was also recorded collecting nesting material at PH5 where alfalfa was present, possibly collecting alfalfa as a substitute for grass, the standard nesting material (Larsen 1993).

Poison Hemlock Interactions

There were 177 photos of riparian brush rabbits interacting with invasive poison hemlock. These interactions included feeding, smelling, and carrying small bundles of poison hemlock at sites PH1, PH2, PH3, and PH4. In one event, an RBR chin-marked poison hemlock at PH3.

Table 15. *Count of photos with each vegetation tag.*

Tag Name	Species	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2	Total
alfalfa	*Medicago sativa*	-	-	4,730	3,540	2,226	-	-	-	10,496
black willow	*Salix gooddingii*	-	-	-	-	-	11	-	-	11
blue elderberry	*Sambucus nigra caerulea*	-	4	-	-	-	-	-	-	4
bundle		-	4	-	-	64	-	-	5	73
CA blackberry	*Rubus ursinus*	-	8	-	-	-	37	-	-	45
CA rose	*Rosa california*	-	-	-	-	-	-	31	-	31
coyote brush	*Baccharis pilularis*	-	-	16	3	-	-	-	9	28
leaf		-	-	-	-	-	-	11	-	11
poison hemlock	*Conium maculatum*	33	21	108	15	-	-	-	-	177
twig		-	-	-	-	-	-	6	-	6
willow	*Salix* species	-	-	-	-	-	16	5	-	21

Riparian Brush Rabbit Behavior Types

Documented RBR behaviors were predominately individual, but at sites PH3, PH4, and PH5, higher frequencies of intraspecific and interspecific behaviors were recorded. Individual behaviors represented over half (64.29%) of all behaviors recorded, followed by intraspecific behaviors (29.78%). In comparison, interspecific behaviors were captured only 6% of the time (Table 16). The variance between the three was not equal ($F_{2,21}$ = 3.89, p = 0.037, Table 17). There was not a significant difference between individual and intraspecific behaviors (two-tailed $t(7)$ = 2.18, p = 0.066, Table 18) or intraspecific and interspecific interactions (two-tailed $t(7)$ = 2.06, p = 0.079, Table 19), however, there was a significant difference between individual and interspecific behaviors (two-tailed $t(7)$ = 2.91, Table 20, p = 0.022, Table 21).

Table 16. *Number of behavior types and individual riparian brush rabbit recordings across sites with proportion calculated as a percentage.*

	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2	Percentage
Individual	1,370	2,563	10,483	591	5,693	1,262	4,518	1,752	64.29%
Intraspecific	57	137	5,505	3,750	3,349	27	173	81	29.78%
Interspecific	19	18	870	890	758	0	34	13	5.93%

Table 17. *Results of single factor analysis of variance (ANOVA) comparing the numbers of individual, intraspecific, and interspecific behaviors.*

Summary

Groups	Count	Sum	Average	Variance
Individual	8	2,8232	3,529	10,934,633
Intraspecific	8	13,079	1,634.875	4,894,290
Interspecific	8	2,602	325.25	182,753.4

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	41,511,577	2	20,755,788	3.888872	0.036577	3.4668
Within Groups	1.12E+08	21	5,337,226	-	-	-
Total	1.54E+08	23	-	-	-	-

Table 18. *Results of t-Test comparing the means of individual and intraspecific behaviors of riparian brush rabbits.*

t-Test: Paired Two Sample for Means

	Individual	Intraspecific
Mean	3,529	1,634.875
Variance	10,934,633.14	4,894,290.41
Observations	8	8
Pearson Correlation	0.66828395	-
Hypothesized Mean Difference	0	-
df	7	-
t Stat	2.177875637	-
P(T<=t) one-tail	0.032923454	-
t Critical one-tail	1.894578605	-
P(T<=t) two-tail	0.065846909	-
t Critical two-tail	2.364624252	-

Table 19. *Results of t-Test comparing means of intraspecific and interspecific interactions.*

t-Test: Paired Two Sample for Means

	Intraspecific	Interspecific
Mean	1,634.88	325.25
Variance	4,894,290.41	182,753.36
Observations	8	8
Pearson Correlation	0.970040937	-
Hypothesized Mean Difference	0	-
df	7	-
t Stat	2.057176857	-
P(T<=t) one-tail	0.039346174	-
t Critical one-tail	1.894578605	-
P(T<=t) two-tail	0.078692348	-
t Critical two-tail	2.364624252	-

Table 20. *Results of t-Test comparing the means of individual and interspecific behaviors of riparian brush rabbits.*

t-Test: Paired Two Sample for Means

	Individual	Interspecific
Mean	3,529	325.25
Variance	10,934,633.14	182,753.3571
Observations	8	8
Pearson Correlation	0.508073859	-
Hypothesized Mean Difference	0	-
df	7	-
t Stat	2.912359683	-
P(T<=t) one-tail	0.011292238	-
t Critical one-tail	1.894578605	-
P(T<=t) two-tail	0.022584476	-
t Critical two-tail	2.364624252	-

Table 21. *Results of Tukey's honest significant difference test comparing means.*

Tukey's Honest Significant Difference (HSD) Test	Results
HSD[.05]	2,911.51
HSD[.01]	3,773.29
Individual vs Intraspecific	nonsignificant
Individual vs Interspecific	$p < 0.05$
Intraspecific vs Interspecific	nonsignificant

Riparian Brush Rabbit Interspecific Interaction

There were 2,296 photos of RBR and other species co-occurring without interaction, referred to as allospecific. Of this total, the alfalfa supplemented sites (i.e. PH3, PH4, and PH5) had more allospecific occurrences ($n \geq 330$) than the other site types ($n \leq 61$). These sites also had the highest numbers of interspecific interactions (Table 22). Despite the differences between sites, there was not a significant difference ($t(7) = -0.68$, $p = 0.26$) between the number of allospecific and interspecific interactions (Table 23).

The number of instances of interspecific and allospecific co-occurrence was different among species (Table 24). Comprising 82% of all co-occurrences, desert cottontails were far more likely than any other species to be photographed with RBR. The desert cottontail was followed by the California quail (*Callipepla californica*) and California ground squirrel (*Otospermophilus beecheyi*). These were followed by granivorous passerine birds spotted towhee (*Pipilo maculatus*) and various sparrows. All of these species, as well as California towhee (*Melozone crissalis*) and golden-crowned sparrow (*Zonotrichia atricapilla*), had higher co-occurrences at PH3, PH4, and PH5 (Table 25). Likewise, many other species had higher co-occurrences at the alfalfa supplemented sites PH3, PH4, and PH5. The other endangered riparian specialist, the riparian woodrat (*Neotoma fuscipes riparia*), had higher co-occurrence in PH3 whereas other native rodents were recorded most at both PH3 and PH1.

Table 22. *Number of photos with riparian brush rabbits and another species co-occurring (Allospecific) and the number of photos with an interspecific interaction.*

	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2	Total
Allospecific	44	60	852	889	330	14	50	57	2,296
Interspecific	19	18	870	890	758	0	34	13	2,602

Table 23. *Results of t-Test comparing the means of allospecific and interspecific riparian brush rabbit photos.*

t-Test: Paired Two Sample for Means

	Allospecific	Interspecific
Mean	287	325.25
Variance	139,664.8571	182,753.3571
Observations	8	8
Pearson Correlation	0.930103511	-
Hypothesized Mean Difference	0	-
df	7	-
t Stat	-0.681165827	-
P(T<=t) one-tail	0.25882935	-
t Critical one-tail	1.894578605	-
P(T<=t) two-tail	0.517658699	-
t Critical two-tail	2.364624252	-

Table 24. *Number of total photos and percentage of riparian brush rabbits co-occurring with other species from highest to lowest number of photos.*

Common Name	Species	Total	Percentage
Desert Cottontail	*Sylvilagus audobonii*	4,032	77.06%
California Quail	*Callipepla californica*	255	4.87%
California Ground Squirrel	*Otospermophilus beecheyi*	217	4.15%
Unknown Sparrow	-	168	3.21%
Spotted Towhee	*Pipilo maculatus*	145	2.77%
Fox Sparrow	*Passerella iliaca*	67	1.28%
California Thrasher	*Toxostoma redivivum*	54	1.03%
California Towhee	*Melozone crissalis*	50	0.96%
Golden-crowned Sparrow	*Zonotrichia atricapilla*	37	0.71%
Unknown Thrush	-	36	0.69%
Riparian Woodrat	*Neotoma fuscipes riparia*	34	0.65%
Unknown Mouse	-	33	0.63%
Hermit Thrush	*Catharus guttatus*	31	0.59%
American Coot	*Fulica americana*	16	0.31%
Black Rat	*Rattus rattus*	15	0.29%
White-crowned Sparrow	*Zonotrichia leucophrys*	12	0.23%
Human	*Homo sapien*	10	0.19%
Coyote	*Canis latrans*	6	0.11%
Common Yellowthroat	*Geothlypis trichas*	5	0.10%
Scrub Jay	*Aphelocoma californica*	4	0.08%
Long-tailed Weasel	*Mustela frenata*	2	0.04%
Domestic Dog	*Canis familiaris*	1	0.02%
Marsh Wren	*Cistothorus palustris*	1	0.02%
Unknown Wren	-	1	0.02%

Table 25. *Number of photos at each site of riparian brush rabbits co-occurring with other species from highest to lowest number of photos.*

Common Name	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2
Desert Cottontail	9	52	1,408	1,595	927	3	36	2
California Quail	6	3	101	76	33	11	18	7
California Ground Squirrel	0	0	55	109	53	0	0	0
unknown Sparrow	0	3	96	33	14	0	4	18
Spotted Towhee	0	20	84	17	24	0	0	0
Fox Sparrow	0	0	53	4	0	0	1	9
California Thrasher	1	2	2	1	9	0	19	20
California Towhee	0	0	9	5	36	0	0	0
Golden-crowned Sparrow	0	0	15	16	2	0	3	1
unknown Thrush	0	0	13	4	0	0	5	14
Riparian Woodrat	5	0	18	0	3	0	3	5
unknown Mouse	11	0	17	0	5	0	0	0
Hermit Thrush	0	0	13	4	0	0	5	9
American Coot	16	0	0	0	0	0	0	0
Black Rat	15	0	0	0	0	0	0	0
White-crowned Sparrow	0	0	9	0	0	0	0	3
Human	0	0	0	10	0	0	0	0
Coyote	0	0	0	0	6	0	0	0
Common Yellowthroat	0	0	0	5	0	0	0	0
Scrub Jay	0	0	0	0	2	0	0	2
Long-tailed Weasel	0	0	0	2	0	0	0	0
Domestic Dog	0	0	0	1	0	0	0	0
Marsh Wren	0	0	1	0	0	0	0	0
unknown Wren	0	0	1	0	0	0	0	0

When examining RBR interspecific interactions with specific species types there were no negative or amicable interactions with potential beneficial species California quail and few interactions with competitors (63) and predators (3). There were no amicable interactions with predatory species. Riparian brush rabbits were mainly captured interacting with their competitors: desert cottontails and California ground squirrels (Table 26). The variance between the negative and amicable interactions was not significantly different ($F_{1,4}$= 0.14, p = 0.73, Table 27). When analyzing the variance by species type there was a significant difference between beneficial and competitor species interactions ($F_{2,3}$= 19.09, p = 0.02, Table 28, p < 0.01, Table 30) and there was a significant difference between competitor and predator interactions (two-tailed $t(5)$ = 2.87, p = 0.035, Table 29, p < 0.01, Table 30). There was no significant difference between RBR interactions with beneficial and predatory species (Table 30).

Table 26. *Number of photos of negative and amicable interaction between riparian brush rabbits and beneficial (CA quail), competitor (desert cottontails and CA ground squirrels) and predatory species.*

	Negative				Amicable	
	Aggression	Chase	Flight	Predation	Rest	Smell
Beneficial	0	0	0	0	0	0
Competitor	6	10	23	0	18	7
Predator	0	0	1	2	0	0

Table 27. *Results of single factor analysis of variance (ANOVA) comparing amicable and negative interspecific interactions.*

Summary

Groups	Count	Sum	Average	Variance
Negative	3	42	14	471
Amicable	3	25	8.33	208.33

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	48.17	1	48.17	0.14	0.73	7.71
Within Groups	1,358.67	4	339.67	-	-	-
Total	1,406.83	5	-	-	-	-

Table 28. *Results of single factor analysis of variance (ANOVA) comparing riparian brush rabbit interspecific interactions with beneficial, competitor, and predatory species.*

Summary

Groups	Count	Sum	Average	Variance
Beneficial	2	0	0	0
Competitor	2	64	32	98
Predator	2	3	1.50	4.50

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	1,304.33	2	652.17	19.09	0.0196	9.55
Within Groups	102.50	3	34.17	-	-	-
Total	1,406.83	5	-	-	-	-

Table 29. *Results of t-Test comparing the means of riparian brush rabbit interactions with competitors and predators.*

t-Test: Paired Two Sample for Means

	Competitor	Predator
Mean	10.67	0.5
Variance	71.07	0.7
Observations	6	6
Pearson Correlation	-0.26	-
Hypothesized Mean Difference	0	-
df	5	-
t Stat	2.87	-
P(T<=t) one-tail	0.018	-
t Critical one-tail	2.015	-
P(T<=t) two-tail	0.035	-
t Critical two-tail	2.57	-

Table 30. *Results of Tukey's honest significant difference test of the means of the species types.*

Tukey's Honest Significant Difference (HSD) Test	Results
HSD[.05]	7.35
HSD[.01]	9.67
Beneficial vs Competitor	$p < 0.01$
Beneficial vs Predator	Nonsignificant
Competitor vs Predator	$p < 0.01$

Documented Animals

A total of 38 animal species were recorded during this study.

Mammals

Thirteen different mammal species were photographed, including 1 marsupial, 2 lagomorphs, 4 rodents, and 5 carnivores.

Lagomorphs. The riparian brush rabbit was the most documented species with a total of 44,053 out of 68,909 photographs taken that included an animal. The desert cottontail was the second most documented species with 14,946 photos (Table 13). Black-tailed jackrabbits (*Lepus californicus*), which are also present on SJRNWR, were not recorded in this study. The ratio of RBR to desert cottontails (52.27%:17.73%) was similar to the proportion documented in refuge levee surveys during the flood (40-70%: 20-40%) (Heffernan and Takahashi 2017).

Six different types of interspecific interactions between the two lagomorph species were recorded. Vigilance was the most recorded interspecific behavior (96.08%), the other five were rare ($n \leq 1.21\%$) in comparison (Table 31).

Table 31. *Interspecific interactions between riparian brush rabbits and desert cottontails.*

Behavior	Number of Photos	Percentage
vigilant	2,232	96.08%
rest	28	1.21%
chase	27	1.16%
flight	24	1.03%
smell	7	0.30%
aggression	5	0.22%

Rodents. Four rodent species were recorded among the sites, most notably the endangered riparian woodrat at PH1, PH3, PH5, Run7, RunB1, and RunB2. The non-native fox squirrel (*Sciurus niger*) was photographed at Run7 and RunB1, but the native western gray squirrel (*Sciurus griseus*), which is also present on the refuge, was not recorded at all.

Predators

There were six native predatory mammals recorded during the study: coyote (*Canis latrans*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), long-tailed weasel (*Mustela frenata*), American mink (*Neovison vison*), and Virginia opossum (*Didelphis virginiana*). Co-occurrence of RBR and these species was rare ($n \leq 0.11\%$). Direct interaction included predation by coyote, where coyotes were photographed carrying dead RBR through the site. There was also indirect predatory interactions recorded, where after a RBR left the photo area, a coyote was immediately photographed following the same path. The only documented RBR interspecific interaction with smaller predators was vigilance as a long-tailed weasel moved through the site.

Coyotes maintained a consistent presence at sites, with possibly different groups as territorial behaviors like marking and defecating were photographed at PH4. Raccoons were mainly documented at PH1, often excavating the inundated shore for food, altering the shoreline. Observations of predatory birds were limited to one occasion where a barn owl (*Tyto alba*) was recorded at site PH1 at night where no RBR or other prey were documented. A gopher snake (*Pituophis catenifer*) was photographed at PH5 while it was being inspected by a desert cottontail. The sequence involved 19 photos without the snake moving in or out of the camera area.

The rest of the predatory species photographed were domestic species: feral cats (*Felis catus*) and pet dogs. It should be noted that the refuge personnel were trapping feral dogs on the levee during the study; however, all dogs photographed were pets, identified by presence of a collar and for one individual, an adjacent human. Humans were only recorded on refuge trails in PH2 and PH4, the photographs at PH2 were of trespassers on a trail that is closed to the general public. Despite the trespassing and off-leash dogs, no harassment of RBR or other species was observed. The closest recording of any impact was an RBR fleeing as an off-leash dog went towards the alfalfa pile it was feeding on. Otherwise there were very few co-occurrences of RBR and these recreation-related species.

Birds

At least 20 bird species were photographed. Most photographed birds were passerine species where 17 species were identified. However, the most photographed species was the California quail (*Callipepla californica*). There was only one species of waterfowl (American coot, *Fulica americana*) photographed and one species of wading bird (black-crowned night-heron, *Nycticorax nycticorax*), both at PH1 when there was water present in the camera area.

Reptiles

Similar to the gopher snake, a western fence lizard (*Sceloporus occidentalis*) was documented at PH2 in ten consecutive photos over 17 minutes where the lizard only moved slightly.

Extent of Habitat Use

Twenty-four RBR behaviors were documented at all sites during this study, including individual, intraspecific, and interspecific behaviors. The frequency of each behavior photographed varied between sites, but *forage* and *vigilant* were the highest cataloged across sites (315-3,844 and 483-7,656 photos, Table 32). Behaviors were not evenly performed across sites, with some behaviors such as *drink* and *predation* being recorded exclusively at a single site (Table 33). Behaviors that were recorded at all sites were recorded more at certain sites: for instance, 44.6% of photos for *feed* were recorded at a single station, PH3 (Table 34).

Table 32. *Total count of behaviors collected and behavior percentage arranged by category from highest to lowest.*

Behavior Categories	Behavior	Total Count	Percentage
Exploratory	vigilant	19,712	35.87%
	forage	11,770	21.42%
Consumption	feed	10,804	19.66%
Movement	travel	3,667	6.67%
	dash	3,529	6.42%
Care	groom	1,755	3.19%
	rest	299	0.54%
	defecation	13	0.02%
	dust bath	12	0.02%
	drink	9	0.02%
Consumption, Exploratory	climb	1,636	2.98%
	stand	195	0.35%
Exploratory, Social, Interspecific	smell	771	1.40%
Social, Interspecific	chase	332	0.60%
Social	agonistic	121	0.22%
	nose touch	43	0.08%
	mark	39	0.07%
Reproductive	carry	87	0.16%
	mating	37	0.07%
Care, Social	vigilance/rest	82	0.15%
	urinate	1	0.00%
Interspecific	flight	25	0.05%
	aggression	6	0.01%
	predation	6	0.01%

Table 33. *Count of photos of each behavior tag among sites.*

Behavior	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2
aggression	0	0	3	2	1	0	0	0
agonistic	4	1	57	16	40	0	2	1
carry	0	4	3	6	65	0	4	5
chase	2	10	150	59	81	0	15	15
climb	0	8	4	416	1,196	0	2	10
dash	117	171	1,186	651	1,035	38	219	112
defecation	0	0	3	0	8	0	1	1
drink	9	0	0	0	0	0	0	0
dust bath	0	0	0	0	12	0	0	0
feed	32	24	4,823	3,545	2,231	53	91	5
flight	0	1	16	4	3	0	1	0
forage	520	742	3,844	1,370	2,118	315	2,186	675
groom	15	93	642	23	873	52	32	25
mark	0	9	23	0	0	0	6	1
mating	0	0	8	2	7	0	11	9
nose touch	3	1	23	3	11	0	2	0
predation	0	0	0	0	6	0	0	0
rest	4	15	140	19	105	6	10	0
smell	43	76	295	12	84	61	175	25
stand	0	14	13	68	10	41	44	5
travel	171	310	1,472	144	735	87	460	288
urinate	0	0	1	0	0	0	0	0
vigilance/rest	0	0	32	10	40	0	0	0
vigilant	483	979	7,656	2,954	5,228	600	1,235	577

Table 34. *Percentage of separate behavior tags represented at each site.*

Behavior	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2
aggression	0	0	50.00	33.33	16.67	0	0	0
agonistic	3.31	0.83	47.11	13.22	33.06	0	1.65	0.83
carry	0	4.60	3.45	6.90	74.71	0	4.60	5.75
chase	0.60	3.01	45.18	17.77	24.40	0	4.52	4.52
climb	0	0.49	0.24	25.43	73.11	0	0.12	0.61
dash	3.32	4.85	33.61	18.45	29.33	1.08	6.21	3.17
defecation	0	0	23.08	0	61.54	0	7.69	7.69
drink	100	0	0	0	0	0	0	0
dust bath	0	0	0	0	100	0	0	0
feed	0.30	0.22	44.64	32.81	20.65	0.49	0.84	0.05
flight	0	4.00	64.00	16.00	12.00	0	4.00	0
forage	4.42	6.30	32.66	11.64	17.99	2.68	18.57	5.73
groom	0.85	5.30	36.58	1.31	49.74	2.96	1.82	1.42
mark	0	23.08	58.97	0	0	0	15.38	2.56
mating	0	0	21.62	5.41	18.92	0	29.73	24.32
nose touch	6.98	2.33	53.49	6.98	25.58	0	4.65	0
predation	0	0	0	0	100	0	0	0
rest	1.34	5.02	46.82	6.35	35.12	2.01	3.34	0
smell	5.58	9.86	38.26	1.56	10.89	7.91	22.70	3.24
stand	0	7.18	6.67	34.87	5.13	21.03	22.56	2.56
travel	4.66	8.45	40.14	3.93	20.04	2.37	12.54	7.85
urinate	0	0	100	0	0	0	0	0
vigilance/rest	0	0	39.02	12.20	48.78	0	0	0
vigilant	2.45	4.97	38.84	14.99	26.52	3.04	6.27	2.93

Vegetation

Plant Community Composition

Camera photos were clear enough to identify plants. Foliage changed during the seasons as denuded vegetation recovered and leaves regrew in RBR forage areas (Figure 17**Error! Reference source not found.**). Riparian brush rabbits were recorded interacting with alfalfa (*Medicago sativa*), black willow (*Salix goodingii*), California blackberry (*Rubus ursinus*), California rose (*Rosa californica*), poison hemlock (*Conium maculatum*), coyote brush (*Baccharis pilularis*), and blue elderberry (*Sambucus nigra cerulea*), and an unidentified willow species (*Salix* sp.). Riparian brush rabbits were not recorded interacting with other plants that were evident in the photographs (e.g., elderberry sprouts and moss).

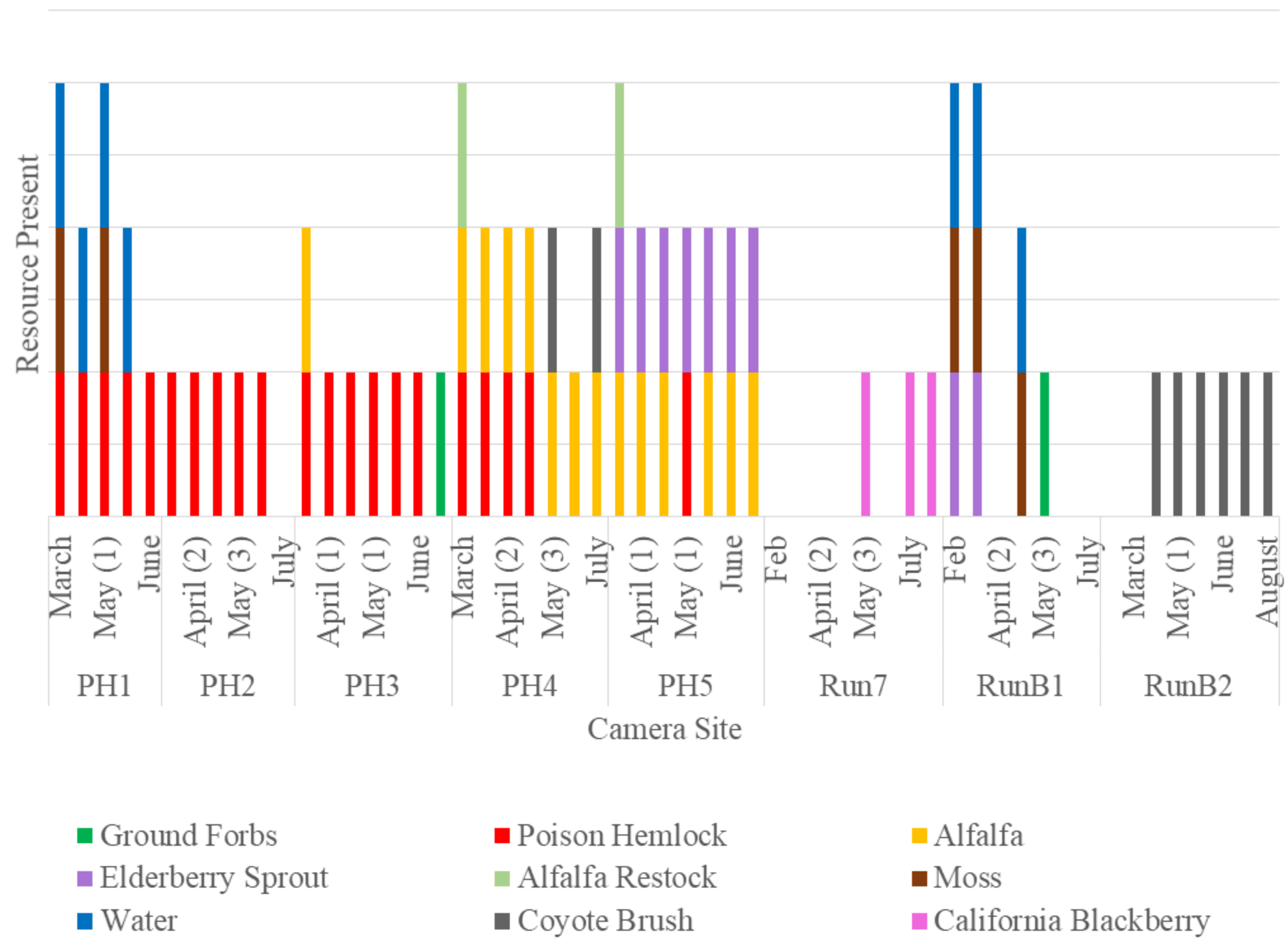

Figure 17. Available resources visible in photos that were accessible to riparian brush rabbits each month (February to August).

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Vegetation Density and Dominance

The vegetation transect survey yielded eleven species and three unidentified guilds (moss, annual grass, unknown forb), including residual alfalfa (Table 35). Of the live plants, six species are known food sources for RBR on the refuge. Two species, perennial pepperweed (*Lepidium latifolium*) and residual poison hemlock, are invasive and, in the case of poison hemlock, toxic. When all site totals are combined the dominant canopy species are two brush species, coyote brush (48.80%) and blue elderberry (22.44%), followed by two scandent species, California rose (12.65%) and California blackberry (9.03%). In the forage area, coyote brush and California blackberry were also dominant. Ground cover was dominated by litter (80.94%) (Table 35).

Three different plant alliances were represented in the project area, all were shrubland alliances (Table 36). Based on the transect surveys, sites PH1, PH3, PH4, PH5, RunB1, and RunB2 were classified *Baccharis pilularis* Shrubland Alliance. Both sites PH1 and RunB2 had California rose as a co-dominant species with the coyote brush (Table 36, Table 37). Blue elderberry was co-dominant in PH5 and RunB1. Coyote brush was only co-dominant at PH2 where blue elderberry was dominant. Run7 was the only site not dominated by large woody shrub species.

Table 35. *Total number of recordings of plant species intercepted in three different cover categories. Percentage calculated based on total for location.*

Location	Environmental Variable	Plant Species	Total	Percentage
Canopy	Black Willow	*Salix gooddingii*	115	5.86%
	Blue Elderberry	*Sambucus nigra cerulea*	440	22.44%
	California Blackberry	*Rubus ursinus*	177	9.03%
	California Rose	*Rosa californica*	248	12.65%
	Coyote Brush	*Baccharis pilularis*	957	48.80%
	Poison Hemlock	*Conium maculatum*	5	0.25%
	Red Willow	*Salix laevigata*	15	0.76%
	Unknown Forb	N/A	4	0.20%
Forage Area	Alfalfa (dried)	*Medicago sativa*	53	9.30%
	Alkali Heliotrope	*Heliotropium curassavicum*	8	1.40%
	Alkali Mallow	*Malvella leprosa*	1	0.18%
	Annual Grass	N/A	15	2.63%
	Black Willow	*Salix gooddingii*	3	0.53%
	Blue Elderberry	*Sambucus nigra cerulea*	34	5.96%
	California Blackberry	*Rubus ursinus*	147	25.79%
	California Rose	*Rosa californica*	88	15.44%
	Coyote Brush	*Baccharis pilularis*	191	33.51%
	Moss	N/A	7	1.23%
	Perennial Pepperweed	*Lepidium latifolium*	1	0.18%
	Poison Hemlock	*Conium maculatum*	2	0.35%
	Red Willow	*Salix laevigata*	7	1.23%
	Unknown Forb	N/A	13	2.28%
Ground	Bare Ground	N/A	247	16.07%
	Litter	N/A	1,244	80.94%
	Rock	N/A	46	2.99%

Table 36. *Each site's vegetation alliance based on the dominant and co-dominant species.*

Site	Dominant	Co-Dominant	Shrubland Alliance
PH1	*Baccharis pilularis*	*Rosa californica*	*Baccharis pilularis*
PH2	*Sambucus nigra cerulea*	*Baccharis pilularis*	*Sambucus nigra*
PH3	*Baccharis pilularis*	-	*Baccharis pilularis*
PH4	*Baccharis pilularis*	-	*Baccharis pilularis*
PH5	*Baccharis pilularis*	*Sambucus cerulea*	*Baccharis pilularis*
Run7	*Rubus ursinus*	*Salix gooddingii*	*Rubus* (*parviflorus, spectabilis, ursinus*)
RunB1	*Baccharis pilularis*	*Sambucus cerulea*	*Baccharis pilularis*
RunB2	*Baccharis pilularis*	*Rosa californica*	*Baccharis pilularis*

Table 37. *Percentage of species or feature within the canopy, forage area, or ground for individual sites.*

	Plant	PH1	PH2	PH3	PH4	PH5	Run7	RunB1	RunB2
Canopy	Black Willow	0	0	0	0	0.71	34.20	0	6.67
	Blue Elderberry	23.53	62.39	11.57	0	40.36	0	35.65	0
	California Blackberry	8.33	0	0	0	0	47.96	9.37	0
	California Rose	15.20	1.38	16.67	0	12.50	0	2.72	42.54
	Coyote Brush	52.94	32.11	71.76	100	41.07	0	50.45	50.79
	Poison Hemlock	0	2.29	0	0	0	0	0	0
	Red Willow	0	0	0	0	5.36	0	0	0
	Unknown	0	1.83	0	0	0	0	0	0
	Empty canopy	0	0	0	0	0	17.84	1.81	0
Forage Area	Alfalfa	0	25.00	16.51	11.29	19.15	0	0	0
	Alkali Heliotrope	0	0	0	0	0	0	14.04	0
	Alkali Mallow	0	0	0	1.61	0	0	0	0
	Annual Grass	0	0	0	0	0	10.27	0	0
	Black Willow	0	0	0	0	0	2.05	0	0
	Blue Elderberry	17.14	17.11	0.92	0	8.51	0	17.54	0
	California Blackberry	2.86	1.32	0	0	0	84.25	35.09	5.26
	California Rose	62.86	11.84	18.35	8.06	19.15	0	8.77	47.37
	Coyote Brush	14.29	19.74	63.30	79.03	46.81	0	22.81	47.37
	Moss	2.86	0	0.92	0	0	3.42	0	0
	Perennial Pepperweed	0	1.32	0	0	0	0	0	0
	Poison Hemlock	0	1.32	0	0	0	0	1.75	0
	Red Willow	0	5.26	0	0	6.38	0	0	0
	Unknown	0	17.11	0	0	0	0	0	0
Ground	Bare Ground	8.54	26.52	22.05	22.99	24.00	12.5	3.02	10.00
	Litter	89.45	71.27	73.33	75.94	76.00	81.25	88.94	90.00
	Rock	2.01	2.21	4.62	1.07	0	6.25	8.04	0

Independence of Sites

The habitat along the levees, which is dominated by coyote brush and blue elderberry, with two climbing species, California rose and blackberry, tends towards homogeneity because it is restored habitat, habitat created using a specific planting regime by River Partners. Alternative sites were limited in representing historical and restoration communities as most areas adjacent to the levees were flooded, or when accessible, had few areas that fit the project parameters. With limited areas to choose from that fit project parameters, such as RBR sign present, presence of alfalfa and/or poison hemlock, wide enough area to avoid risk of animals colliding with cameras, and being undetectable to Refuge visitors, sites were unsystematic and at times in relatively close proximity to one another (Figure 2).

CHAPTER V

DISCUSSION

Riparian Brush Riparian Activity

The primary objective of this study was to determine if riparian brush rabbits have a defined activity period. Larsen (1993) reported that riparian brush rabbits were crepuscular, active from sunset to 02:00 and again from 06:00 to 10:00, and resting and grooming in between these periods. Given this, I expected that RBR would have a crepuscular activity pattern. My data contradicted my hypothesis and did not find RBR to be definitively crepuscular ($F_{2,3}$ = 0.19, p = 0.83, Table 8). In this study, the activity periods of the riparian brush rabbit varied between sites, and documented activity patterns were neither strictly diurnal nor strictly nocturnal (Figure 7, Figure 8). However, the activity peaks distributed across day and night hours do not reflect a strictly crepuscular life style either, suggesting that activity is influenced by multiple factors. There was a lack of variance between day, night, dawn, and dusk ($F_{3,4}$ = 0.44, p = 0.74) suggesting that there is not a defined activity period (Table 7). Although RBR were active at all hours, there were declines in activity in the morning, and around midday and midnight. The peaks in the late morning (09:00-11:00) suggest that future live-trapping efforts would benefit from extending trap check times to late morning when feasible.

In a live-trapping study on Año Nuevo Island, Zoloth (1969) documented brush rabbit peak activity at 10:00 and low activity at 06:00, similar findings to this study, 10:00 and 07:00, respectively. These similarities in timing of activity, despite the very different techniques used in the two projects, support the idea that the RBR has a morning peak around 10:00 and morning low between 06:00 and 07:00. Further, the Zoloth study took place in summer, when food was plentiful, on an island with less brush and no known predators. This is important because the comparable results for these two very different studies suggest that camera trapping may be as effective as live-trapping for understanding brush rabbit activity patterns. Live-trapping can be stressful, even harmful, to animals. If cameras can capture equivalent data, they are a preferable alternative, especially for sensitive species such as RBR. However, deployment of multiple cameras across multiple seasons in different habitat types would be needed to get a more complete picture of activity patterns since those patterns can vary between camera sites (Figure 6) as well as by season and habitat.

Riparian Brush Rabbit Activity versus Rest

Early in the project, I assumed that rest and active periods would not coincide and possibly be inverse. However, although significant, there was less of a difference than expected ($t(3) = -2.54$, $p = 0.045$, Table 9, Table 10), and rest and active peaks occurred at similar times (Figure 7, Figure 8, Figure 9, Figure 10). The lowest amounts of *rest* recorded were at 00:00 (none), 01:00 (none), 06:00 (none), 07:00, 08:00, 13:00, and 21:00 (Figure 9, Figure 10). This suggests that RBR would be most active at these times, but this was not the case. The resting peaks at 11:00 and 14:00 may be more for thermoregulation purposes than sleep. The relatively low frequency of *rest* behaviors may in part be a product of the limitations of the camera placement.

The cameras may have not been covering areas in which RBR generally rest. Most *rest* photos came from PH3 and PH5, both sites differing from all other sites in that they had alfalfa and dense canopy cover. Canopy cover may be a more important determining factor on whether an RBR will feel safe enough to rest or not.

There is a possibility that the categorization of vigilance as an energy conservation behavior rather than an active one would provide a greater understanding of RBR rest. As vigilance was recorded more often, using *vigilant* photos to represent *rest* may compensate for gaps in data when recordings of *rest* are low. Since this study found that excluding *vigilant* photos from the dataset did not affect interpretations about activity levels ($F_{1,6}$ = 0.65, p > 0.05, Table 11), that may also be a better option for interpreting rest. However, this may result in an inflation of rest periods and would require further delimitation of *vigilance* based on posture such as vigilance while standing, or lying down. In conclusion, fully understanding RBR rest and resting periods requires further study with a more specialized study design.

Riparian Brush Rabbit Interactions

The second objective of this study was to understand what behaviors and activities are most representative of the riparian brush rabbit repertoire. I had hypothesized that RBR, being a cryptic species, would be primarily solitary and that individual behaviors would be predominant. My hypothesis was supported as over half of the behavior photos were of individual behaviors (64.29%) with intraspecific behaviors representing over a quarter of behaviors recorded (29.78%). Despite this disparity, the individual and intraspecific means did not differ significantly whereas the difference between individual and interspecific was significant ($p < 0.05$, Table 21). This suggests that individual and intraspecific interactions are more significant to RBR ecology than interspecific interactions. A more thorough review of RBR behavior is discussed in Appendix E, where the results of behavior tags are examined individually.

Intraspecific Interactions

Riparian brush rabbits were mainly recorded in photographs as lone individuals. Although there were many photographs with two RBR present, photographs of single RBR predominate across all sites, and the number of photos with increasing numbers of RBR steadily declined (Table 14). Photos with more than two RBR were only captured at the alfalfa sites (PH3, PH4, and PH5). The ample and concentrated food source at those sites, with little alternative natural forage, likely resulted in the rabbits congregating in the area. The overall photographic results suggest a somewhat solitary lifestyle but with increased co-occurrence and tolerance at feeding sites. Nevertheless, photos with over five individuals present were very rare despite the concentration of rabbits (Table 14). This suggests that RBR were not lingering at the alfalfa piles but were visitors. This would be adaptive since there would be a greater opportunity for predation and disease transmission at food sites with multiple RBR in close proximity.

Interspecific Interactions

The third aim of this project was to understand how riparian brush rabbits interact with other species. My hypotheses were that RBR would act amicably towards potentially beneficial species and aggressively towards competitors and predators. The data did not support my hypothesis. There were as no negative or amicable interactions with beneficial species and few interactions with competitors ($n = 64$) and predators ($n = 3$, Table 26). There was not a significant variance between the number of negative and amicable interactions ($p = 0.73$, Table 27) suggesting that such interactions are not a large part of the RBR behavioral repertoire. Competitor interactions were more significantly different than interactions with predatory ($p < 0.01$) and beneficial species ($p < 0.01$), reflected in the photoset where RBR were mainly captured co-occurring with desert cottontails and California ground squirrels, their primary competitors (Table 24, Table 25, Table 26, Table 30).

Lagomorph Interactions. Among all species, desert cottontails had the highest documented co-occurrence with RBR. The interactions between these species were limited to six behaviors, but *vigilant* accounted for 96% of the interactions (2,232/2,323, Table 31). Conversely, the desert cottontail was the only mammalian species RBR would rest in the presence of ($n = 28$). Two negative behaviors, *chase* and *flight*, were recorded about equally in the presence of desert cottontails (n = 27 and 24, respectively). Riparian brush rabbits seemed to avoid confrontation with desert cottontails as they rarely would smell ($n = 7$) or act aggressively ($n = 5$) towards them. Although their relationship seemed not completely congenial, this seemingly tolerant relationship may explain how these two *Sylvilagus* species, one a specialist and the other a generalist, can coexist.

The larger proportion of RBR to desert cottontails photographed during the flood may have been because RBR were more abundant in the study area or perhaps it was a result of species differences (Table 13). The larger body size of the desert cottontails may have been harder to maintain through the food shortage of the prolonged flood leading to increased mortality. However, refuge data showed a downward trend in desert cottontail numbers even after supplemental feed was distributed, suggesting that starvation may not have been a significant factor in the decline of desert cottontail numbers (Heffernan and Takahashi 2017). A potentially more important factor may have been the behavioral differences between the two species in relation to predation. Unlike RBR, which stay in or close to cover at all times, desert cottontails exhibit bold behavior, readily leaving cover to forage in large open spaces, resting in exposed areas, and even being active around humans. Because of the widespread flooding on the refuge, predator activity was concentrated along the levee roads. It is therefore reasonable to assume that more bold rabbits, primarily desert cottontails, have a higher probability of being preyed upon. Thus, RBR may have a competitive advantage over desert cottontails during extreme flood events.

Predator Interactions. Riparian brush rabbits were very rarely photographed simultaneously with known predators (Table 24). There were six *predation* interactions with coyotes and a single *vigilance* event with a long-tailed weasel. Riparian brush rabbit response to human presence seemed variable. Ordinarily, RBR would continue to feed on alfalfa piles, but on one occasion when a truck was driving by, one RBR continued feeding while another fled. It may be that potential predators like weasels and humans are not perceived as direct threats, warranting caution, but rarely avoidance. This response differs from known predators, coyotes and raccoons, where there were few co-occurrences despite their presence in the community (Table 13). Consequently, RBR may avoid areas when either is present, explaining the limited photographs. However, the low rate of co-occurrence with predators may be normal, even with the continuous observation by camera traps. A recent investigation of camera trap effectiveness in capturing predation yielded relatively low captures of predator response (52/268 observations) and attacks (21/268 observations) to artificial prey presence (Akcali et al. 2019). This suggests that predation is rarely captured, even with a consistent prey presence, and that future RBR ecological studies using camera traps will need to consider this limitation.

Limited information on the impact of domesticated dogs was generated by this study. Most dog photos were taken at PH4 where the camera could capture visitors and vehicles if they were close to the side of the trail. Despite human disturbance, RBR were often present, possibly due to the presence of the alfalfa. However, RBR were mostly absent when dogs were present; one RBR was feeding on alfalfa at PH4 when a leashed dog went off trail but then was gone in the next photograph, suggesting a quick flight from the area. Of three instances where dogs were captured on camera, two were the same off-leash dog as it traveled off trail at PH4 and PH5, on a similar route also used by (photographed) coyotes. The absence of RBR despite alfalfa being present suggests that dogs are perceived as more of a threat than humans on their own. Multiple visitors with loose dogs were observed, prompting the refuge staff to post signs explicitly stating the regulation against off-leash dogs. Subsequently, off-leash dogs were not captured on the cameras, highlighting the importance of signage and monitoring threats to the RBR community during critical times of stress for the species.

Bird Interactions. In co-occurring with RBR, the California quail was the most recorded bird species (n = 255), followed by six granivorous passerine species (n = 479, Table 24). The most direct interaction RBR had with all of these bird species was *vigilance*, otherwise RBR continued with their activities. Although the interaction rate may seem low, and could be a consequence of no or low competition or predatory threat between these species living in the brush, there could also be an element of commensalism between the species with regard to predator detection. For example, a recently published study showed that grey squirrels can infer safety from bird chatter (Lilly et al. 2019). Whether RBR would assess safety in a similar manner is beyond the scope of this study's methods as bird vocalizing cannot be discerned in the Cuddeback's photographs.

Apart from the quail and the passerines, a black-crowned night heron was recorded at PH1 without co-occurrence with RBR (Table 13). Open water, like was present at PH1, could bring in wading birds such as night herons or great blue herons (*Ardea herodias*) that may prey on small riparian brush rabbits, perhaps explaining the lack of co-occurrence. Further heron studies should be done on the refuge to better understand flood impacts within the context of shifting predation pressures.

Reptile Interactions. The camera traps did not capture reptiles co-occurring with RBR. On one occasion, a desert cottontail was photographed inspecting a gopher snake at PH5. This active engagement was different than the only RBR co-occurrence, documented during live observation, where RBR stood vigilant as a gopher snake traveled past them. Gopher snakes were regularly encountered in the live observation meadow and may have a higher presence there than along the levees. Riparian brush rabbits may be somewhat habituated to them and may not flee when in close proximity but still remain alert. This highlights the necessity of camera traps in multiple plant communities as the low co-occurrence of reptiles may have resulted from low presence in the levee area.

Riparian Brush Rabbit Interactions in Summary

The greater number of intra and interspecific behaviors documented at PH3, PH4, and PH5 compared to other sites are likely a result of the fact that those three sites were consistently supplied with supplemental food, whereas the five other sites (PH1, PH2, Run7, RunB1, and RunB2) lacked consistent food sources and thus, were mainly transit sites. As transit sites, there was little to attract RBR and other species as well as to retain them at the site for extended periods of time. Transit sites were less likely to bring different individuals and species together at the same time compared to sites with alfalfa piles. The alfalfa presence during a time of food shortage may have attracted more RBR and other herbivorous species, and they in turn would attract more predators in response to the increased and consistent presence of prey. With much of the Refuge flooded for an extended period and natural forage in low supply, areas with high concentrations of supplemental food were more likely to keep rabbits concentrated for longer periods than the natural vegetation, which was mainly brush. Under normal conditions, brush is a natural part of the diet of brush rabbits, but they also feed heavily on herbaceous material. Brush differs as a food source in that accessible leaves are completely browsed in less time than a pile of alfalfa that, although easily accessible, would take a longer period to be exhausted. Future rescue efforts may need to consider distributing supplemental feed to more closely mimic natural sources to reduce species concentrations and conflicts, perhaps by dispersing feed in smaller piles over wider areas.

The rate of intraspecific interaction may have been inflated because of the methodology used in evaluating photographs. RBR within 2 meters of each other were considered to be engaged in an intraspecific interaction. By contrast, interspecific interactions were not distance based. If an RBR and another species were in the same photograph, and the RBR exhibited *vigilance*, the interaction was considered interspecific. Thus, the methodology may have inflated the number of intraspecific interactions. However, the constant food supply at the three alfalfa sites, alfalfa in a single pile, brought more RBR, and other species, closer together and for more extended periods, thus increasing the numbers of both intra- and interspecific interactions.

The high individual, low interspecific proportion of behaviors at transit sites suggest that RBR may not interact extensively with other species outside of feeding areas (Table 16). This proportion, along with the increased intra- and interspecific behaviors recorded specifically at alfalfa sites suggest a relatively solitary lifestyle. Indeed, when Stoner et al. (2003) evaluated pelage coloration in lagomorphs, they found that coloration of extremities, such as ear tips and tails, was more associated with sociality than with environmental variables. Dark-tipped ears, a feature that desert cottontails have and RBR lack, is associated with sociality for intraspecific signaling (Stoner et al., 2003). This suggests that sociality is more important for desert cottontails than it is for RBR. Furthermore, white tails is a trait that is associated with intraspecific signaling (Stoner et al., 2003), specifically for flight, a trait that is muted in RBR. This combination of uniform ear color and small, less conspicuous tails may suggest that for RBR intraspecific signaling may be reserved more for signaling danger than for other social purposes.

The inconspicuous features of RBR with the high proportion of individual behaviors could possibly reflect a species that is solitary, only engaging in intraspecific interactions for territorial and reproductive purposes, and reserving intraspecific signaling for times of emergency. The fact that the RBR geographic range overlaps with two other lagomorph species, desert cottontails and black-tailed jackrabbits, that have black-tipped ears and large white tails associated with sociality illustrate the unique niche that RBR fit into. The grassland-associated jackrabbit (large black patches on the ears and tail that is black on top and white underneath), followed by the generalist desert cottontail (black-tipped ears and a large white tail), and then the brush specialist RBR (unmarked ears and a small white tail) show a definitive reduction from most to least conspicuous markings. The range of markings is matched by a range of sizes from large, fast jackrabbits living in the open, to small, cryptic brush rabbits hiding in the sheltered, dense protection of the brush, and the generalist desert cottontail in between those two extremes. These variations in morphology and behavior may explain how three lagomorph species can coexist on the refuge.

Results Compared to Previous Brush Rabbit Behavior Studies

There is only one other known study of behavior in brush rabbits. Zoloth (1969) studied a population of introduced brush rabbits on Año Nuevo island, but this study is not directly comparable with this study because of differences in habitat and subspecies. Nevertheless, aggressive behavior was documented where rabbits would chase one another if one came within an average of “approximately one foot” of the other (Zoloth 1969). The Año Nuevo study further does not align with the refuge study since *chase* and *agonistic* behaviors were inconsistent and relatively rare in proportion to the number of non-agonistic interactions recorded. The differences between the studies could be due to differences between subspecies, populations, habitat, or disturbance (flood). Further, the lush environment of the riparian communities on the Refuge support not only RBR, but a larger number and diversity of predators than Año Nuevo. Further, the Refuge’s proximity to human development adds feral cats and dogs to its community, which is not a concern for Año Nuevo. Possibly due to their cautious nature, RBR may not be as aggressive as other subspecies, constantly chasing and fighting exposes them to more danger than intraspecific avoidance. Additional studies on brush rabbit behavior, but in different habitats and environments, would be very helpful.

Riparian Brush Rabbit Habitat Use

Coyote brush dominated the brush at all camera sites, except for PH2 and Run7, resulting in limited documented RBR use of refuge plant communities. Other brush communities (e.g., rose and willow thickets), as well as grasslands, were in the floodplain and mostly inundated. Despite the low diversity of plant communities available, a variety of RBR environmental interactions were captured.

RBR showed some adaptability in foraging behavior with their use of a novel food source (alfalfa) and a nonnative toxic plant (poison hemlock). This suggests that RBR will interact with novel plants, which is advantageous as they used supplied alfalfa, avoiding starvation, and harmful in that poison hemlock exposed them to toxins.

The types of plants used by RBR to line nests has not been previously evaluated. In this study, RBR were photographed carrying bundles of sticks including poison hemlock, rose twigs, and alfalfa stems. We might assume that California rose would not be used to line nests because of its thorns, but it may be used to provide cover and camouflage for a nest. The short supply of grass and herbaceous growth, the normal material used to line nests (Larsen 1993) may have forced pregnant rabbits to instead collect rose and poison hemlock. The possible dual usage of dried alfalfa, as food and as nesting material, suggests that alfalfa pile placement could further benefit female rabbits when grass is unavailable for nesting. Although no nests were found and no small juveniles were photographed, the results of this study suggest that RBR that live under adverse conditions still make nests and give birth to young. The results further suggest that RBR will use whatever nesting material is available. Consequently, land managers that need to supplement resources in future floods might want to also take the availability of nesting material into account.

Native Plant Species Interactions

Riparian brush rabbits were photographed utilizing native species in a variety of ways. Riparian brush rabbits would feed on native species such as willow, blackberry, and rose, even when alfalfa was available and arguably more accessible. Also, despite the presence of alfalfa, RBR were seen climbing to access native plants, suggesting that they readily climb into shrubs under normal, non-flood conditions. This is further supported by observations of RBR climbing to feed on vegetation during earlier live-trapping studies (M. Lloyd pers. comm.).

Riparian brush rabbits interacted more with coyote brush and California rose than any other plant species. This study showed that RBR occasionally chin-marked coyote brush. Coyote brush was also the only plant species that RBR climbed into by more than 0.5 m. Coyote brush dominates the levee habitat, and its growth form allows rabbits to use it for movement, protection, and cover. However, RBR were not photographed feeding on coyote brush, but they may climb it to access California rose, which often grows into the canopy of coyote brush. California rose can exist as standalone bushes and thickets, especially on the floodplain, as well as vines that use coyote brush or other shrub species to provide a ladder to the canopy. In the floodplain, RBR climb directly into rose bushes to forage, but in the study area where rose vines are more common, they may use coyote brush to access the rose, one of their preferred foods (P. Kelly pers. comm.). Both coyote brush and rose were collected by RBR for nesting material, illustrating the role this chaparral community plays in RBR survival.

Riparian brush rabbits were photographed climbing coyote brush on five occasions and directly observed climbing in quail bush on one occasion. Both of these woody species are characterized by thick lateral branches with smaller branches that can layer one on top of another. Riparian brush rabbits were recorded climbing California rose once and blackberry twice, all were similar in that they had low, dense growth forms. This suggests that for shrubs to be climbable by RBR, they must have if not low lateral branches, layers of smaller woody branches that can create a structure stable enough for the rabbit's weight. Thus, habitat evaluation should include assessing the distribution and abundance of food plants that have these growth patterns in the plant community to better characterize the overall ecological value to RBR. These characteristics can be used to evaluate habitat for vertical foraging. However, RBR were only regularly documented climbing at PH4 and PH5, and that was to feed on alfalfa, a non-natural food source. In summary, the frequency and consistency at which RBR climb into shrubs to forage is still poorly understood and needs further evaluation.

Non-native Plant Species Interactions: Poison Hemlock and Alfalfa

An unforeseen consequence of the flood was the impact of poison hemlock and the lack of alternative herbaceous forage. Multiple poison hemlock plants were clipped by herbivores, presumably rabbits. United States Fish and Wildlife Service staff submitted for necropsy 13 RBR carcasses collected in January and February 2017 to the Diagnostic Services Section of the Southeastern Cooperative Wildlife Disease Study at the University of Georgia. Only one showed trace amounts of the alkaloid coniine, a toxin found in poison hemlock, but not enough to have been the cause of death. All 13 rabbits were in poor to fair body condition, often with little fat stores, suggesting starvation rather than poisoning as a mortality factor (Ruder and Fischer 2017). These findings are supported by the camera study. There was little interaction with poison hemlock, suggesting that it had little effect on the survival of RBR. It is possible that RBR sampled hemlock, but did not ingest much, finding it unpalatable. The necropsy and camera results suggest that RBR may not eat toxic plants, even when starving.

The photos of RBR carrying poison hemlock suggest that they may have used it for nesting material. Whether this would affect offspring survival is unknown. Very few studies have been conducted on the effects of poison hemlock ingestion on rabbits. Forsyth and Frank (1993) and Short and Edwards (1989) found negative effects on fetal development as well as death with high exposure in New Zealand white rabbits (*Oryctolagus cuniculus*). Since RBR were exhibiting reproductive behavior, ingesting at least some poison hemlock, and seemingly using it for nesting material, it is possible that the survivorship of young RBR was affected. However, as the recorded feeding on poison hemlock was low compared to feeding on alfalfa and other plants, the impact may not have been significant. Nevertheless, the scarcity of data on how RBR use poison hemlock and how it impacts adults and offspring highlight the need for further research.

Alfalfa was distributed along levee roads once the impact of the flooding was realized; habitat conditions were deteriorating rapidly under pressure from the high densities of rabbits (Table 13). The rabbits readily fed on this new and novel food supply. However, since RBR can be challenging to trap, there was a possibility they would avoid or not be interested in a new food source. Basey (1990) evaluated ten different bait types, but he concluded that only one, rolled oats, was effective and feasible for trapping RBR. Subsequent research and the captive breeding program have used traps that are baited with horse meal (sweet COB: corn, oats, and barley with molasses) with additional attractants (apple pieces, apple sauce, walnuts) added when rabbits exhibit trap-shyness (P. Kelly pers. comm., M. Lloyd pers. comm.). The large amount and variety of attractants required for trapping this animal further illustrates RBR as a novelty-shy species. Conversely, the large number of photos of RBR feeding on alfalfa demonstrated forage flexibility, at least when other food sources are scarce. Further, their use of alfalfa for nesting suggests that providing forage substitutes is an important management action during periods of severe flooding.

Effects of the 2017 Flood on the Riparian Brush Rabbits of San Joaquin River National Wildlife Refuge

Floods are periodic but normal occurrences in riparian habitat. Depending on their severity and duration, they can pose a significant threat to RBR populations. RBR are able to swim and they can climb to escape floodwater, at least to a certain extent in both cases, but on the refuge they are limited by access to sheltered refugia that has enough forage to support them through a prolonged flood (E. Hopson pers. comm.). The effects of floods on the refuge RBR population have not been extensively studied. The 2017 flood created a unique opportunity to study RBR activity and behavior within the context of a major flood.

Unexpected photographic captures of human visitors and off-leash dogs in closed areas illustrate the overlap between RBR habitat and recreation, especially during flood periods. At PH2, visitors used a trail that was off-limits, seemingly to view the floodwaters. On another occasion, a man with a drone was encountered with plans film the flooding with his drone, an activity that is prohibited on National Wildlife Refuges unless the operator has a special use permit. Other visitors were reported to have walked closed areas of the levee, meaning that RBR did not have a refuge away from human disturbance. The novelty of extreme flooding may possibly attract more visitation and trespassing than usual, and thereby increase the likelihood of conflict with RBR and other wildlife. Future flood response may need to include monitoring visitation levels and impacts when recreation areas are a significant proportion of flood refuge for RBR.

An estimated 930 riparian brush rabbits inhabited the San Joaquin River National Wildlife Refuge in April 2017, after the peak of the flood in March (Takahashi 2017). Based on counts of dead rabbits found on flood refugia during the peak of the flood, the RBR population prior to the flood was high (P. Kelly pers. comm.). It is unknown if rabbit distribution will return to previous levels as before the flooding as there were not enough collection periods in this study to collect distribution data. Quantitive studies on the size of the RBR population have not been conducted in recent years, but camera trapping in different habitat types in winter 2018 and spring 2018 revealed that RBR were present on all of the previously flooded riparian areas adjacent to my study area (P. Kelly pers. comm.). The flooding may have increased forage and revitalized the restoration site plants, bettering the habitat available and lead to a population rebound or even increase. However, after the water fully receded there were noticeable differences in the landscape as grasslands that were underwater were slow to recover and herbaceous species, including invasive stinkwort (*Dittrichia graveolens*), were more prevalent in the plant community than previous visits. It may be just as likely that the flood weakened the native plant communities, exposing them or increasing their susceptibility to invasive species. As RBR recovery is dependent on the recovery of native plant communities, the effects of the flood may extend years beyond water receding, impacting recovery efforts. Plant community composition should be increasingly monitored after flood events to prevent habitat loss or degradation by colonizing invasive species.

The high rates of *vigilance*, *travel*, and *foraging* may in part be a consequence of the flood. The increased predator concentration on levee roads could have required RBR to be more vigilant and mobile than usual. Predator concentration could further explain why there was little rest recorded and RBR activity was recorded at all hours of the day and night at some sites with little fluctuation. Foraging may have increased due to the sparse resources, causing RBR to expend more energy. The food stress and threatened starvation may have trumped territoriality or other social behaviors, increasing the proportion of the solitary behaviors. Future studies should focus on refining our understanding of the behavioral repertoire and activity under more normal conditions. With a standard model, the effect of flooding on the population can be better understood. By having a reference to measure the deviation of proportions during a flood event, it may be easier to determine the degree of stress RBR are experiencing and interpret the impacts of such a natural disturbance.

The 2017 flood demonstrated that disturbances like the floods not only cause direct mortality from drowning and exposure, but continue to affect the population through loss of food, reduction in shelter, concentration of predators, increase in toxic plants, and loss of nesting material and sites. The flood substantially affected population size and hindered recovery through resource depletion. It is understudied how RBR habitat recovered post-flood and whether RBR were redistributing to areas with habitat improved or deteriorated. If large floods damage the productivity of RBR habitat or render it less resilient to invasive species, flood impacts on RBR recovery may extend far beyond the floodwater receding. Nevertheless, the situation would likely have been more extreme without the supplemental provisioning of alfalfa by USFWS.

Future Research

Riparian Brush Rabbit Behavior and Ecology

This study focused on RBR behavior during a major flood event. Although the results expanded our understanding of RBR behavior, they point to the need to study the animals during more average conditions, without the major disturbance of a large flood, to better understand RBR ecology as a whole.

The variety of behaviors collected demonstrates the compatibility of camera traps and riparian brush rabbits, that this technology provides the means to study in-depth the ecology and life history of this cryptic species. That said, within the somewhat narrow scope of this project, the photographs yielded important data on RBR behavior and ecology during a major flood. Beyond feeding and foraging, the rabbits were engaging in social interactions and even reproducing, behavior sets that are more illustrative of population survival and vitality. Future ecological studies would benefit from employing camera traps to study riparian brush rabbits.

Research Response to Flood Events

Floods are a periodic but normal occurrence in riparian habitat. As such, the behavioral ecology of RBR should include adaptation to flood events. Since the RBR release program began on the refuge in 2002, major floods in 2006, 2011, and 2017 have impacted the RBR population, (Phillips et al. 2005, Kelt et al. 2014, Kelly

2018). The 2017 flood provided an opportunity to gather data on RBR during a flood, data that would otherwise be challenging to acquire.

Concurrent with the camera project, USFWS biologists were conducting a monitoring project, counting the number of RBR and desert cottontails along the levees throughout the flood (Heffernan and Takahashi 2017). The USFWS biologists documented a change in the proportion of desert cottontails to RBR over time. This could only be done during the flood because both species were concentrated and often visible on the levees. A repeat of this quantitative survey during floods could aid in teasing out the niche differences between these similar species.

As flooding is a periodic event, protocols for data acquisition, as well as salvage and rescue, are necessary for species recovery. Data collection could work in tandem with salvage, rescue, and monitoring efforts during floods. Examples of useful data include but are not limited to genetic samples, body condition (mass/parasites/disease/etc.), sex, reproductive status, disposition, and GPS information (collection/release site). This would allow biologists and Refuge management to get a snapshot of the demographic and genetic diversity of the Refuge. Released RBR could also be marked with PIT tags or ear tags, the latter being detectable by camera traps.

Usage of Camera Traps in Behavioral Studies

Prior to this project there had only been one published study that used camera traps to study riparian brush rabbits (Elsholz 2010). The focus on the study, performed at Caswell Memorial State Park, was characterizing RBR habitat through vegetation and RBR presence surveys. Elsholz (2010) additionally evaluated the performance of camera traps and track plates for surveying RBR presence. Although successful at detecting RBR at four out of 125 sites, the capture success compared to this study's results is curiously low considering Caswell MSP is one of the residual habitats for RBR. However the study design was quite different, in Elsholz (2010) cameras ran for four days for each of the 125 sites between July and October, effectively collecting one sample per site compared to my study which sampled few sites multiple times. These differences between methods and results suggest that camera trap methods can influence data collection and that RBR camera surveys require specific tailoring to meet project objectives, whether the objectives are presence or behavior. Further details on the effectiveness of camera traps for this project are discussed in Appendix F.

A concern with the behavior tag system for this project was how different tags were treated as active and inactive. This primarily concerned the behavior *vigilance* as to whether its classification as active or inactive would impact the interpretation of RBR rest. As this study took place during a natural disaster for the population, the differentiation of RBR fully resting was important to separate from activity to record possible impacts of flood on RBR rest and energy conservation. However when examining activity without *vigilance* included there was little difference despite the prevalence of the behavior. Further study of the significance of vigilance as an active or inactive behavior should be done.

Vigilance is significant area of study for prey species for multiple reasons. An animal scanning for threats loses some of its energy conservation potential and is additionally distracted from energy gain, thus excessive vigilance can have an impact on animal survival (Presser et al. 2005). Understanding vigilance can also provide further interpretation of community health as rabbit studies found a link between body condition and amount of vigilance (Monclús & Rödel 2009). The proportion of full sleep to resting while vigilant may provide context for the animals' level of stress or possibly energy usage during a period of environmental disaster. However, since most rabbit vigilance studies were dependent on live observation and adjoining methodologies, the results determined by camera ethological studies may be completely different and possibly not comparable (Monclús & Rödel 2009, Monclús et al. 2006). It may be that more specialized methods are required for technological ethological studies than traditional live observation. RBR lack observation studies in general and require both live and technological observation to create a full picture of their behavior.

In Conclusion

Details of the activity patterns and behaviors of the riparian brush rabbit illustrate the unique niche it occupies within the riparian areas. Riparian brush rabbits demonstrate a plasticity within their habitat, interacting with familiar and unfamiliar vegetation in multiple ways not often attributed to environmental specialists. That being said, their interaction with toxic poison hemlock highlights that as riparian brush rabbit habitats increase and the species recovers, there may be the emergence of a new limitation on their recovery and survival. The potential impact of invasive plant species may need to be considered as much as impacts of development and invasive animal species. Particular plants that need to be studied are toxic species that can dominate RBR forage areas, particularly during times of the year when ground forage is less available. As such, there may be a requirement for habitat assessments of forage availability shifts over multiple seasons, with specific surveys of flood refugia included. Furthermore, RBR collecting material for nesting highlights the need to understand the seasonal habitat requirements of this species within the context of reproduction and whether current flood refugia can meet this need.

Riparian brush rabbit foraging needs to be further assessed, specifically foraging in the canopy via climbing. The role of climbing in foraging needs to be established to understand how RBR are fully using their habitat. If canopy foraging is a significant part of their diet, it may further illustrate the differences and co-habitation of RBR and desert cottontails. It may also reveal more the relationship between riparian plants and RBR, if RBR are not concentrated foragers it may have evolved to better allow plants to weather flooding periods where there would be more herbivore pressure. They could potentially be the medium level vertical forager, where ground squirrels can easily and fully access the entire canopy and desert cottontails restricted to the ground, RBR may be filling the niche in between that. Thus, the regularity of climbing and foraging needs to be assessed further to determine its role in RBR ecology.

Based on the results of this research, it appears that RBR are capable of being active at all hours. However, there appears to be a peak in activity between 09:00 and 11:00 and perhaps another one at 20:00. Paradoxically, the peaks in rest also occurred at these times. Perhaps this flexibility allows them to better adapt to abrupt environmental changes such as floods so they can take advantage of shifting predatory pressure and maximize foraging when resources are sparse. It is possible that RBR have circadian plasticity in response to environmental stress, similar to nocturnal mice shifting to a diurnal phenotype when enduring energetically challenging conditions (van der Vinne et al. 2014). Riparian brush rabbit activity needs to be evaluated outside of floods and stressful conditions to better determine if there is a defined activity period and thus circadian plasticity.

The somewhat solitary nature of the riparian brush rabbit may be an adaptation to evade predation. That nature may possibly reduce the energetic cost of agonistic social interactions. Stress from intraspecific conflicts has been linked to increased disease susceptibility in European wild rabbit, a rabbit species with aggression-based social hierarchies (von Holst et al. 1999). Avoiding confrontation may aid in survival and reduce intraspecific and interspecific conflict. Further, the apparent docility of RBR seems to benefit other species, as RBR do not obstruct food resources, even when food is limited.

Riparian brush rabbits demonstrate specialization to riparian habitats through adaptations to floods, climbing to access foliage during food shortages, all while maintaining energy expensive social and reproductive behaviors. This elasticity and resilience suggest that RBR ecology will be compatible with restoration activities as the Refuge continues to transition to larger expanses of restored habitat. It also highlights the importance of recovering this species to improve the resilience of the riparian community. As RBR are prey to many predatory mammals and birds, their resilience during flood periods support the larger community. This may further expand what their role is in comparison to the desert cottontail. If floods typically follow the pattern of 2017 with the reduction of desert cottontails and persistence of RBR, the riparian brush rabbit provides a critical prey base during long floods.

The resilience of riparian brush rabbits to multiple disturbance events suggests that when the riparian and upland habitats on the San Joaquin River National Wildlife Refuge are fully restored, the rabbits have the potential to thrive if not fully recover. In 1993 the riparian brush rabbit was only known from Caswell Memorial State Park, and there was widespread concern that the rabbit could “become extinct during a single catastrophic event” (Larsen 1993). As a consequence, various things were set in motion: the subsequent endangered listings by state and federal authorities; a massive captive breeding program; and extensive habitat restoration. Yet, riparian brush rabbit populations continue to experience extreme events, major floods and wildfires, that threaten their survival. This project demonstrated a new perspective that is relevant to riparian brush rabbit recovery that RBR retain a behavioral resilience despite an impacted environment and that recovery efforts are not in vain but should continue to adapt to a changing Central Valley.

This study demonstrates the insight gained from focusing on behavior within the context of a threatening event. It highlights the need to understand the compounding effects of punctuating events in species conservation as well as the role behavioral studies can play in interpreting the impacts (Berger-Tal et al. 2011, Caravaggi et al. 2017). Additionally, it establishes the need to identify behavioral indicators of stress to interpret management success and shortcomings of species recovery efforts (Lindell 2008, Berger-Tal et al. 2011). With many other specialist leporid species threatened, perhaps a route to more targeted recovery is the inclusion of behavior-based management, particularly with camera traps (Chapman et al. 1990, Caravaggi et al. 2017, Smith et al. 2018). In conclusion, the results of this study emphasize the importance of studying behavior as a component of lagomorph conservation and support the pursuit of behavioral research of the riparian brush rabbit and other endangered lagomorphs.

REFERENCES

REFERENCES

Addin Technology Inc. 2018. Kutools for Excel [Microsoft Excel add-in]. Retrieved from https://www.extendoffice.com

Akcali, C.K., Adán Pérez-Mendoza, H., Salazar-Valenzuela, D., Kikuchi, D.W., Guayasamin J.M., and D.W. Pfennig. 2019. Evaluating the utility of camera traps in field studies of predation. PeerJ, 7:e6487. doi:10.7717/peerj.6487.

Basey, G. 1990. Distribution, ecology, and population status of the riparian brush rabbit *(Sylvilagus bachmani riparius)* [dissertation]. California State University, Stanislaus. 76 pp.

Blumstein, D.T., and E. Fernández-Juricic. 2004. The Emergence of Conservation Behavior. Conservation Biology 18:1175-177.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B., and D. Saltz. 2011. Integrating animal behavior and conservation biology: A conceptual framework. Behavioral Ecology 22:236-239.

Camera Bits, Inc. 2016. Photo Mechanic 5 [Computer software]. Retrieved from https://camerabits.com

Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., and M.D. Wood. 2017. A review of camera trapping for conservation behaviour research. Remote Sens Ecol Conserv 3:109-122. doi:10.1002/rse2.48

Caro, T.M. 1998. The Significance of Behavioral Ecology for Conservation Biology. Pp. 3-26 in Behavioral Ecology and Conservation Biology (T.M. Caro ed.). Oxford University Press, Inc. New York, 565 pp.

Chapman, J.A. 1971. Orientation and homing of the brush rabbit (*Sylvilagus bachmani*). Journal of Mammalogy 52:686-699.

Chapman, J.A. 1974. *Sylvilagus bachmani*. Mammalian Species, 34:1-4.

Chapman, J.A. and G. Ceballos. 1990. Chapter 5: The Cottontails. Pp. 95-110 in Rabbits, Hares, and Pikas Status Survey and Conservation Action Plan (J.A. Chapman and J.E.C. Flux, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 168 pp.

Chapman, J.A. and J.E.C. Flux. 1990. Chapter 1:Introduction and Overview of the Lagomorphs. Pp.1-6 in Rabbits, Hares, and Pikas Status Survey and Conservation Action Plan (J.A. Chapman and J.E.C. Flux, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 168 pp.

Chapman, J.A. and J.E.C. Flux. 2008. Introduction to the Lagomorphs. Pp. 1-9 in Lagomorph Biology: Evolution, Ecology, and Conservation (P.C. Alves, N. Ferrad, and K Hackländer, eds). Springer-Verlag Berlin Heidelberg, New York, 413 pp.

Chapman, J.A., Flux, J.E.C., Smith, A.T., Bell, D.J., Ceballos, G.G., Dixon, K.R., Dobler, F.C., Formozov, N.A., Ghose, R.K., Oliver, W.L.R., Robinson, T., Schneider, E., Stuart, S.N., Sugimurua, K. and Z. Changlin. 1990. Chapter 14:

Conservation Action Needed for Rabbits, Hares and Pikas. Pp. 154-167 in in Rabbits, Hares, and Pikas Status Survey and Conservation Action Plan (J.A. Chapman and J.E.C. Flux, eds.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 168 pp.

Close, C.L. and D.F. Williams. 1998. Habitat management for riparian brush rabbits and woodrats with special attention to fire and flood, final report in partial fulfillment of the Central Valley Project Improvement Act, Section 3406(b)(1). Endangered Species Recovery Program, Department of Biological Sciences, California State University, Stanislaus.

Connell, J.H. 1954. Home range and mobility of brush rabbits in California chaparral. Journal of Mammalogy 35:392-405.

CNPS (California Native Plant Society). 2019. A Manual of California Vegetation, Online Edition. <http://www.cnps.org/cnps/vegetation/>. Accessed 2019 Apr 5.

Delibes-Mateos, M., Smith, A.T., Slobodchikoff, C.N., and J.E. Swenson. 2011. The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. Biological Conservation 144:1335-1346.

Elsholz, C.R. 2010. Riparian brush rabbit habitat requirements in Caswell Memorial State Park. San Jose State University, Department of Environmental Studies, Master’s Thesis. Paper 3857. 83 pp.

Fisher, P.G., and J.W. Carpenter. 2012. Chapter 19: Neurologic and Musculoskeletal Diseases. Pp. 245-256, in Ferrets, Rabbits, and Rodents: Clinical Medicine and Surgery. 3rd Edition (K.E. Quesenberry and J.W. Carpenter, eds.). Saunders, Elsevier Inc., St. Louis, Missouri, 608 pp.

Forsyth, C.S., and A.A. Frank. 1993. Evaluation of developmental toxicity of coniine to rats and rabbits. Teratology 48:59-64.

Greggor, A.L., Blumstein, D.T., Wong, B.B.M., and O. Berger-Tal. 2019. Using animal behavior in conservation management: a series of systematic reviews and maps. Environmental Evidence 8(Suppl 1):23. <https://doi.org/10.1186/s13750-019-0164-4>

Hamilton, L.P., Kelly, P.A., Williams, D.F., Kelt, D.A., and H.U. Wittmer. 2010. Factors associated with survival of reintroduced riparian brush rabbits in California. Biological Conservation 143:999-1007.

Hickman, K. 2016. Up close and personal with wild pygmies and pikas: How advances
in camera trap technology are expanding wild lagomorph research capabilities. Presented at 5th World Lagomorph Conference. Proceedings of the 5th World Lagomorph Conference; Turlock CA.

Higgins, K.F., Jenkins, K.J., Clambey, G.K., Uresk, D.W., Naugle, D.E., Klaver, R.W., Norland, J.E., Jensen, K.C., and W.T. Barker. 2012. Vegetation Sampling and Measurement. Pp. 381-409, in The Wildlife Techniques

Manual, Volume 1 Research. 7th edition. (N.J. Silvy ed.). The John Hopkins University Press. Baltimore, Maryland, 686 pp.

Hobbs, M.T., and C.S. Brehme. 2017. An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. PloS one, 12(10), e0185026.

Kelly, P.A. 2018. Reintroduction of the riparian brush rabbit in the San Joaquin Valley, California, USA. Global Reintroduction Perspectives: 2018, Case studies from around the globe.

Kelt, D.A., Kelly, P.A., Phillips, S.E., and D.F. Williams. 2014. Home range size and habitat selection of reintroduced *Sylvilagus bachmani riparius*. Journal of Mammalogy 95:516-524.

Lacher, Jr, T.E., Murphy, W.J., Rogan, J., Smith, A.T., and N.S. Upham. 2016. Evolution, Phylogeny, Ecology, and Conservation of the Clade Glires: Lagomorpha and Rodentia. Pp.15-26, in Handbook of the Mammals of the World: Volume 6. Lagomorphs and Rodents I, (D.E. Wilson, T.E. Lacher, Jr, and R.A. Mittermeier, eds). Lynx Ediciones, Barcelona, Spain, 987 pp.

Larrucea, E.S., and P.F. Brussard. 2008a. Efficiency of various methods used to detect presence of pygmy rabbits in summer. Western North American Naturalist 68:303-310.

Larrucea, E.S., and P.F. Brussard. 2008b. Habitat selection and current distribution of the pygmy rabbit in Nevada and California, USA. Journal of Mammalogy 89:691-699.

Larrucea, E.S., and P.F. Brussard. 2009. Diel and seasonal activity patterns of pygmy rabbits (*Brachylagus idahoensis*). Journal of Mammalogy 90:1176-1183.

Larsen, C.J. 1993. Report to the fish and game commission: status review of the riparian brush rabbit (*Sylvilagus bachmani riparius*) in California. State of California, Department of Fish and Game. Wildlife Management Division. Nongame Bird and Mammal Section Report 93-12.

Lee, J.E., Larsen, R.T., Flinders, J.T., and D.L. Eggett. 2010. Daily and seasonal patterns of activity at pygmy rabbit burrows in Utah. Western North American Naturalist 70:189-197.

Lehner, P.N. 1979. Chapter 3B How to Describe Behavior, pp. 43-52, Handbook of Ethological Methods. Garland STPM Press, New York, NY. 403 pp.

Lindell, C.A. 2008. The value of animal behavior in evaluations of restoration success. Restoration Ecology 16:197-203. doi:10.1111/j.1526-100X.2008.00389.x

Lilly, M.V., Lucore E.C., and K.A. Tarvin. 2019. Eavesdropping grey squirrels infer safety from bird chatter. PLoS ONE 14: e0221279.

Lowry, R. 2020. Vassarstats One-Way Analysis of Variance for Independent or Correlated Samples. VassarStats: Website for Statistical Computation [Online Statistical Calculator]. Vassar College. Poughkeepsie, NY. <http://vassarstats.net/anova1u.html>. Accessed 2020 Feb 11.

McCain, C.M. and S.R. King. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology 20:1760-1769.

Monclús, R. and H.G. Rödel, 2009. Influence of different individual traits on vigilance behaviour in European rabbits. Ethology 115:758-766.

Monclús, R., Rödel, H.G. and D. von Holst. 2006. Fox odour increases vigilance in European rabbits: A study under semi-natural conditions. Ethology 112:1186-1193.

Orr, R.T. 1940. The rabbits of California. Occasional Papers of San Francisco California Academy of Sciences. 19:1-227.

Phillips, S.E., Hamilton, L.P., and P.A. Kelly. 2005. Assessment of habitat conditions for the Riparian Brush Rabbit on the San Joaquin River National Wildlife Refuge, California. Endangered Species Recovery Program.

Pierce, J.E., Larsen, R.T., Flinders, J.T., and J.C. Whiting. 2011. Fragmentation of sagebrush communities: does an increase in habitat edge impact pygmy rabbits? Animal Conservation 14:314-321.

Preisser, E.L., Bolnick, D.I., and M.E. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

Rippert, J., Matocq, M., Feldman, C., and P. Weisberg. 2017. Population genetics and functional connectivity of the Riparian Brush Rabbit (*Sylvilagus bachmani riparius*): Implications for the conservation of an endangered lagomorph [dissertation]. University of Nevada, Reno. 65 pp.

Ruder, M.G., and J.R. Fischer. 2017. Final Report Case Number CC17-320A-M. Diagnostic Services Section. Southeastern Cooperative Wildlife Disease Study (SCWDS) College of Veterinary Medicine. The University of Georgia.

Shields, P.W. 1960. Movement patterns of brush rabbits in northwestern California. Journal of Wildlife Management 24:381-386.

Short, S.B., and W.C. Edwards. 1989. Accidental *Conium maculata* poisoning in the rabbit. Veterinary and Human Toxicology, 31:54-57.

Smith, A.T. 2008. Conservation of Endangered Lagomorphs. Pp. 297-315 in Lagomorph Biology: Evolution, Ecology, and Conservation (P.C. Alves, N. Ferrad, and K Hackländer, eds). Springer-Verlag Berlin Heidelberg, New York, 413 pp.

Smith, A.T., Johnson, C.H., Alves, P.C., and K. Hackländer. 2018. Lagomorphs: pikas, rabbits, and hares of the world. John Hopkins University Press, Baltimore, Maryland, 266 pp.

State of Washington. 2005. Data model – Sunrise/sunset. [Microsoft Excel workbook]. Research & Data, Department of Ecology, State of Washington. Retrieved from https://ecology.wa.gov/Research-Data?topics=&cats=29

Stoner, C., Bininda-Emonds, O., and T. Caro. 2003. The adaptive significance of coloration in lagomorphs. Biological Journal of the Linnean Society. 79:309-328.

Tyndale-Biscoe, C.H. 1953. A method of marking rabbits for field studies. The Journal of

Wildlife Management. 17:42-45.

Welbourne, D.J., Paull, D.J., Claridge, A.W., and F. Frederic. 2017. A frontier in the use of camera traps: Surveying terrestrial squamate assemblages. Remote Sensing in Ecology and Conservation. 3:133-145.

Williams, D.F. 1986. Mammalian Species of Special Concern in California. State of California, The Resources Agency, Department of Fish and Game, Wildlife Management Division Administrative Report. California Department of Fish and Game. 86-1:23-24.

Williams, D.F. 1988. Ecology and management of the riparian brush rabbit in Caswell Memorial State Park. Department of Biological Sciences, California State University, Stanislaus.

Williams, D.F. 1993. Population censuses of riparian brush rabbits and riparian woodrats at Caswell Memorial State Park during January 1993. California Department of Parks and Recreation.

Williams, D.F., and G.E. Basey. 1986. Population Status of the Riparian Brush Rabbit (*Sylvilagus bachmani riparius*). Contract Final Report. Wildlife Management Division, Nongame Bird and Mammal Section. State of California Department of Fish and Game.

Williams, D.F., Hamilton, L.P., Lloyd, M.R., Vincent, E., Lee, C., Edmondson, A., Youngbloom, J.J., Gilardi, K., and P.A. Kelly. 2002. Controlled propagation and translocation of riparian brush rabbits: Annual report for 2002.

Endangered Species Recovery Program, Department of Biological Sciences, California State University, Stanislaus.

Williams, D.F., Kelly, P.A., Hamilton, L.P., Lloyd, M.R., Williams, E.A., and J.J. Youngblom. 2008. Recovering the endangered riparian brush rabbit (*Sylvilagus bachmani riparius):*Reproduction and growth in confinement and survival after

Translocation. Pp 349-361 in Lagomorph Biology: Evolution, Ecology, and Conservation (P.C. Alves, N. Ferrad, and K Hackländer, eds). Springer-Verlag Berlin Heidelberg, New York, 413 pp.

Wittmer, H.U., Kelt, D.A., Kelly, P.A., and D.F. Williams. 2016. Use of simulation modeling to evaluate management strategies for reintroduced riparian brush rabbits in California. Journal of Fish and Wildlife Management. 7:334-346.

United States Fish and Wildlife Service (USFWS). 1998. Recovery plan for upland species of the San Joaquin Valley, California. Region 1, Portland Oregon. 319 pp.

United States Fish and Wildlife Service (USFWS). 2000. Endangered and threatened wildlife and plants; final rule to list the riparian brush rabbit and the riparian, or San Joaquin Valley, woodrat as Endangered. Federal Register. 65:8881-8890.

van der Vinne, V., Riede, S.J., Gorter, J.A., Eijer, W.G., Sellix, M.T., Manaker, M., Daan, S., Pilorz, V., and R.A. Hut. 2014. Cold and hunger induce diurnality in a nocturnal mammal. Proceedings of the National Academy of Sciences of the United States of America. 111:15256-15260.

von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., and R. Schönheiter. 1999. Social rank, stress, fitness, and life expectancy in wild rabbits. Naturwissenschaften 86:388–393.

Zoloth, S.R. 1969. Observations of the population of brush rabbits on Año Nuevo Island, California. Wasmann Journal of Biology 27:149-161.

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In. Litt. References

Heffernan, K. and Takahashi, F. 2017. Riparian Brush Rabbit Surveys During Flood Event 2017, San Luis National Wildlife Refuge Complex 2017. San Luis National Wildlife Refuge Complex, CA.

Takahashi, F. 2017. Brush Rabbit Flood Issues Fact Sheet, USFWS January-April 2017. U.S. Fish and Wildlife Service. San Luis National Wildlife Refuge Complex, CA.

Takahashi, F. 2017. 2017 Riparian Brush Rabbit Flooding Mortality Report. U.S. Fish and Wildlife Service. San Luis National Wildlife Refuge Complex, CA.

APPENDICES

APPENDIX A

CAMERA SITE SUMMARIES

The purpose of this appendix is to document the field of view of the camera sites utilized in this project. Photos from the beginning of the survey and the end of the survey are provided to catalog the changes of the site's environment. Photos with riparian brush rabbits were selected to provide a sense of scale within the context of the focal species. The resources in the photos are listed in Table 3 and illustrated in Figure 17. Details of the camera orientations and alterations are listed in Table 4.

PH1

Figure 18. PH1 in March 2017. PH1 was established to view riparian brush rabbit interactions with poison hemlock. Its view is parallel to the lower Pelican Trail facing west. It was attached to a stake approximately 2 meters north of RunB1. Note the "V" shaped dried stem in the bottom right corner that is not inundated by the water in the upper right of the photograph.

Figure 19. PH1 in April 2017. Rainfall and flooding continued through March into April 2017. The bank was eroded in part by raccoons, photographed on multiple occasions excavating it for food. Note how the "V" shaped stem at the right is underwater due to the continued flooding in the area.

Figure 20. PH1 in June 2017. The lower trail was dry and subsequently reopened later in June. With that, PH1 was completely exposed to theft and thus retired.

PH2

Figure 21. PH2 in March 2017. The PH2 camera was attached to an elderberry trunk to view riparian brush rabbit interactions with poison hemlock. It faced west towards a lower road of the Vierra levee. It was next to a coyote brush adjacent to a road connecting the upper levee of the Pelican trail to the lower road. During the flood the camera photographed trespassers on the lower trail that were examining the water.

Figure 22. PH2 in July 2017. As the poison hemlock died it revealed the California blackberry growing in the upper left corner. The PH2 camera was often tilted by California ground squirrels climbing up the elderberry to strip its bark. In one event, a coyote pulled the camera off its mount, dropping it a meter away from the site.

PH3

Figure 23. PH3 in March 2017. The PH3 camera was set at a pre-existing alfalfa pile where poison hemlock was present. The camera was attached to a coyote brush facing West. The blue in the far background is water from the flooded lower road.

Figure 24. PH3 in July 2017. The alfalfa pile was not replenished after exhausted but some poison hemlock remained. The shallow hole the RBR is facing may have been used as a nest but was unconfirmed in field and in photos as of 2020.

PH4

Figure 25. PH4 in March 2017. PH4 was set on a pre-existing pile of alfalfa where poison hemlock was present. The camera was facing North, parallel to the levee road in the upper right corner. Note the high forage lines on the coyote brush in the background, a condition found throughout the upland area.

Figure 26. PH4 in March 2017. A full bale of alfalfa ended up at the site during alfalfa distributions. Riparian brush rabbits fed on top of the bale, despite the exposure, climbing to the top from the lower part of the slope. Note the condition of the bale in this photo, taken March 6, compared to the previous photo, taken on March 7. During this time, the peak of the flooding, Alfalfa sites had high usage and notable changes in the amount of alfalfa present.

Figure 27. PH4 in June 2017. The last photo of a riparian brush rabbit taken at PH4. Alfalfa was present into August but riparian brush rabbit visitation declined.

PH5

Figure 28. PH5 in March 2017. The PH5 camera site viewed an existing alfalfa pile where poison hemlock was not present. The camera faced south, parallel to the upper trail (top left), and was attached to a stake.

Figure 29. PH5 in July 2017. Due to the fast growth of elderberry sprouts (seen in photo), the camera was moved from its low stake to an elderberry trunk 0.5m to the right in May 2017. Alfalfa was always present but riparian brush rabbit visitation declined over time.

Run7

Figure 30. Run7 in February 2017. The Run7 camera was set on stake within the California blackberry next to the upper Pelican trail, facing Hospital Creek. The entire site was composed of a California blackberry understory and black willow overstory. The blackberry contributed to the canopy as part of it was above riparian brush rabbit foraging height, as shown in the photo of a riparian brush rabbit standing.

Figure 31. Run7 in August 2017. Run7 camera was moved in July 2017 due to the defoliation of the blackberry exposing the camera. This position matched pre-flood camera position, placing the camera perpendicular to the upper Pelican trail rather than parallel. Blackberry leaves grew in the foraging area later in the season but were subsequently eaten by standing riparian brush rabbits.

RunB1

Figure 32. RunB1 in February 2017. The RunB1 camera was attached to stake secured to coyote brush, facing the lower Pelican trail. The blue in the top left behind the California rose is the water of the flooded trail.

Figure 33. RunB1 in July 2017. In July 2017 the lower Pelican trail was fully dry and reopened, exposing the camera. Prior to the flood, the California rose visible in the camera's prior location could obscure the camera from view, however, the slow recovery of the plant’s canopy post-flood left the camera exposed. Thus the camera was moved behind the coyote brush trunk, shifting its view to the right of the site.

RunB2

Figure 34. RunB2 in March 2017. The RunB2 camera was attached to the trunk of a coyote brush. The upper Pelican Trail can be seen in top right.

Figure 35. RunB2 in August 2017. In June 2017 an adjacent coyote brush collapsed on the site, adding branches to the camera's view and obscuring the camera's view of the upper trail.

APPENDIX B

ETHOGRAM AND BEHAVIOR TAGS

Table 38. *Ethogram with tags used for photos and detailed descriptions for each tag.*

Type	Behavior	Tag	Description	Specifications
Individual	Carry	carry	Hold object in mouth for multiple photos or moves with it	*plant species*
	Climb	climb	Either actively climbing or off the ground on top of object	
	Coprophagy	*Not identified*		
	Dash	dash	Quick movement across site	
	Defecation	defecation	RBR in position or appearance of scat following photo	
	Drink	drink	Nose and mouth to water	
	Dust Bath	dust bath	Consecutive photos of laying down in different positions	
	Feed	feed	Actively eating, vegetation in mouth, or sitting at alfalfa	*plant species, stand*
	Foraging	forage	RBR nose to ground or objects as moving around site	*stand*
	Grooming	groom	Includes grooming by licking, scratching, or shaking body	*shake OR scratch*
	Mark	mark	Rub chin and/or cheeks on object	
	Rest	rest	Sitting with ears down, not actively scanning / lying on front or side	*sit OR lay down*
	Smell	smell	Nose on same spot or object for 2 or more consecutive photos	*stand*
	Stand	stand	Standing on hind legs with front legs in air	
	Travel	travel	Slow crossing of site	
	Urination	urinate	RBR in position and no scat	
	Vigilance	vigilant	Still but alert (ears up, nose twitching, scanning)	*stand*
Intraspecies	Agonistic	agonistic	Fight or standoff between multiple RBR	
	Chase	chase	One individual chases another with purpose and speed	
	Grooming	groom	Grooms in presence of another RBR	
	Mating	mating	In the act or one following another with nose close to rear	
	Nose Touch	nose touch	2 RBR touch noses or smells the other's face	
	Smell	smell	One RBR smells another RBR anywhere but the head	
	Travel	travel	Multiple RBR moving together as group, slow movement	
	Vigilance/Rest	vigilance/rest	One RBR alert while another RBR rests	
Interspecies	Aggression	aggression	RBR chases or fights another species	*Group, Class, species*
	Chase	chase	Other species chases RBR	*Group, Class, species*
	Flight	flight	RBR leaves as other species arrives	*Group, Class, species*
	Predation	predation	Other species kills RBR or photographed holding dead RBR	*Group, Class, species*
	Rest	rest	RBR at rest while other species present	*Group, Class, species*
	Smell	smell	RBR smells other species	*Group, Class, species*
	Vigilance	vigilant	RBR vigilant while other species present	*Group, Class, species*

APPENDIX C

PHOTOGRAPH TAG ASSIGNMENT AND DEFINITIONS

Table 39. *Order of photograph tag assignment.*

Class	Group	Species	# RBR	# Species	Group	Species	Interaction	Behavior	Specification
Mammal	Lagomorph	RBR						carry	*Plant species*
								climb	
								dash	
								defecation	
								drink	
								dust bath	
								feed	*Plant species*
								forage	stand
								groom	scratch /shake
								mark	*Plant species*
								rest	sit /lay down
								smell	
								stand	
								travel	
								urinate	
								vigilant	stand
Mammal	Lagomorph	RBR	2				intra	agonistic	
			3					chase	
			4					forage	
			5					groom	
			6					mating	
			7					nose touch	
			8					smell	
			9					travel	
			10					Vigilance /rest	
Mammal	Lagomorph	RBR	2	multiple	bird	*species*	inter	aggression	
			3		Predator			chase	
			4		Rodent			flight	
			5		herp			predation	
			6					rest	
			7					smell	
								vigilant	
Mammal	Predator	*species*							
bird	Rodent								
herp									

Table 40. *Vegetation tags and definitions.*

Vegetation Tag	Tag Definition
Alfalfa	Dried *Medicago sativa* scattered off-trail by USFWS as food supplement
black willow	*Salix gooddingii* plant material
bundle	Bundle of vegetation and/or sticks carried by RBR for nesting purposes
CA blackberry	*Rubus ursinus* plant material
CA rose	*Rosa californica* plant material
leaf	Leaf of undetermined species of plant
Poison Hemlock	*Conium maculatum* plant material
twig	Twig of undetermined species of plant
willow	Leaf of undetermined species of *Salix*

APPENDIX D

LOG OF CAMERA STATUS

Table 41. *Log of camera status for each site per month. Camera malfunctions of active cameras included sessions with only photos of setup and takedown (A), sessions of the camera sliding down obscuring its vision (B), camera tilted obscuring the view (C), camera tilted by raccoons (C*), camera knocked down (D) or in the case of D*, carried by a coyote and dropped a 1 meter away, and vegetation moved and obscured view (E).*

	February	March	April 1	April 2	May 1	May 3	June	July	August
Run7	C	C	Not set	C	C	Active	A	Active	Active
RunB1	C*	Active	Not set	C	Active	Active	Active	Active	removed
RunB2	Not set yet	Active	Not set	C*	C	Active	A	C	Active
PH1	Not set yet	Active	Not set	Active	Active	Active	Active	removed	
PH2	Not set yet	D	Not set	D*	Active	Active	Active	C	removed
PH3	Not set yet	Active	Active	Active	Active	C	Active	Active	removed
PH4	Not set yet	Active	C	C	Active	Active	Active	C	removed
PH5	Not set yet	Active	C	Active	B	Active	Active	E	removed

APPENDIX E

DISCUSSION OF THE BEHAVIORAL REPERTOIRE OF THE RIPARIAN BRUSH RABBIT

Behavior Tag Summaries

In this section, I discuss the behaviors individually to provide a broader context for frequently photographed behaviors and expand on infrequently photographed behaviors in the total data (Table 32) and at individual sites (Table 33). Examining tagged behaviors individually provides details that better illustrate the ecology of riparian brush rabbit.

Agonistic

Agonistic behaviors involve intraspecific aggression, such as standoffs with RBR leaping at each other followed by chasing. There were 121 recordings in total involving all sites except Run7, with most photos taken at PH3 (57), PH5 (40), and PH4 (16); photographs from the other sites contained less than 7 percent of this interaction (Table 32, Table 34).

A possible reason for the high number of agonistic behavior photos at PH3 and PH5 may have been the fact they both have a more expanded viewing area perhaps allowing more to be captured by the cameras. Agonistic interactions typically use more space than other intraspecific interactions and could be confused for a chase without additional photos of the interaction. The high number of agonistic behavior photos may also be due to the differences between the three sites PH3 and PH5 are both covered and protected, whereas PH4 is almost completely exposed. It was probably not due to the presence of alfalfa because PH3's alfalfa was exhausted and never replenished, whereas the other two sites always had alfalfa present but had different numbers of agonistic behaviors (Figure 17, Table 33**Error! Reference source not found.**). Another possibility is that agonistic interactions may not be driven by food alone. They may be driven by other factors, accounting for this interaction in sites without food available. The increase of agonistic interactions at alfalfa sites may be a product of RBR concentrated near the food source and thus interacting more often than if food was evenly distributed.

Aggression

Aggression is a tag used to refer to RBR engaging in a fight or confrontation with another species. This involves similar actions to agonistic interactions such as a standoff and the RBR leaping towards the other individuals. It also included events where an RBR would chase another species. It was a relatively rare behavior, documented only six times, each an individual act of aggression. Five of these six events involved RBR being aggressive toward desert cottontails at PH3 (2), PH4 (2), and PH5. The other event involved an RBR leaping from the pile of alfalfa in PH3 towards a ground squirrel, seemingly as a territorial action over its food source. These six events all occurred at sites with alfalfa, possibly because of increased competition for the limited food resource. However, considering that alfalfa was present for five months in some sites, one might have expected more frequent aggressive interactions.

RBR may not generally engage in interspecific confrontations or may not be habitually aggressive.

Figure 36. An riparian brush rabbit aggressively leaps at a California ground squirrel at PH3.

Carry (Nesting)

The tag *carry* is defined as an RBR collecting or traveling with a leaf or bundle of vegetation in its mouth as nesting material. *Sylvilagus* rabbits do not collect and store plant material for food; it is a component of their nesting behaviors (Smith et al. 2018). None of the photos recorded the act of building a nest; however, *carry* is also referred to as *nesting* since it was the only nesting related behavior recorded.

Nesting was observed in 87 photos between March through May: PH2 (4 photos), PH3 (3), PH4 (6), PH5 (65), RunB1 (4) and RunB2 (5). In RunB2 a rabbit with a bundle of sticks, most likely coyote brush, was recorded during the day. Other possible *nesting* recordings were at RunB1 where an RBR was observed picking up and carrying a rose leaf and PH3 where an RBR carried poison hemlock. At PH3 and PH4, RBR were carrying single pieces of alfalfa, possibly carrying the food to a different location to eat, a behavior I could not confirm.

Although photos of RBR with bundles were taken during the day and night, photos were predominately captured at night (70 photos; 80%). The night photos were all at PH5 and of the same individual, identified by an ear notch and the continuous timeframe of the photos. The rabbit was documented over two hours (04:15 to 06:09) continuously traveling in front of the camera, collecting a bundle in the distance, then passing to a location behind the camera. Identified species in its bundles were California rose (*Rosa californica*; identified by its thorns) and alfalfa (the site was covered in alfalfa and the material was light-colored and straight). Two photos captured the same rabbit with bundles of material in daylight, one at 07:56 and the second 15 minutes later, 08:11. If these three consecutive events are treated as a single event, then they would be one of 11 nesting events. The continuous collection at PH5 suggests that the nest was nearby. The other nesting events happened on different dates with unmarked rabbits, so it is presumed that these were different rabbits. With so few separate events, the preference for nocturnal gathering would have to be evaluated further during a non-flood year.

Documenting nesting behavior between March and May corresponded with Basey (1990) who found RBR to be reproductive January through June. Basey documented young RBR from March through July, but young rabbits were rarely recorded in the photographs taken on this project (<10). Reproduction may have been curtailed during the flood; only two separate females were observed with nesting material, both in single time periods suggesting each had only one litter in the area and Basey estimated RBR to have three to four litters a season (Basey 1990). Alternatively, as the floodwater receded, pregnant females and young may have dispersed to the recently exposed habitat areas.

Figure 37. Riparian brush rabbit carrying a bundle of nesting material at PH5.

Chase

The behavior tag *chase* refers to an event where an RBR is involved in a pursuit. It could be intraspecific or interspecific depending on whether the RBR was the aggressor (intraspecific) or the species being chased (interspecific). It is different from *agonistic* in that it is only a pursuit; the chase may be to drive away a competitor or pursue a potential mate. Most of the *chase* photos captured were intraspecific events (314/336, Table 33). A total of 16 interspecific *chase* events were recorded in 18 photos, all involving desert cottontails, a much lower rate than intraspecific interactions (Table 16). It may be that the overall low rate of occurrence of interspecific interaction is due to RBR avoiding confrontation with a larger competitor, perhaps by keeping a safe distance.

Overall, *chase* was most recorded in alfalfa sites, supporting a territorial purpose for interspecific chases as the concentrated communal food source would bring more species into close contact with each other and the shortage of other forage would increase the likelihood of territorial behaviors.

Climb

The tag *climb* refers to the act of climbing or an RBR being on an elevated surface. Although climbing on alfalfa bales was photographed both during the day and night, cameras only captured brush climbing during the day. There were eight photos of RBR climbing blackberry, all at PH2 comprising two separate events. In B1 there was one event of an RBR climbing California rose in two photos. There were 16 photos of RBR climbing coyote brush covering five separate events: two at PH3, one at PH4, and two at RunB2.

Riparian brush rabbits climbing to access food resources may not be restricted to floods. At Caswell Memorial State Park, Basey (1990) observed RBR climbing about 0.5 m up a blackberry bush to access blackberry and rose during a time where there was not a flood or food shortage. Indeed, during live observation in this study, an RBR was witnessed hopping into and climbing a quail bush to eat the leaves above the over-browsed forage area despite plenty of annual grass adjacent to the bush that other RBR primarily fed on. These observations suggest that RBR may climb to forage even when ground-level food is readily available, possibly to access a greater variety of forage or more nutritious food sources (Basey 1990). However, based on the observed climbing abilities of RBR, climbing may be more opportunistic than habitual since RBR were only recorded climbing on lateral branches (horizontal or gently sloping). The RBR climbing event during direct observation started with the RBR hopping onto a low lateral branch of the quail bush, then proceeding to use thinner, secondary branches like steps to scale up the shrub, stopping at a point where it could reach leaves and eat. While stationary in the shrub, its feet were distributed among branches to evenly balance while reaching for far leaves. Similarly, climbing captured by camera traps showed use of lateral branches on coyote brush or branches to the tops of alfalfa bales, both giving the rabbit a platform to feed. In all of these instances RBR were positioned to view the open area adjacent to their climb, most likely to maintain vigilance for predators. RBR were not recorded climbing shrubs without these characteristics, suggesting climbing is an environment-dependent behavior.

Figure 38. Riparian brush rabbits were recorded climbing shrubs and downed vegetation to access resources.

Dash

Photos were tagged as *dash* if the RBR was blurred as if it was in fast motion or it was captured in no more than 2 of 5 photos in a series, indicating fast movement through the site. If used in a photo that was also tagged as intraspecific, it referred to an RBR moving through a site while another RBR is present, but not traveling with the focal RBR which was not performing other behaviors such as *feed* or *vigilant*.

Dash was recorded at all sites with most recordings at PH3 and PH5. In total, 3,529 photos were tagged with *dash*, 6.4% of all behaviors tagged, similar to *travel* (3,667 photos, 6.7%; Table 32). Perhaps *dash* and *travel* had similar numbers because they are both about RBR in transit and possibly interrelated. In future studies, having more tags to refer to different movement-related behaviors may yield more descriptive data. Simply combining *dash* and *travel* results in 7,196 photos, 13.09% of all behavior tags recorded, placing these behaviors as the fourth largest behavior set and demonstrating the considerable role of movement behaviors in RBR ecology (Table 32).

Defecation

Defecation was one of the rarest tags used in the study. This is because identification required a clear sequence of photos that showed the appearance of scat after an RBR moved and the body posture was too similar to grooming. There were 11 separate events recorded: RunB1 (1), RunB2 (1), PH3 (3), and PH5 (6). With the exception at one event at PH5 with three photos, all events consisted of a single photo. Four of these events were during the day and seven were at night. Most of the recordings were at PH3 and PH5, perhaps due to RBR spending more time at these sites for longer periods of time. Despite the extended time RBR spent at these sites, body postures indicative of coprophagy could not be distinguished in the photos. The low number of *defecation* tags may be due to limitations of the camera, photo resolution perhaps, especially since the pellets are so small (~5 mm). Further, because the captured instances were single, individual photo events, this behavior may be too fast for the cameras to capture adequately.

Drink

Drink was a tag for photos where an RBR has its face to water. It was recorded at 4 separate events, all at PH1. Only two sites had water, PH1 and RunB1, and the latter's camera angle was not conducive to assessing the behavior (Figure 17, Figure 32). Also, it is possible that RBR were not actually drinking, but sampling duckweed (*Lemna* sp.) that accumulated near the shore; however, considering the few instances *drink* was captured, it seems unlikely that RBR were using duckweed as a food source. It may be that RBR do not drink often, primarily depending on vegetation for moisture. Further, the water at the camera stations may not have been ideal. The water at PH1 and RunB1 was overflow from the flood and was sitting stagnant. Walking through it released the smell of sulfur, a sign of stagnation and poor water quality. Riparian brush rabbits may have traveled across the levee to Hospital Creek to drink from the fresh water of the creek.

Dust Bath

The behavior *dustbath* was identified as an RBR laying down and changing position rapidly in consecutive photos. Alternatively, if a single shot, it would be an RBR laying in a contorted position. Twelve photos were collected of two events, one night photo from March and one 2-minute event (11 photos) during the day in May. Dust baths were fast, not lasting more than a few moments; whether this is the norm or a product of the high predator presence is unknown. The sites also had significant canopy, whether this encourages dust-bathing by removing the threat of predation from above would need further study.

The act of dust bathing was only captured at PH5, possibly because of the unique microenvironment underneath a mature elderberry where there was finer soil and litter. PH2 was the only other site beneath elderberry, but it had a ground covering of thick litter and poison hemlock. At the live observation study site, VPMC, dust bathing was recorded at a site (VPMC5) similar to PH5, although with a different brush species, a large, mature quail bush, shading an area of fine litter and soil. In further research of the habitat requirements of dust baths, more substrate and environmental data should be collected as dust bathing is likely an important environmentally dependent behavior.

Feed

Photos were tagged *feed* if they contained an RBR holding plant material in a way where it could consume the material while scanning. It also included photos of individuals actively feeding on vegetation and photos where vegetation is visibly altered after an RBR was in contact with it. If the RBR had to stand on its hind legs to feed both *feed* and *stand* tags would be included. The tag *climb* was also included if the RBR was feeding on top of a bale of alfalfa or in a shrub.

In total, *feed* was the third most common behavior, comprising 19.66% of all behaviors photographed (Table 32). Material from some species, such as black willow and California rose, were acquired from leaves that fell from the canopy above. California rose was only eaten in 13 events, all at RunB1, two with RBR standing to reach foliage and the rest depending on fallen rose leaves (Table 15). All seven events (21 photos) of RBR eating willow, four (11 photos) of black willow specifically, were of fallen leaves. Black willow feeding was restricted to Run7, the only site with black willow. California blackberry was only present at Run7 (37 photos). Two events were recorded in August where an RBR stood on its hind legs, browsing blackberry leaves of the canopy. It moved from leaf to leaf, eating until no more were accessible. Whether RBR typically stand while feeding until the source is exhausted is unknown.

Alfalfa feeding had a slightly different tagging method: any photo where an RBR was at or on top of alfalfa was tagged as *feed*, even if their head was raised as if vigilant. This was based on live observation of RBR feeding on grass in a meadow where they would lower their head to quickly clip the grass then hold their head up, vigilant, as they masticated. In photos, this action set could appear as vigilant even though it is done with the purpose of eating. Since alfalfa is a food source similar to meadow grass and RBR were regularly observed feeding on alfalfa in this manner on the levee, an RBR orientated towards alfalfa in this way was tagged as *feed*. Consequently, alfalfa was the most eaten plant material with 10,498 out of the 10,804 feed photos recorded with alfalfa (Table 15, Table 32).

There were 160 photos of RBR eating poison hemlock, which although eaten more than the native plants, was more likely eaten due to availability over preference (Table 15, Figure 17). It was a very low proportion of *feed* recordings compared to the number of photos with RBR eating alfalfa, as if RBR were sampling the plant. A few of these recordings were of RBR feeding on poison hemlock when alfalfa is present suggesting the RBR will try to maintain a varied diet, even if that involves sampling unpalatable species. Whether RBR will sample this plant outside of a flood event is unknown and needs to be evaluated.

Flight

Flight was when a RBR would dash out of the camera view when another species entered the photo view. There were 24 separate events recorded, twelve at night and twelve during the day. One RBR flight was in response to a passing truck at PH4. Nineteen *flight* events were in response to desert cottontails. Eight of the 24 photos, one with the truck and seven with desert cottontails had multiple RBR present, in five of these photos the other RBR do not flee, but are vigilant or feeding. This suggests that some RBR may be habituated to disturbances and gauge the threat, whereas others are more likely to flee at the appearance of a perceived threat.

Figure 39. One riparian brush rabbit flees from a passing truck while the other remains at the alfalfa bale.

Forage

Forage was a sequence dependent behavior that involved consecutive photos of RBR moving through the site with their nose to the ground. If an RBR was examining different objects in consecutive photos the photo would be tagged *forage* instead of *smell*. It was the second most captured behavior at 11,770 photos, 21.41% of behaviors recorded, and was recorded in all sites (Table 32, Table 33). There is the possibility that the percentage of foraging is higher than normal due to the food shortage from the flood. However, with the exception of RunB1, the highest recordings were at alfalfa sites, suggesting that RBR forage more at food sites (Table 34). This fits with RunB1, a site that was formerly a food site before its rose was over browsed. It suggests that RBR will have different behavior patterns at different site types and that creation of food sites can alter this pattern. The number of photos may have been artificially low due to identification error as there may not have been enough space to differentiate this behavior from traveling in the small areas of sites PH2 and Run7.

Groom

The tag *groom* includes multiple behaviors involved in hygiene such cleaning, shaking, and scratching. The base tag for grooming referred to an RBR cleaning itself by rubbing its mouth on parts of its body, presumably licking dirt and debris. It does not include dust bathing. It is unknown if RBR dust bathe for hygiene or purely thermoregulation. *Groom* had subtags *shake* and *scratch* as they are related to hygiene, but are more responses to the external environment, particularly parasites. *Scratch* was the most recorded at 212 photos whereas *shake* was recorded in 72 photos. One of the reasons scratching was included in *groom* was that it would sometimes be a component of self-cleaning or it could be done as an independent behavior. Sometimes a *scratch* would turn into *groom* as an RBR would first scratch with the back leg, then extend its foot and clean it, similar to grooming, where an RBR would lick its forepaws before rubbing them over its face. These subtags represented a small component of total *groom* photos (1,755), most of which were RBR cleaning their fur. Groom was photographed about the same amount as climbing, suggesting it is a relatively minor part of RBR behavioral ecology (Table 32).

A potential shortcoming with this behavior tag was that it could include *coprophagy* without knowing or identifying it because it is indistinguishable from grooming in still photographs.

Mark

The tag *mark* refers to RBR scent marking an object by touching the object with its chin or cheek. There were 39 photos of this behavior in 26 events. *Mark* was mainly captured at site PH3, perhaps because there was a low branch from the coyote brush that was accessible for marking. However, PH3 was the only site where an RBR marked a sprout of poison hemlock. Although this behavior was documented more at sites with alfalfa, it wasn't always done when alfalfa was present, suggesting that territorial marking is not related to food resources but rather for some other territorial or social reason, such as reproduction. It could be a response to the large number of RBR at alfalfa sites; however, most marking was captured in April and May, whereas the peak concentration of RBR was in March (Heffernan and Takahashi 2017). As all sites with *mark* photos had low or grounded branches, future camera studies evaluating this behavior would benefit from choosing locations with similar features.

Mating

The tag *mating* includes RBR in the act of mating as well as pre-mating behaviors, such as when one rabbit closely follows another with its nose low or in close contact with the rear of the leading female. Nineteen events were captured; nine took place at night and the rest during the day. The night events happened in March (PH4 and PH5), April (RunB1 and PH5), and July (RunB2). Daytime events were in March (PH4), August (RunB1 and RunB2), and April through July (PH3). At all of these sites, the collection of nesting material (*carry*) was recorded as well. The dates of mating and pre-mating behavior differ somewhat from the reproductive period recorded by Williams (1988) and Basey (1990), January through June. Moreover, Williams et al. (2002) did not find juveniles after September 19, setting the end of the mating period in July. The difference in dates may be due to the flood event shifting the reproductive season. During the captive breeding program, RBR in the propagation enclosures were reproductive year round, suggesting that RBR may alter reproductive behavior in atypical situations or environments (M. Lloyd pers. comm.). However, the differing reproductive periods may also be due to population differences as both the Williams and Basey studies were at Caswell MSP. In conclusion, the discrepancies between this project and previous studies highlight the need to continue research on RBR reproduction.

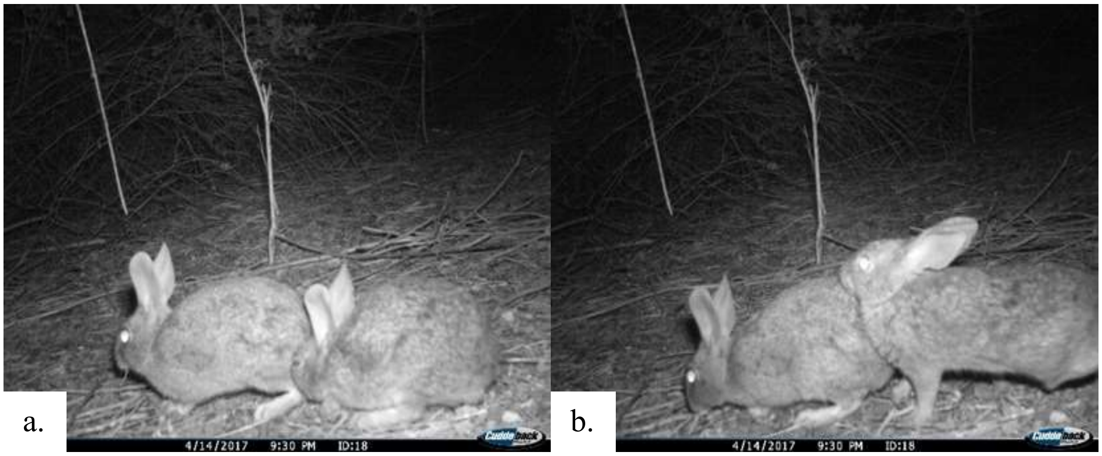

Figure 40. Pre-mating behaviors included close following (a.) with subsequent smelling (a. and b.).

Nose touch

Nose touch refers to a social behavior where a riparian brush rabbit smells another RBR's face. There were 35 separate events recorded with different outcomes. Zoloth (1969) observed this behavior as an infrequent interaction preliminary to chase interactions between juveniles and between juveniles and adults. Only eight events photographed resulted in a chase, suggesting that *nose touch* may not be limited to a territorial or dominance interaction. Indeed, two *nose touch* interactions resulted in copulation suggesting that this behavior is related to reproduction as well. The other 25 *nose touch* interactions did not seem to result in any further interaction.

This behavior was recorded at all sites, except Run7 and RunB2. This disparity may be due to the nature of these sites. As travel site there was nothing attracting RBR to linger there and thus less opportunity for intraspecific encounters (Table 3). However, it may also be that these sites, which had fewer photos due to camera interference, were not active enough to capture this relatively rare behavior.

Predation

Predation involves any interaction between a predator and RBR, whether pursuit, killing or carrying an RBR carcass. A shortcoming with this definition is that some predators were photographed carrying a dead RBR, but it is unknown if the RBR was hunted or found dead. Few acts of predation were captured in the 100,000+ photos used in this study despite 4,925 photos of predators. In the tagged photos there were only two separate events of predation over six photographs, both involving a coyote carrying an RBR out of the deep brush during the day.

In separate camera studies outside of this project, two predatory events were recorded: a Cooper's hawk (*Accipiter cooperii*) perched on a dead RBR and two raccoons were captured pulling a dead RBR apart, but in both events, the hunt was not recorded. Further, during field trials, a Cuddeback camera revealed sign of a quail kill in front of it, and the camera had one photo showing the teeth of a coyote without any footage before or after. All of this suggests that *predation* happens too fast for these cameras to capture. Consequently, *predation* is inferred from context photos such as pursuit, carrying, or feeding on the carcass. It may mean that researching RBR and predator dynamics requires a more specialized approach, perhaps the use of video cameras.

Rest

Rest is a varied behavior, but was only recorded in 299 photos (0.54%). It was used if an RBR had its one or both of its ears back, head down, and eyes possibly closed in one of two body positions, sitting or lying down. Subtags *sit* and *lay down* were included as RBR lying down could be resting for thermoregulation purposes, not purely to conserve energy. *Lay down* involved the RBR lying on its side or lying on its front, sometimes with its head and ears up as if *vigilant,* but its body relaxed. The tag *sit* referred to an RBR sitting with its body compact, sometimes with one ear up or both ears back and eyes fully open, aware of its surroundings. Possibly the only time an RBR would be completely asleep was if it was compact or lying down with ears flat on its back and eyes closed. This was rarely captured, possibly because cameras were stationed at sites of transit or feeding, both of which might not be conducive to RBR sleep.

The low number of *rest* photos may be a consequence of camera trap placement. The cameras may not have been placed at sites where that behavior is performed, especially if behaviors like sleeping are done in specific, confined environments. It could also be that while RBR seem comfortable performing other behaviors around the cameras, they may not feel secure enough to fully rest there. During live observation of RBR at rest, they would have their head or an ear raised, even if lying down, possibly due to the presence of an observer. Observer impact could be affecting RBR behaviors in the study site. Perhaps even the camera is having an effect on whether they rest or not.

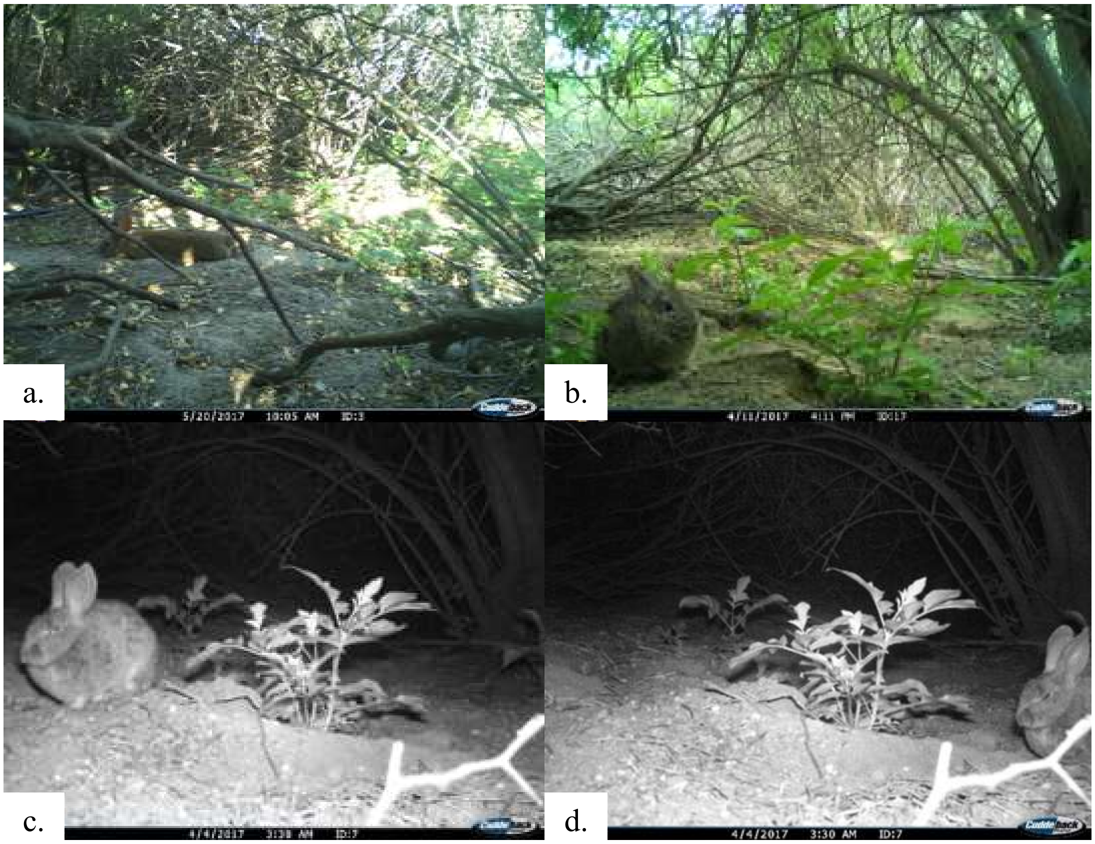

Figure 41. Riparian brush rabbits were captured resting in different positions: lying down (a.), sitting, compact with ears back and eyes open (b.), sitting, compact with ears up (c.), and sitting, compact with eyes closed (d.).

Smell

Smell refers to examining something, in two or more consecutive photos, or another animal with its nose. It differs from foraging in that they are standing still to examine something, whereas in foraging they are exploring while in transit. Interspecific *smell* involves another species; however, intraspecific *smell* involves smelling another RBR's body, but not the face—that behavior is covered by *nose touch*. *Smell* only accounted for 1.4% of behaviors recorded (Table 32). The low count of this behavior compared to other exploratory behaviors like *vigilant* and *forage*, may suggest that RBR may rely more on vision and hearing to assess their environment when stationary, and possibly using olfactory senses more while moving through a site.

Stand

Stand refers to an RBR standing on its hind feet with its front legs off the ground. If the RBR was performing another behavior while standing, that behavior was added to the metadata. Co-occurring behaviors included *vigilant*, *feed*, *forage*, and *smell*. *Smell* was when an RBR would stand to examine a single spot or branch above its head, possibly scenting other animals. *Stand* combined with *forage* referred to an RBR examining multiple points of the canopy as if searching for food. *Stand* was recorded at every station except PH1, possibly because of the relative openness of the site and the forage was inaccessible even when standing.

Basey (1990) found that RBR would stand on their hind legs to reach growing tips of blackberry and California rose. Similarly, RBR have been seen on a number of occasions along the Hospital Creek levee road standing on their hind feet to feed on overhanging willow branches (P. Kelly pers. comm.). Similar behavior was captured in this study of RBR feeding on blackberry leaves and attempting to access rose and willow. The apparent willingness of RBR to stand while browsing on shrubs and vines, along with their willingness to climb on and into them, suggest that these resources be assessed quantitatively for better management prescriptions in times of flooding.

Travel

Travel refers to the individual behavior of an RBR moving slowly through a site, the slow pace identified by the lack of blurring and shorter distances moved in photographic sequences. Intraspecific *travel* involved multiple RBR moving together, and was rarely not involved in mating behavior, 431 of 3,667 photos. This suggests that RBR may generally move about solitarily. Movement related behaviors such as *travel* may be inflated because of the sparse resources and apparently high concentration of predators that could have required RBR to move more often than they would otherwise.

Figure 42. Riparian brush rabbits traveling to the brush in PH4.

Urinate

The *urinate* tag is based on the body position of an RBR in a photo. Surprisingly, this tag was used only once. Possible explanations include the challenge of identifying the behavior in photographs, the behavior being too fast to photograph, or perhaps RBR did not urinate much at the camera stations.

Figure 43. The only photo of a riparian brush rabbit urinating, taken at PH3.

Vigilant

The tag *vigilant* was used when an RBR would be stationary with ears raised and eyes open as if alert or scanning. The only subtag used with *vigilant* was 'inter', which would be included if another species was present. *Vigilant* was recorded at all sites, was the most recorded behavior (35.9%), and ranged from vigilance while alone to being vigilant while near conspecifics or other species. The high frequency of vigilance behavior may have been a consequence of the high density of animals on the levee, requiring RBR to always be more alert, especially with the ever-present threat of predation. Alternatively, the high number of *vigilant* photos could be partly due to the camera equipment; any slight noise from the camera, or just the presence of the novel object in their environment, may have caused an RBR to be on increased alert.

Figure 44. A riparian brush rabbit is vigilant at RunB1 with ears upright and eyes open, alert and scanning.

Vigilance/Rest

Vigilance/Rest is a variant on *vigilant* that describes a specific type of interaction, an intraspecific interaction between RBR that appeared cooperative. A photo tagged with this behavior would have at least one RBR vigilant and at least one at rest in the same photo. There were 23 separate events, 82 photos, with this tag, less than 1% of all tagged RBR photos. Eight of these events occurred at night, mostly at PH3 and PH5, but with one at PH4. The daytime events also occurred at these alfalfa stations, mostly at PH3 and PH5. Those sites had greater numbers of photos of multiple RBR. The intraspecific combination of vigilance and rest, a behavior that appears cooperative, warrants more detailed study.

Figure 45. Vigilance/rest photograph taken at PH5 where the riparian brush rabbit in the foreground is at rest and other riparian brush rabbits are vigilant.

Behavior Results

The results of the camera study, combined with live observations, suggest that RBR maintain a high level of vigilance. RBR maintain vigilance even in the presence of larger numbers of RBR during the flood. Further, few recordings of cooperative behaviors, such as co-occurring vigilance and rest, suggest a somewhat solitary lifestyle. Nevertheless, RBR seem relatively passive in social situations. Despite engaging in occasional territorial behavior, RBR did not seem to hinder conspecifics from accessing alfalfa, a limited food resource that brought feeding rabbits in close proximity. Riparian brush rabbits seemed passive with other species as well, where even with the limited resources available, they rarely were in conflict.

Despite the stressed conditions of the flood, when supplemental food was provided (alfalfa), RBR seemed to engage in energy-expensive behaviors. They performed territorial behaviors such as marking, chasing, and agonistic interactions. They also engaged in reproductive behaviors such as mating and nesting. With supplemental feeding, the flood-marooned RBR were able to maintain social relationships, demonstrating a resilience and adaptation to the disturbance that characterizes their namesake habitats.

APPENDIX F

EFFECTIVENESS OF CAMERA TRAPS TO STUDY RIPARIAN BRUSH RABBIT BEHAVIOR

Impacts of Site Choice and Design

The differences in results between camera sites highlight how site choice can heavily influence the amount and type of data gathered (Table 3, Table 5, Figure 17). It is questionable whether cameras at stations with alfalfa are analogous to natural food sources like meadows or analogous to baited stations in other studies. Future RBR behavioral studies may need to evaluate if there are differences in recorded behaviors between natural forage and baited camera sites as well as unbaited, runway sites. Baited or food-supplemented stations will typically provide a higher number of photographs and therefore a greater quantity and variety of behavioral data. This is what happened in this study, however, whether this can be replicated with RBR during non-flood years, when there is plenty of food, needs evaluation. Observational behavioral ecology studies typically involve techniques with minimal manipulation of the environment, similar to the unbaited camera sites. As there is little manipulation in unbaited sites, it may be assumed that any activity and behavior data closer matches natural proportions. Future RBR behavioral ecology studies will need to strike a balance between these perspectives to evaluate RBR behavior with camera traps.

Future studies need to take these factors into account as well as the feasibility of the study's design. Forage sites may have more promise for quality behavioral data, however, there are more challenges associated with forage sites. Some of the optimal forage sites seemed to be edge habitats (brush/meadow), locations where cameras can be more exposed than when hidden in the brush. During the flood, most of the optimal sites were on levees that double as a public trail. This limited what sites could serve as camera sites due to increased risk of camera tampering and theft.

Camera Model Performance

Based on the variety of behaviors captured with the Cuddeback Black Flash E3 Model, it appears that the camera had little impact on RBR. There was a possibility of low capture rates due to the presence of the unnatural object, especially when it was often placed low enough for RBR to interact with it. However, the high proportion of photos containing RBR suggest that disturbance was minimal, possibly because of the device's minimal noise, compact size, and simple design. These features also facilitated the deployment of cameras close to trails, preventing human interference by being inconspicuous and easily hidden.

The compact design and minimal disturbance were disadvantageous in that under certain circumstances animals would interfere with the cameras. At RunB2, an RBR climbed on top of the camera that was attached to a coyote brush trunk to scale the brush, tilting the camera. This happened at PH2 as well where California ground squirrels would climb the camera to access the elderberry it was attached to. Both of these unexpected events illustrate the need to attach small cameras to a stake, rather than plants, in habitats where animals may use it as a platform to climb. In another event at PH2, a coyote pulled the camera off of its mount, carried and dropped it on the ground about 1 m away, but despite the impact the camera continued to operate. At PH1, raccoons digging into the mud on the waterlogged bank handled the camera to examine it, covering it in mud.

The small size and light weight of the cameras appeared to make them more sensitive to vibrations, such as from a traveling animal, when they were set close to the ground. For example, at PH5 the camera's strap slipped down its stake. At Run7, the memory card of the camera slipped out of position multiple times, even with different cameras, which may have been responsible for the low and inconsistent number of photos collected. Since Run7 was the most constricted space of all eight camera sites and the Black Flash E3 Model does not have a memory card lock, the most likely explanation was passing animals caused vibrations or jarred the camera.

Despite these disadvantages, considering the number of photos in non-food areas, future RBR studies would benefit from choosing cameras with similar features to the Black Flash E3 Model.

Studying the Riparian Brush Rabbit's Activity

Cameras were the optimal means for studying RBR activity because they could operate for days or weeks, collecting activity continuously, something that is very challenging to with direct (live) observation or live-trapping. A main concern for studying activity was whether the camera was in an optimal location to capture RBR resting and whether it was set to motion trigger or interval. All of the sites in this study had different activity periods resulting in high variance for each time period (Figure 5). This variation most likely stemmed from some cameras being at runway sites while others were at provisioned sites, and the rabbits remaining longer at the latter. However, it may also have been that at transit sites, RBR were moving so fast that they were not captured on camera. Additionally, the count of RBR rest may have been underestimated due to the cameras only activating with motion. An RBR resting for long periods may not have triggered the camera for the duration of its presence, resulting in fewer photos of RBR rest captured. These problems can be addressed in future activity studies by setting the cameras to photograph at intervals rather than by motion activation or set more camera stations in different areas.

Studying Riparian Brush Rabbit Behavior and Intraspecific Interactions

The behavior results were determined to a certain extent by the parameters set for each behavior tag (Table 38). For example, tagging photos as intraspecific if RBR were within 2 meters of each other may have inflated the number of those occurrences. That distance was meant to convey that the RBR were within visible distance of one another, and therefore interacting, and also to differentiate those photos from ones where an RBR was far in the background and only captured incidentally. The estimated distance of 2 meters may have overestimated or underestimated the actual social distance for RBR.

The presence of the camera may have inflated the number of *vigilant* photos. Although the Cuddeback camera is small, its presence could increase the wariness of an animal. However, the large variety of behaviors captured suggests that the disturbance is relatively minimal. Further, direct observation on a calm, quiet day from a hunting blind, found that RBR, although first fleeing, would return and resume activities as soon as 30 minutes after setup. The high numbers for vigilance may in part be due to the limitations of the camera. When feeding, RBR lift their head to scan (vigilance), often while still masticating. In live observation, this happens so often in a minute that it is easier to record this dual action of feeding while vigilant as a single behavior. In camera surveys, the cameras may only capture the more frequent behavior, vigilance, and the observer may not be able to distinguish whether a photo is an independent act of vigilance or part of the dual feeding/vigilant behavior.

Similarly, there is a possibility that an intraspecific *chase* event may not be an isolated behavior, but part of a larger interaction, presumably *agonistic*. In more confined areas, the camera could miss the full picture of an *agonistic* event, only capturing part of the chase component. Thus, a variety of sites with narrow and wide views is required to get a more complete picture of RBR behavior.

Studying Riparian Brush Rabbit Interspecific Interactions and Community Ecology

Riparian brush rabbit interspecific interactions with the surrounding community may not have been completely documented in this study, particularly with amphibians and reptiles. One of the major weaknesses of PIR camera traps is capturing ectotherms, primarily due to their body temperature hardly differing from the surrounding environment, thus not triggering the infrared sensor (Hobbs &

Brehme 2017). The, at times, slow movements and stillness of reptiles and amphibians combined with ectothermy result in inconsistent photo capture without an ectotherm-specific methodology (Welbourne et al. 2017, Hobbs and Brehme 2017). In this survey the only instances where reptiles were documented was when there was environmental movement, such as an endotherm present, despite being present near multiple sites. American bullfrogs (*Lithobates catesbeianus*) were consistently encountered when traveling through water to PH1 and RunB1, but none were recorded despite PH1 having a clear enough view of the water to capture aquatic birds swimming in the background. Similarly, a garter snake (*Thamnophis sirtalis fitchi*) was observed basking on an exposed pile of alfalfa, but was never recorded at a camera station. Although the low presence of amphibians and reptiles might be a consequence of the flooding, the very low number of camera captures (2), suggests that the Cuddeback cameras were not always triggered by amphibians and reptiles. Future camera studies on the biodiversity of RBR habitat and RBR interspecific interactions may need to employ different methods to document amphibians and reptiles (Welbourne et al. 2017, Hobbs and Brehme 2017).