Resource partitioning between Monterey dusky-footed woodrats (*Neotoma fuscipes luciana*) and brush rabbits (*Sylvilagus bachmani*) in maritime chaparral habitat

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Abstract

Resource partitioning is an ecological and evolutionary mechanism that allows species to share resources such as food or space. Resource partitioning may be key to reducing competition and promoting species coexistence. Resource partitioning occurs differently in various habitats but there are few field studies done on small mammals in an undisturbed chaparral habitat. Browsers in a central California maritime chaparral, Fort Ord Natural Reserve, could be partitioning sandmat manzanita (*Arctostaphylos pumila*). My study used motion-sensitive cameras to passively observe browsing activity of two dominant browsers, Monterey dusky-footed woodrat (*Neotoma fuscipes luciana)* and brush rabbit (*Sylvilagus bachmani*). I compared browsing activity to see how woodrats and rabbits are partitioning sandmat manzanita. I also compared browsing activity near and far to oak woodlands and if predator activity was a possible influence on browsing activity. My results suggest that woodrats and rabbits are partitioning sandmat manzanita by browsing height and across the reserve by location, near and away oak woodlands. Woodrats browsed at higher heights and closer to oak woodlands than rabbits. Assessing how predators influence browsing activity of woodrats and rabbits requires additional data. Documenting resource partitioning in an undisturbed habitat is beneficial for understanding the plant-animal interactions and predict the possible consequences of disturbances, such as fire, that would change the composition of the habitat.

Keywords

Resource partitioning, chaparral, manzanita, browsing, woodrat, rabbit

Introduction

Species sharing the same abiotic and biotic conditions (niche) may have to compete for resources (Hutchinson 1957). This competition for resources can be interspecific (different species) or intraspecific (same species) and can lead to resource partitioning, an ecological and evolutionary mechanism that allows species to share their resources and reduce competition (Chesson 2000; Morris 2003). How species partition and what factors influence resource partitioning are common questions asked in research to understand how species coexist to maintain the biodiversity of an ecosystem.

Resource partitioning occurs when species share resources, such as space, time, or food, and partitioning varies with different species and ecosystems (Schoener 1976). Resource partitioning differs among animal species and habitats (Farnworth et al 2002; Makhabu 2018; Singer 2007; Cameron and Toit 2003). As an example, resource partitioning among 3 sympatric species of woodrats (*Neotoma albigula*, *N. devia*, and *N. stephensi*) in scrub desert and juniper woodland habitats occurs in both space and time. The woodrats partition by having diet preference for different genera of evergreen plants and dominance for den space based on aggression levels (Dial 1988). Another example is in brown hares (*Lephus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in pastural farmlands, where the species partitioned their diet by selecting different species of grasses (Lush et al 2017).

As a way to partition their food and reduce competition, browsers may feed at different vegetation heights due to their body size and/or behaviors. This feeding-height separation hypothesis was first tested in 4 different sized species of browsers, giraffe, kudu, impala, and steenbok, in an African savanna habitat (du Toit 1990). Giraffes are capable of feeding on the lower vegetation heights but feed at higher vegetation heights when smaller browsers are present. This feeding height preference helps reduce the long-term exploitative competition with the smaller species of browsers that rely on the lower vegetation. Hulbert and Andersen’s (2001) study on partitioning between roe deer and brown hares also supported the feeding-height separation hypothesis with roe deer feeding more on higher browse and brown hares on grass.

In some cases where resources are not limited, predator-prey interactions or past competition may influence how species use resources. Predators affect resource partitioning and competition between their prey by changing the behavior of their prey, specifically anti-predator adaptions. Some anti-predation behaviors observed in small mammals have been temporal changes in activity (Fenn and Macdonald 1994), reduced activity range (Borowski 1998) and differences in foraging efforts in locations with high or low predation risk (Koivisto and Pusenius 2003).

Partitioning among mammals has not been studied in maritime chaparral habitats. Fort Ord Natural Reserve (FONR) has a maritime chaparral habitat dominated by sandmat manzanitas (*Arctostaphylos pumila*; manzanita hereafter). My study used motion-sensitive cameras to passively document resource partitioning at FONR between two browsers that both utilize manzanita, the Monterey dusky-footed woodrat (*Neotoma fuscipes luciana*; woodrat hereafter) and brush rabbit (*Sylvilagus bachmani*; rabbit hereafter). The body size of both woodrats and rabbits make it easier than other browsers to passively observe browsing activities within the dense chaparral shrubs. Hypothesizing that woodrats and rabbits partition manzanita, my specific questions are: 1) Are the two browsers partitioning manzanita by height? and 2) Are the two browsers partitioning across the reserve by location near and away from oak woodland and if so, does predator activity affect that?

To address these questions, I first, documented plant use by woodrats, which can climb, and rabbits, which are not known to climb. I predicted that woodrats and rabbits partition manzanita by browsing height, following the feeding-height-separation hypothesis (du Toit

1990). Woodrats would browse more on manzanita branches that are higher than where rabbits browse. Secondly, I documented the distribution of different browsing height in an area close to oak woodlands and an area that is away from oak woodland and compared it to the number of predators in the specific area. I predicted (1) more browsing activity on manzanita on higher branches than on lower branches in area close to oak woodlands; (2) more browsing activity on manzanita on low branches in area away from oak woodland; (3) less browsing activity when there is more predator activity; and (4) more browsing by woodrat near oak woodlands and more browsing by rabbits away from oak woodland in more a chaparral habitat.

Documenting how species partition resources contribute to the study of the effects of species loss on an ecosystem. This will help to better implement conservation of the ecosystem, especially when faced with ecological changes such as in climate or frequency of disturbances.

Methods and Materials

Study area

I conducted my research at the Fort Ord Natural Reserve (FONR), part of an old army base in Marina, CA (36.680924^{o}N, -121.7794933^{o}W). Surrounded by farmlands and urbanization, FONR is approximately 242 hectares of central California maritime chaparral mixed with oak woodlands. Many endemic species, found only at FONR, are also species of conservation concern (Griffin 1978; Sawyer et al. 2009). Maritime chaparral communities are shrubland habitats along the coast of California, bordering the Pacific Ocean.

Much of California has a Mediterranean-like climate. Mediterranean-like climate consists of summer months that are generally dry and wet winters. Winter in Mediterranean-like climate varies in length year to year but is generally shorter than summer. During my study period, July 2018-December 2018, the summer at FONR was generally dry and foggy (average temperature =

15.6°C) until approximately September when the rainfall started. Historical reports show a decrease in frequent fires in the Monterey Bay (central California coast) (Greenlee and Langenheim 1990). Without frequent fires or other disturbances, FONR mainly consists of matured shrubs.

Study Organisms

Undisturbed by fire, manzanita dominates the chaparral at FONR and both woodrats and rabbits utilize manzanita for either nest building or their diet. The size of woodrats and rabbits is ideal to passively observe browsing activities because I am able to accurately identify them browsing in videos. For these reasons, I have chosen woodrats, rabbits, and manzanita as my study organisms.

Monterey dusky-footed woodrats are a subspecies of woodrat endemic the Monterey Bay area. Woodrats utilize their surroundings to build nests from plant material such as twigs. Woodrat nests are often passed down to other woodrats and shared with other species (Meserve 1974; Cranford 1982; Carraway and Verts 1991). This unique nest-building behavior allows their nest to be studied and to get a better understanding of the environment’s natural history through their building material used. Woodrats nest mainly in oak woodland, but are also found in chaparral (Horton and Wright 1944). Woodrats breed between March and April (Donat 1933). The home range of woodrats is 0.17-7.38 ha. Males generally have larger home range than females (Innes et al. 2009). Individual woodrat nests may lay central to their home range and activities (McGinley 1984).

Brush rabbits live in ground burrows underneath dense vegetation cover, like chaparral (Orr 1935; Chapman and Litvaitis 2003). They breed between January to May (Mossman 1955;

Chapman and Harman 1972). Rabbit home ranges in chaparral habitat are 0.14-0.57 ha (Connell 1954). Population density possibly influences the home range of rabbits (Zoloth 1969).

Arctostaphylos pumila (sandmat manzanita) is an endemic shrub found at FONR (http://ucjeps.berkeley.edu/eflora/). Manzanita is one of the dominant shrubs at FONR; it is abundant and spread throughout the chaparral. Manzanita grows as dense mounds that provide cover to many mammalian species such as the brush rabbit.

Transects

I set up 4 transect lines that started from the western borders of polygons A1 and A3 as a baseline to move cameras and document browsing heights. Each transect was about 100m apart and was in oak woodlands and chaparral habitats at different segments of the transects. The length of transect segments varied depending on the chaparral growth. Some chaparral shrubs were too dense for me to navigate through, so I restarted the transects at the other side of the dense vegetation.

Browsing Height

From late July 2018 to December 2018, I studied browsing heights of both woodrats and rabbits by documenting their browsing activity within manzanita in the northern reserve of FONR (Figure 1); with 4 motion-sensitive cameras (Browning dark ops2017, model BTC-6HD-940). I set out my cameras for a total of 298 camera days, starting at FONR’s western border in polygons A1 and A3. After 3 to 7 days at a time, I moved my cameras east approximately 40m apart along the 4 transects. I set up each motion-sensitive camera in front of an individual manzanita where I had observed browsing (e.g. clipped branches, piles of litterfall). I disregarded the age of the manzanita. The cameras recorded 1 min videos when triggered by motion with 30 sec intervals before responding to motion again. The cameras captured 604 counts of activities from 15 different species (Table 1) from July 2018 to December 2018. I measured browsing height of woodrat and rabbits in videos using ImageJ (ImageJ 1.52a) with images of the specific manzanita. I included a one-meter stick in the still photo of each manzanita that I had a camera viewing to calibrate ImageJ. I tested the accuracy of heights measured by ImageJ by taking photos of the manzanita from the same positions as when I recorded browsing and measured actual heights of different branches. I measured the height of the same branches on ImageJ to compare to the actual heights ($y= 1.2116x + 0.2882$, $R^2 = 0.9284$; Figure 2).

Browsing Activity and Predators

I studied the effects of predators on the number of browsing episodes and the location of browsing by recording the browsing height that I saw along the same 4 transects as my cameras but only used data across the A1 and A3 polygon. Only data from polygon A1 and A3 was used because they were the closest polygons to the stationary cameras at FONR that I had data from (Figure 1). I used data from 2 stationary cameras at FONR that faced chaparral and chaparral/oak woodland border with wide viewing scope that captured both vegetation and predator activity. The stationary cameras were on for the entire duration of the month. For the browsing height, I only compared data from A1 and A3 polygons during August 2018 and September 2018 because they were the two polygons with the most consist overlap in data from both the stationary cameras at FONR and my camera data. I recorded data from the stationary cameras at FONR which included the species seen in the picture and the date the picture. I used a one-meter stick to measure browsing heights along the transects . Then I categorized browsing height as low (0-30cm) or high (30-60cm and up). The average distance of each browsing observation from oak woodland was measured using Google Earth Pro.

Data Analysis

I used Adobe Bridge CC 2019 to record video data from my 4 cameras. I tagged the full common name of species seen in the video, polygon, type of activity and the height of any browsing. I had 3 subcategories of activities: browsing, foraging, and others. I called an activity “browsing” if I saw an individual actively removing biomass from manzanita. “Foraging” is species actively searching for food such as nose down and scratching at parts of the manzanita shrub. The “Others” category included other activities such as walking by the camera. I only used browsing activities of woodrats and rabbits in analyzing browsing heights; I compared heights using a t-test with unequal variance (Microsoft Office 365, Excel).

For the browsing activity in regard to predator activity, I used my camera data from polygon A1 and A3 and the camera data from the 2 stationary FONR cameras. There was a combined total of 314 camera days from my cameras and the stationary cameras in polygons A1 and A3 from July 2018 to December 2018 (Figure 4), which was used to compare the relative number of species at the polygons. I categorized species from my data and the stationary cameras at FONR into their trophic level; omnivore, herbivore, seed feeder, or predator (Table 2). I found the number of observations per day of each category by dividing the number of species seen by the camera’s total of days deployed, which accounts for the varying differences in the length of camera deployments. I compared the low and high browsing heights that I observed on the transects in A1 and A3 during August and September to the monthly number of predators seen on the FONR cameras in the same polygons during the same time. From browsing height activities that I observed from my camera data (Figure 3), I associated low browsing heights with rabbits (0cm to 30cm) and high browsing heights with woodrats (30cm and up). I compared the average distance of browsing observations from oak woodland using a t-test with unequal variance (Microsoft Office 365, Excel).

Results

I set out my cameras for a total of 298 camera days, from late July 2018 to December 2018. The 4 motion-sensitive cameras captured 604 counts of activities from 15 different species.

Browsing Height

Woodrats and rabbits were in 349 of the 604 total counts of activity. Woodrats were in 221 out of the 349 total counts of recorded activity, but only browsed 14 separate times. Within the same time frame, there were fewer rabbits (128), but rabbits actively browsed in approximately half of those (51 times).

Both woodrats and rabbits browsed at a wide range of heights with some overlap but there was a clear distinction in their average browsing height. Woodrats browsed at heights from 0cm (ground level) to 56cm. Rabbits browsed at heights from 0cm to 30cm. Overall, woodrats browsed significantly higher on the manzanitas and over a wider range of heights than rabbits (31.2cm ± 4.7cm (SE), and 6.4cm ±1.7cm (SE), respectively; $t(14)= 4.9$, $p = 0.00022$; Figure 3).

Browsing Activity and Predators

Surprisingly, there were more predators than seed feeders, omnivores, and herbivores during July 2018 and August 2018 in polygons A1 and A3. Predator activity declined during September 2018 before rising again in November 2018 and December 2018 (Figure 5). No predator data from the stationary FONR camera was available for October 2018.

Woodrat browsing activity on manzanita along transects in polygon A1 was significantly ($t(8) =5.185$, $p=0.00084$) closer to oak woodlands (mean = 11.9m ± 7.4m (SE)) than in polygon A3 (mean = 54.21m ± 22.40m (SE)). There were more woodrat browsing activity than rabbit browsing activity in polygon A1 during August 2018 and September 2018 (Figure 6a), but more rabbit browsing activity than woodrat browsing activity in polygon A3 during the same time (Figure 6b). In polygons A1 and A3 during August 2018, there were more predators seen on the stationary FONR cameras than woodrat and rabbit browsing activity observed on the transects (Figure 6a, 6b). In polygons A1 and A3 during September 2018, there were fewer predators seen than browsing observed (Figure 6a, 6b).

Discussion

Browsing Height

The woodrats and rabbits at FONR browsed at different heights on manzanita, an unlimited resource at FONR. Prior to this study, partitioning by feeding height was mainly supported between significantly larger browsers and small browsers in other ecosystems (du Toit 1999; Hulbert and Andersen 2001). It is possible that the feeding-height separation I observed between woodrats and rabbits at FONR could be influenced by another factor other than body size.

My study was limited in that it documented browsing only during the months of July-December. A long-term study that accounts for breeding seasons, of the woodrats and rabbits, and environmental variability, such as more rainfall, that could affect browsing activity would be best to accurately conclude that woodrats and rabbits do browse at different heights, supporting the feeding-height separation hypothesis. Future studies could also see what specific parts of manzanita woodrats and rabbits are using.

Browsing and Predators

From the browsing heights of woodrats and rabbits measured in my study, I hypothesized that the low browsing on manzanita that I observed on my transects was from rabbits and the high browsing were from woodrats. Based on this, I conclude that woodrats browse closer to oak woodlands while rabbits browse farther away. Woodrats center activities around their nests (Horton and Wright 1944) and as expected, from reduced activity range as an anti-predator response, would be browsing closer to their nests to reduce the risk of predation. Similarly, rabbits would browse closer to their burrows under dense chaparral shrubs (Chapman and Litvaitis 2003). Although risk of predation is a plausible explanation for the difference in browsing location between woodrats and rabbits, it is not the only possible explanation. Foraging energetic cost could influence how far woodrats and rabbits browse and furthermore, vary with breeding season (Horton and Wright 1944; Chapman and Litvaitis 2003)

My study was limited in the range of data. I only compared data in polygons A1 and A3 during August and September because it was the months and polygons that I had the most consistent data. A long-term study with consistent data from other polygons and longer duration would be best to account for possible variations like weather. A long-term study would also assess the possible explanation that browsing range varies due to breeding season. My study only measured the distance of browsing observations to nearby oak woodland. It would be more accurate to compare distance from oak woodland if there was also an assessment of the number of woodrat nests and rabbit burrows in the same areas.

Conclusion

My short-term study on the browsing activities of woodrats and rabbits suggest that they are partitioning manzanita by browsing height. Data from both my study and stationary cameras at FONR also suggest that they may be partitioning at a larger spatial scale with woodrats closer to oak woodlands and rabbits closer to chaparral. A long-term study on the browsing activities of FONR would be best to support the findings of my study. Documentation of browsing activities at FONR is beneficial in understanding the plant-animal interactions of the undisturbed chaparral and predict the possible consequences of disturbances, such as fire, that would change the composition of the habitat.

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Tables

Table 1. Summary of observations: The number of separate observations of browse, forage, and "others" activities for species (rows) in the videos from my camera data. The total sum of individual species is given in the far-right column; the bottom row is the total sum of the 3 categories of activities.

Species	**Browse**	**Forage**	**Others**	**Total**
Misc. bird	1	15	105	121
Bobcat	0	0	12	12
Quail	0	0	1	1
Coyote	0	0	1	1
Deer	0	1	6	7
Fox	0	0	1	1
Lizard	0	0	3	3
Opossum	0	0	2	2
Rabbit	51	10	67	128
Raccoon	0	0	14	14
Red squirrel	0	0	3	3
Scrub jay	0	1	0	1
Skunk	0	0	1	1
Small mammal	1	8	79	88
Woodrat	14	15	192	221
Grand Total	**67**	**50**	**487**	**604**

Table 2. Species classified by trophic role: Specific species (left column) were classified into their trophic role of either herbivore, omnivore, predator, or seed feeder (right column).

Species	**Role**
Deer	Herbivore
Rabbit	Herbivore
Woodrat	Herbivore
Opossum	Omnivore
Quail	Omnivore
Raccoon	Omnivore
Skunk	Omnivore
Bobcat	Predator
Coyote	Predator
Fox	Predator
Mountain lion	Predator
Turkey vulture	Predator
White tailed kite	Predator
Misc. bird	Seed feeder
Blue jay	Seed feeder
California thrasher	Seed feeder
Small mammal	Seed feeder
Squirrel	Seed feeder

Figures

Figure 1. Fort Ord Natural Reserve, Northern Reserve: The Northern Reserve is the largest of two parts of FONR. The reserve is divided into polygons. I collected browsing heights of woodrats and rabbits within the polygons shown (red). Only browsing observations and predator activity from polygons A1 and A3 during August and September were used to compare browsing activity to predator activity.

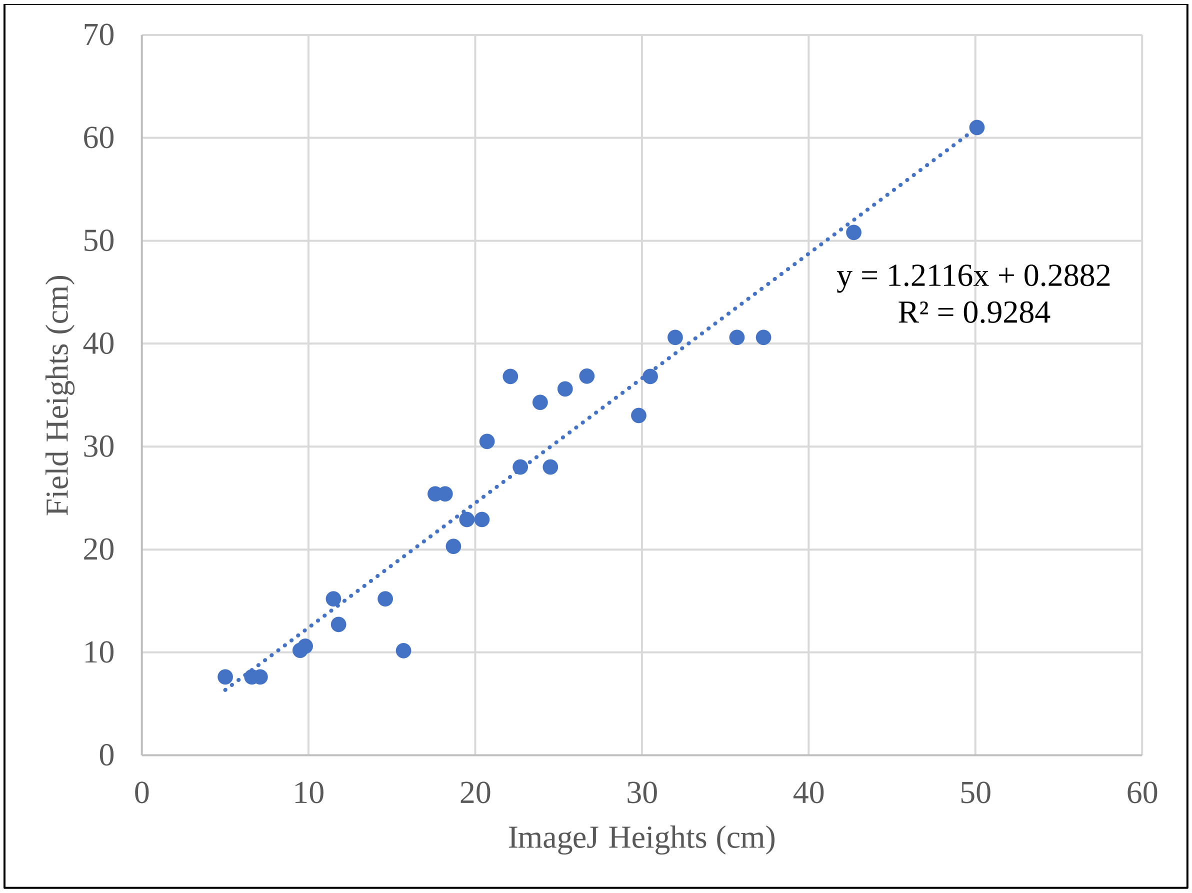

Figure 2. Heights measured from ImageJ compared to the actual browsing height measured in the field: Browsing height in videos could predict the actual browsing height in the field (y= 1.2116x + 0.2882; R^2 = 0.9284).

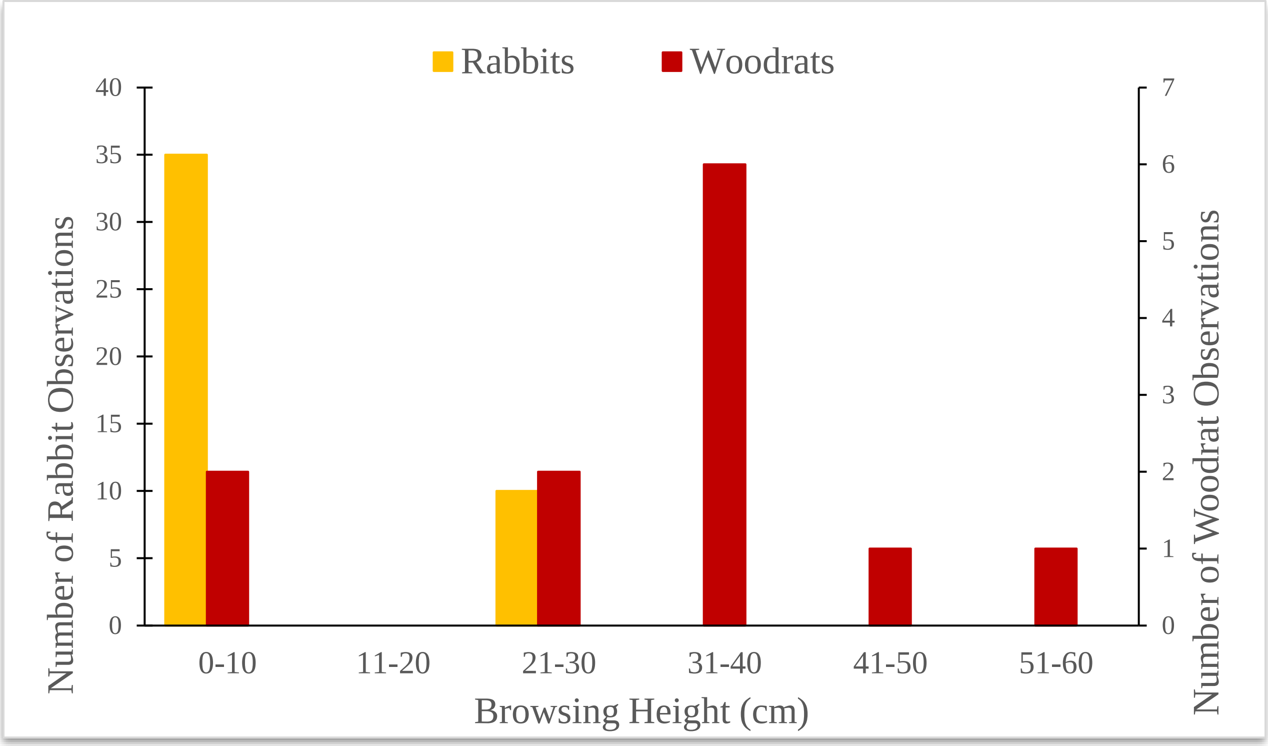

Figure 3. Browsing heights of rabbits (*Sylvilagus bachmani*) and woodrats (*Neotoma fuscipes luciana*) across FONR (Fig 1) from July 2019 to December 2019 was measured using ImageJ in the videos. Rabbits browsed more in low heights while woodrats browsed more in high heights. The browsing heights of woodrats and rabbits overlapped in the lower browsing heights.

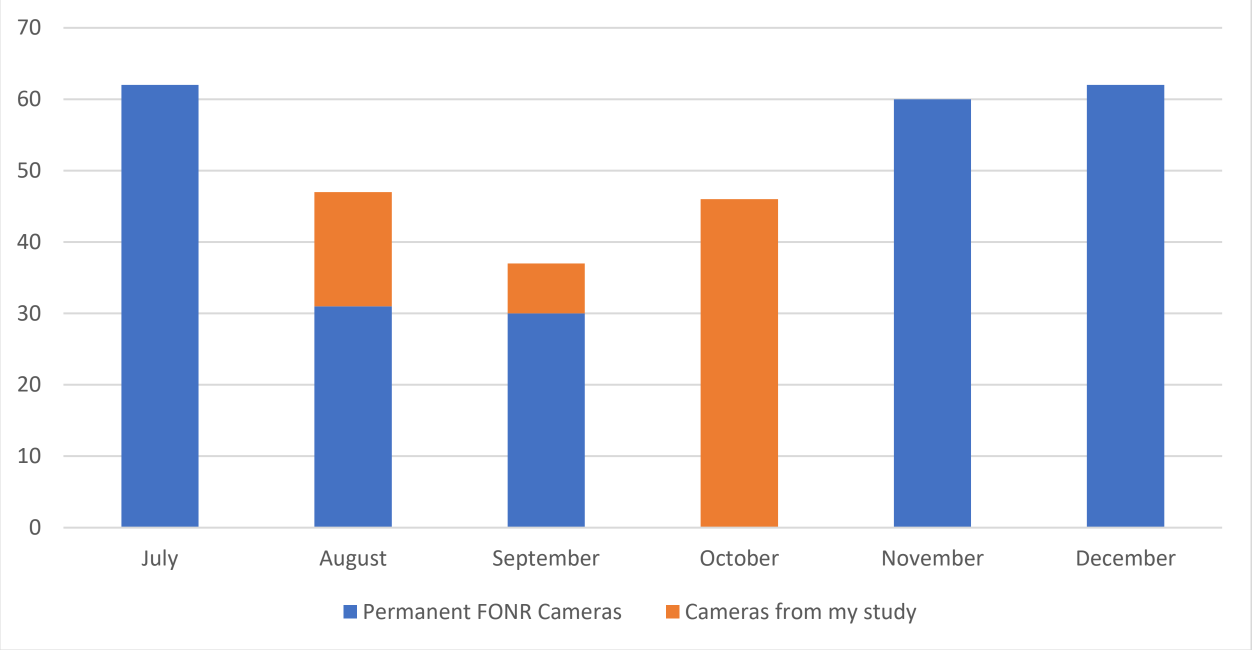

Figure 4. Total number of camera days per month in polygons A1 and A3 during July 2018 through December 2018: During the month of October 2018, no data from stationary FONR cameras was available which explains the missing predator activity data during that month (Figure 5).

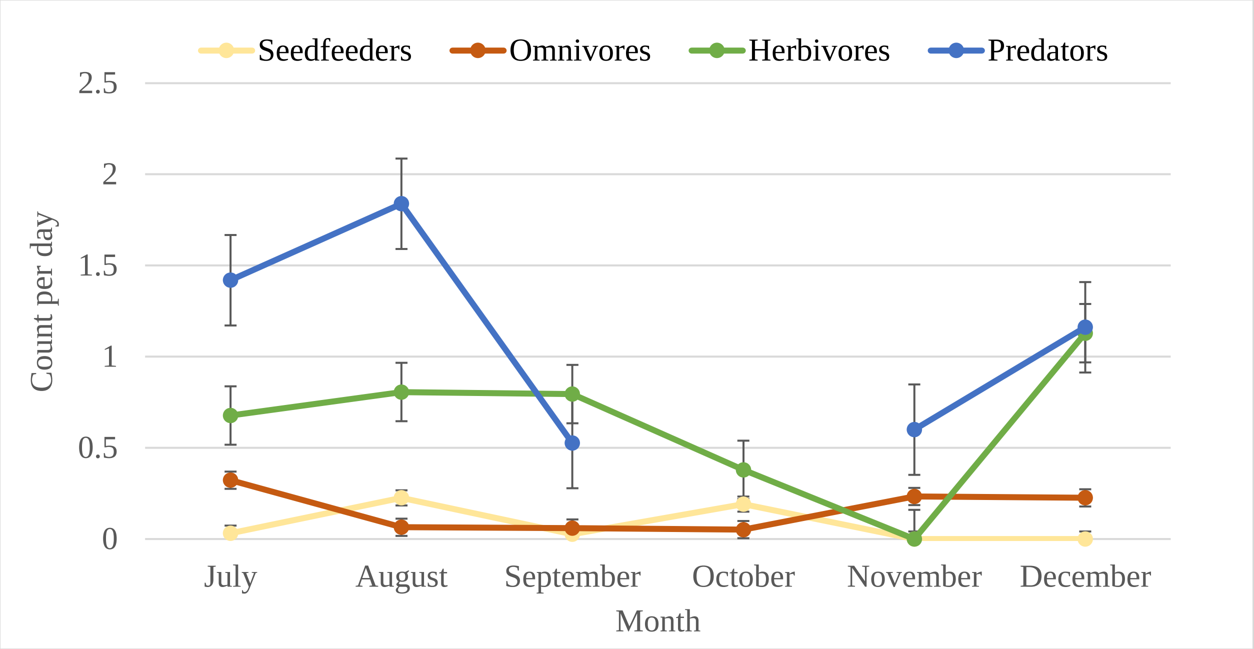

Figure 5. Daily number of seed feeders, omnivores, herbivores and predators from my data and FONR cameras: During July 2018 to August 2018, there were more predator activities compared to total seed feeders, omnivores, and herbivores in polygons A1 and A3. This trend was reversed during the months of September 2018 but reversed again during November 2018 and December 2018. There are no predator data from the FONR cameras for the month of October 2018.

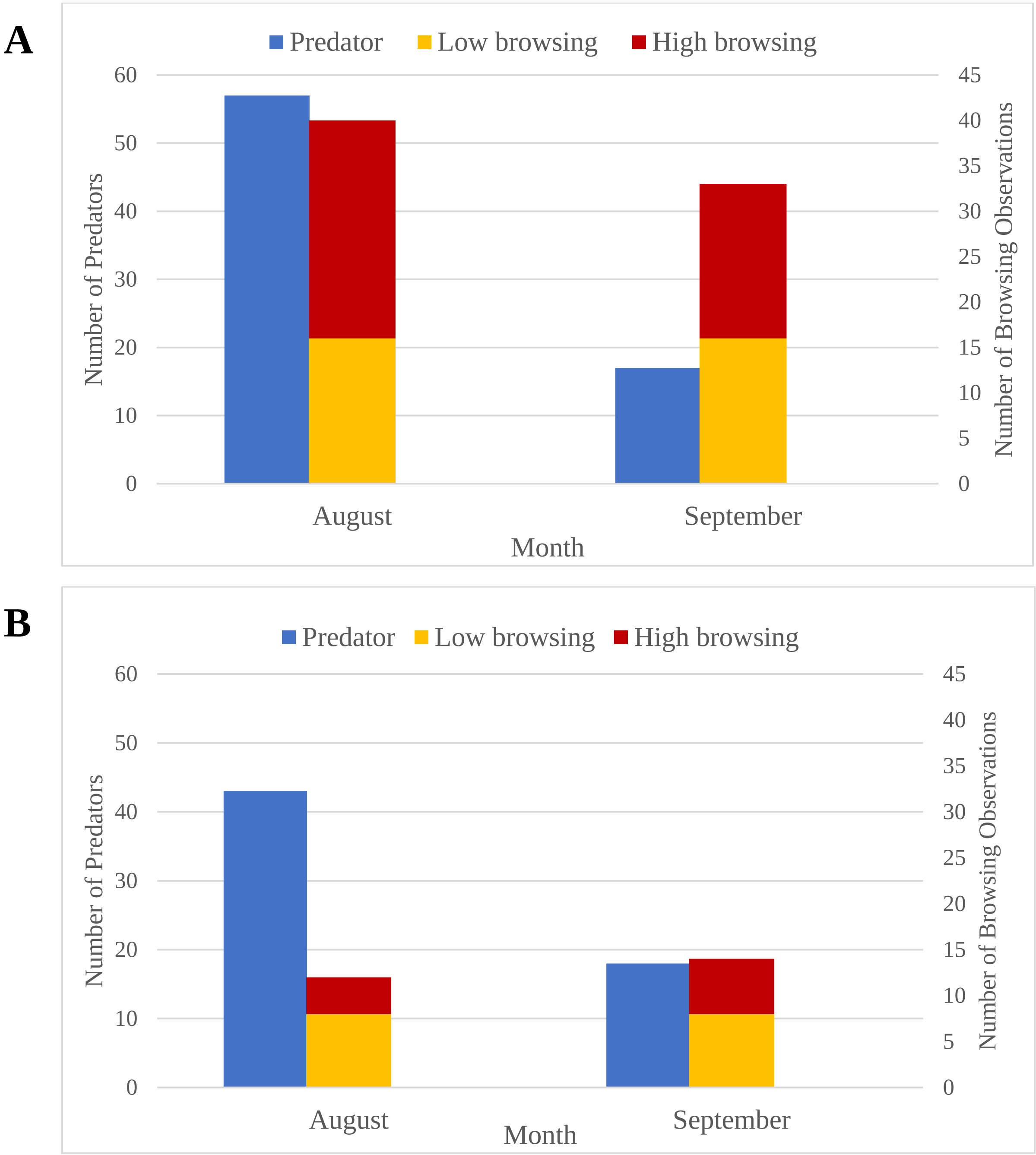

Figure 6. The number of low/high browsing observed on transects and predators on stationary FONR cameras during August and September in polygons A1(a) and A3(b). Both polygons had high and low browsing but A1 had more total browsing than A3. A1 which is closer to oak woodlands had more browsing observed at high heights while A3 which is farther from oak woodland had more browsing at low heights. The number of predators and browsing observations in polygon A1 were higher in August 2018 than September 2018. In polygon A3, the number of predators was higher in August 2018 than September 2018, but there were more browsing observations in September 2018 than August 2018.