

**SPATIOTEMPORAL ACTIVITY PATTERNS OF THE CARNIVORE GUILD
ON THE APOSTLE ISLANDS, WISCONSIN**

by

Morgan J. Farmer

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Chapter I

Spatiotemporal activity overlap of the carnivore guild in the Apostle Islands National Lakeshore, Wisconsin.

Abstract

Carnivore communities can be diverse and complex, with interactions ranging from predation to niche partitioning. For conservation strategies to be effective, we must understand the magnitude and direction of intraguild interactions. To determine how intraguild interactions may be affecting the spatiotemporal activity distributions of the carnivore guild on the Apostle Islands National Lakeshore, I monitored the carnivore population using a grid of camera traps from 2014-2018, during which time I collected 257,358 photographs with 8,869 independent detection events. I used generalized linear mixed effects models at two different scales to test whether subordinate carnivore presence is related to dominant carnivore relative abundance or to island biogeography variables. At the island-level, the island biogeography variables were in the top models for all of the subordinate species, except for fisher, while dominant carnivore relative abundance was in the top models for all of the subordinate species, except for grey fox. At the camera-level, dominant carnivore relative abundance was not a significant predictor of subordinate carnivore presence. To determine whether subordinate carnivores are using temporal partitioning, I calculated temporal overlap between each pair of subordinate and dominant species, and all pairs exhibited high or neutral temporal overlap. Despite the minimal evidence for spatial or temporal partitioning between the carnivore guild on the Apostle Islands, the subordinate carnivores could be partitioning at a finer scale than I was able to measure, highlighting the need to measure niche partitioning at multiple scales.

Introduction

Carnivores perform essential functions within ecosystems, including nutrient cycling (Estes et al 2011, Holtgrieve et al 2009, Ripple et al 2014, Schmitz et al 2010), zoonotic disease regulation (Estes et al 2011, Ripple et al 2014), and maintaining biodiversity (Estes et al 2011, Ripple et al 2014). Carnivores also exert population control on prey (Berger et al 2001, Preisser et al 2005), leading to large-scale effects in the ecosystem, including erosion prevention (Beschta and Ripple 2011, Ripple et al 2014) and increased tree recruitment (Beschta and Ripple 2009, Estes et al 2011). Natural experiments, where carnivores have been extirpated, provide evidence for the necessity of carnivores for a healthy ecosystem (Berger et al 2001, Ford and Goheen 2015, Hebblewhite et al 2005).

Guilds of sympatric carnivores can be diverse and complex. Within carnivore guilds, competition for prey species and other resources is common and can have effects ranging from indirect effects, such as where a decrease in the abundance of a shared prey resource results in a decrease in abundance of one of the carnivore species (Linnell and Strand 2008), to direct effects, such as intraguild predation, where a carnivore preys on a closely related species (Arim and Marquet 2004, Linnell and Strand 2008, Palomares and Caro 1999).

Due to the negative effects of intraguild competition, carnivore coexistence is often facilitated through niche partitioning. Niche partitioning can be achieved through separation in spatial and/or temporal dimensions, morphological divergence, or through diet selection (Davies et al 2007, Di Bitetti et al 2010, Hayward and Slotow 2009,

Schuetz et al 2013). For example, the African large carnivore guild, which includes lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*), exhibits spatial, temporal, and resource partitioning that tends to associate with mass, with niches of smaller species based on the niches of larger species (Caro and Stoner 2003, Durant 2002, Hayward and Kerley 2008, Hayward and Slotow 2009, Schuetz et al 2013, Swanson et al 2014).

Temporal partitioning occurs when a species shifts its temporal activity patterns to minimize competition and predation risk from a competitor, such as when African wild dogs hunt during the day to minimize exposure to the dominant carnivores that tend to hunt at night (Dröge et al 2016). In contrast, spatial partitioning occurs when a species shifts its physical location to minimize risk from a competitor (Durant 2002). African wild dogs also exhibit spatial partitioning and tend to altogether avoid areas with lions (Dröge et al 2016, Swanson et al 2014, Vanak et al 2013). Cheetahs and leopards exhibit spatial partitioning at the landscape scale, with cheetahs selecting for grasslands and leopards selecting for wooded areas, but they also tend to partition at a finer-scale and will occupy similar areas as dominant carnivores (Swanson et al 2014, Vanak et al 2013).

Finally, resource partitioning occurs when a species shifts its resource use so that its habitat or prey use overlap less with its competitor, and morphological partitioning occurs when some change in morphology (i.e. body size) decreases resource overlap between competitors, thereby minimizing risk (Hayward and Kerley 2008). For example, lions and hyenas tend to specialize on wildebeest, an energetically favorable prey item, while cheetahs, leopards, and other subordinate carnivores tend to have broader diets that

include smaller and rarer prey (Dröge et al 2016, Hayward and Kerley 2008, Vanak et al 2013). By niche partitioning, carnivores can alleviate intraguild competition and successfully coexist.

Worldwide, carnivore populations, especially those of large-bodied or specialized carnivores, are declining, resulting in a conservation crisis and a need for information pertaining to carnivore community dynamics. The Apostle Islands of the Apostle Islands National Lakeshore (APIS) is an optimal island system to explore how intraguild interactions affect carnivore communities in temperate North America. Currently, a most island-based community research is conducted in the tropics, so it is largely unknown whether temperate island wildlife communities follow the same trends. My objectives were to explore spatiotemporal species distributions within the Apostle Island carnivore guild based on intraguild competition. I hypothesized that subordinate carnivore species will use either spatial or temporal niche partitioning to facilitate coexistence with dominant carnivores within the archipelago. Therefore, I expect that subordinate carnivore species will exhibit minimal temporal activity overlap with dominant carnivores or that subordinate carnivore presence will be predicted by dominant carnivore relative abundance at either the island or camera site level.

Methods

Study Area

The Apostle Islands National Lakeshore (APIS) consists of twenty-one of the twenty-two islands that make up the archipelago in southwestern Lake Superior

(Wisconsin, USA). The islands were designated as a national lakeshore in 1970 despite a history of logging, quarrying, and private residences. Madeline Island was excluded from the national lakeshore due to an already established year-round community. The archipelago was originally connected to mainland Wisconsin but was isolated by glacial scouring during the Pleistocene epoch. Erosion is still a major agent of change within the islands as evidenced by the disappearance of Little Steamboat Island by 1898 (Judziewicz and Koch 1993) and the sea caves, which attract many visitors throughout the year to the national lakeshore. The archipelago is located within a transition zone between northern boreal coniferous forest and deciduous forest, which results in a rich matrix of habitat types (Craven and Lev 1987). This, in addition to the individual islands' exposure to wind and waves, often creates complex microclimates.

Historical temperature and precipitation data through 1972 have been collected on Madeline Island (Phillips and McCulloch 1972). Maximum daily temperatures ranged from 25.5°C to -4.5°C while average annual precipitation was 75 cm with 200 cm of snow (Judziewicz and Koch 1993). During this study (September 2014 – November 2018), temperatures ranged from -30.0°C to 36.1°C, with an average of 3.6°C, and annual precipitation averaged 81.77 cm of rain and 142.41 cm of snow (National Centers for Environmental Information 2019). Within Bayfield Harbor, located on the mainland adjacent to Madeline Island, lake ice cover has decreased at a rate of 3 days/decade over the past 150 years (Howk 2009). Ice bridges between islands in the Great Lakes region and the mainland have proven to be essential to preventing genetic isolation in carnivore

populations (Adams et al 2011, Lomolino 1988), so decreasing ice cover could pose a serious threat to the carnivore community on APIS.

Camera traps

Carnivores can be cryptic and difficult to monitor due to large home ranges and low population densities (Allen et al 2016, Krofel 2012); however, camera traps can be an effective and relatively low-effort tool for monitoring carnivore populations (Allen et al 2018). To understand the effects of anthropogenic activity and structures on the carnivore community of the Apostle Islands, I used a grid of camera traps deployed across the island system to determine spatial and temporal activity patterns for the carnivore community and the individual carnivore species.

National Park Service employees, University of Wisconsin – Madison graduate students, and Northland college students deployed and checked camera traps from fall 2014 to fall 2018. Along with the collaborators, I deployed camera traps on the islands following a randomized systematic design to maximize carnivore detections and camera independence. We overlaid a 1 km² grid on each island and created a center point for each grid cell that contained >50% land. I adjusted camera trap density on each island using the following power law equation based on island size (x):

$$y = 2.0826x^{-0.369}$$

so that smaller islands received a higher density of cameras (Allen et al 2019). When placing the cameras within each grid cell, we navigated to the center point and then walked outwards in concentric circles until we found a location that would maximize

carnivore detections, such as an area along a game trail or a relatively open area that could facilitate animal travel. Once a suitable location was found, we installed a camera trap (HC600 Hyperfire™ High Output Covert, PC 800 Hyperfire Professional Semi-covert, and HC500 Hyperfire Semi-covert cams; RECONYX, Inc., Holmen, WI, USA) on a tree and then recorded its coordinates using a handheld GPS unit. We selected the height and orientation of each camera to maximize wildlife detection, and we programmed the camera traps to take a burst of three pictures with no refractory period when triggered and to record the date, time, and temperature for each detection.

We surveyed 164 camera-trap sites on 19 islands between 2014 and 2018 (Figure 1). Camera traps remained on the islands year-round, and we checked the camera traps approximately every six months to replace batteries and memory cards. A random selection of half of the cameras on each island received a scent lure (~3-4 m of the ground in field of view or placed on downed, woody vegetation in field of view) using a commercial predator lure (Caven's Gusto, Minnesota Trapline Products Inc., Pennock MN) during the first six-month period. When we checked camera traps after the first six months, cameras that were not previously baited received bait. Once we collected the memory cards from the camera traps, we downloaded and identified all species in the photographs.

Statistical Analyses

I performed all statistical analyses using R version 3.5.3 (R Core Team 2019) and considered $p < 0.05$ to be significant.

I first calculated a relative abundance index (*RAB*) at each camera trap site for each species as:

$$RAB = \frac{D}{TN} \times 100$$

where *D* is the number of detections and *TN* is the total number of trap nights that a camera trap was active (Jenks et al 2011, Farmer and Allen 2019). To calculate the number of detections, I considered multiple photographs of a species that occurred within thirty minutes of each other to be the same detection. This accounts for pseudoreplication and provides a more accurate measure of wildlife presence. I calculated *RAB* instead of using the raw counts from each photograph or the number of detections because relative abundance can be used as an accurate proxy for abundance (Parsons et al 2017).

I then identified pairs of subordinate and dominant species based on a range of factors including body size and evidence of intraguild predation (Table 1). After, I calculated temporal activity overlap and spatial activity overlap for each pair of species using the following methods.

Spatial Activity Overlap

To determine whether spatial distribution of subordinate species is affected by dominant species, I tested a set of *a-priori* hypotheses (Table 2) using generalized linear mixed effects models with a binomial distribution in the *lme4* package (Bates et al 2015) to determine whether the presence of a subordinate species was related to the *RAB* of a dominant species at both the island-level and the camera-level. At the island-level, I tested whether the presence of a subordinate species on an island was related to the

overall RAB of the dominant species, and whether dominant carnivore RAB, island biogeography variables, or both were the best predictor of subordinate species presence on an island. I compared the models based on AIC values, and considered the top model for each subordinate species to be the model with the lowest AIC value (Burnham and Anderson 2002).

In addition to testing whether the presence of a subordinate species on an island is related to the dominant species RAB, I included three island biogeography variables in my *a-priori* hypotheses: island size and distance from mainland and nearest island, which are both measures of island connectivity. Island connectivity, along with island size, can both affect species distributions among an island system. Previous research on the carnivore community on the Apostle Islands has determined that island connectivity, including swimming and crossing ice bridges, may be essential to the longevity of the carnivore guild and is an important predictor of carnivore occupancy (Allen et al 2018). Therefore, I included island biogeography variables to determine whether the addition of the dominant carnivore RAB improved the island biogeography, or whether the dominant carnivore RAB was a better predictor of subordinate species presence than island biogeography.

At the camera-level, I tested whether the presence of a subordinate species at a given camera on a given island was related to the RAB of the dominant species at the given camera (Bates et al 2015). I included 'island' as a random effect in our camera-level models and only included data from the islands on which I detected both species. Then, I built receiver operating characteristic curves (roc) and calculated the area under

the curve (AUC) to determine whether the relationship between presence of subordinate species and RAB of dominant species at camera-level is due to chance, uninformative, or perfectly aligned (Robin et al 2011).

Temporal Activity Overlap

I used the *activity* (Meredith and Ridout 2017) and *overlap* (Rowcliffe 2016) packages to compare temporal activity distributions of a subset of carnivore species detected on the Apostle Islands, including: coyote, fisher, gray fox, American marten, red fox, and bobcat. I selected these specific species because they are either within the canid guild or the mustelid guild, or in the case of bobcats, are similar in size to the other species. First, I converted the timestamp for each detection event into radians and then into kernel densities. Next, I calculated temporal overlap between each pair of species as $\hat{\Delta}_4$ with a 95% confidence interval for the temporal overlap value. $\hat{\Delta}_4$ is a value between 0 and 1, where 0 indicates no temporal activity overlap and 1 indicates perfect temporal activity overlap. I used $\hat{\Delta}_4$ rather than $\hat{\Delta}_1$ because all carnivore species tested had at least 50 observations (Meredith and Ridout 2017). To calculate the confidence intervals, I used the bootstrap method with 1000 bootstrap samples (Farmer and Allen 2019, Ridout and Linkie 2009). Pairs of species with $\hat{\Delta}_4$ values greater than 0.5 with a confidence interval that did not overlap 0.5, had high temporal activity overlap, and pairs of species with $\hat{\Delta}_4$ values less than 0.5 with a confidence interval that did not overlap 0.5, had low temporal activity overlap. Pairs of species with a confidence interval that overlapped 0.5 had

neutral overlap and did not exhibit either avoidance (low overlap) or aggregation (high overlap).

Results

Summary statistics

I had 164 camera traps functioning across 5 years for a total of 88,712 trap nights. I obtained 257,358 photographs, with 8,869 independent detection events of 17 mammal species. Thus far, camera traps installed on the islands since 2014 have detected twelve carnivore species, including two semi-aquatic species. Detected carnivore species include: American marten (*Martes americana*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), gray fox (*Urocyon cinereoargenteus*), gray wolf (*Canis lupus*), mink (*Neovision vision*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), river otter (*Lontra canadensis*), and weasels (*Mustela spp.*) (Allen et al 2018).

Spatial Activity Overlap

At the island level, global models, including dominant carnivore RAB and island biogeography variables were the top model for both red fox (wAIC = 0.86) and marten (wAIC = 0.41) (Table 3). The global model with coyote RAB was supported as the top model for red fox presence (wAIC = 0.86), and the second-best model was the dominant carnivore model with coyote RAB (wAIC = 0.12). For marten, the global model

including bobcat RAB and the global model including red fox RAB contained almost equal AIC weight ($wAIC = 0.41$ and $wAIC = 0.39$, respectively). Gray fox presence was best predicted by the island biogeography variables ($wAIC = 0.44$); however, all three global models for gray fox had some support ($wAIC = 0.16$ for all three models). The top model for fisher was the dominant carnivore model with bobcat RAB ($wAIC = 0.75$) (Table 3).

At the site level, dominant carnivore RAB does not appear to predict subordinate carnivore presence at a given camera site. All p-values were insignificant and AUC values ranged from 0.4723 (Gray Fox – Coyote) to 0.6224 (Marten – Coyote), indicating that for all pairs, the RAB of the dominant carnivore is uninformative relative to the presence of the subordinate carnivore (Table 4).

Temporal Activity Overlap

All of the pairs of dominant and subordinate species exhibited high or neutral temporal overlap. Nine species pairs, including Gray Fox – Bobcat ($\hat{\Delta}_4 = 0.92$, 95% $CI = 0.82 - 1.00$, *Figure 2d*), Marten – Bobcat ($\hat{\Delta}_4 = 0.91$, 95% $CI = 0.80 - 1.00$, *Figure 2i*), Fisher – Bobcat ($\hat{\Delta}_4 = 0.91$, 95% $CI = 0.83 - 0.99$, *Figure 2g*), Gray Fox – Coyote ($\hat{\Delta}_4 = 0.90$, 95% $CI = 0.80 - 0.98$, *Figure 2c*), Fisher-Coyote ($\hat{\Delta}_4 = 0.87$, 95% $CI = 0.78 - 0.96$, *Figure 2f*), Marten – Coyote ($\hat{\Delta}_4 = 0.84$, 95% $CI = 0.76 - 0.91$, *Figure 2h*), Red Fox – Bobcat ($\hat{\Delta}_4 = 0.83$, 95% $CI = 0.68 - 0.96$, *Figure 2b*), Red Fox-Coyote ($\hat{\Delta}_4 = 0.79$, 95% $CI = 0.67 - 0.90$, *Figure 2a*), and Gray Fox – Red Fox ($\hat{\Delta}_4 = 0.75$, 95% $CI = 0.58 - 0.90$, *Figure 2e*) had high temporal

overlap (Table 5). The remaining two pairs of dominant and subordinate species displayed neither aggregation nor avoidance in time (Table 5, Figures 2j-k). In terms of body size and family group, there did not appear to be any trends in temporal overlap, as all a strong majority of the species pairs tested showed high temporal overlap.

Discussion

Carnivore communities can be diverse and complex, and intraguild interactions between species can range from direct (predation) to indirect (niche partitioning) (Arim and Marquet 2004, Linnell and Strand 2008, Palomares and Caro 1999). Gaps in knowledge regarding intraguild interactions can preclude effective conservation of carnivore species (Krofel et al 2016). I used an array of camera traps to monitor the carnivore guild on the Apostle Islands and to determine whether species were using spatial or temporal partitioning to facilitate coexistence. I found some evidence of spatial partitioning at the island-level, no evidence of spatial partitioning at the camera-level, and no evidence of temporal partitioning. Contrary to my hypotheses, a majority of the tested pairs had high temporal overlap, while the rest were uninformative.

Niche partitioning is a well-documented risk-management strategy used by carnivores to minimize risk from competition and predation. Many of the carnivores that were detected on the Apostle Islands use some form of niche partitioning on mainland North America. For example, red foxes and especially gray foxes can exhibit spatial avoidance of coyotes and bobcats across the United States (Fedriani et al 2000, Gosselink et al 2003, Harrison et al 1989, Henke and Bryant 1999). Similarly, Fisher et al (2012)

found that the absence of marten or fisher was significantly related to the presence of the other species. However, my hypotheses of temporal partitioning and spatial partitioning (with the exception of fisher and red fox at the island-level), was only minimally supported by my analyses for any pair of species. This supports other recent research on the carnivore guild that shows a lack of separation between carnivores, despite competition (Allen et al 2018, Balme et al 2017, Steinmetz et al 2013).

Surprisingly, there were no trends in spatial or temporal partitioning related to body size or taxonomic family, with the exception of bobcat RAB being included in both of the top models for fisher and marten. Additionally, there was no evidence of spatial or temporal partitioning within the taxonomic families (canids or mustelids). My results are supported by Manlick et al (2017), who also found no evidence of temporal partitioning or spatial partitioning between marten and fisher in northern Wisconsin. Aside from temporal and spatial partitioning, sympatric species can use dietary or morphological partitioning to facilitate coexistence. While I did not test for dietary overlap, Manlick et al (2017) found no evidence of dietary partitioning among the mainland Wisconsin population of fishers and martens, which is supported by mustelid research outside of Wisconsin (Lanszki and Heltai 2011, McDonald 2002). Canids can also vary in whether or not they display spatial partitioning (Lesmeister et al 2015, Neale and Sacks 2001). Within an urban matrix that approximates an island system, Mueller et al (2018) observed coyotes and red foxes partitioning by habitat type, but additionally recorded several interactions between coyotes and red foxes during which no interspecific aggression occurred.

While my results contradict a large portion of the literature on intraguild interactions, there is some support for carnivore coexistence without spatial or temporal partitioning (Allen et al 2018, Balme et al 2017, Steinmetz et al 2013). However, my results do not necessarily prove that the subordinate carnivores are not using spatial or temporal partitioning. The carnivore community could be partitioning at a finer scale than what I was able to test at (Sultaire 2016). Fine-scale partitioning can manifest as an interaction between spatial and temporal partitioning, where a subordinate carnivore uses the same general area as a dominant carnivore, but will either avoid areas that the dominant carnivore recently used or will maintain some minimum distance from the dominant carnivore (Swanson et al 2014, Vanak et al 2013). Fine-scale partitioning could also manifest as seasonal partitioning, where species' niches and resource use shift based on the season, whether it be weather or natural history related (Monterroso et al 2016, Vanak et al 2013). Alternatively, niche partitioning is based on the availability and range of resources, whether the resource is space, time, or prey. In a system with limited prey species richness, carnivores may be unable to partition prey resources, resulting in a prey-driven system.

Within the Apostle Islands, a remote and temperate archipelago, the carnivore community displayed some evidence of spatial niche partitioning and no evidence of temporal niche partitioning. Based on my results and the competitive exclusion principle, I suspect that the carnivore community may either be partitioning prey through differences in morphology and/or diet selection or may be partitioning space or time at finer scales than I was able to measure. Identifying how carnivore species are coexisting

would provide critical information on their realized niches and allow for more effective conservation. Future research should attempt to assess whether the carnivore community on the Apostle Islands is using prey and morphological partitioning or finer-scale spatiotemporal partitioning to facilitate coexistence.

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Table 1. Subordinate and dominant species as determined by body size and published accounts of intraguild predation and the islands on which each pair were both detected.

Subordinate	Dominant	Islands with detections of both species
Red fox	Coyote	Bear, Hermit, Manitou, Oak, Stockton
Red fox	Bobcat	Oak, Stockton
Gray fox	Coyote	Basswood, Oak, Stockton
Gray fox	Bobcat	Basswood, Oak, Stockton
Gray fox	Red fox	Oak, Stockton
Fisher	Coyote	Basswood, Oak, Stockton
Fisher	Bobcat	Basswood, Oak, Stockton
American marten	Coyote	Bear, Manitou, Outer, Stockton
American marten	Bobcat	Stockton
American marten	Red fox	Bear, Manitou, Stockton
American marten	Fisher	Cat, Rocky, Stockton

Table 2. Model table with *a-priori* models to determine influences of subordinate carnivore island occupation.

Model name	Variables	Hypothesis
Dominant Carnivore	Dominant carnivore RAB	Two strong competitors cannot coexist, so dominant carnivore RAB will be an important predictor of subordinate species presence (Durant 2002, Fedriani et al 2000)
Island Biogeography	Island size + Distance from mainland + Distance from nearest island	The larger and closer that an island is to the mainland or other islands, the more resources that are available and the easier it is to colonize, so island biogeography will be an important predictor of subordinate species presence (Millien-Parra and Jaeger 2001)
Global Model	Dominant carnivore RAB + Island size + Distance from mainland + Distance from nearest island	
Null Model	-	

1 Table 3. Generalized linear mixed effects model results at the island level.

Subordinate	Dominant	Global model AIC (<i>wAIC</i>)	Dominant carnivore model AIC (<i>wAIC</i>)	Island Biogeography model AIC (<i>wAIC</i>)	Null model AIC (<i>wAIC</i>)
Red Fox	Coyote	10.000 (0.86)	14.008 (0.12)	18.128 (0.01)	28.920 (0.00)
	Bobcat	20.116 (0.01)	26.781 (0.00)		
Gray Fox	Coyote	10.000 (0.16)	26.286 (0.00)	8.000 (0.44)	24.493 (0.00)
	Bobcat	10.000 (0.16)	11.481 (0.08)		
	Red Fox	10.000 (0.16)	26.493 (0.00)		
Fisher	Coyote	24.932 (0.05)	29.892 (0.00)	23.404 (0.10)	27.898 (0.01)
	Bobcat	23.880 (0.08)	19.442 (0.75)		
Marten	Coyote	26.418 (0.01)	29.213 (0.00)	25.341 (0.02)	27.898 (0.00)
	Bobcat	18.898 (0.41)	29.897 (0.00)		
	Red Fox	18.979 (0.39)	27.047 (0.01)		
	Fisher	20.897 (0.15)	29.079 (0.00)		

2 Bold results indicate the top model for each subordinate carnivore.

Table 4. Generalized linear mixed effects model results at the camera site-level.

Subordinate	Dominant	P Value	AUC
Red Fox	Coyote	0.396	0.5922
	Bobcat	0.685	0.5338
Gray Fox	Coyote	0.728	0.4723
	Bobcat	0.572	0.4973
	Red Fox	0.745	0.5641
Fisher	Coyote	0.998	0.4944
	Bobcat	0.384	0.5407
Marten	Coyote	0.492	0.6224
	Bobcat	0.536	0.6018
	Red Fox	0.273	0.5642
	Fisher	0.751	0.6159

Table 5. Temporal overlap results with 95% confidence intervals.

Species Pairs	$\hat{\Delta}_4$	95% CI
Gray Fox-Bobcat	0.92	0.82-1.00
Marten-Bobcat	0.91	0.80-1.00
Fisher-Bobcat	0.91	0.83-0.99
Gray Fox-Coyote	0.90	0.80-0.98
Fisher-Coyote	0.87	0.78-0.96
Marten-Coyote	0.84	0.76-0.91
Red Fox-Bobcat	0.83	0.68-0.96
Red Fox-Coyote	0.79	0.67-0.90
Gray Fox-Red Fox	0.75	0.58-0.90
Marten-Red Fox	0.68	0.49-0.84
Marten-Fisher	0.65	0.44-0.84

Figure 1. Locations of camera traps placed within the Apostle Islands National Lakeshore (WI, USA) as part of the carnivore monitoring project.

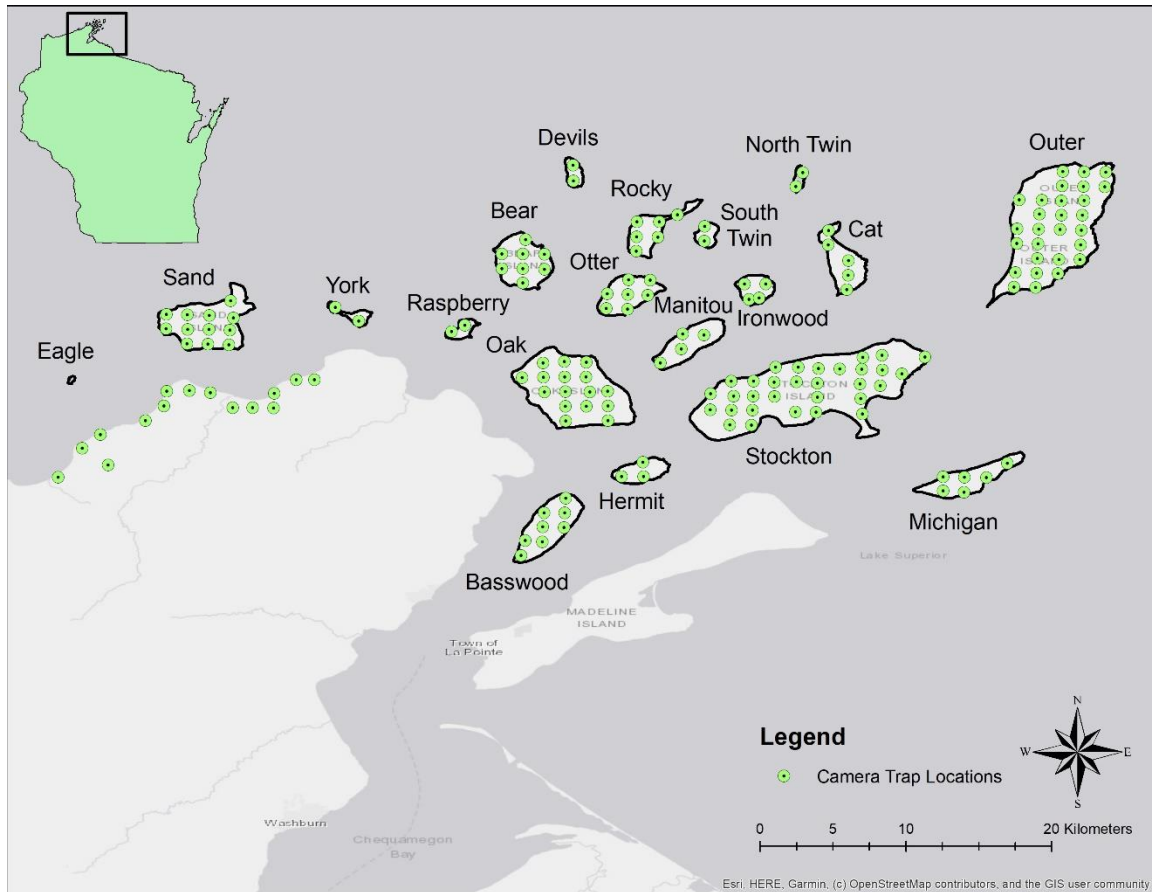


Figure 2a-k. Temporal activity overlap plots comparing the temporal activity of six of the carnivores detected using camera traps in the Apostle Islands National Lakeshore (WI, USA).

Figure 2a. Red fox and coyote temporal activity overlap.

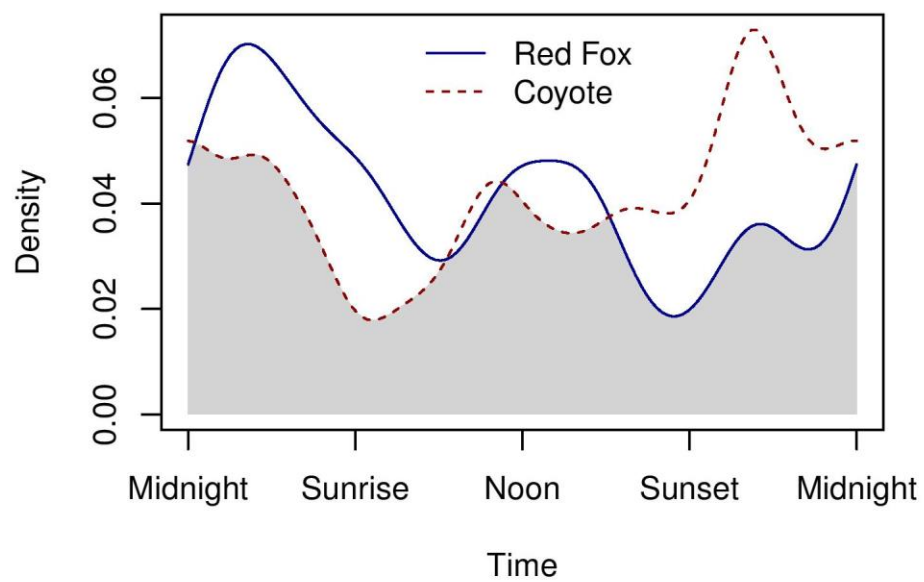


Figure 2b. Red fox and bobcat temporal activity overlap.

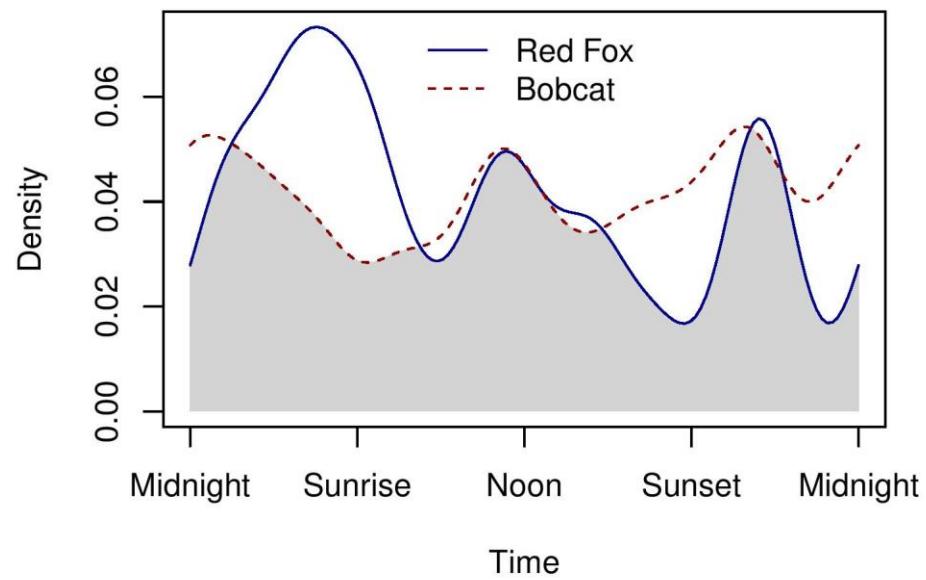


Figure 2c. Grey fox and coyote temporal activity overlap.

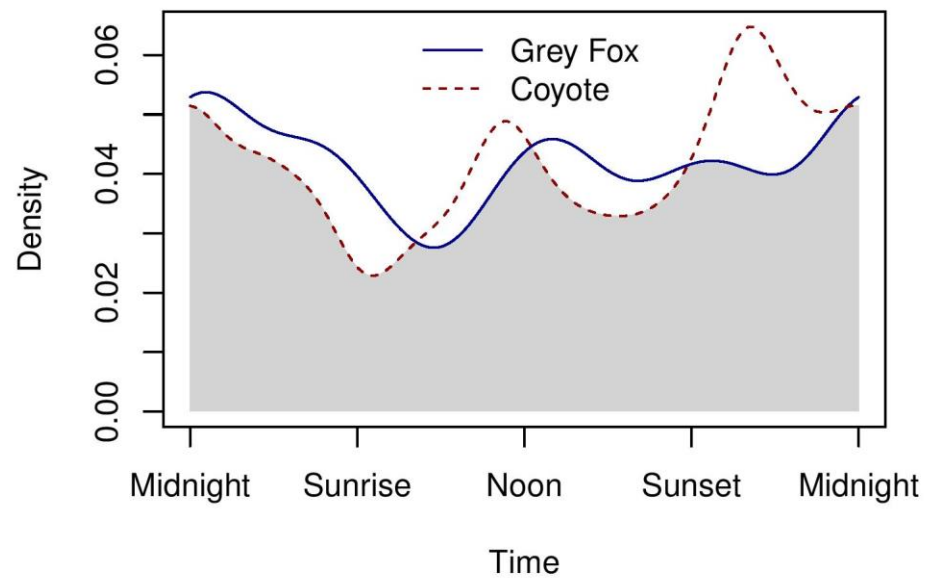


Figure 2d. Grey fox and bobcat temporal activity overlap.

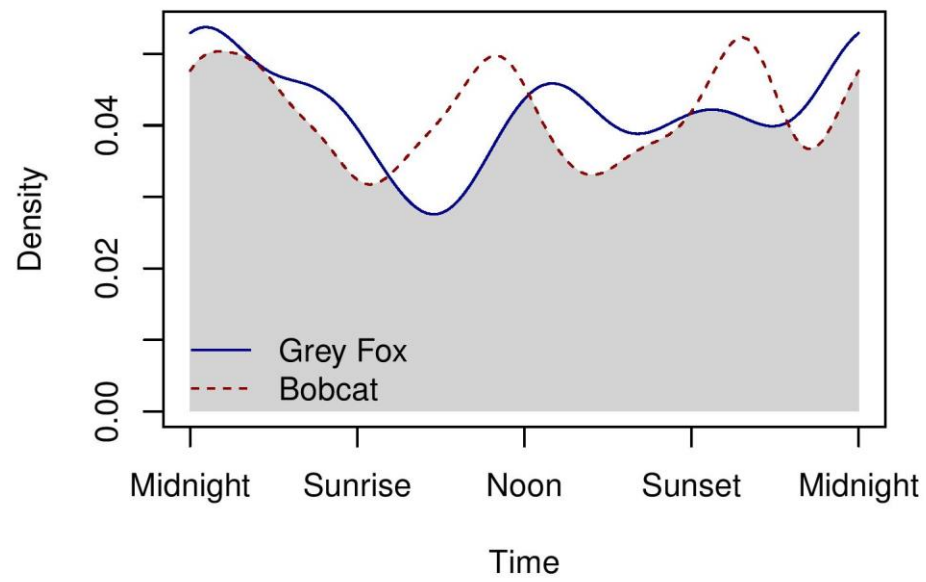


Figure 2e. Grey fox and red fox temporal activity overlap.

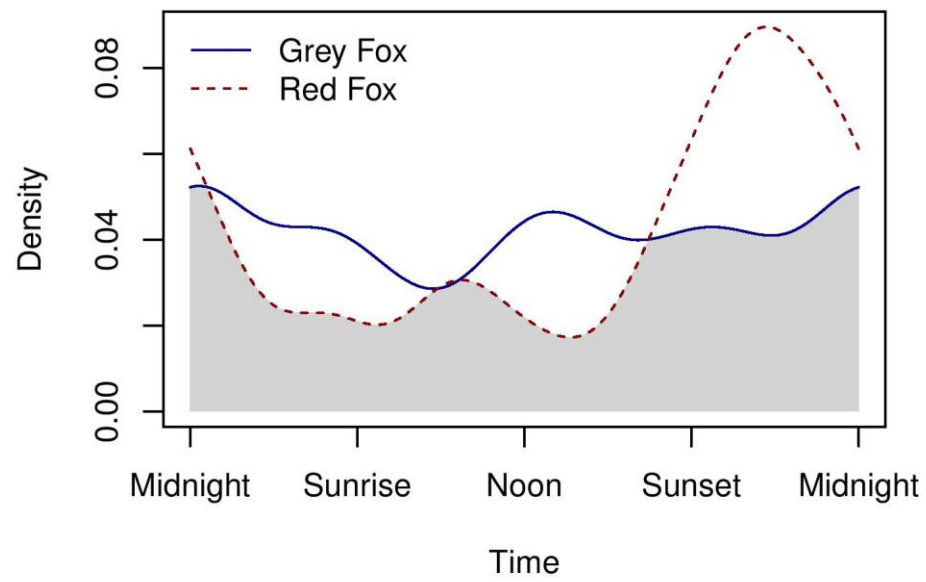


Figure 2f. Fisher and coyote temporal activity overlap.

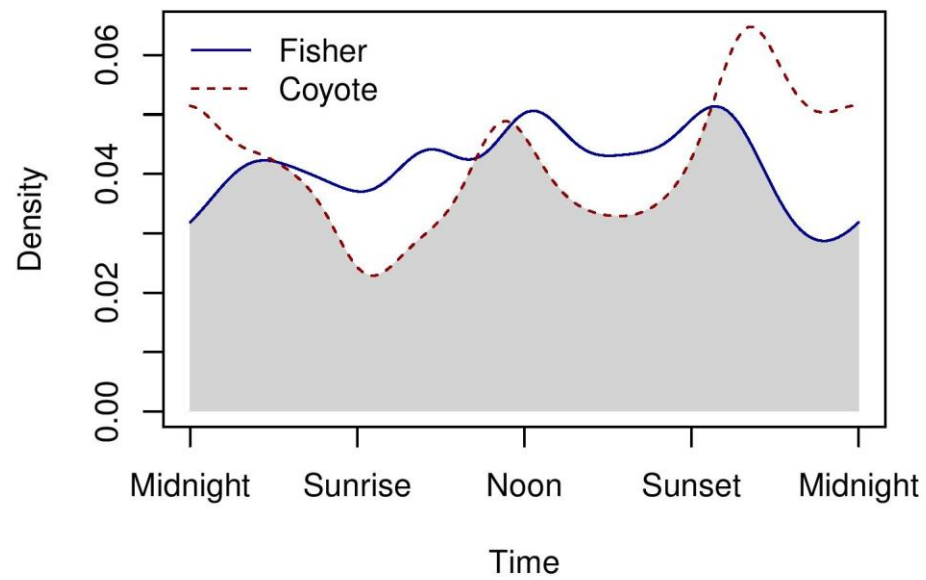


Figure 2h. Marten and coyote temporal activity overlap.

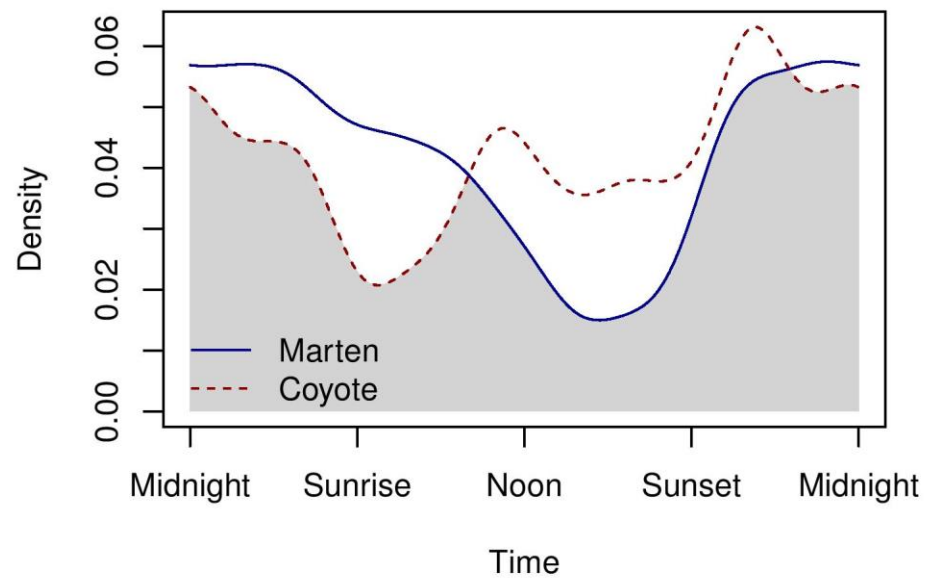


Figure 2i. Marten and bobcat temporal activity overlap.

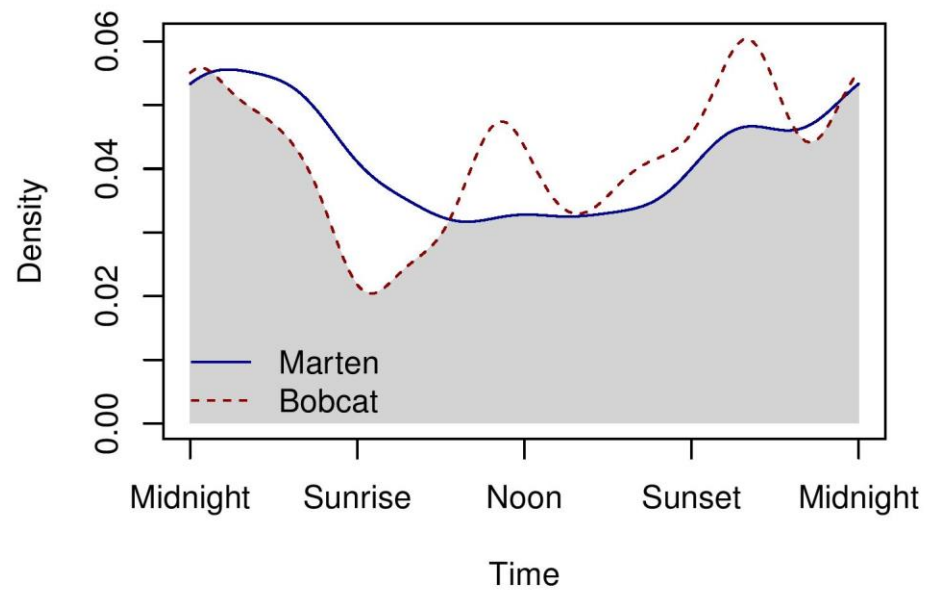


Figure 2j. Marten and red fox temporal activity overlap.

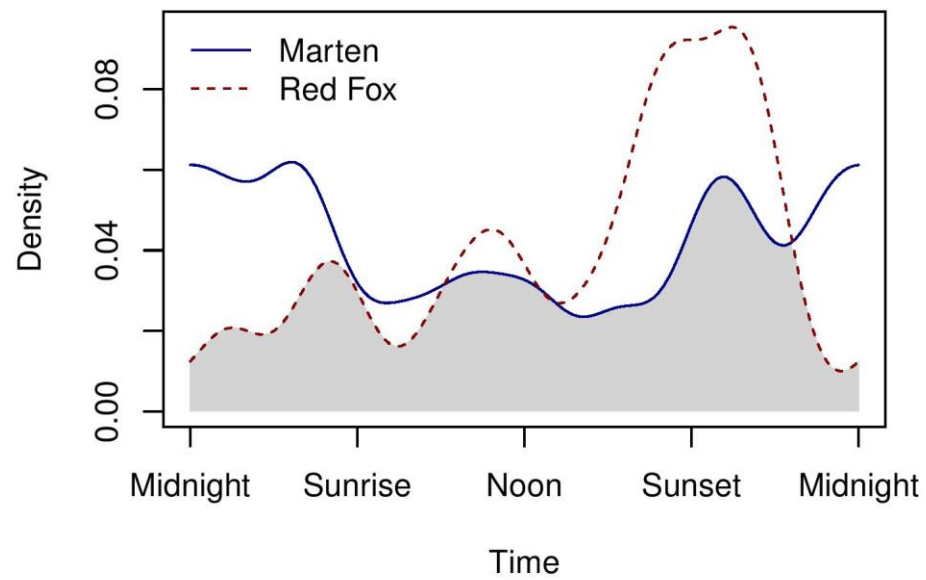
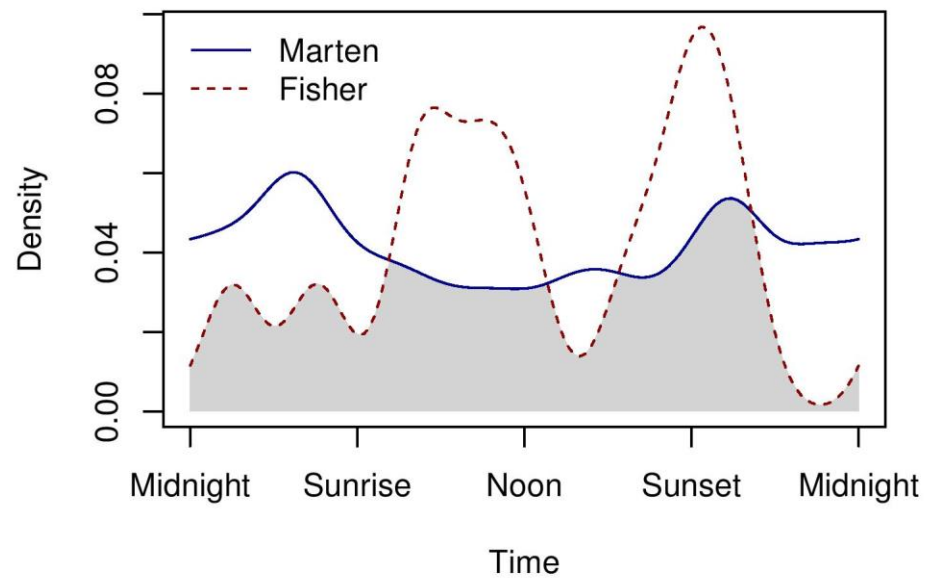


Figure 2k. Marten and fisher temporal activity overlap.



Chapter II

Effects of anthropogenic activity and structures on the spatiotemporal activity patterns of the carnivore community on a temperate, protected archipelago

Abstract

Anthropogenic impacts on wildlife have well-documented, varied effects, and understanding both the magnitude and direction of these effects is necessary for effective conservation of wildlife species. While protected areas are often considered to be strongholds for wildlife populations, recent research on anthropogenic impacts on wildlife in protected areas has highlighted that even nonconsumptive activities can be detrimental to wildlife populations. To determine how anthropogenic activity and structures affect the spatiotemporal activity distribution of the carnivore guild on the Apostle Islands National Lakeshore, I monitored the carnivore population using a grid of camera traps from 2014 to 2018. Over the four-year period, I collected 257,358 total photographs, of which there were 8,869 independent detection events of 12 carnivore species. I used generalized linear mixed effects models to test whether carnivore community and carnivore species relative abundance at the camera site is related to distance from nearest structure or type of nearest structure. At the community level, all structure types tested were significant and negatively related to carnivore community relative abundance, except for campgrounds, which was significant and positively related to carnivore community relative abundance. Responses of individual carnivore species to anthropogenic structures varied. To determine whether anthropogenic activity has affected the temporal activity patterns of the carnivore community, I compared carnivore nocturnality along a gradient of anthropogenic activity, and my results indicate that the carnivore community is not becoming more nocturnal as expected with increasing

anthropogenic activity. Within the Apostle Islands National Lakeshore, a remote and temperate archipelago, the carnivore community displayed spatial avoidance of current and historical anthropogenic structures, potentially reducing the effective area of the protected lakeshore.

Introduction

Anthropogenic impacts on wildlife are varied and can be positive or negative, ranging from habitat loss to food subsidies (Brashares et al 2001, Fahrig 1997, Halpern et al 2008, Liu et al 2001, Newsome 2014, Rodewald 2011). These impacts can be accidental or deliberate; for example, gray wolves (*Canis lupus*) have been extirpated from much of their North American range due to a purposeful removal campaign in the early 1900s (Leopold 1947), but have also been brought back to the lower 48 states through deliberate reintroductions and conservation actions (Smith et al 2003). The effects can also be unintentional, with large decreases in raptor populations due to DDT and other pesticides (Hartley and Douthwaite 1994, Wallin 1984), but also skyscrapers providing habitat for peregrine falcons at high concentrations (Bolen 1991). Further variation and complexity occur when anthropogenic impacts on wildlife species are propagated indirectly through cascading effects. In the late 1800s, small Indian mongooses (*Herpestes javanicus*) were introduced to Jamaica and several other Caribbean islands with the intention of controlling rodent populations. While the introduced mongooses did decrease the rodent populations, they also decimated the native bird and small mammal populations (Hays and Conant 2007).

With the advent of conservation, humans have made targeted efforts to conserve wildlife populations; however, conservation efforts tend to be concentrated on charismatic mammals, including large carnivores (Lindsey et al 2007, Walpole and Leader-Williams 2002). Historically, anthropogenic impacts on carnivores have been detrimental (Karanth and Chellam 2009, Kellert et al 1996, Ripple et al 2014), which is

partially due to carnivore biology. For example, carnivores tend to occur at low populations densities because they require large home ranges to meet their nutritional needs (Ripple et al 2014). Additionally, humans have viewed many carnivore species as pests or competitors for resources such as deer and other game species (Ripple et al 2014). More recently, anthropogenic alteration of habitat has been a major cause of carnivore population decline (Crooks 2002, Crooks et al. 2011), and in some cases, has exacerbated human-wildlife conflict (Michalski 2006). While some species, such as coyotes and foxes have been able to adapt their behavior to a highly-altered environment (Mueller et al. 2018), other carnivores such as some species of bears and mountain lions have not adapted to living in close proximity to developed areas (Baruch-Mordo 2014, Beckmann and Lackey 2008, Gibeau et al 2002, Riley et al 2014, Smith et al 2017).

In addition to impacts from development, humans are impacting carnivores through non-consumptive recreation (George and Crooks 2006, Reed and Merenlender 2011). Studies of effects of non-consumptive recreation on the taxonomic families Canidae, Felidae, and Ursidae, found significant negative results (Larson et al 2016). Outdoor activities such as hiking, bicycling, and boating can displace carnivores spatially and temporally (Larson et al 2016). In California, coyotes and other carnivores such as bobcats, display both spatial shifts due to human recreation and temporal shifts due to dogs (*Canis familiaris*) accompanying their owners (George and Crooks 2006, Reed and Merenlender 2011). Cases with neutral or even positive effects from non-consumptive recreation on carnivores are often explained by habituation to humans (Larson et al 2016) or exploitation of food subsidies (George and Crooks 2006).

The Apostle Islands National Lakeshore (APIS) has a rich history of human use, and as part of the National Park Service, is currently a popular destination for hiking, camping, and boating. My objectives were to explore spatiotemporal species interactions within the Apostle Islands carnivore guild based on disturbance in the form of 1) current anthropogenic structures, 2) historical anthropogenic structures, and 3) a gradient of anthropogenic activity. I hypothesized that carnivore community relative abundance and individual species relative abundance will be positively correlated with distance from closest structure, negatively related to current structures, and positively correlated to historical structures, and that the carnivore community will be more nocturnal on islands with greater anthropogenic activity.

Methods

Study Area

The Apostle Islands National Lakeshore (APIS), an archipelago of twenty-one islands in Lake Superior, Wisconsin, USA, has a varied and rich history of human use (Figure 1). Native American settlements on Madeline Island, the only island in the archipelago not included in the national lakeshore designation due to an already established year-round community, were the first human uses of the islands (Beals and Cottam 1960). In the late 1600s, French explorers established La Pointe, a trading post on Madeline Island. La Pointe quickly became a center for trade within the Lake Superior region for the next two hundred years (Judziewicz and Koch 1993). During this time, the region's economy was based primarily on the fur trade. Gradually, fish, lumber, and

sandstone replaced fur as the basis of the economy. Fishermen established three fishing camps, which were operational until the 1980s, on Rocky and South Twin Island.

Companies such as John Schroeder Lumber Company, established logging operations on Outer (1920s), Bear, Oak, and Stockton islands, with a total of thirty-four logging camps.

Companies such as Strong, French and Co. and Bass Island Brownstone Co. quarried brownstone, a brown variety of sandstone, from Basswood, Hermit, and Stockton beginning in the late 1860s. Removal of brownstone followed boom and bust cycles as demand changed, until the quarries permanently closed in 1893. In addition to commercial ventures, several islands, including Sand and Basswood, had private farms (seven total) and residences (Feldman 2011).

In 1930, Harlan Kelsey, a landscape architect, visited APIS to determine if the islands were eligible for national park status. Kelsey not only reported that “the project does not meet National Park Service standards”, but also predicted that “the whole area would soon become a smoldering, desolate waste” due to logging and forest fires, both of which were evident while Kelsey was touring the islands (Feldman 2011). Contrary to Kelsey’s prediction, in 1970, Congress designated twenty-one of the islands in the archipelago as a national lakeshore. Inclusion in the national park system solidified a management shift from “resource-production” to “tourism”, a shift sparked from both the national park designation and failing timber resources. In 2004, eighty-percent of APIS was designated as the Gaylord Nelson Wilderness, further protecting the islands from additional anthropogenic development (Feldman 2011).

Since the wilderness designation in 2004, APIS has been managed to retain wilderness qualities while incorporating cultural resources and recreational opportunities. Historical structures, such as the quarry on Basswood Island, are managed as cultural resources. Within the twenty-one islands, there are 187 historic structures, ten of which are included in the National Register of Historic Places. Recreational opportunities include hiking, boating, and camping. Within APIS, the National Park System oversees 62.4 miles of trail, 67 campsites, 3 visitor centers, and 8 lighthouse towers (National Park Service 2015).

As part of the APIS management plan, graduate students from the University of Wisconsin – Madison, students from Northland College, and National Park Service employees installed camera traps within APIS beginning in 2013 to establish baseline information on carnivore distribution. Thus far, camera traps have detected twelve carnivore species, including two semi-aquatic species. Detected carnivores species include: American marten (*Martes americana*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennant*), gray fox (*Urocyon cinereoargenteus*), gray wolf (*Canis lupus*), mink (*Neovision vision*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), river otter (*Lontra canadensis*), and weasels (*Mustela spp.*).

The archipelago was originally connected to mainland Wisconsin but was carved out by glacial retreat during the Pleistocene epoch. Erosion is still a major agent of change within the islands as evidenced by the disappearance of Little Steamboat Island by 1898 (Judziewicz and Koch 1993) and the sea caves, which attract many visitors

throughout the year to the national lakeshore. The archipelago is located within a transition zone between northern boreal coniferous forest and deciduous forest, which results in a rich matrix of habitat types (Craven and Lev 2015). This, in addition to the individual islands' exposure to wind and waves, often creates microclimates.

Historical temperature and precipitation data have been collected on Madeline Island and were summarized in 1972 (Phillips and McCulloch). Maximum daily historical temperatures ranged from 25.5°C to -4.5°C while average annual historical precipitation was 75 cm with 200 cm of snow (Judziewicz and Koch 1993). During this study (September 2014 – November 2018), temperatures ranged from -30.0°C to 36.1°C, with an average of 3.6°C, and annual precipitation averaged 81.77 cm of rain and 142.41 cm of snow (National Centers for Environmental Information 2019). Within Bayfield Harbor, located on the mainland adjacent to Madeline Island, lake ice cover has decreased at a rate of 3 days/decade over the past 150 years (Howk 2009). Ice bridges between islands in the Great Lakes region and the mainland have proven to be essential to preventing genetic isolation in carnivores (Adams et al 2011, Lomolino 1988), so decreasing ice cover could pose a serious threat to the carnivore community on APIS.

Camera traps

Carnivores can be cryptic and difficult to monitor due to large home ranges and low population densities (Allen et al 2016, Krofel and Jerina 2012); however, camera traps can be an effective and relatively low-effort tool for monitoring carnivore populations (Allen et al 2018). To understand the effects of anthropogenic activity and

structures on the carnivore community of the Apostle Islands, I used a grid of camera traps deployed across the island system to determine spatial and temporal activity patterns for the carnivore community and the individual carnivore species.

National Park Service employees, University of Wisconsin – Madison graduate students, and Northland college students deployed and checked camera traps from fall 2014 to fall 2018. Along with the collaborators, I deployed camera traps on the islands following a randomized systematic design to maximize carnivore detections and camera independence. We overlaid a 1 km² grid on each island and created a center point for each grid cell that contained >50% land. We adjusted camera trap density on each island using the following power law equation based on island size (x):

$$y = 2.0826x^{-0.369}$$

so that smaller islands received a higher density of cameras (Allen et al. 2019). When placing the cameras within each grid cell, we navigated to the center point and then walked outwards in concentric circles until we found a location that would maximize carnivore detections, such as an area along a game trail or a relatively open area that could facilitate animal travel. Once a suitable location was found, we installed a camera trap (HC600 Hyperfire™ High Output Covert, PC 800 Hyperfire Professional Semi-covert, and HC500 Hyperfire Semi-covert cams; RECONYX, Inc., Holmen, WI, USA) on a tree and then recorded its coordinates using a handheld GPS unit. We selected the height and orientation of each camera to maximize wildlife detection, and we programmed the camera traps to take a burst of three pictures when triggered and to record the date, time, and temperature for each detection.

We surveyed 164 camera-trap sites on 19 islands between 2014 and 2018 (Figure 1). Camera traps remained on the islands year-round, and we checked the camera traps approximately every six months to replace batteries and memory cards. A random selection of half of the cameras on each island received a scent lure (~3-4 m off the ground in field of view or placed on downed, woody vegetation in field of view) using a commercial predator lure (Caven's Gusto, Minnesota Trapline Products Inc., Pennock MN) during the first six-month period. When we checked camera traps after the first six months, cameras that were not previously baited received bait. Once we collected the memory cards from the camera traps, we downloaded and identified all species in the photographs.

Statistical Analyses

I performed all statistical analysis using R version 3.5.3 (R Core Team 2019) and ArcGIS version 10.5.1 (Environmental Systems Research Institute 2017). I considered $p < 0.05$ to be significant.

I first calculated annual carnivore species richness for each island as the number of carnivore species detected in a calendar year. I then classified whether the species richness on each island was increasing over all years, decreasing over all years, or variable. Next, I calculated a relative abundance index (*RAB*) at each camera trap site for each species as:

$$RAB = \frac{D}{TN} \times 100$$

where D is the number of detections and TN is the total number of trap nights that a camera trap was active (Jenks et al. 2011, Farmer and Allen 2019). To calculate the number of detections, I considered multiple photographs of a species that occurred within thirty minutes of each other to be the same detection. This accounts for pseudoreplication and provides a more accurate measure of wildlife presence. I calculated RAB instead of using the raw counts from each photograph or the number of detections because relative abundance can be used as an accurate proxy for abundance (Parsons et al. 2017).

Human structures

APIS contains both current and historical anthropogenic structures (Figure 2). Current anthropogenic structures include campsites, lighthouses, and other structures that are maintained by the National Park Service (NPS) and were built after 1970. Historical anthropogenic structures include structures such as abandoned farms and quarries that were maintained by public or private parties but are no longer in use. I identified current and historic structures from NPS maps, and then determined exact GPS coordinates for both current and historical anthropogenic structures using satellite imagery from Google Earth (Google Inc. 2018).

To determine if distance from historical or current anthropogenic structures is driving carnivore spatial use of the islands, I began by creating a point layer with locations for all of the camera trap sites and then joined the relative abundance value for each carnivore species at each site to the point layer. I also created a point layer with locations for all current and historical structures within the national lakeshore, which I

classified as either ‘Campground’, ‘Historical site’, ‘Lighthouse’, or ‘Park Service’, which included ranger stations and visitor centers. I calculated the distance from the closest structure (up to 10 km away) to each camera located on the same island using proximity analysis. For example, I calculated the distance from each camera trap on Oak island to the closest structure on Oak island. I then rounded the RAB for the community and for each species to the nearest integer and used a generalized linear mixed effects model with a Poisson distribution (log link) in the *lme4* package to test whether distance from the closest structure and the classification of the structure affected relative abundance of the carnivore community and the individual carnivore species at each camera site (Bates et al. 2015). I used relative abundance of a carnivore as our dependent variable, distance from nearest structure and type of nearest structure as our fixed independent variables, and ‘island’ as a random effect.

Nocturnality

Anthropogenic activity within the National Lakeshore is limited by the wilderness designation, and includes boating, camping, and hiking. Overnight camping on the islands is permitted through the National Park Service, which maintains individual campgrounds, with a maximum occupancy of 7 people, and group campgrounds, with a maximum occupancy of 21 people, on 18 of the islands and in the mainland unit. Based on maximum campground capacity and census data, I selected two islands and the mainland unit to use as a gradient of anthropogenic activity: mainland unit (high), Stockton island (medium), and Outer island (low). Both Stockton island and Outer island

are approximately the same area, but have vastly different maximum human populations. Stockton island has 21 individual campsites and 2 group campsites, for a maximum campsite occupancy of 189 people, while Outer island has 1 individual campsite and a maximum campsite occupancy of 7 people. The mainland unit includes the Little Sand Bay Campground, which has 32 RV sites, 6 individual campsites, and 1 group campsite.

To determine whether anthropogenic activity is affecting the carnivore community, I chose to compare nocturnality of carnivores on the mainland, Stockton, and Outer island. Using the timestamps on the camera trap photographs and the `sunTime` function in the *overlap* package (Meredith and Ridout 2017), I converted each detection time from ‘clock time’ to ‘sun time’. Sun time, also known as Solar time, bases the passage of time on sun position. For example, at a given location, solar noon is when the sun is due south of the location. Sun time is a more accurate scale for daily activity patterns due to variation in daylight length that isn’t accounted for with clock time, especially in temperate areas. I split the detections into Summer/Fall (June – November) and Winter/Spring (December – May) since anthropogenic activity and tourism is much higher during the summer and fall months. Next, I used the sun times to calculate the percentage of detections of carnivores for each island that occurred at night. I compared nocturnal detections between islands and the mainland by calculating a risk ratio with a 95% confidence interval using the number of nocturnal detections and the number of total detections in each of the three sites and the *fmsb* package (Gaynor et al. 2018, Nakazawa 2018).

Results

Summary statistics

Over the five-year study period, I had 164 camera traps operating for 88,712 trap nights. Out of 257,358 total photographs, I had 8,869 independent detection events of 12 carnivore species. Average carnivore species richness was relatively stable between 2 and 3 species for the duration of the study; however, half of the islands displayed either an increasing (25% of island), decreasing (10% of islands), or variable (15% of islands) trend in annual species richness. Six of the twelve detected carnivore species, including black bear, bobcat, coyote, fisher, grey fox, red fox, and American marten, were detected in all five years. I detected common raccoon and gray wolf in four out of five years, while weasels (*Mustela spp.*), otter, and mink were detected in three or fewer years. Due to low detection rates, mink, weasel spp. and otter were not included in the spatial analysis.

Human structures

For the carnivore community, all structure types had a significant relationship with carnivore RAB. Campgrounds had a positive effect ($p < 2e-16$), while all other buildings (lighthouses ($p = 3.4e-13$), historical sites ($p = 0.004$), and Park Service ($p = 0.007$)) had a negative effect. Distance to nearest structure was not significant (Table 1).

The RAB of canids (including gray wolf, coyote, red fox, and grey fox), exhibited negative or non-significant relationships with distance and all structure types. Red foxes and grey wolves had significant negative relationships with campgrounds ($p = 0.002$ and

$p = 6.58e-5$, respectively). The RAB of coyotes had a significant negative relationship with historical sites ($p = 0.044$). Grey foxes were the only carnivore species tested that had a significant negative relationship with distance to nearest structure ($p = 3.75e-4$). All other combinations of distance and structure types with canid species were not significant (Table 1).

The RAB of mustelids, including fisher and American marten, had a significant and negative relationship to campgrounds ($p = 0.005$ and $p = 3.05e-7$, respectively). Fishers and American martens both displayed no significant relationship with distance to nearest structure. Neither of the mustelids had a significant relationship with lighthouses, park service buildings, or historical sites (Table 1).

Black bear and bobcat were the only detected members of their respective families (ursids and felids). The RAB of black bears had a significant negative relationship with lighthouses ($p = 2.06e-5$) and Park Service buildings ($p = 3.45e-4$), but a significant positive relationship with campgrounds ($p < 2e-16$). In contrast, bobcat RAB had a significant negative relationship with campgrounds ($p = 2.07e-5$), but no other structure type or distance was significant (Table 1).

Nocturnality

To determine whether anthropogenic activity has affected the temporal activity patterns of the carnivore community, I compared nocturnality along a gradient of anthropogenic activity, and there was minimal difference in nocturnality between the mainland unit, Stockton island, and Outer island. Risk ratio values for all three units

during the summer and fall seasons are effectively equal and indicate no change in temporal activity patterns due to anthropogenic activity; however, risk ratio values during winter and spring indicated an increase in nocturnality on Outer island relative to both Stockton island and the mainland unit compared to summer and fall. There was no difference across seasons between the mainland unit and Stockton island (Table 2).

Discussion

Anthropogenic impacts on wildlife have well-documented, varied effects, and understanding both the magnitude and direction of these effects is necessary for effective conservation of wildlife species (Gaynor et al 2018, Larson et al 2016). While protected areas are often considered strongholds for wildlife populations, recent research on the effects of anthropogenic activities in protected areas, such as recreation, tourism, livestock grazing, and development have highlighted that wildlife within protected areas are still exhibiting negative effects that may reduce individual fitness (Baker and Leberg 2018, M'soka et al 2017, Oladeji et al 2012, Pangle and Holekamp 2010, Pelletier 2006). Carnivores can be especially sensitive to anthropogenic impacts due to their body size, home range requirements, slow reproduction, and low population densities (Cardillo et al 2004, Cardillo et al 2005, Purvis et al 2000).

I used a grid of camera traps to monitor the carnivore community on the Apostle Islands and to determine how anthropogenic activity and structures affected the spatiotemporal distributions of the carnivore community. I found no evidence that distance to nearest structure affected carnivore community or carnivore species spatial

distribution, with the exception of grey foxes. At the community level, all structure types were significant and negatively related to carnivore community relative abundance, except for campgrounds, which was significant and positively related to carnivore community relative abundance. I also found little evidence of increased nocturnality among the carnivore community in relation to anthropogenic activity on the islands.

Wildlife species tend to spatially avoid most forms of anthropogenic development, including exurban residential development, energy development, and road networks (Hansen et al. 2005, Hovick et al. 2014, Northrup and Wittemyer 2012, Taylor and Goldingay 2010). On the Apostle Islands, the carnivore community and the individual species, with the exception of black bears, followed this trend of spatial avoidance of anthropogenic structures. Lighthouses and Park Service buildings were both significant and negatively related to the carnivore community and black bears, which supports my hypothesis that carnivores would tend to avoid anthropogenic structures. Similarly, historical sites were significant and negatively related to the carnivore community but had no relation to the individual carnivore species, except for coyotes. Within the national lakeshore, building type is likely correlated to degree of anthropogenic activity; however, the National Park Service does not track anthropogenic activity due to the logistical difficulties involved with rigorously monitoring a wilderness area. For example, Apostle Islands Cruises, a National Park Service authorized concessioner, provides daily boat cruises that visit several of the lighthouses within the island system, resulting in relatively high anthropogenic activity.

Of the current structures maintained by the National Park Service, campgrounds were the most likely to be significantly related to carnivore relative abundance. Small- and medium-bodied carnivore RAB was generally significant and negatively related to campgrounds, while the two large-bodied species (gray wolf and black bear) had significant but opposite effects from campgrounds. Black bears and the carnivore community as a whole, had a positive relationship with campgrounds while all other individual carnivore species had a negative relationship with campgrounds. This difference could be due to anthropogenic food subsidies at campgrounds that draw in black bears, similar to urban food subsidies (Backmann and Berger 2003, Hopkins III et al 2014). Season could also be influencing carnivore use of campgrounds since the campgrounds are much more likely to be occupied during the summer months than during the winter months (Wilton and Wirjanto 1998). If carnivores are taking advantage of a food subsidy or avoiding anthropogenic activity, then the effect of campgrounds would likely be dependent on the season.

Contrary to my hypotheses, the carnivore community exhibited no differences in nocturnality between the mainland unit, Stockton island, and Outer island. The lack of significance could possibly be because I tested nocturnality at the community level rather than the individual species level. Even though carnivores generally show an increase in nocturnality in response to anthropogenic activity and development, humans can have a differential effect on individual species (Crooks 2002, Gaynor et al. 2018). Body size and degree of specialization are often related to the magnitude of anthropogenic effect (Devictor et al. 2008, Gaynor et al. 2018, Larson et al 2016, Taylor and Knight 2003).

For example, larger-bodied animals tend to be more negatively affected than smaller-bodied animals, and specialists tend to be more negatively affected than generalists. Since the carnivore community on the Apostle Islands ranges in body size and degree of specialization, individual species could be decreasing or increasing nocturnality in response to anthropogenic activity.

Within the Apostle Islands, a remote and temperate archipelago, the carnivore community displayed spatial avoidance of anthropogenic structures but no change in temporal activity relative to anthropogenic activity. Since season and type of structure are likely correlated to the level of anthropogenic activity, it is important to be able to accurately track the amount of anthropogenic activity within island systems. Future research should focus on the possible role that seasonality plays in the spatiotemporal distribution of the carnivore community.

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Table 1. P-values and effect directions from generalized linear mixed effects models with species relative abundance as the dependent variable and distance and type of nearest structure as the fixed, independent variables.

Species	Distance to nearest structure		Campgrounds		Historical sites		Lighthouses		Park Service Buildings	
Community ^o	0.050	-	<2e-16	+	0.004	-	3.4e-13	-	0.007	-
Black Bear	0.048	-	<2e-16	+	0.147	-	2.06e-5	-	3.45e-4	-
Bobcat	0.982	+	2.07e-5	-	0.802	-	0.993	-	0.554	-
Gray wolf	0.875	-	6.58e-5	-	0.996	-	0.995	-	0.899	-
Coyote	0.829	+	0.247	-	0.044	-	0.158	-	0.052	+
Red Fox	0.090	-	0.002	-	0.922	-	0.827	-	0.606	-
Gray Fox	3.27e-4	-	0.892	-	0.993	-	0.989	-	0.718	-
Fisher	0.136	-	0.005	-	0.889	-	0.995	-	0.997	-
American marten	0.135	+	3.05e-7	-	0.142	-	0.697	+	0.987	-

^oCommunity includes all species listed in the table.

Bolded values indicate significance at $p < 0.05$.

Table 2. Risk ratios with 95% confidence intervals comparing nocturnality along a gradient of anthropogenic activity of the carnivore community of the Apostle Islands. Values close to 1 indicate little difference in nocturnality, values greater than 1 indicate increased nocturnality, and values less than 1 indicate a lesser degree of nocturnality.

High activity	Low activity	Summer/Fall	Winter/Spring
Stockton	Outer	0.9 (0.69-1.19)	1.4 (0.94-2.09)
Mainland	Outer	0.9 (0.66-1.33)	1.3 (0.89-1.90)
Mainland	Stockton	1.0 (0.79-1.35)	0.9 (0.7-1.19)

Figure 1. Map of the Apostle Islands National Lakeshore, Wisconsin, USA with camera trap locations.

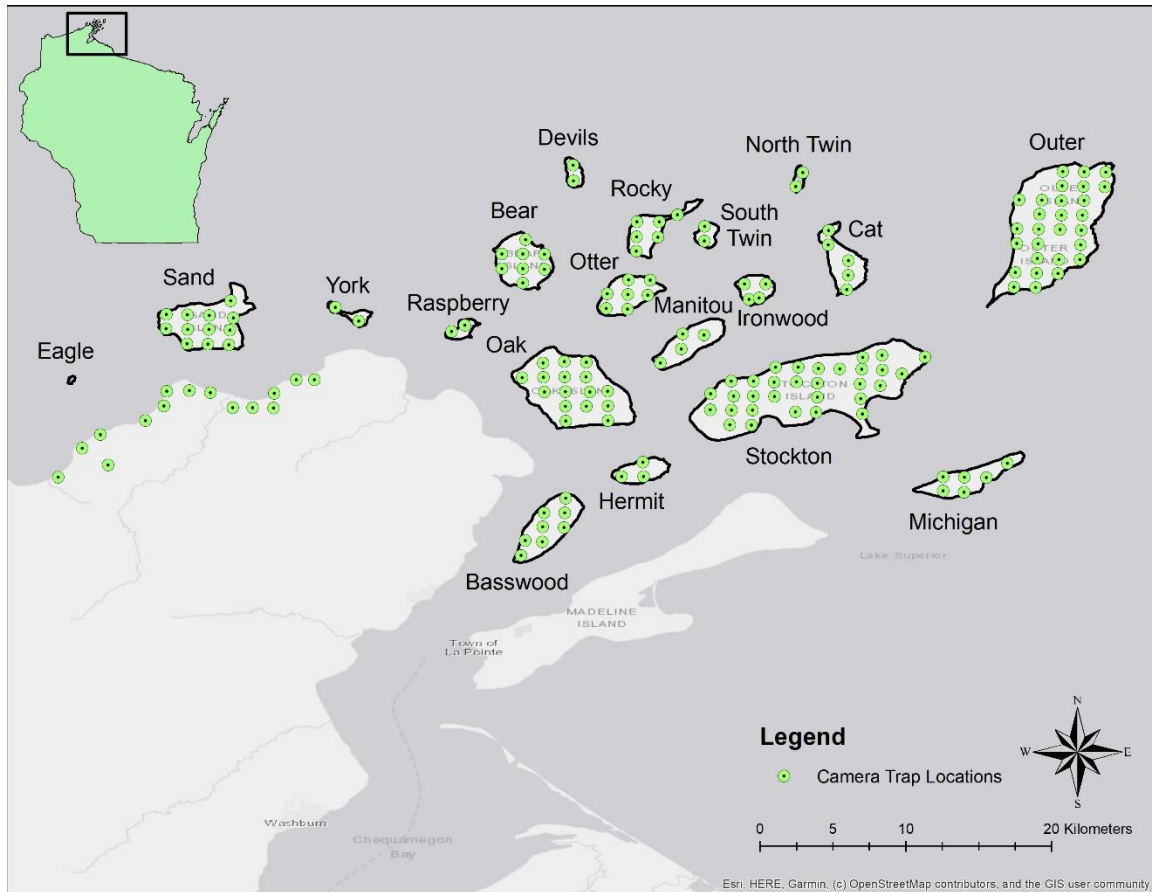


Figure 2. Location of current and historical anthropogenic structures within the Apostle Islands National Lakeshore.

