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SUMMARY AND ACKNOWLEDGEMENTS

This is the annual report for Great Lakes Northern Forest CESU Cooperative Agreement P14AC01180 between the United States Department of Interior and University of Wisconsin-Madison, entitled “Survey Carnivores at Apostle Islands National Lakeshore using Camera Traps.”

The Apostle Islands carnivore guild assessment project was a 4-year cooperative investigation between researchers at the University of Wisconsin-Madison, Northland College, and the National Park Service (NPS), Apostle Islands National Lakeshore (APIS). Researchers from all three groups contributed to the study design, along with placement and maintenance of camera traps. Researchers at the University of Wisconsin provided statistical analyses and reporting, and will ensure that results will be published in peer-reviewed journals.

We thank the personnel from each group that contributed to this project, especially APIS staff and volunteers, graduate students from the Van Deelen lab at the University of Wisconsin – Madison, and students from Northland College that provided assistance over the course of the project. The support and cooperative spirit between these three groups was key to the success of this project.
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ABSTRACT

Carnivores are important components of ecosystems with wide-ranging effects on ecological communities. These wide-ranging effects are complex and vary with carnivore size, natural history, and hunting tactics, and researchers and managers must understand the ecological roles of carnivores and their interactions with their local environment. We studied the carnivore guild in the Apostle Islands National Lakeshore (APIS), where the distribution, abundance, and occupancy of carnivores was largely unknown. This knowledge was needed to understand island-level variation in carnivore communities and how this variation affects the community-level ecology of APIS. We developed a systematic method to deploy a grid of camera traps while targeting fine-scale features to maximize carnivore detection (Appendix 1) and for organizing and tagging the resulting photograph data (Appendix 2).

In this report, we document our findings from deploying 160 camera traps on 19 islands and mainland Wisconsin from 2014-2017. We collected 203,385 photographs across 49,280 trap nights, with 7,291 total wildlife events and 1,970 carnivore events. We had a mean 7.68 functioning camera traps per island (range 1-30), and our camera trap density averaged 1.89 (range 0.75-12.50) camera traps/ km². We detected 10 terrestrial carnivores among 21 unique species detected, including unanticipated detections of American martens (Martes americana) and gray wolves (Canis lupus). The mean richness of carnivores on an island was 3.10 (range 0-10) species/island.

The most supported single variable to explain carnivore richness on the Apostle Islands was island size, while the most supported model was island biogeography, which included island size (positive correlation), distance to mainland (negative correlation), and distance to nearest island (negative correlation). The relative abundance of a species was significantly correlated with the number of islands on which they were found. Mean carnivore occupancy across islands ranged from 0.24 for gray wolves to a high of 0.93 for black bears (Ursus americanus). Detection rates for species were generally higher in summer than winter, with the exception of coyotes (Canis latrans) and red foxes (Vulpes vulpes).
Low levels of human activity and development in APIS may play a role in supporting carnivore species that tend to avoid human disturbance. However, none of the islands in the archipelago are likely large enough to sustain populations of mammalian carnivores in the face of demographic stochasticity or the genetic effects of small population size. Therefore, one important area for future study is determining how carnivores colonize and move between islands, as well as how the carnivore guild interacts and affects each other. Fuller understanding of APIS ecology will require on-going monitoring of carnivores to evaluate temporal dynamics as well as related ecological evaluations (e.g. small mammal dynamics, plant community dynamics) to understand trophic effects.


*Photograph 1. Black bear cubs with their mother during autumn on Hermit Island.*
INTRODUCTION


Given their effects on ecological communities, loss of carnivores may change ecosystem dynamics. Worldwide and throughout the USA, many carnivore populations are threatened and diminished over the last century (Laliberte and Ripple 2004, Ripple et al. 2014). Carnivores are among the most charismatic wildlife species (Kellert 1997, Ray et al. 2013) and are important to consider in the management of National Parks. The National Park System (NPS) mission is to “preserve unimpaired the natural and cultural resources and values of the NPS for the enjoyment, education, and inspiration of this and future generations” (Anderson and Barbour...
Wildlife viewing opportunities are an important part of a park visitor’s experience, and many visitors are interested in seeing unique native wildlife, with large carnivores often drawing more attention than other species (Okello et al. 2008). Carnivores are therefore critical components of ecosystems and the experience of a park’s constituents, and it is important for the National Park Service to manage carnivore communities within respective parks.

Niche partitioning allows species to reduce competition for selected resources (Carvalho and Gomes 2004, Schuette et al. 2013), and partitioning frequently occurs with respect to selected prey and spatiotemporal activity (du Preez et al. 2017, Wang et al. 2015). Despite the difficulty in measuring precise levels of partitioning between sympatric species, determining how plastic or rigid species niches and distributions are in relation to interspecific competition is important in further understanding the mechanisms that affect species assemblages. The intensity of interspecific competition of sympatric carnivores may vary with seasonal prey abundance, life history similarity, habitat homogeneity, and competitor distribution (Gompper et al. 2013, du Preez et al. 2017, Manlick et al. 2017). In many cases, carnivores exhibit spatial or temporal partitioning loosely based on body size, with smaller carnivores tending to avoid areas or time periods where they are more susceptible to intraguild predation (Di Bitetti et al. 2010, Schuette et al. 2013, Wang et al. 2015).

The Apostle Islands National Lakeshore (APIS, acronym based on NPS standards) was established in 1970 and included 21 of the 22 islands to protect their unique cultural and natural value (Busch 2008). Human use is limited to recreational and land management activities (Feldman 2004), but the presence and distribution of carnivore populations in APIS was largely unknown. Recent wildlife research includes black bear (Ursus americanus) population dynamics (Belant et al. 2005), which found substantial black bear immigration from mainland populations.
A historical observational report recorded the presence of red fox (*Vulpes vulpes*) on the islands, and coyotes (*Canis latrans*) were observed traveling on the ice (Jackson 1920). Reintroductions of American martens (*Martes americana*) occurred in APIS during the 1950’s (Williams et al. 2007), but these reintroductions were assumed to have failed (Williams et al. 2007). Formal studies of carnivore distribution in the archipelago are needed to better understand the island-level variation in presence, distribution, and composition of carnivore communities, and how this affected the ecology of APIS.

*Photograph 2. A coyote walking along a lagoon on Stockton Island.*

Monitoring distribution and trends in population sizes of species are a fundamental part of wildlife management. Carnivores, however, can be difficult to monitor rigorously due to their low population densities and cryptic behaviors (Harmsen et al. 2010, Krofel et al. 2012, Allen et al. 2016b). Surveys performed via camera traps are a potential solution to the difficulty of monitoring the carnivore community in APIS. Camera trapping has been successfully used to
assess occupancy dynamics for single or multiple species across large regions in many biomes (Rich et al. 2017, Steenweg et al. 2016). The reliability of camera traps combined with well-developed occupancy models has made camera trapping an indispensable tool for monitoring wildlife populations. The optimal survey design and analytical techniques for camera trapping vary widely and efforts to develop and standardize optimal procedures are ongoing (see review in Burton et al. 2015). The design used depends critically on the monitoring goals and the logistical constraints associated with camera trap deployment, data recovery, and visitation to and within the study site.

This project builds on a previous cooperative agreement between the NPS and the University of Wisconsin-Madison to design a rigorous monitoring program for large carnivores in APIS. Our original project objectives, as noted in the grant proposal and grant agreement between the University of Wisconsin - Madison and NPS were:

1) Develop protocols for using camera traps to determine the occurrence of carnivores, including relative abundance, where possible. Ensure that protocols can be used throughout the park and are readily transferrable to other remote areas.

2) As part of protocol development, obtain: estimates of detection probabilities for each carnivore species to understand how long camera traps need to be deployed; determine the season of greatest detection probability to understand time of year camera traps should be deployed; and through sub-sampling of camera traps, know the camera trap density needed to detect species of interest.

3) For the pilot location, Stockton Island, determine which carnivore species are present and their distribution. If possible, determine relative abundance.

In consultation with APIS staff, we have expanded beyond the scope of these objectives,
including expanding our monitoring efforts beyond Stockton Island. Additional goals of the project included examining the dynamics of the islands’ carnivore guild using occupancy modeling and inferring how these processes reflect theory from island biogeography and community ecology. In this report we document our findings from deploying 160 camera traps on 19 of 21 islands and mainland Wisconsin from 2014-2017 (Table 1). Islands not surveyed include Gull Island (3 acres) and Long Island (a barrier spit). Our findings include a) the species richness of each of the islands we monitored, b) the distribution, relative abundance, and mean relative abundance of carnivore species, c) the occupancy and detection rates of each carnivore species. We also provide the methodology we developed for establishing a camera trap monitoring project (Appendix 1), including systematic methods for organizing and tagging the photograph data (Appendix 2). We conclude with recommendations and potential areas of future research.

*Photograph 3. A bobcat resting in a forest on Oak Island.*
METHODS

Study Area

The Apostle Islands are an archipelago of Pleistocene relict sandstone islands located in southwestern Lake Superior, Wisconsin, USA. Since glacial retreat, processes of erosion and deposition have created a dynamic island system. For example, erosion washed away Little Steamboat Island by around 1898, and continues to erode others such as Gull Island (Judziewicz and Koch 1993). In contrast, deposition has united islands such as the tombolo between Presque Isle and Stockton Island (Judziewicz and Koch 1993). Today, the products of post-glacial erosion can be witnessed as red-toned rock outcrops and cliffs throughout the shores of the islands. Microclimatic conditions, which influence vegetative communities, are highly variable between islands depending on their size, elevation, and location with respect to Lake Superior (Table 1) (Judziewicz and Koch 1993). For instance, islands situated farther north and northwest in the archipelago experience the brunt of prevailing northerly storm winds, resulting in cooler conditions, whereas islands with higher elevation and larger size, such as Oak Island, tend to experience warmer microclimates (Judziewicz and Koch 1993).

The islands are in the transition zone between northern boreal coniferous forest and deciduous forest, which creates a diverse vegetative structure (Craven and Lev 2017). Poorly drained clay soils lay the foundation for hemlock, white pine, northern hardwood, and boreal forest communities (Judziewicz and Koch 1993). The vegetation present on a given island is strongly affected by variation in logging history, fire, and deer herbivory (Beals and Cottam 1960). The most common forest type present today is maple-yellow birch northern hardwoods forest (65%), followed by white-cedar-boreal conifer mesic forest (13%), and then north-central hemlock-hardwood forest (<1%) (Hop et al. 2010). The understory primarily consists of American yew (Taxus canadensis), mountain maple (Acer spicatum), beaked hazelnut (Corylus
cornuta), skunk currant (Ribes glandulosum), juneberries (Amelanchier spp.), fly honeysuckles (Lonicera canadensis) and bush-honeysuckle (Diervilla lonicera) (Judziewicz and Koch 1993).

Table 1. Characteristics of the individual islands monitored within the Apostle Islands National Lakeshore, Wisconsin (USA, 2014-2017).

<table>
<thead>
<tr>
<th>Island</th>
<th>Island Size (km²)</th>
<th>Distance to Mainland (km)</th>
<th>Distance to Nearest Island (km)</th>
<th>Maximum Elevation (m)</th>
<th>Mean Elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basswood</td>
<td>7.74</td>
<td>1.87</td>
<td>2.20</td>
<td>58</td>
<td>32.3</td>
</tr>
<tr>
<td>Bear</td>
<td>7.34</td>
<td>7.23</td>
<td>2.84</td>
<td>72</td>
<td>26.9</td>
</tr>
<tr>
<td>Cat</td>
<td>5.41</td>
<td>18.03</td>
<td>2.74</td>
<td>25</td>
<td>13.3</td>
</tr>
<tr>
<td>Devils</td>
<td>1.25</td>
<td>14.33</td>
<td>3.36</td>
<td>21</td>
<td>10.6</td>
</tr>
<tr>
<td>Eagle</td>
<td>0.08</td>
<td>3.54</td>
<td>5.13</td>
<td>8</td>
<td>5.4</td>
</tr>
<tr>
<td>Hermit</td>
<td>3.17</td>
<td>3.67</td>
<td>2.20</td>
<td>56</td>
<td>21.7</td>
</tr>
<tr>
<td>Ironwood</td>
<td>2.69</td>
<td>14.44</td>
<td>1.66</td>
<td>27</td>
<td>15.3</td>
</tr>
<tr>
<td>Manitou</td>
<td>5.36</td>
<td>8.43</td>
<td>1.66</td>
<td>43</td>
<td>19.7</td>
</tr>
<tr>
<td>Michigan</td>
<td>6.18</td>
<td>17.86</td>
<td>4.09</td>
<td>29</td>
<td>15.0</td>
</tr>
<tr>
<td>North Twin</td>
<td>0.65</td>
<td>20.76</td>
<td>2.73</td>
<td>13</td>
<td>8.4</td>
</tr>
<tr>
<td>Oak</td>
<td>20.32</td>
<td>2.12</td>
<td>2.22</td>
<td>147</td>
<td>66.8</td>
</tr>
<tr>
<td>Otter</td>
<td>5.35</td>
<td>8.43</td>
<td>1.29</td>
<td>44</td>
<td>24.4</td>
</tr>
<tr>
<td>Outer</td>
<td>21.78</td>
<td>23.83</td>
<td>4.28</td>
<td>83</td>
<td>31.7</td>
</tr>
<tr>
<td>Raspberry</td>
<td>1.16</td>
<td>2.69</td>
<td>2.91</td>
<td>30</td>
<td>15.4</td>
</tr>
<tr>
<td>Rocky</td>
<td>4.24</td>
<td>12.41</td>
<td>1.05</td>
<td>31</td>
<td>14.4</td>
</tr>
<tr>
<td>Sand</td>
<td>11.58</td>
<td>2.04</td>
<td>3.47</td>
<td>19</td>
<td>9.6</td>
</tr>
<tr>
<td>South Twin</td>
<td>1.36</td>
<td>15.06</td>
<td>1.05</td>
<td>15</td>
<td>8.3</td>
</tr>
<tr>
<td>Stockton</td>
<td>40.00</td>
<td>7.84</td>
<td>2.15</td>
<td>61</td>
<td>25.7</td>
</tr>
<tr>
<td>York</td>
<td>1.10</td>
<td>1.48</td>
<td>3.47</td>
<td>12</td>
<td>6.3</td>
</tr>
</tbody>
</table>

The earliest human presence on the Apostle Islands was Native American settlements on Madeline Island (Beals and Cottam 1960). Later, French explorers established a trading post on Madeline Island in 1693, called La Pointe, which was the hub for commerce of the Lake Superior region in the 18th and early 19th centuries (Judziewicz and Koch 1993). As the fur trade declined during the late 19th century, logging and mining became the main economic pursuit on the Apostle Islands (Beals and Cottam 1960). Today human use within APIS is limited to recreational and land management activities (Busch 2008).
Photograph 4. A trio of black bear cubs with their mother on Bear Island.

Historical temperature data collected from Madeline Island reported maximum daily mean temperatures ranging from 25.5°C in July to -4.5°C in January. Low and high temperature records are -35°C and 38°C, respectively. Historical precipitation has averaged about 75 cm annually with 200 cm of snow (Judziewicz and Koch 1993). The average temperature for the duration of this study was 4.4°C, with minimum and maximum temperatures ranging from -30.0°C to 32.8°C, respectively. Average annual precipitation for the three years in this study was 82.8 cm of rainfall and 197.4 cm of snowfall (National Centers for Environmental Information 2017).

Ice cover is an important factor for mammalian community structure in temperate archipelagos, influencing the propensity for immigration and emigration (Lomolino 1988). Ice cover in the Bayfield harbor, which is indicative of overall lake trends, has decreased over the past 150 years at a rate of about 3 days/decade (Howk 2009). Since 1975, the ice season has
begun an average of 11.7 days later and ended 3.0 days earlier every decade (Howk 2009). This is consistent with declining number of days between freeze-up and break-up in lakes and rivers throughout the northern hemisphere during the 19th and 20th centuries (Magnuson et al. 2000).

**Field Methods and Design**

Careful and deliberate camera trap placement is critical for accurately and efficiently documenting carnivores with camera traps (Krofel et al. 2012, Taylor et al. 2015, Allen et al. 2016b) and estimating their distributions and abundance (Chandler and Royle 2013, Burton et al. 2015, Rich et al. 2017). We developed a systematic method to deploy camera traps (Appendix 1), where camera traps were placed near the center of 1 km² grids that were overlain on the islands. We then created a ‘camera trap deployment location’ at the center of each grid cell whose surface area contained >50% land. For Stockton Island, 34 grid points were generated; however because we only had 30 camera trap traps available we randomly omitted four deployment locations from the final configuration. In subsequent camera trap deployments, we adjusted camera trap density \( y, \text{camera traps/km}^2 \) using a power law curve based on island size \( x, \text{km}^2 \) to ensure smaller islands were surveyed more intensively (Figure 1). We used the following power law curve equation:

\[
y = 2.0826x^{-0.369}
\]

On Oak Island, two camera trap locations were omitted according to our power law curve for camera trap density. We omitted one location that was in an area of high human use and a second location due to access issues (e.g., steep ravine). For some of the smaller islands we relaxed our >50% of grid cell surface area on land to ensure adequate camera trap densities. For example, Eagle Island was ~0.1 km², thus, no camera trap locations would meet the >50% of grid surface area on land requirement. We explicitly targeted fine-scale features (i.e. camera trap height,
orientation, and distance to wildlife sign) to maximize carnivore detection when placing camera traps. We would walk in concentric circles from the grid point until a suitable location was found. We recorded the coordinates of each camera trap site with a handheld GPS unit, but did not place flagging or physically mark any of the sites, and then placed the camera trap.

![Photograph 5. An American marten in a winter forest.](image)

We used our protocol to place 164 camera traps (HC600 Hyperfire™ High Output Covert, PC 800 Hyperfire Professional Semi-covert, and HC500 Hyperfire Semi-covert cams; RECONYX, Inc., Holmen, WI, USA) on 19 islands (Table 1). These camera traps have an infrared flash, trigger speed of 1/5 sec, and a 1080p high definition image resolution. We programmed camera traps to take a photograph when triggered by an animal and also to take a “time-lapse” photograph every day at 11 am or 12pm to create a systematic sampling of changing ecological conditions (see below). We programmed the camera traps to record the time, date, temperature, and moon phase for each photograph. We initially programmed the camera traps on Stockton Island to take 5 photographs, 1 sec between each photograph, and a 15 sec
delay between events. We then changed our programming to take 3 photographs, with no refractory period between each event as we expanded our camera trap grid to other islands. We conducted camera trapping year-round to encompass seasonal changes in carnivore activity and visual obstructions caused by changes in vegetation. We returned to each of the camera trap sites approximately six months after the initial deployment date to replace batteries and memory cards. On each island, we randomly assigned a lure treatment to half of the camera trap sites for that island. We placed aerial call lures (~3-4 m) and local lures (on downed woody vegetation) to draw carnivores into the camera trap’s core detection area. Sites received a commercial predator trapping scent lure (Caven’s Gusto, Minnesota Trapline Products Inc.) during the first 6-month deployment, and later we rotated sites and all previously non-lured sites received lure during the second 6-month deployment.

We defined a carnivore event as any series of 3-5 photographs (as programmed) triggered by a carnivore species. We used the carnivore events to determine the relative abundance of carnivores and their presence at each camera trap site. To reduce pseudo-replication when calculating relative abundance, we considered multiple photographs of a species within 30 min of a previous photograph to be the same event (Wang et al. 2015, Rich et al. 2017).

**Statistical Analyses**

We used the program R version 3.3.1 (R Core Team 2016) for all of our statistical analyses, and in each analysis we considered $p < 0.05$ to be statistically significant.

We calculated carnivore species richness as the number of carnivore species detected on a given island. We then tested *a-priori* hypotheses (Table 2) of variation in carnivore species richness using linear regression. We used the carnivore species richness as our dependent
variable and island size (km²), distance to mainland (km), distance to nearest island (km), maximum elevation (km), and trap nights as our independent variables. We compared models using AIC weight, with AICc values in each of our models due to low sample sizes (Burnham and Anderson 2002). When interpreting models we considered our top models to be those before a cumulative wAIC threshold of 0.90 (Burnham and Anderson 2002).

**Table 2.** Our a-priori models for factors determining carnivore richness among islands. We provide the name of the model, the variables included (ISSZ = island size, MLDI = distance to mainland, ISDI = distance to nearest island, ELEV = elevation, TRAP = trap nights) and the hypothesis/reasoning behind the model.

<table>
<thead>
<tr>
<th>Name</th>
<th>Variables</th>
<th>Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island Size</td>
<td>ISSZ</td>
<td>Larger islands will support greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Distance to Mainland</td>
<td>MLDI</td>
<td>Larger islands closer to the source population will support greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Distance to Nearest Island</td>
<td>ISDI</td>
<td>Less isolated islands will support greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Immigration Island Biogeography</td>
<td>ISSZ * MLDI</td>
<td>Larger islands that are less isolated from the source population will support immigration and therefore greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Island Size and Elevation</td>
<td>ISSZ * ELEV</td>
<td>Larger islands with greater elevation range will provide a diversity of habitats that will increase carnivore richness (MacArthur and Wilson 1967, Wilson 2009).</td>
</tr>
<tr>
<td>Island Biogeography</td>
<td>ISSZ * ISDI * MLDI</td>
<td>Larger, less isolated islands will support greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Elevation and Island Biogeography</td>
<td>ISSZ * ISDI * MLDI * ELEV</td>
<td>Larger, less isolated, and more habitat diverse islands will support greater species richness (MacArthur and Wilson 1967, Wilson 2009)</td>
</tr>
<tr>
<td>Trapping Effort</td>
<td>TRAP</td>
<td>The mean number of trap nights per camera trap is a potential source of bias, and carnivores detected may simply be based on trap nights (e.g., Larrucea et al. 2007).</td>
</tr>
</tbody>
</table>
We determined the distribution of each terrestrial carnivore species across the islands based on the distributions of camera traps with an event. We then calculated relative abundance (RA) for each carnivore species as:

\[
RA = \frac{D}{TN} \times 100
\]

where \(D\) is the number of detections and \(TN\) is the total number of trap nights at a camera, and overall relative abundance is the mean of all cameras. We then tested whether the mean relative abundance of a carnivore was correlated with the number of islands the carnivore was found on using linear regression.

We used occupancy models (MacKenzie et al. 2006) to estimate the occurrence of carnivore species across islands. Succinctly, occupancy models assume that an animal’s presence at a specific site \(i\) \((z_i)\), is distributed as Bernoulli \((\psi)\), and that observed presence or absence at specific sites over \(j\) repeated intervals \((y_{i,j})\) is distributed as Bernoulli \((z_i \times p)\), where \(p\) is the probability of detecting a present species. Both occupancy probability \((\psi)\) or detection probability may vary as a function of site-specific or site and interval-specific covariates, e.g.:

\[
\text{logit}(\psi_i) = \beta_0 + \beta_1 X_{1,i}; \text{ if no temporal variation in } p \text{ is considered within a model, } y_{i,j} \text{ can be reformulated as a Binomial count—e.g., } y_i \sim \text{Binomial} (z_i \times p, k) \text{—for increased computational efficiency.}
\]

We subdivided the monitoring periods into two seasons: summer (May through October) and winter (November through April), and calculated the number of camera trap nights per island within these periods and the number of 24 h periods in which our focal species were each detected. We used these detection and effort metrics as inputs for multi-species occupancy models (Dorazio and Royle 2005): extensions of single-species models that treat species-level parameters \((s)\) as random effects drawn from a common distribution: e.g., \(\text{logit} (\beta_s) \sim \text{Normal} (\mu_\beta, \sigma_\beta)\).
σβ). We modeled occupancy variability as logit \( \psi_{i,s} = \beta_{0,s} + \beta_{1,s}\text{IslandSize}_i + \beta_{2,s}\text{IslandDistance}_i + \beta_{3,s}\text{MainlandDistance}_i + \beta_{4,s}\text{MaxElev}_i \), with species-specific probabilities of detection (p) varying between summer and winter, where \( p = \text{season} + \epsilon \), where \( \epsilon \) is the species error term x site. Given the small number of islands, we expected the full model to be over-parameterized, and we used indicator variable selection (Kuo and Mallick 1998) to select suitable and parsimonious models for each species. Indicator variable selection associates each coefficient with a binary random variable \( w_\theta \) that iteratively dictates whether a term is included within a model: when \( w = 0 \), the term is not included within the model, and when \( w = 1 \), the term is (i.e., logit \( \psi_{i,s} = \beta_{0,s} + \beta_{1,s}\text{IslandSize}_i w_{1,s} \)). The posterior mean of any \( w_\theta \) is equivalent to the probability that the model term should be included within the predictive model, with values > 0.5 generally considered to be useful terms.

We fit models using MCMC using JAGS (Plummer 2003) through the jagsUI package, and used appropriately balanced priors for beta coefficients within logistic models (Gelman and Hill 2007) and Uniform (0, 1) priors for probability parameters. We considered models to have converged if traceplots exhibited adequate mixing and if point estimates of the Gelman-Rubin convergence statistic were less than 1.1 (Gelman and Rubin 1992). We used posterior samples from the fitted model to derive several additional metrics of interest. First, we report finite-sample occupancy estimates for each carnivore on each island (i.e., the posterior mean of \( \hat{z}_{\text{species, island}} \)), and estimates of the proportion of islands in which each species was present (\( \overline{PAO} \)). Because estimated detection probability per trap-night was small for each species, we report derived detection probabilities for each season per 100 trap-nights (a more realistic unit of monitoring effort).
RESULTS

Summary Statistics

We collected data from 160 camera traps on 19 islands and mainland Wisconsin in APIS, but had 4 camera traps malfunction, so they did not record any data and were excluded from our analyses. We had a mean 7.68 (±1.87 SE) functioning camera traps per island (range 1-30) (Table 3). Our camera trap density on islands averaged 1.89 (±0.60 SE, range 0.75-12.50) functioning camera traps/km² (Table 3). We collected 203,385 photographs across 49,280 trap nights. We documented 7,291 wildlife events, including 1,970 carnivore events.

Table 3. Characteristics of sampling effort for camera traps deployed on each island within the Apostle Islands National Lakeshore, Wisconsin (USA, 2014-2017).

<table>
<thead>
<tr>
<th>Island</th>
<th>Functioning Camera Traps</th>
<th>Total Trap Nights</th>
<th>Mean Nights Per Camera Trap</th>
<th>Camera Trap Density (cams/km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basswood</td>
<td>8</td>
<td>1736</td>
<td>217.0</td>
<td>1.03</td>
</tr>
<tr>
<td>Bear</td>
<td>8</td>
<td>4104</td>
<td>513.0</td>
<td>1.09</td>
</tr>
<tr>
<td>Cat</td>
<td>5</td>
<td>2433</td>
<td>486.6</td>
<td>0.92</td>
</tr>
<tr>
<td>Devils</td>
<td>2</td>
<td>712</td>
<td>356.0</td>
<td>1.59</td>
</tr>
<tr>
<td>Eagle</td>
<td>1</td>
<td>536</td>
<td>536.0</td>
<td>12.50</td>
</tr>
<tr>
<td>Hermit</td>
<td>3</td>
<td>1618</td>
<td>539.3</td>
<td>0.95</td>
</tr>
<tr>
<td>Ironwood</td>
<td>4</td>
<td>635</td>
<td>158.8</td>
<td>1.49</td>
</tr>
<tr>
<td>Manitou</td>
<td>4</td>
<td>1859</td>
<td>464.8</td>
<td>0.75</td>
</tr>
<tr>
<td>Michigan</td>
<td>6</td>
<td>1229</td>
<td>204.8</td>
<td>0.97</td>
</tr>
<tr>
<td>North Twin</td>
<td>2</td>
<td>861</td>
<td>430.5</td>
<td>3.08</td>
</tr>
<tr>
<td>Oak</td>
<td>16</td>
<td>6549</td>
<td>409.3</td>
<td>0.79</td>
</tr>
<tr>
<td>Otter</td>
<td>7</td>
<td>3277</td>
<td>468.1</td>
<td>1.31</td>
</tr>
<tr>
<td>Outer</td>
<td>26</td>
<td>6935</td>
<td>266.7</td>
<td>1.19</td>
</tr>
<tr>
<td>Raspberry</td>
<td>2</td>
<td>743</td>
<td>371.5</td>
<td>1.72</td>
</tr>
<tr>
<td>Rocky</td>
<td>6</td>
<td>3196</td>
<td>532.7</td>
<td>1.41</td>
</tr>
<tr>
<td>Sand</td>
<td>12</td>
<td>2333</td>
<td>194.4</td>
<td>1.04</td>
</tr>
<tr>
<td>South Twin</td>
<td>2</td>
<td>952</td>
<td>476.0</td>
<td>1.47</td>
</tr>
<tr>
<td>Stockton</td>
<td>30</td>
<td>7330</td>
<td>244.3</td>
<td>0.75</td>
</tr>
<tr>
<td>York</td>
<td>2</td>
<td>422</td>
<td>211.0</td>
<td>1.82</td>
</tr>
</tbody>
</table>
Camera Trap Deployment Protocol

We developed a standardized protocol for placing camera traps to detect terrestrial carnivores in APIS (Appendix 1). We also developed a photograph-tagging protocol for use in interpreting and analyzing data obtained from camera traps. This protocol was used during the study and can also be used for future studies in APIS or other NPS units, and is explained in detail in Appendix 2.

We found that the protocol successfully detected the presence of terrestrial carnivores across islands of different sizes and various habitats. We detected 21 unique species and 6 other groups of species (raptors, small rodents, songbirds, squirrels, waterfowl, weasels), including 10 terrestrial carnivores and two semi-aquatic carnivores (mink, *Neovison vison*, and river otter, *Lontra canadensis*). Each of the terrestrial carnivores was found on 2 to 13 islands (Figure 1).

![Carnivore Species](image)

*Figure 1. The number of islands which each terrestrial carnivore was documented (drawing by Yiwei Wang). All carnivores except for American marten and gray fox were also detected on the mainland.*
**Carnivore Species Richness**

The mean richness of carnivores detected on the islands was 3.10 (±0.62 SE), and varied from 0 (Eagle, North Twin, and York) to 10 (Stockton Island) (Figure 2).

![Figure 2. Map of carnivore species richness for each of our study islands.](image)

**Table 4. Results from our a-priori modeling of carnivore richness by island in the Apostle Island National Lakeshore (2014-2017).**

<table>
<thead>
<tr>
<th>Model (see Table 2)</th>
<th>AICc</th>
<th>wAIC AICc</th>
<th>wAIC AICc</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island Biogeography</td>
<td>60.25</td>
<td>0.9960</td>
<td>0.9960</td>
<td>0.92</td>
</tr>
<tr>
<td>Immigration Island Biogeography</td>
<td>72.92</td>
<td>0.0018</td>
<td>0.9978</td>
<td>0.80</td>
</tr>
<tr>
<td>Island Size and Elevation</td>
<td>73.26</td>
<td>0.0015</td>
<td>0.9993</td>
<td>0.80</td>
</tr>
<tr>
<td>Island Size</td>
<td>74.64</td>
<td>0.0007</td>
<td>1.0000</td>
<td>0.69</td>
</tr>
<tr>
<td>Distance to Nearest Island</td>
<td>93.86</td>
<td>0.0000</td>
<td>1.0000</td>
<td>0.14</td>
</tr>
<tr>
<td>Distance to Mainland</td>
<td>94.80</td>
<td>0.0000</td>
<td>1.0000</td>
<td>0.09</td>
</tr>
<tr>
<td>Trapping Effort</td>
<td>96.61</td>
<td>0.0000</td>
<td>1.0000</td>
<td>0.01</td>
</tr>
<tr>
<td>Elevation and Island Biogeography</td>
<td>655.23</td>
<td>0.0000</td>
<td>1.0000</td>
<td>0.99</td>
</tr>
</tbody>
</table>
Our top model for carnivore richness was Island Biogeography (\(a\text{AIC} = 0.9960, R^2 = 0.92\)), which was our only model with substantial support (Table 4). Island size had a positive effect on carnivore richness (\(\beta = 0.29\)), distance to mainland had a negative effect (\(\beta = -0.32\)), and distance to nearest island had a negative effect (\(\beta = -1.38\)).

**Carnivore Relative Abundance and Distribution**

The mean relative abundance (number of detections per 100 trap nights) of species had a significant strong relationship with the number of islands they were found on \((F_{1, 8} = 8.55, R^2 = 0.82, p = 0.0034)\), but this relationship varied. For example, black bears were found on a high number of islands \((n = 13)\) (Figure 3b) and had a high relative abundance \((2.01)\) (Figure 4), but red fox were distributed on a high number of islands \((n = 9)\) (Figure 3i) and had a low relative abundance \((0.31)\). The species distribution and relative abundance at each camera site over the course of the study are represented in Figures 3a-3j.
Figure 3b: Black Bear

Relative Abundance
- Not Detected
- < 2.0
- 2.0 - 4.0
- 4.0 - 6.0
- > 10.0

Figure 3c: Bobcat

Relative Abundance
- Not Detected
- < 0.5
- 0.5 - 1.0
- 1.0 - 1.5
- 1.5 - 2.0
- 2.0 - 2.5
- 2.5 - 3.0
- > 3.0

No Data
Figure 3f: Gray Fox

Relative Abundance

- Not Detected
- < 0.5
- 0.5 - 1.0
- 1.0 - 1.5
- 1.5 - 2.0
- 2.0 - 2.5
- 2.5 - 3.0
- No Data

Figure 3g: Gray Wolf

Relative Abundance

- Not Detected
- < 0.5
- 0.5 - 1.0
- 1.0 - 1.5
- 1.5 - 2.0
- 2.0 - 2.5
- 2.5 - 3.0
- No Data
Figure 3h: Raccoon

Figure 3i: Red Fox
Mean relative abundances across APIS for carnivores ranged from a low of 0.01 (±0.01 SE) for weasels (*Mustela spp.*) to a high of 2.08 (±0.47 SE) for black bears (Figure 4).

*Figure 4. Mean relative abundance and standard error for the 10 terrestrial carnivores detected on 19 islands in APIS (drawing by Yiwei Wang).*
**Carnivore Occupancy and Detection Rates**

Occupancy of carnivores varied across islands (Table 5). APIS-wide distribution based on observed and predicted occupancy (defined as island-level values of ≥0.50) varied from 18 islands for black bears and raccoons to 1 island for gray wolves. Perfect positive occupancy (1.00) was frequent among species and associated with actual observations on islands, while perfect negative occupancy (0.00) was not predicted for any carnivore species on any island despite the absence of actual observations on some islands. Mean occupancy (predicted and observed) across islands varied from a low of 0.24 (± 0.04 SE) for gray wolves to a high of 0.93 (± 0.04 SE) for raccoons and 0.89 (± 0.05 SE) for black bears.

<table>
<thead>
<tr>
<th>Carnivore Species</th>
<th>Island</th>
<th>American Marten</th>
<th>Black Bear</th>
<th>Bobcat</th>
<th>Coyote</th>
<th>Fisher</th>
<th>Gray Fox</th>
<th>Gray Wolf</th>
<th>Raccoon</th>
<th>Red Fox</th>
<th>Weasel</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Basswood</td>
<td>0.31</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.16</td>
<td>0.97</td>
<td>0.74</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Bear</td>
<td>1.00</td>
<td>1.00</td>
<td>0.48</td>
<td>1.00</td>
<td>0.63</td>
<td>0.26</td>
<td>0.09</td>
<td>0.99</td>
<td>1.00</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Cat</td>
<td>1.00</td>
<td>1.00</td>
<td>0.40</td>
<td>0.31</td>
<td>0.46</td>
<td>0.21</td>
<td>0.30</td>
<td>1.00</td>
<td>0.38</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>Devils</td>
<td>0.61</td>
<td>0.80</td>
<td>0.45</td>
<td>0.52</td>
<td>0.49</td>
<td>0.27</td>
<td>0.31</td>
<td>0.97</td>
<td>0.54</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Eagle</td>
<td>0.26</td>
<td>0.64</td>
<td>0.64</td>
<td>0.60</td>
<td>0.51</td>
<td>0.50</td>
<td>0.30</td>
<td>0.85</td>
<td>0.40</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>Hermit</td>
<td>0.38</td>
<td>1.00</td>
<td>0.55</td>
<td>1.00</td>
<td>0.67</td>
<td>0.28</td>
<td>0.13</td>
<td>0.99</td>
<td>1.00</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Ironwood</td>
<td>0.71</td>
<td>1.00</td>
<td>0.42</td>
<td>0.46</td>
<td>0.63</td>
<td>0.26</td>
<td>0.22</td>
<td>0.97</td>
<td>0.56</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td>Manitou</td>
<td>1.00</td>
<td>1.00</td>
<td>0.46</td>
<td>1.00</td>
<td>0.64</td>
<td>0.27</td>
<td>0.15</td>
<td>0.99</td>
<td>1.00</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>Michigan</td>
<td>0.60</td>
<td>0.84</td>
<td>0.43</td>
<td>0.51</td>
<td>0.50</td>
<td>0.24</td>
<td>0.22</td>
<td>0.98</td>
<td>0.50</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>North Twin</td>
<td>0.08</td>
<td>0.16</td>
<td>0.36</td>
<td>0.30</td>
<td>0.67</td>
<td>0.14</td>
<td>0.39</td>
<td>0.31</td>
<td>0.11</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Oak</td>
<td>0.12</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.19</td>
<td>1.00</td>
<td>1.00</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Otter</td>
<td>1.00</td>
<td>1.00</td>
<td>0.49</td>
<td>0.83</td>
<td>0.64</td>
<td>0.29</td>
<td>0.06</td>
<td>1.00</td>
<td>1.00</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Outer</td>
<td>1.00</td>
<td>1.00</td>
<td>0.40</td>
<td>1.00</td>
<td>0.50</td>
<td>0.15</td>
<td>0.19</td>
<td>0.98</td>
<td>0.46</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Raspberry</td>
<td>0.43</td>
<td>0.93</td>
<td>0.56</td>
<td>1.00</td>
<td>0.68</td>
<td>0.33</td>
<td>0.08</td>
<td>0.99</td>
<td>1.00</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>Rocky</td>
<td>1.00</td>
<td>1.00</td>
<td>0.44</td>
<td>0.52</td>
<td>1.00</td>
<td>0.18</td>
<td>0.14</td>
<td>0.99</td>
<td>0.59</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>0.20</td>
<td>1.00</td>
<td>0.63</td>
<td>1.00</td>
<td>0.65</td>
<td>0.40</td>
<td>0.17</td>
<td>1.00</td>
<td>0.59</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>South Twin</td>
<td>0.66</td>
<td>0.73</td>
<td>0.40</td>
<td>0.31</td>
<td>0.54</td>
<td>0.19</td>
<td>0.31</td>
<td>0.90</td>
<td>1.00</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Stockton</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>York</td>
<td>0.31</td>
<td>0.87</td>
<td>0.62</td>
<td>0.96</td>
<td>0.69</td>
<td>0.44</td>
<td>0.07</td>
<td>0.96</td>
<td>0.72</td>
<td>0.41</td>
</tr>
</tbody>
</table>
Table 6. The estimates of detection parameters for carnivores on 19 islands in APIS (Table 3) by season (summer and winter). We report detection probability over a 100 trap-night effort, and 95% confidence intervals.

<table>
<thead>
<tr>
<th>Species</th>
<th>Summer $\hat{p}$</th>
<th>95% CI</th>
<th>Winter $\hat{p}$</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Marten</td>
<td>0.136</td>
<td>0.012 - 0.519</td>
<td>0.119</td>
<td>0.088 - 0.159</td>
</tr>
<tr>
<td>Black Bear</td>
<td>0.338</td>
<td>0.095 - 0.739</td>
<td>0.076</td>
<td>0.061 - 0.094</td>
</tr>
<tr>
<td>Bobcat</td>
<td>0.024</td>
<td>0.000 - 0.411</td>
<td>0.015</td>
<td>0.007 - 0.028</td>
</tr>
<tr>
<td>Coyote</td>
<td>0.082</td>
<td>0.014 - 0.339</td>
<td>0.151</td>
<td>0.117 - 0.192</td>
</tr>
<tr>
<td>Fisher</td>
<td>0.021</td>
<td>0.001 - 0.257</td>
<td>0.014</td>
<td>0.008 - 0.027</td>
</tr>
<tr>
<td>Gray Fox</td>
<td>0.044</td>
<td>0.001 - 0.505</td>
<td>0.024</td>
<td>0.130 - 0.044</td>
</tr>
<tr>
<td>Gray Wolf</td>
<td>0.041</td>
<td>0.000 - 1.000</td>
<td>0.006</td>
<td>0.001 - 0.026</td>
</tr>
<tr>
<td>Raccoon</td>
<td>0.010</td>
<td>0.001 - 0.047</td>
<td>0.007</td>
<td>0.003 - 0.017</td>
</tr>
<tr>
<td>Red Fox</td>
<td>0.051</td>
<td>0.007 - 0.230</td>
<td>0.061</td>
<td>0.036 - 0.103</td>
</tr>
<tr>
<td>Weasel</td>
<td>0.008</td>
<td>0.000 - 0.138</td>
<td>0.002</td>
<td>0.000 - 0.012</td>
</tr>
</tbody>
</table>

Our detection probabilities (for 100 trap nights of effort) for carnivores in summer ranged from 0.053 for weasels to 0.957 for black bear, and in winter ranged from 0.056 for weasel to 0.635 for coyote (Table 6).

Photograph 6. An unusual winter detection of a black bear
DISCUSSION

The Carnivore Community

We used a systematic grid of camera traps to monitor cryptic carnivore species in APIS, and found higher carnivore richness, abundance, and occupancy than we expected. The richness of the carnivore community was surprising, because we expected to document coyote and black bear, but considered other species including gray wolf, red fox, and fisher (Pekania pennanti) as only potentially present on the archipelago. Although we could not identify weasel detections to species, the 10 terrestrial carnivores we were able to identify to species potentially represent all but two of the native terrestrial carnivores present in Wisconsin, (exceptions: American Badgers (Taxidea taxus) and striped skunks (Mephitis mephitis)). Capturing all but two of the native carnivore species indicated the success of our monitoring protocol for monitoring and describing the carnivore community in APIS. Our results also highlight the importance of an increased emphasis by the NPS on understanding the carnivore community, as our study fills knowledge gaps in the presence and distribution of carnivores in the archipelago, and provides a foundation for understanding the community ecology dynamics in greater detail.

It is important to consider the full spectrum of species’ distributions, abundances, and occupancy rates to understand a given carnivore species and their ecological role within APIS. Some species, such as black bears, had a high abundance and occupancy, and were distributed on all but the smallest islands. In contrast, red foxes were found on many islands, but usually at low relative densities. We were surprised by detections of American martens and gray wolves, however martens were widely distributed, while gray wolves were only found on the largest island and the mainland. It is only when considering distribution, abundance, and occupancy that we can understand the patterns of the carnivore species on the islands. As such, an important area
of future research will be to determine how intraguild interactions affect each of the carnivore species that we documented on the islands (e.g., Lesmeister et al. 2015, Wang et al. 2015). Additionally, the absence of high levels of human activity and development may also play a role in supporting carnivore species (such as fishers, bobcats, *Lynx rufus*; and gray wolves) that tend otherwise to avoid human disturbance (Haskell et al. 2013, Wang et al. 2015). There was also a noticeable trend of absence (striped skunk) or low abundance (raccoon) of synanthropic carnivore species. These species are relatively common on the nearby mainland (E. Olson, personal observation), and may be limited due to the limited effects of humans on the islands, or their strategy of winter torpor may play a role in limiting their ability to inhabit the archipelago (e.g., Jackson 1920).

Abundance of prey may be an important aspect of sustaining the carnivore community, but it was not something we could accurately measure through camera trapping. The carnivore species documented appear to outnumber the identified potential prey species and this raises questions about what sustains the larger carnivores. Red squirrels (*Tamiasciurus hudsonicus*) seem abundant, while other rodents and hares were less frequently documented by camera traps. However, camera traps are more likely to be triggered by larger animals, and camera traps deployed as in this study may not be an effective method of documenting prey populations. Implementing small-mammal trapping or other measures may inform our understanding of carnivore community dynamics and competition. Deer present a more substantial food source for gray wolves and coyotes (Arjo et al. 2002, DelGiudice et al. 2009), as well as the rest of the carnivore community when available as carrion (DeVault et al. 2003, Allen et al. 2015). Deer populations may be an important aspect of carnivore diet on the islands, but further study of
carnivore diets is needed to understand if prey availability affects carnivore populations over time in APIS.

Photograph 7. An example of our surprising documentation of American martens in APIS

One observation of particular interest was our detection of American martens. Martens were extirpated from the state of Wisconsin in the 1920s (Williams et al. 2007), and after reintroduction efforts on Stockton Island in the 1950s (Williams et al. 2007), martens had not been formally documented in APIS until this study. Since no focused survey efforts have been conducted on Stockton Island until this camera trapping project, it is difficult to confirm the source of the current martens inhabiting the island. It is possible that a relict population survived the extirpation of martens on mainland Wisconsin, the martens are descendants of the 1950s reintroductions, or that they have naturally colonized from reintroductions on the mainland. Martens had the second highest relative abundance among our carnivore species, which is surprising considering that martens are the only mammal listed as state-endangered in Wisconsin. The marten population in APIS may have important implications for the conservation
of the mainland population, and it is therefore important to try and understand the factors that drive their distribution and abundance in APIS.

The Importance of Island Biogeography

One of the most important outcomes of our study was understanding how island biogeography theory (e.g., MacArthur and Wilson 1967, Wilson 2009) explains carnivore richness on islands in the archipelago. ‘Island Biogeography’ (a combination of island size, distance to mainland, and distance to nearest island) was our top model, and was our only model with substantial support (wAIC = 1.00). This model is a combination of resource availability (island size) and immigration ability which can buffer for stochasticity in the island environment (distance to the mainland and nearest island). Species richness appears most dependent on increasing size of the island, but also decreased with an island’s distance from the mainland or other islands. Most previous studies involving island biogeography have been in tropical systems with innately high levels of biodiversity. Our study informs island biogeography theory by showing that these trends hold true in temperate systems, and relation to complex species (carnivores). Therefore APIS is a model system for studying the effects of island biogeography on the carnivore community, and we encourage future ecological studies both in APIS and in archipelagos in the Great Lakes Region.

Island size was the most important variable in our top model, suggesting that resource availability is important, while long-term trends may be dictated by immigration and stochasticity. Size of an island likely dictates the diversity and abundance of resources, such as prey and habitat that are available for carnivores. Prey abundance reduces avoidance behavior between sympatric and otherwise antagonistic carnivores (Grassel et al. 2015). A larger diversity of habitat also allows carnivores that compete for the same resources to establish foraging or
behavioral niches to partition resources (Lesmeister et al. 2015, Wang et al. 2015). It is therefore not surprising that larger islands, possibly with more diverse prey or habitat, support more carnivore species. There were, however, exceptions: seven of ten carnivore species were never detected on Sand Island, one of the larger islands that is also close to the mainland, even though many were found on the nearby mainland. APIS recently completed a substantial deer reduction on Sand Island – hence the lack of predator diversity may reflect a lack of prey or carrion resources. Further, the distribution of American marten did not align with the predicted distribution of our island biogeography hypothesis, as they were completely absent from the inner ring of islands (Sand, York, Raspberry, Oak, Hermit, and Basswood Islands) and the mainland. In addition, some of their highest relative abundance values were on islands far from the mainland (Cat and Outer Island).

The importance of distances to mainland Wisconsin and to the nearest neighboring island suggests that the populations of a given carnivore species on an island may be dependent on periodic influxes of individuals, particularly from the mainland to maintain their population. This may be because in an island system, the end of the archipelago acts as a geographical limit to the dispersal of young animals, or islands far from the mainland may act as population sinks. None of the islands in the archipelago are likely large enough to sustain populations of mammalian carnivores in the face of demographic stochasticity or the genetic effects of small population size. Long-term monitoring would help elucidate trends in carnivore community dynamics on the islands and reveal whether the current diversity of carnivores is sustainable. Future studies in the APIS have the opportunity to examine how emigration and immigration are affected by the various life histories employed by the target carnivore species.
In APIS, the movement of mammals between the islands and outside of the archipelago occurs through either swimming or travel across ice bridges in winter, and so community dynamics may therefore be mediated by the effects of a warming climate. Reports exist of some mammal species swimming long distances between islands and the mainland (Jackson 1920, Pauli 2005, Wilton et al. 2015), but the role of long-distance swimming as a dispersal strategy for terrestrial carnivores is poorly understood. Alternatively, species can immigrate and emigrate from the archipelago during winter, when ice forms connective bridges between the islands and the mainland. For example, gray wolves originally populated Isle Royale National Park in the late 1940s by crossing an ice bridge connecting the island to mainland Ontario (Adams et al. 2011). Over the last 150 years, limnologists have documented declines in the duration of lake ice in the northern hemisphere (Magnuson et al. 2000), suggesting that if travel across the ice is the primary mode of recolonization, rates of recolonization may be affected by climate change. This may in turn change the dynamics of the carnivore community in APIS, as the existence of some species on the islands may be dependent on ice bridges to maintain a stable population (e.g., wolves, coyotes and red foxes) while others may not be (e.g., black bears). Future work should attempt to assess the effects of changes in connectivity associated with intermittent or persistent ice bridge formation between islands and the mainland during the winter months.

**Camera Trap Monitoring Protocol**

Our camera trap monitoring protocol was successful for monitoring carnivores in APIS. Using these methods we documented a suite of terrestrial carnivore species, along with several non-target species. The wealth of data collected has allowed us to calculate a variety of measurements, including species richness, relative abundance, distribution, detection
probabilities, and occupancy. APIS is remote and difficult to access, so installing camera traps is an ideal method for the monitoring the ecological system. Using these methods long-term will allow APIS to document trends in carnivore richness, distribution, and occupancy. Data from camera trapping grids can also be used for other analyses, from population estimates to animal behavior and ecological dynamics. These data are particularly well-suited to population estimates using n-mixture models (Royle 2004) or spatially-explicit capture recapture (SECR) models (Chandler and Royle 2013), and creating population estimates of carnivores in APIS would be a valuable follow-up study.

Photograph 8. A surprising detection of a gray wolf on Stockton Island.

When creating a sampling grid for other ecosystems and species, it is important to consider our methodologies, but not necessarily the specifics we used. In our experience a 1x1 km grid worked well for the terrestrial carnivore guild of APIS; however, this should be tailored to a given set of target species, and study goals. For example, our protocol was designed for
terrestrial carnivores and other large mammals, but if researchers were attempting to document semi-aquatic mammals they would likely use different sampling methods. In the case of semi-aquatic mammals, a modified linear grid that follows the shoreline of rivers, lakes, and wetlands would be more effective, as well as aiming the camera traps towards water rather than toward openings in the forest. In addition, potentially diminished detection probability should be accounted for (see Lerone et al. 2015, Evans 2017). Also, if targeting a specific terrestrial carnivore rather than the community as a whole, the grid density could be increased or focused on particular habitat or features. Similarly, if targeting smaller or less active species, the camera traps may need to be set out for longer times or at higher density.

This project was logistically challenging, in part, due to the large number of people required to maintain and install camera traps across the various islands, and the access limitations associated with working on a Lake Superior archipelago. This project was only possible because of the large number of volunteers, but working with volunteers can have some drawbacks, including inconsistency in data collection. Volunteers were, however, comparable to project personnel, in terms of: data collection, camera trap placement, and following protocol, and reduced costs for project personnel, which would have otherwise been prohibitive. Despite the large number of volunteers involved in this project minor issues arose (e.g., failure to program time-lapse settings for the camera trap, variation in the number of photographs taken or duration of the refractory period, or in some cases camera traps were set upside down). Improved training methods, a clearer camera trapping protocol, and ensuring adequate training dramatically led to reduced errors, and should be continued in the future.
Conclusions

The remarkable diversity and abundance of carnivores detected in the APIS archipelago exceeded our expectations and created an opportunity to investigate multiple aspects of their ecology. The camera traps collected information on species ranging in size from weasels to black bears, in addition to relative abundances of species from single-camera trap detections to near-ubiquitous. Our methodology appears to be an effective approach to monitoring across such diverse criteria, and the wealth of data produced can inform park management as well as broader wildlife issues. Camera traps that are rugged enough for long-term monitoring under extreme environmental conditions are a relatively recent advance and the statistical and data-management techniques for optimizing large databases of camera trap-generated information are also currently evolving. These advances will enable more precise resolution of ecological patterns at finer temporal and spatial scales with reduced costs for labor and material. Managers should plan to exploit these technological trends to deal with emergent threats to the ecological integrity of protected areas such as those posed by climate change, increasing human impacts, invasive species, and reduced connectivity. Greater understanding of APIS ecology will require on-going monitoring of carnivores to evaluate temporal dynamics as well as related ecological evaluations (e.g. small mammal dynamics, plant community dynamics) to understand trophic effects.
LITERATURE CITED


Appendix 1
Protocol for Creating and Setting a Camera Trap Grid

From:
Survey techniques, detection probabilities,
and the relative abundance of the carnivore guild
on the Apostle Islands (2014-2016)

Final Report
December 15, 2016

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Report to the National Park Service.
Creating a Sampling Grid for Camera Trap Deployment

Effective camera trap designs for monitoring wildlife depend on sampling in a standardized and rigorous method. One of the most effective designs for monitoring is to create a sampling grid on which to place camera traps because it enables both systematic (sample all grid cells) and systematic-random (sample a randomly chosen subset of grid cells) designs for unbiased camera placement. The density of camera traps in the grid used is dependent on both the monitoring goals and logistical constraints of a project. The spacing of the camera traps is dependent on the detection probabilities and home range size of the target species.

To meet the goals of this project we overlaid satellite imagery of the APIS area with a 1km² grid. We then created a ‘camera trap deployment location’ at the center of each grid cell whose surface area contained >50% land (Figure 9). This allowed standardized (even and repeatable) camera trap placement across all islands, at a scale that we thought would be rigorous enough to meet the detection and abundance measurement goals of our project based on previous experience with an earlier study on Sand Island (Bartnick, et al. 2013).

Different models and brands of camera traps vary in their performance. To ensure standardized monitoring we used the same model of camera traps for all of our monitoring. For this study we used RECONYX HC600 Hyperfire™ High Output Covert infrared digital game camera (RECONYX, Inc., Holmen, Wisc., USA).

Camera Trap Placement

We created standardized and documented procedures for placing camera traps in strategic locations. This allowed for multiple field staff, with varying levels of skill, to set camera traps in a similar pattern and maximize the detection of our target species (e.g., O’Connell et al 2011).
We created a systematic naming system for each of our camera trap deployment locations for consistency and accuracy in tracking the data. Our naming system included: A two-letter notation for the project (“CN” for the Carnivore project), the two first letters of the island, a two-digit number unique to the camera trap deployment location and whether it had lure or not (presence or absence of L). For example:

CNOA01L = Carnivore Project, Oak Island, Camera Trap Deployment Location 1, lure used
CNST14 = Carnivore Project, Stockton Island, Camera Trap Deployment Location 14, no lure used

![Photograph 9. Our field staff hiking in to place camera traps on Stockton Island.](image)

We split our camera trap placement procedure into 6 steps:

1) *Selection of camera trap location*

We navigated to our target camera trap deployment location (the center of a grid cell) using handheld GPS units. Upon arriving we walked in concentric circles until we intersected animal
sign, a clearing, a trail, or other site relatively free of obstructions that would serve as a natural travel route for a large mammal. Most suitable high-use areas were characterized by a small opening in the vegetative cover where ≥2 trails intersected, and included trees for camera trap placement, and adequate space (≥3 m, ≤7 m) between a suitable tree and the trail intersection. We suspect several target carnivores are attracted to large, downed woody debris, and therefore we prioritized sites with logs or stumps if available. Generally, this allowed for ideal placement of camera traps and reduced the amount of vegetation in front of camera traps that could cause false triggers or obscure the camera trap images.

2) Programming of camera trap settings

It is important camera trap settings are the same to ensure even and accurate sampling across all sites. In order to do this, we turned the camera trap on, entered the security code (if applicable) and then set the appropriate settings. The following is an example of how we set the camera traps for the RECONYX HC600 Hyperfire™ High Output Covert infrared digital game camera (RECONYX, Inc., Holmen, Wisc., USA):

a) Change Setup → OK; Advanced → OK; Trigger → OK; Motion Sensor → ON; Sensitivity → HIGH; Pics per Trigger → 3; Picture Interval → RAPIDFIRE; Quiet Period → NO; Finished → OK (This sequence sets the motion sensor on with the high sensitivity and programs the camera trap to take 3 photographs in rapid sequence after each trigger)

b) Change Setup → OK; Advanced → OK; Time Lapse → OK; AM Period → ON; AM Start → 11:00 AM; AM End → 12:00 PM; PM Period → OFF; Picture Interval → 1
HOUR; Finished → OK (This sequence programs the camera trap to take a single photograph each day at 11 am)

c) Change Setup → OK; Advanced → OK; Night Mode → OK; High Quality → ON; Finished → OK (This sequence programs the camera trap to operate at night using infrared illumination)

d) Change Setup → OK; Advanced → OK; Date/Time/Temp > OK; Finished → OK (This sequence programs the camera trap to record date, time and temperature with each image)

e) ARM CAMERA → OK (This sequence programs the camera trap to begin monitoring)

The red light on camera trap front should flash, and the camera trap is now ready to be deployed.

Optional steps include:

f) Change Setup → OK; Advanced → OK; User Label > OK; Choose Add OR View/Change, and enter your unique user label; Finished → OK (This sequence adds a unique user label for all of the images taken)

g) Change Setup → OK; Battery Type →Lithium; Finished → OK (This sequence optimizes camera trap function for different battery types)

3) Deploy the camera trap

We affixed camera traps to a tree approximately 0.75-1.5 m above the ground level. We placed camera traps 3-5 m from the trail intersection, and faced the camera traps at a 45-degree angle in relation to the most traveled section of trail. A small stick can be placed behind the camera trap
between the tree and cable lock to provide a downward angle and ensure the camera trap captures the entire area you are trying to survey. It was important make sure there were no large trees or objects in the main field of view of the camera trap, as this could adversely affect motion detection and nighttime flash range and light balance of the photograph. We avoided setting camera traps in a location where branches or vegetation of any kind could block the camera trap or grow in front of the camera trap.

![Photograph 10. Field staff placing a camera trap](image)

4) *Testing the camera trap*

To ensure our target location and camera trap placement is optimal, we took a photograph on a handheld camera trap. We placed the camera trap right in front of the lens of the motion-triggered camera trap, allowing us to take a photograph that shows the expected view of the motion-triggered camera trap. The goal was for the test photograph to focus on the focal point, including a targeted trail junction or downed log/tree.
It was sometimes necessary to take multiple photographs and adjust the placement of the camera trap accordingly until it was optimally placed. Alternatively, a handheld photograph viewers (such as a Cuddeback® Cuddeview, Park Falls, Wisc., USA) could be used to view photographs taken by the motion-triggered camera trap itself.

5) Record the data
We marked and labeled the coordinates of each camera trap site with a handheld GPS unit and recorded the coordinate location of the camera trap on datasheets. Optionally, notes were taken on habitat, animal sign seen, any potential problems with the camera trap, or other relevant observations. We did not place flagging or physically mark any of the camera trap sites in case that might influence the behavior of animals, or increase the risk of theft or damage to the camera trap.

6) Optional: Lure placement
We speculated that placing an olfactory or visual lure could increase the probability of detection for some carnivores (Long et al. 2008). Our system for olfactory lures was to place a small amount of lure (Caven’s Gusto lure, Minnesota Trapline Products, Pennock, MN) inside of a holder and hang it from a tree ~5ft high within the camera trap’s field of view. Holders for lure can be as simple as placing the lure on a cotton ball within a Dixie cup or film canister. We also placed another small amount of lure in a crack or under bark on a log, stump, or tree within the focal area of the camera trap’s field of view, and we placed the stick used to apply lure in the middle of the focal area.
Checking and Retrieving Camera Traps

We left the camera traps to monitor for approximately six months, and then revisited to collect SD memory cards and exchange batteries as needed. Stockton Island camera traps were deployed for a second six-month interval, and then removed during the fall of 2015 to establish grids on other islands, which were also maintained for at least one full year.

Steps for retrieving data from camera traps:

1) When approaching a deployed camera trap, walk in front of the camera trap to trigger a picture on the camera trap to provide an exact record of the date and time retrieved, and checked if the camera trap was still taking pictures when opened. If not, we noted this on the
data sheet to help track when a camera trap was not functional throughout the entire monitoring period.

2) When checking a camera trap, adjust the setup according to your judgement if any changes had occurred (often the result of black bear investigating the camera traps).

3) We then turned the camera trap on and checked the following data:

   Pressing ‘OK’ led to a screen which indicated # PICS (the number of photographs taken), %FULL (how full the memory card was) and %LITH (the available battery power remaining). We recorded #PICS & %LITH on the data sheet.

4) If the batteries were ≤90%, we replaced them.

5) We removed the SD card containing data and replaced it with a new SD card. The full SD card was stored in a paper envelope labeled with the date, the name of the camera trap deployment location, and the observer.

Camera Trap Data Management

All SD memory cards were labeled with the camera trap deployment location to avoid misidentification, and then the data were downloaded and stored in duplicate locations (which can be distributed among collaborators). We organized all photographs in a database master file, backed up through cloud hosting, consisting of folders for each camera trap for each period of monitoring. We then tagged the individual photograph files using a standardized tagging procedure (see Appendix 2).
Appendix 2
Protocol for Tagging Photograph Data from Camera Traps

From:
Survey techniques, detection probabilities,
and the relative abundance of the carnivore guild
on the Apostle Islands (2014-2016)

Final Report
December 15, 2016

Suggested Citation:
Report to the National Park Service.
Introduction

This protocol uses Reconyx® proprietary software to facilitate classification of camera trap photographs and to create a database of camera trap meta-data. The software is provided with the purchase of Reconyx® camera traps and is available online (http://www.reconyx.com/software/mapview). Use of this software does not imply an endorsement by the USDI Park Service or its collaborators.

Setting up Reconyx Software and Loading Images

1) Open **MapView Professional**, and click *Install* if prompted.

2) To confirm that image data will be linked to the correct project, navigate to the top panel of the RECONYX homepage and click **Tools - Image Folders...** and then click *Edit*. You can type the path or click the box “…” to browse.

3) From the RECONYX homepage, go to the left panel and under **Choose a site** either:
   a) Select the SITE from the pull-down menu where the camera trap you will be tagging belongs (as an example, for the APIS project each island where camera traps have been deployed is listed as a site)
   b) Or, you can create a NEW SITE and it will then be visible for the project.
4) Back in the homepage, navigate to the lower center box. Any previously tagged camera traps in that site will be visible here.

a) To create a new camera trap, click the Add box on the right hand side. Naming conventions vary, but must be unique to each individual camera trap deployment location (see Appendix 1 for an example where CNBE01L and CNOA02 are two camera trap deployment locations).

b) To add images, select the site and then navigate to the upper left hand console, just below File, and click the down arrow ▼ beside View/Load New Images & Videos.

c) Select From Another Folder, then navigate to your project directory, double click the camera trap folder, hit OK when prompted.

d) In the Reonyx dialog box, select Check All at the top of the window, ensure the Checked/Total shows all images, and then click OK at the bottom. Loading may take several minutes for many images; once it is completed click Finish at the bottom right.
e) If multiple folders contain images, load them sequentially into the same camera trap site.

**Creating the Keyword List and Progress Tracking Document**

1) For initial setup or the first use of RECONYX software on a new computer, you must create a *Keyword List* to ensure consistent tags are applied. From the homepage, select a camera trap site from the lower middle window and click **View Pics/Vids** to the right.

2) In the image Viewer window, go to the Image Toolbox on the right hand side and select **Setup** from the option near **Keywords**.

3) Click **Add** to make a new list, being careful to Name it consistently and select the correct list Type (for APIS, use **Categorical Census**, which allows a count of the number of individuals of the same species).

4) In the box for **New**, add each possible trigger cause for your project (these include species found in your study area, and may include other causes such as false triggers, camera trap setup or take down, etc.). An example list of the tags used for the APIS project is provided.

5) If you later encounter a new species, it can be added to this list. We recommend immediately updating the master list to include the new keyword, and notifying any collaborators of the addition.
6) We also recommend maintaining a Word document for tracking image tagging progress and recording information about camera trap site quality, uncertain animal identifications, and especially high quality images. For APIS, this document includes columns for a) Camera Trap ID b) Image tagger initials and the dates started / completed c) List of species detected and d) Notes / Uncertain / Good. In this final column, note any days the camera trap was blocked by snow or vegetation, highlight any animal tags that need to be reviewed by an expert, and list file names for any particularly good images. This document can also be used to assign different individuals or teams specific camera trap sites to tag in order to avoid redundancy.

**Image Tagging Protocol**

1) From the RECONYX homepage, add all images to the camera trap site you wish to tag and then select it in the lower middle window and click **View Pics/Vids** to the right

2) In the image viewing window, individual pictures are in the column on the far left. Each image is named with the date, time, and indicator “T” for Timelapse or “M #_#” for Motion trigger.

   a) Timelapse images are recorded at predetermined time each day and may or may not be present depending on the project goals and camera trap settings.
b) For Motion images, the numbers indicate the order in which each image was recorded if the camera trap was set for a RapidFire burst. For the APIS project, bursts of five were used, so images M 1_5, M 2_5… M 5_5 result from each trigger event. Other projects may use longer bursts, or only single images per trigger event.

c) All Timelapse images must be viewed and tagged either as Timelapse or as a species tag if an animal is visible. You can sort among these by selecting “All”, “Timer” or “Motion” at the upper left to either tag Timelapse separately or simultaneously with Motion triggers.

3) Motion images resulting from RapidFire burst are tagged as a group.

a) To view a series of images, click on the first image, and then use the keyboard down arrows to scroll through, examining each image for the cause of the trigger. Because several bursts of images may have the same cause, continue down the list until the cause changes.

Example: if you have looked through 15 images featuring a squirrel and then a new set features a deer, stop on that first image of the new set.

b) When the cause of the trigger changes, you have reached the end of that group. Hold SHIFT+UP to select back to the first image, which will be shown by blue highlighting. If the final image is not also selected, hold SHIFT+DOWN until the entire group ends is selected (for APIS, this will always mean the last image is M 5_5).

c) DO NOT TAG INDIVIDUAL MOTION IMAGES. If RapidFire was used, always tag every image in the group consistently.

Example: if the first two images appear blank, but a deer is visible in the final three, tag all M 1_5 to M 5_5 as Deer).
4) To apply an image tag after identifying the cause of the trigger and selecting the group, click the blue underlined **apply keyword** on the right. In the dialog box that opens, check the box to the left of the correct tag and click **OK**.

5) **If multiple individuals are present:**
   a) The default count is “1” when you click the check box beside a tag. If more than a single individual of the same species is confirmed within that burst of three images, manually apply the correct count.
   b) **ONLY** count the number of individuals that can be confirmed within a single burst of three images (though there may be single images where not all individuals are visible). Do not assume that the maximum visible from a previous or following trigger are present.

6) **If multiple species are present:**
   a) **ONLY APPLY A SINGLE SPECIES TAG** (do not check more than one box).
   b) Apply the tag for the larger species.
   c) Add the other species name in the Narrative box.
   d) Include a detailed account in the Word document, with the names of all images.

Example: “For the images 2016-06-08 14:55:00 to 2016-06-08 15:03:00, a deer was present browsing in the focal area but several songbirds are also visible in the trees”
7) If the trigger is cause by people:
   
a) For images of the deployment team setting up the camera trap, checking it or taking it down, apply the tag Setup. A count of individuals is not necessary here. For other human activity at the camera trap site, apply the tag People and record count data.
   
   Note: You may encounter people walking dogs. For images with both dogs and humans, tag as People, for bursts with only the dog tag as Domestic_dog. Apply a Narrative comment and a note in the tracking document.

8) If there is no clear cause:
   
a) If there are no animals present in any of the images from the event, tag as False_trigger.
   
b) If there is potentially a blurry animal but not enough information to identify, tag as False_trigger and make a note in the Word document with the image name and that it was unidentifiable.
   
c) If there is an animal but you are uncertain in your ID, apply the species tag that you believe it is and make a note in the Word document, clearly indicating that the images need to be DOUBLE-CHECKED during a quality control meeting after tagging. You can also comment in the Narrative box, but we recommend having a protocol in place to remove this comment after the images have been resolved.

9) If the image is compromised:
   
a) Multiple things can interfere with the quality of the images (e.g., vegetation blocking the view, snow accumulation, change in the camera trap view point, moisture condensation on lenses, malfunctioning IR illuminator). For these, note in the Word document and include the date range, if the situation worsens or when it improves.
Exporting Images

When all images are tagged, before closing the window go up to **Image** and select **Export**

**Image Data**

1) Switch the default to **All images in this list**

2) Save as a CSV file into the correct folder, and we suggest naming with the same conventions for making the camera trap site in the Reconyx software, with an additional indicator for which deployment was tagged if camera traps are revisited multiple times

3) Do not close the program while it is exporting, and when prompted select **Open File** to review the exported data
   a) Check that the correct number of rows are present
   b) Go to the last column and scroll through to ensure that every row received a SPECIES tag
   c) If you had any uncertain tags, highlight these rows in the CSV file

4) Review the Word document, add any comments, and save it with the current date

5) We recommend going through the image folder and copying any uncertain images, or images of especially good quality, and save those into a special folder. To assist finding good example images later, rename these images with the species, anything of note, and the camera trap name. Example: “Bear with three cubs CNHE02”.
A suggested *Species List* for the APIS and surrounding area:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bear</td>
<td>Fisher</td>
</tr>
<tr>
<td>Beaver</td>
<td>Fox_gray</td>
</tr>
<tr>
<td>Bird_corvid</td>
<td>Fox_red</td>
</tr>
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*Photograph 12. A red fox pausing close to a winter camera trap.*