

# Agonistic interactions and island biogeography as drivers of carnivore spatial and temporal activity at multiple scales

M.J. Farmer, M.L. Allen, E.R. Olson, J. Van Stappen, and T.R. Van Deelen

**Abstract:** Carnivore communities can be diverse and complex, and lack of knowledge regarding intraguild interactions and alternative drivers of carnivore distributions can preclude effective conservation of co-occurring species. As such, our objectives were to evaluate the relative importance of intraguild interactions and island biogeography to carnivore community spatiotemporal activity at multiple spatial scales. We monitored the carnivore community of the Apostle Islands National Lakeshore (Wisconsin, USA) using a grid of camera traps from 2014 to 2018. We used generalized linear mixed-effects models and information-theoretic model selection to evaluate whether subordinate carnivore presence was related to dominant carnivore relative abundance (interactions) or to island biogeography at the island level and camera site level, and we calculated temporal overlap between each pair of species to determine whether subordinate carnivores were using temporal segregation. At the island level, the relative importance of interactions and island biogeography was species dependent. At the site level, relative abundance of dominant carnivores was not a significant predictor of subordinate carnivore presence, and all pairs exhibited high or neutral temporal overlap. At the island level, island biogeography and interactions may both impact species distributions; however, at finer spatial scales, the carnivore community may be using alternative segregation strategies, or the island system may preclude segregation.

**Key words:** Apostle Islands, camera traps, carnivores, island biogeography, spatial segregation, temporal segregation.

**Résumé :** Une grande diversité et une grande complexité peuvent caractériser les communautés de carnivores, et un manque de connaissances sur les interactions intraguilides et d'autres facteurs influant sur la répartition des carnivores peut faire obstacle à la conservation efficace d'espèces cooccurrentes. Nos objectifs consistaient donc à évaluer l'importance relative des interactions intraguilides et de la biogéographie insulaire pour l'activité spatiotemporelle de communautés de carnivores à différentes échelles spatiales. Nous avons surveillé la communauté de carnivores de la réserve Apostle Islands National Lakeshore (Wisconsin, États-Unis) de 2014 à 2018 à l'aide d'un réseau de pièges photographiques. Nous avons utilisé des modèles linéaires généralisés à effets mixtes et la sélection de modèles basée sur la théorie de l'information pour évaluer si la présence de carnivores subordonnés était reliée à l'abondance relative de carnivores dominants (interactions) ou à la biogéographie de l'île aux échelles de l'île et du site du piège photographique, et nous avons calculé le chevauchement dans le temps de chaque paire d'espèces afin de déterminer si les carnivores subordonnés faisaient preuve de ségrégation temporelle. À l'échelle de l'île, l'importance relative des interactions et de la biogéographie de l'île dépend de l'espèce. À l'échelle du site, l'abondance relative des carnivores dominants n'était pas une variable prédictive significative de la présence de carnivores subordonnés, et toutes les paires présentaient un chevauchement temporel élevé ou neutre. À l'échelle de l'île, la biogéographie de l'île et les interactions pourraient toutes deux avoir une incidence sur la répartition des espèces, alors qu'à des échelles spatiales plus fines, la communauté de carnivores pourrait employer d'autres stratégies de ségrégation, ou le système de l'île pourrait faire en sorte que la ségrégation n'est pas possible. [Traduit par la Rédaction]

**Mots-clés :** îles Apostle, pièges photographiques, carnivores, biogéographie insulaire, ségrégation spatiale, ségrégation temporelle.

## Introduction

Carnivores perform essential functions within ecosystems, including nutrient cycling (Schmitz et al. 2010; Estes et al. 2011), zoonotic disease regulation (Estes et al. 2011; Ripple et al. 2014), and biodiversity maintenance (Estes et al. 2011; Ripple et al. 2014). Carnivores also influence prey populations (Berger et al. 2001; Preisser et al. 2005), sometimes leading to cascading, large-scale effects in ecosystems, including carbon sequestration (Ripple et al. 2014) and increased tree recruitment (Estes et al. 2011). Despite their importance, many carnivore populations, especially

those of large-bodied or specialized carnivores, are declining worldwide (Ripple et al. 2014). For conservation measures to be effective, managers must understand both biotic and abiotic factors that influence carnivore population distribution.

Inter- and intra-specific agonistic interactions with other carnivores is often a driving force of carnivore population spatiotemporal distributions. Between sympatric carnivore species, agonistic interactions, including competition for prey and other resources, are common and can have a range of direct and indirect effects. Direct effects include intraguild predation (Palomares and Caro

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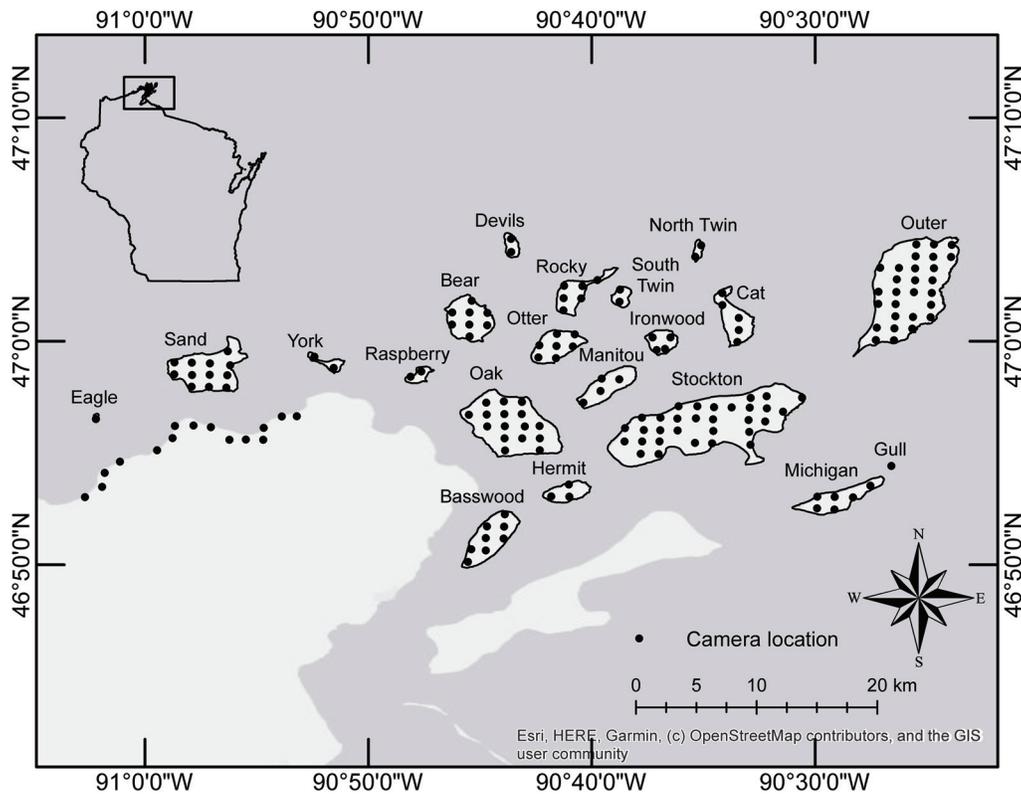
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**Fig. 1.** Camera trap locations within the Apostle Islands, Wisconsin, USA, as part of the carnivore species monitoring project conducted from September 2014 to November 2018. Figure was created using ArcMap version 10.5.1 (Esri, Inc. 2017) and assembled from the following data sources (shapefiles): camera point locations and island labels and boundary lines (M.J. Farmer, this study) and State of Wisconsin Boundary 24K (Wisconsin Department of Natural Resources; <https://data-wi-dnr.opendata.arcgis.com/datasets/wisconsin-state-boundary-24k>). Base map from ArcMap version 10.5.1, courtesy of Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS user community.



1999; Linnell and Strand 2000; Arim and Marquet 2004), while indirect effects can affect foraging efficiency and potentially result in a loss of fitness (Linnell and Strand 2000). As such, spatial segregation (i.e., a species shifts its physical location to minimize risk of agonistic interactions; Durant 1998) and temporal segregation (i.e., a species shifts its temporal activity to minimize risk of agonistic interactions; Wang et al. 2015) are possible mechanisms of avoidance among co-occurring carnivores. For example, red foxes (*Vulpes vulpes* (Linnaeus, 1758)) and especially gray foxes (*Urocyon cinereoargenteus* (Schreber, 1775)) exhibit spatial avoidance of coyotes (*Canis latrans* Say, 1823) and bobcats (*Lynx rufus* (Schreber, 1777)) across the United States (Harrison et al. 1989; Henke and Bryant 1999; Fedriani et al. 2000; Gosselink et al. 2003). Similarly, American marten (*Martes americana* (Turton, 1806)) and fisher (*Pekania pennanti* (Erxleben, 1777)) selected habitat based on habitat characteristics as well as occurrence of the other species (Fisher et al. 2013).

However, in metapopulations where populations persist in isolated patches (such as islands) embedded in an unsuitable matrix, island biogeography is a driving force of population spatial distributions. Island biogeography theory predicts species richness and distribution based on various island characteristics, including island size and distance from the mainland under an equilibrium assumption that species have had adequate time to colonize islands subject to island characteristics (MacArthur and Wilson 1967). Island biogeography theory assumes that species richness is an equilibrium between species-specific colonization and extinction rates, which are random events in which all species have an equal ability to immigrate and to go extinct (Sax and Gaines 2011). However, nonvolant mammals are often limited by dispersal ability, so a dispersal-limited nonequilibrium model of

island biogeography better explains patterns of nonvolant mammal species richness (Sax and Gaines 2011). Based on island biogeography theory, larger islands that are closer to the mainland or to other islands should have greater species richness because they are easier to colonize, assuming that distance constrains dispersal (MacArthur and Wilson 1967). Currently, most island-based community research comes from the Tropics, and it is largely unknown whether temperate island wildlife communities follow the same island biogeography and life-history trends (see, however, Allen et al. 2018, 2019). As such, the Apostle Islands archipelago, located in Lake Superior (USA) and composed of 22 islands that vary in size and isolation, is an ideal system to research drivers of carnivore community distribution in temperate North America (Allen et al. 2018, 2019).

Our objectives were to evaluate the relative importance of life-history drivers and island biogeography to carnivore community spatiotemporal activity patterns at multiple spatial scales. We hypothesized that inter-island distribution of a given carnivore species would be driven by the size and isolation of the island and top-down trophic effects as evidenced by spatial filtering, while intra-island distribution of a given carnivore species would be driven by top-down trophic effects as evidenced by spatial and temporal filtering. Therefore, we expected that subordinate carnivore species would exhibit minimal temporal activity overlap with dominant carnivores or that subordinate carnivore presence would be negatively associated with dominant carnivore relative abundance at either the island or site level. We also expected carnivore presence to be positively associated with island size, and negatively associated with distance from mainland and distance from nearest island.

**Table 1.** A priori models with corresponding independent variables and hypothesized effect on subordinate carnivore species presence based on scientific literature and ecological theory.

Model name	Variables	Hypothesis
Interaction	Dominant carnivore RAI	Dominant carnivore relative abundance (RAI) will predict subordinate species presence since dominant carnivores would be able to outcompete subordinate carnivores if resources are limiting (Durant 1998; Fedriani et al. 2000)
IB	Island size (km <sup>2</sup> ) + Distance from mainland (km) + Distance from nearest island (km)	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 (Millien-Parra and Jaeger 1999)
Interaction + IB	One dominant carnivore RAI + Island size + Distance from mainland + Distance from nearest island	Presence of a subordinate carnivore will be a function of both dominant carnivore relative abundance (RAI) and IB
Global model	All dominant carnivore RAIs + Island size + Distance from mainland + Distance from nearest island	Presence of a subordinate carnivore will be a function of both dominant carnivore relative abundance (RAI) and IB
Null model	—	Presence of a subordinate carnivore is random relative to dominant carnivore relative abundance (RAI) and IB

Note: RAI is relative abundance index. IB is island biogeography.

## Materials and methods

### Study area

The Apostle Islands are an archipelago of 22 islands in south-western Lake Superior (Wisconsin, USA), 21 of which were protected as part of the Apostle Island National Lakeshore in 1970. The islands range in size from 0.08 km<sup>2</sup> (Eagle island) to 40 km<sup>2</sup> (Stockton island), in distance to the mainland from 1.48 km (York island) to 23.83 km (Outer island), and in distance to the nearest island from 1.05 km (South Twin and Rocky islands) to 5.13 km (Eagle island). The archipelago was connected to mainland Wisconsin but was isolated by glacial scouring and the creation of the glacial Lake Duluth during the Pleistocene epoch (Judziewicz and Koch 1993). The archipelago is located within a transition zone between northern boreal coniferous forest and deciduous forest, which results in a rich mix of habitat types (Craven and Lev 1987). During this study (September 2014 – November 2018), temperatures ranged from –30.0 to 36.1 °C, with a mean 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).

### Camera traps

Camera traps can be effective for monitoring cryptic carnivore populations and communities (Allen et al. 2014, 2020). We deployed and maintained a grid of 164 camera traps across 19 islands from September 2014 to November 2018 (Fig. 1). We deployed camera traps on the islands following a randomized systematic design to maximize carnivore detections and camera independence. We overlaid a 1 km<sup>2</sup> grid on each island and created a camera location at the center point for each grid cell that contained >50% land area to exclude cells that were mostly water. We adjusted the number of camera traps ( $y$ ) on each island using the following power law equation based on island size ( $x$ ):

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

to ensure that each island, regardless of size, received at least two cameras, to account for intermediate islands of unique shape, and to purposefully undersample larger islands due to logistical constraints (Allen et al. 2018; Farmer 2020). When placing cameras, we navigated to grid center points 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, Wisconsin, USA) on a tree. We selected the height and orientation of each camera to maximize wildlife detections, and we programmed camera traps to take a burst of three pictures with no refractory period when triggered and to record date, time, and temperature for each detection following Allen et al. (2018) and Farmer (2020).

Owing to the logistical difficulties of traveling to remote islands, only a portion of the possible camera sites were active at any given time during the study. Camera traps remained on islands year-round, and we checked camera traps approximately every 6 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, Minnesota, USA) during the first 6-month period. When we checked camera traps after the first 6 months, cameras that we had not previously baited received a scent lure. After the first two camera checks, each camera had received one scent lure treatment, and we then switched to randomly selecting cameras for a scent lure during each subsequent camera check (Farmer 2020).

### Statistical analyses

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

To determine how intraguild agonistic interactions and island biogeography affected spatial and temporal activity patterns of carnivore species, we used generalized linear mixed-effects models (GLMMs) and temporal activity overlap plots. We fit GLMMs at two different spatial scales to determine whether agonistic interactions or island biogeography are better predictors of subordinate carnivore spatial activity distribution. We calculated temporal overlap and built temporal activity overlap plots for pairs of subordinate and dominant species to determine whether subordinate carnivores were temporally segregating.

We first calculated a relative abundance index (RAI) at each camera trap site for each species as

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

where  $D$  is the number of detections of a given species 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, we considered multiple photographs of a species that occurred within 30 min of each other to be the same detection (Wang et al. 2015; Olson et al. 2019). This mitigates against pseudoreplication and provides a more accurate measure of wildlife presence. We calculated RAI 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) or site use (Sollmann 2018).

We then identified pairs of subordinate and dominant species based on a range of factors including body size and evidence of intraguild predation from published literature (Supplementary Table S1).<sup>1</sup>

### Spatial activity overlap

To determine whether spatial distribution of subordinate species is affected by dominant species or island biogeography at two different spatial scales, we evaluated two sets of a priori hypotheses posed as models (GLMMs; Table 1) with a binomial response in the “lme4” package (Bates et al. 2015). At the island level, we tested whether the presence of a subordinate species on an island was related to the RAI of the dominant species, and whether dominant carnivore RAI, island biogeography variables (island size (km<sup>2</sup>), distance from the mainland (km), and distance from nearest island (km); Allen et al. 2018), or both were the best predictors of subordinate species presence on an island. Within our dataset, we coded presence of a subordinate species as a “0” if the species was not detected on a given island and a “1” if the species was detected. Since only a portion of the possible camera sites were active at any given time, we based presence on the entire long-term monitoring period. Before running the models, we tested for correlation among the three island biogeography variables using Pearson’s correlation test or the Spearman’s rank correlation coefficient if one of the variables was not normally distributed. Correlation coefficients for each possible pair of island biogeography variables were not significantly correlated (all coefficients < |0.05| and all  $p > 0.05$ ). We compared the models based on Akaike’s information criterion corrected for small sample size (AIC<sub>c</sub>) and considered the top models for each subordinate species to be the models within a cumulative AIC<sub>c</sub> weight of 0.90 (Burnham and Anderson 2002). We also used the conditional probabilities (AIC<sub>c</sub> weights ( $w$ )) of each model to determine how well supported each model was relative to the other models (Olson et al. 2019) and calculated evidence ratios as a measure of comparative support for hypotheses reflecting island biogeography and interactions with dominant species (Burnham and Anderson 2002).

At the site level, we tested whether the presence of a subordinate species at a given camera site on a given island was related to the RAI of the dominant species at that site (Bates et al. 2015). We coded presence of a subordinate species as a “0” if the species was not detected at a given camera site and a “1” if the species was detected. In this case, we again based presence on the entire long-term monitoring period. We included “island” as a random effect in our site-level models and only included data from the islands on which we detected both species. Data from the mainland unit was not used in this analysis. Finally, we built receiver operating characteristic curves (ROC) and calculated the area under the curve (AUC) to evaluate each model’s performance (Robin et al. 2011). We used ROC and AUC rather than  $w$  to evaluate model performance at the site level because dominant carnivore was the only applicable model.

### Temporal activity overlap

We used the “activity” (Rowcliffe 2016) and “overlap” (Meredith and Ridout 2017) packages in R to compare temporal activity distributions of a subset of carnivore species detected including: coyote, fisher, gray fox, American marten, red fox, and bobcat. We selected these species because they are relatively common in the island system compared with other carnivore species and because they represent meaningful variation in body size.

First, we converted the timestamp for each detection event into radians and then into kernel densities. We then converted each detection time from “clock time” to “sun time” using the sunTime function in the “overlap” package (Meredith and Ridout 2017). Sun time, also known as solar time, bases the passage of time on sun position and is a more accurate scale for daily activity patterns in temperate areas due to cyclic variation in daylight length that is asynchronous with clock time (Nouvellet et al. 2012). We then calculated temporal overlap between each pair of species as  $\hat{\Delta}_4$  if both of the species in a pair had at least 50 observations or  $\hat{\Delta}_1$  if one of the species had less than 50 observations (both are values between zero and one, where zero indicates no temporal activity overlap and one indicates perfect temporal activity overlap; Meredith and Ridout 2017) with a 95% confidence interval for the temporal overlap value (Farmer and Allen 2019). To calculate the confidence intervals, we used bootstrapping with 1000 bootstrapped samples (Ridout and Linkie 2009; Farmer and Allen 2019). Pairs of species with  $\hat{\Delta}_4$  values > 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 < 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

We had 164 camera trap sites, with a mean of 52 active camera traps per year over 5 years on 19 islands for a total of 88 712 trap-nights. We obtained 257 358 photographs, representing 8 869 independent detections of 17 mammal species. We detected 12 carnivore species: American marten, black bear (*Ursus americanus* Pallas, 1780), bobcat, coyote, fisher, gray fox, gray wolf (*Canis lupus* Linnaeus, 1758), mink (*Mustela vison* Schreber, 1777), raccoon (*Procyon lotor* (Linnaeus, 1758)), red fox, river otter (*Lontra canadensis* (Schreber, 1777)), and weasels (genus *Mustela* Linnaeus, 1758). Of our focal species, coyotes were the most detected (514 detections), followed by American marten (262 detections), red fox (113 detections), fisher (86 detections), bobcat (68 detections), and gray fox (66 detections).

### Spatial activity overlap

At the island level, island biogeography and interactions with any of the dominant species were both well-supported explanations of carnivore species distributions. The interaction and island biogeography model with coyote RAI was the most supported model for red fox presence ( $w_{\text{Interaction+IB}} = 0.7$ ; Table 2), and the second most supported model was the global model ( $w_{\text{Global}} = 0.2$ ; Table 2). For red fox, evidence ratios suggested that the island biogeography and interaction hypotheses are both supported explanations; however, the evidence for interactions was much stronger. Evidence ratios for red fox indicated that it was 10 times more likely that the AIC<sub>c</sub>-model included island biogeography, 101 times more likely to include an interaction with coyotes, and 99 times more likely to include an interaction with any of the dominant species (bobcat or coyote) (Supplementary Table S2).<sup>1</sup> There was minimal support for including an

<sup>1</sup>Supplementary tables are available with the article at <https://doi.org/10.1139/cjz-2020-0195>.

**Table 2.** Top generalized linear mixed-effects model comparison results of dominant carnivore species relative abundance (RAI), island biogeography, and a global model at the island-level for red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), fisher (*Pekania pennanti*), and American marten (*Martes americana*) between September 2014 and November 2018 in the Apostle Islands, Wisconsin, USA.

Subordinate species	Model	Variable	Coefficient estimate	AIC <sub>c</sub>	w	Cumulative w	
Red fox	Interaction + IB	Coyote RAI	17 010.93	10	0.7	0.66	
		Island size (km <sup>2</sup> )	-32.77				
		Distance from mainland (km)	-25.32				
	Global	Distance from island (km)	-157.61	12	0.2	0.9	
		Coyote RAI	17 151.95				
		Bobcat RAI	-24 840.6				
Gray fox	IB	Island size	-33.04	8	0.4	0.43	
		Distance from mainland	-25.53				
		Distance from island	-158.92				
	Interaction + IB	Coyote RAI	37.799	10	0.2	0.59	
		Island size	34.692				
		Distance from mainland	-9.185				
	Interaction + IB	Distance from island	-130.145	10	0.2	0.75	
		Bobcat RAI	272.623				
		Island size	2.714				
	Fisher	Interaction + IB	Distance from mainland	1.007	10	0.2	0.91
			Distance from island	-1.727			
			Red fox RAI	113.742			
Interaction + IB		Island size	19.522	19.4	0.7	0.71	
		Distance from mainland	-4.237				
		Distance from island	-70.379				
American marten	Interaction + IB	Distance from island	-70.379	23.4	0.1	0.81	
		Bobcat RAI	92.861				
		Island size RAI	0.239				
	Interaction + IB	Distance from mainland	-0.108	23.9	0.1	0.89	
		Distance from island	-0.909				
		Bobcat RAI	86.34				
	Interaction + IB	Island size	0.169	24.9	0.1	0.95	
		Distance from mainland	-0.048				
		Distance from island	-0.676				
		Coyote RAI	-0.887				
		Island size	0.228				
		Distance from mainland	-0.133				
American marten	Global	Distance from island	-0.808	16	0.6	0.64	
		Coyote RAI	-468.2				
		Bobcat RAI	-431.1				
		Red fox RAI	-1095				
		Fisher RAI	-1104				
		Island size	61.7				
	Interaction + IB	Distance from mainland	7.53	18.9	0.2	0.79	
		Distance from island	-99.78				
		Bobcat RAI	-118.849				
		Island size	1.627				
		Distance from mainland	0.492				
		Distance from island	-3.849				
Interaction + IB	Red fox RAI	-83.765	19	0.1	0.93		
	Island size	0.718					
	Distance from mainland	-0.131					
	Distance from island	-2.635					

**Note:** AIC<sub>c</sub> is Akaike's information criterion corrected for small sample size. w is AIC<sub>c</sub> weights. IB is island biogeography. RAI is relative abundance index.

interaction with bobcats ( $ER_{\text{Bobcat}} = 0.32$ ) (Supplementary Table S2).<sup>1</sup> Gray fox presence was best predicted by the island biogeography model, but support for the top model reflected model selection uncertainty ( $w_{\text{IB}} = 0.4$ ; Table 2). The interaction and island biogeography models for gray fox were supported as well ( $w_{\text{Interaction+IB}} = 0.2$  for all three models; Table 2).

However, models with island biogeography showed 11.5 times as much support as models without, while evidence for interactions was minimal ( $ER_{\text{Dominant}} = 1.51$ ,  $ER_{\text{Bobcat}} = 0.44$ ,  $ER_{\text{Coyote}} = 0.19$ ,  $ER_{\text{Red fox}} = 0.20$ ) (Supplementary Table S2).<sup>1</sup>

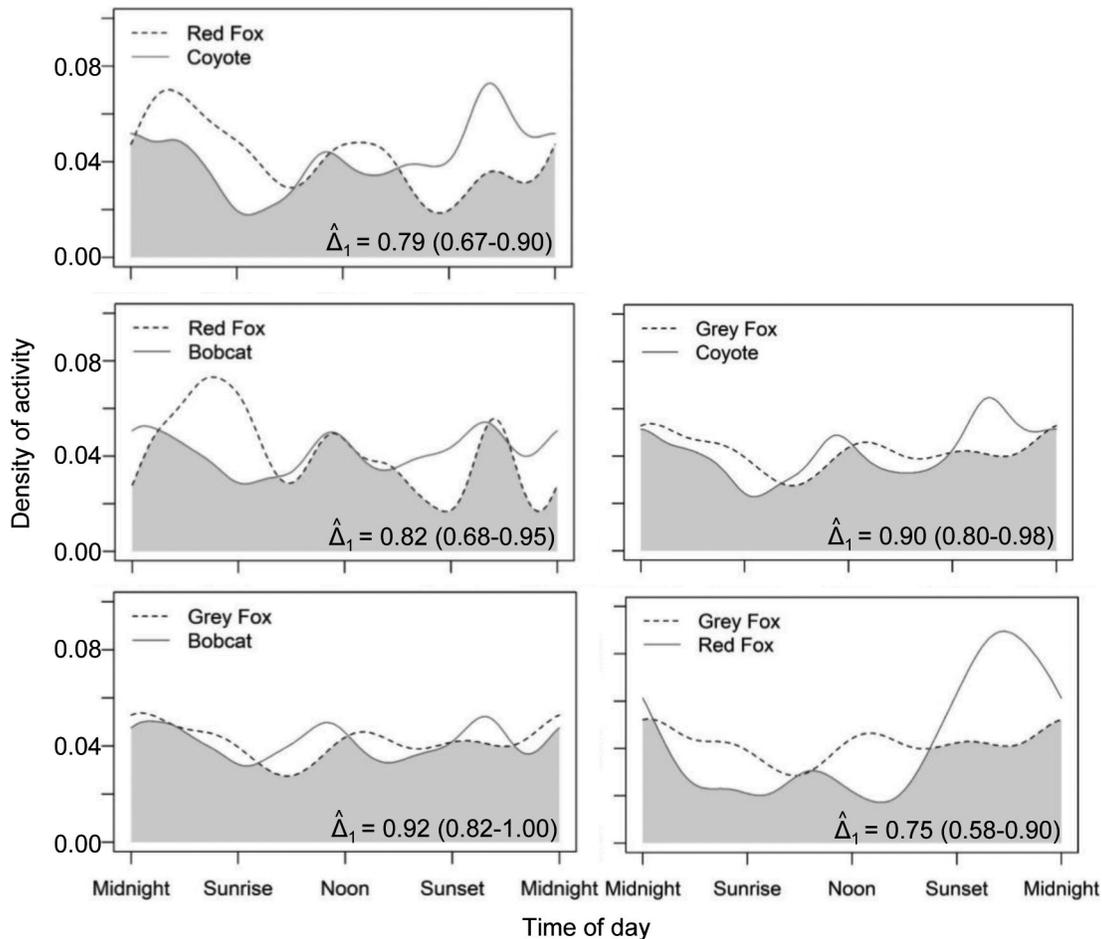
The most supported model for fisher was the interaction model with bobcat RAI ( $w_{\text{Interaction}} = 0.7$ ; Table 2). The island biogeography

**Table 3.** Generalized linear mixed-effects model results of dominant carnivore relative abundance (RAI) at the site level for a selection of carnivores detected between September 2014 and November 2018 in the Apostle Islands, Wisconsin, USA.

Subordinate	Dominant	Coefficient estimate	<i>p</i>	AUC
Red fox, <i>Vulpes vulpes</i>	Coyote, <i>Canis latrans</i>	0.081	0.40	0.59
	Bobcat, <i>Lynx rufus</i>	0.296	0.69	0.53
Gray fox, <i>Urocyon cinereoargenteus</i>	Coyote	0.035	0.73	0.47
	Bobcat	0.406	0.57	0.50
	Red fox	0.276	0.75	0.56
Fisher, <i>Pekania pennanti</i>	Coyote	<0.001	0.10	0.49
	Bobcat	-0.623	0.38	0.54
American marten, <i>Martes americana</i>	Coyote	-0.078	0.49	0.62
	Bobcat	-0.514	0.54	0.60
	Red fox	1.234	0.27	0.56
	Fisher	0.509	0.75	0.62

Note: AUC is area under the receiver operating characteristic curve.

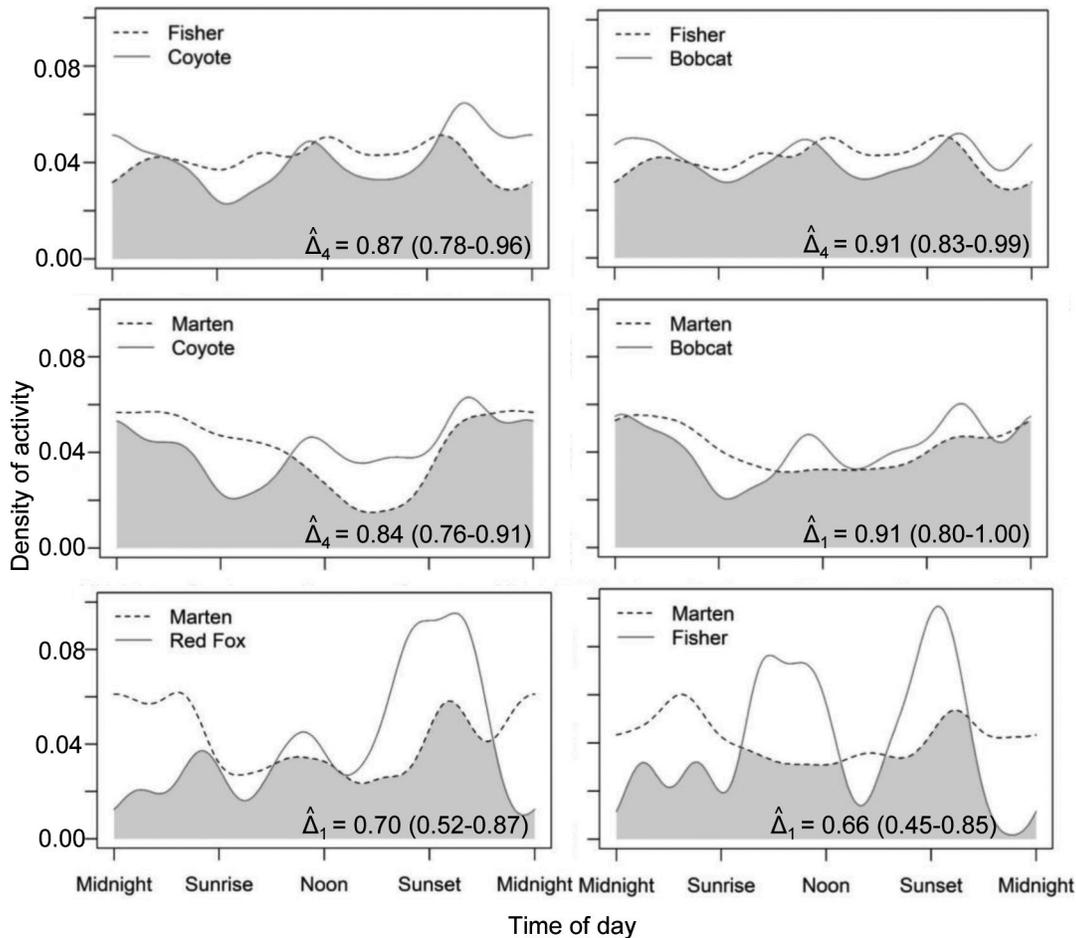
**Fig. 2.** Temporal activity overlap plots comparing the activity of canids and felids detected using camera traps between September 2014 and November 2018 in the Apostle Islands, Wisconsin, USA.  $\hat{\Delta}_1$  is a measure of the temporal overlap between each pair of species that ranges between zero (no temporal activity overlap) and one (perfect temporal activity overlap) (Meredith and Ridout 2017).



model ( $w_{IB} = 0.1$ ) and the interaction and island biogeography models with bobcat and coyote ( $w_{Interaction+IB} = 0.1$  and  $w_{Interaction+IB} = 0.1$ , respectively; Table 2) were also included among the >90% confidence model set for fisher. Based on the evidence ratios, top models for fisher were 5 times more likely to include an interaction with bobcats and 8 times more likely to include an interaction with any of the dominant species (bobcat or coyote), while evidence for both

island biogeography and interaction with coyotes were minimal ( $ER_{IB} = 0.40$  and  $ER_{Coyote} = 0.11$ ) (Supplementary Table S2).<sup>1</sup> For American marten, the global model including all dominant carnivores and the island biogeography variables was the most supported model ( $w_{Global} = 0.6$ ; Table 2). The interaction and island biogeography models with bobcat and red fox were also supported as top models for American marten distribution ( $w_{Interaction+IB} = 0.2$

**Fig. 3.** Temporal activity overlap plots comparing the activity of two mustelid species (fisher (*Pekania pennanti*) and American marten (*Martes americana*)) with potential dominant carnivores detected using camera traps between September 2014 and November 2018 in the Apostle Islands, Wisconsin, USA.  $\hat{\Delta}_4$  and  $\hat{\Delta}_1$  are measures of temporal overlap between each pair of species that ranges between zero (no temporal activity overlap) and one (perfect temporal activity overlap) (Meredith and Ridout 2017).



and  $w_{\text{Interaction+IB}} = 0.1$ , respectively; Table 2). Models without island biogeography received no support, and evidence ratios indicated that top models were 49 times more likely to include an interaction with any of the dominant species (bobcat, coyote, red fox, or fisher) and 4 times more likely to include an interaction with bobcats or an interaction with red foxes. There was minimal evidence supporting interactions with either coyotes or fishers ( $ER_{\text{Coyote}} = 1.77$  and  $ER_{\text{Fisher}} = 2.22$ ) (Supplementary Table S2).<sup>1</sup>

At the camera level, all models were insignificant and AUC values ranged from 0.47 (gray fox–coyote) to 0.62 (marten–coyote), indicating that for all pairings, the RAI of the dominant carnivore was uninformative for predicting the presence of the subordinate carnivore (Table 3).

### Temporal overlap

All pairings of dominant and subordinate species exhibited high ( $\hat{\Delta}_4$  or  $\hat{\Delta}_1$  values  $> 0.5$ ) or neutral temporal overlap ( $\hat{\Delta}_4$  or  $\hat{\Delta}_1$  values = 0.5). Nine pairings had high temporal overlap (Figs. 2 and 3). The remaining two pairings of dominant and subordinate species (marten–red fox and marten–fisher) displayed neither aggregation nor avoidance in time (Fig. 3).

### Discussion

Carnivore communities can be diverse and complex, and gaps in knowledge regarding intraguild interactions can preclude

effective conservation of co-occurring species (Krofel and Jerina 2016). Intraguild agonistic interactions can range from direct (predation) to indirect (spatiotemporal segregation) (Palomares and Caro 1999; Linnell and Strand 2000; Arim and Marquet 2004). We used an array of camera traps to monitor carnivore communities on the Apostle Islands and to determine whether species were using spatial or temporal segregation to facilitate coexistence, whether spatiotemporal segregation between carnivore species occurs at different spatial scales, and whether island biogeography, agonistic interactions, or both are structuring the carnivore community. We found some evidence of spatial segregation at the island level, but no evidence of spatial segregation at the camera level, and no evidence of temporal segregation. This suggests that at the island level, island biogeography and species interactions may both impact species distributions, and that the carnivore community may be using alternative strategies to coexist at fine spatial scales, or that the island system or prey base may preclude strict resource segregation.

Within the Apostle Islands, spatial distributions of carnivores were largely structured by island size and isolation (e.g., Allen et al. 2019). Island systems are typically more dynamic than continental systems due to variation in rates of colonization and extinction, and species may not have time to segregate to relieve agonistic interactions before they or their potential competitor goes extinct on an island (MacArthur and Wilson 1967). Island

biogeography measures were included in nearly all the top models for all species, except for fisher, indicating that the assumption of equilibrium between colonization and extinction rates is reasonable for this system and that island biogeography is important in structuring the carnivore community.

The relative importance of island biogeography and agonistic interactions in determining subordinate carnivore distributions depended on the subordinate carnivore species. For example, evidence ratios indicated that island biogeography was important for gray fox and interactions were important for fisher, while both island biogeography and interactions were important with red fox and marten. American martens are an especially interesting case within the Apostle Islands because they had a positive relationship with distance to the mainland and negative relationships with most dominant carnivores. This could be a case of large-scale spatiotemporal segregation across the island system (Allen et al. 2019), as contrary to island biogeography theory, martens are less likely to be found on the islands closest to the mainland. Despite the importance of island biogeography to carnivore distribution, immigration ability could be even more important to the structure of the carnivore community. Equilibrium island biogeography assumes that every species has equal immigration ability, but this assumption has been widely challenged (Diamond 1974; Simberloff 1978; Cole 1981; Lomolino 2000) and seems tenuous based on the range of body size and life-history traits (e.g., hibernation) exhibited by the Apostle Island carnivore community. Additionally, island biogeography theory assumes that islands and immigration filters (Lake Superior, in our case) are homogenous (Lomolino 2000), which is likely untrue based on currents and ice cover in Lake Superior. For example, with decreasing ice cover, ice bridges that wildlife may depend on to immigrate between islands (Lomolino 1988; Adams et al. 2011) are becoming less common and could pose a serious threat to the long-term viability of the carnivore community on the Apostle Islands.

Spatiotemporal segregation is a well-documented risk-mitigation strategy used by carnivores to minimize risk from agonistic interactions and predation. Contrary to our hypotheses, at the camera level, none of the subordinate carnivores exhibited spatial avoidance and most of the tested pairs had high temporal overlap. While many of the carnivores that were detected on the Apostle Islands use some form of fine-scale spatiotemporal segregation on mainland North America, our results are supported by Manlick et al. (2017), who also found no evidence of temporal or spatial segregation between American marten and fisher on the mainland in northern Wisconsin. Aside from temporal and spatial segregation, sympatric species can use dietary or morphological segregation to facilitate coexistence. Dietary segregation occurs when a species shifts its resource use so that its use of foraging habitat or prey overlaps less with a competitor, and morphological segregation occurs when some difference in morphology (i.e., body size) decreases resource overlap between competitors due to correlations between predator body size and prey body size (Radloff and Du Toit 2004). While we did not test for dietary overlap, Manlick et al. (2017) found no evidence of dietary segregation among the mainland Wisconsin population of fishers and American martens, which is supported by mustelid research outside of Wisconsin (McDonald 2002; Lanszki and Heltai 2011). Canids can also vary in whether or not they display spatial segregation (Neale and Sacks 2001; Lesmeister et al. 2015). Within an urban matrix with habitat patches that are similar to an island system, Mueller et al. (2018) observed coyotes and red foxes segregating by habitat type, but also recorded several interactions between coyotes and red foxes during which no interspecific aggression occurred.

Our results do not necessarily indicate that the subordinate carnivores are not using spatial or temporal segregation since dominant species had a much stronger effect on subordinate

species presence at the island level than the camera level. Scale is a central component of ecology (Levin 1992) and clearly an important factor in our island system. As such, the carnivore community could be segregating at multiple scales, including an even finer scale than we tested. Fine-scale segregation can manifest as an interaction between spatial and temporal segregation, 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 (Vanak et al. 2013; Swanson et al. 2014). Fine-scale segregation could also manifest as seasonal segregation, where resource use shifts based on the season (Vanak et al. 2013; Monterroso et al. 2016). Alternatively, spatiotemporal segregation is based on the availability and distribution of resources, whether the resource is space, time, or food. While no research has yet been published on the Apostle Island prey community, systems with limited prey species richness are generally prey-driven and carnivores may be unable to segregate prey resources. Similarly, the distributions of prey species are also subject to island biogeography, which could result in limited prey species richness and abundance on smaller or more isolated islands.

Based on our results and the competitive exclusion principle, we suspect that the carnivore community may either be segregating prey through differences in morphology and (or) diet selection or may be segregating space or time at finer scales than we were able to measure. It may also be that with so many overlapping carnivore species, the interactions are too complex to detect with analyses of species pairs. Identifying how carnivore species are coexisting would provide critical information on their realized niches and allow for more effective conservation of multiple carnivore species (e.g., Krofel and Jerina 2016). Future research should focus on determining colonization and extinction of islands for carnivore species, individual-level effects of agonistic interactions with other carnivores, and trends in carnivore populations across the archipelago.

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