

Responses of wildlife to tourism and glacial recession in
Glacier Bay National Park, Alaska

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Abstract

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Wildlife have varying responses to disturbances depending on the duration, severity, and type of disturbance event. Some disturbances modify wildlife habitat, and can impact community assembly and patterns of diversity, while others can modify wildlife behavior. Human disturbance often elicits two opposite behavioral response from wildlife, one in which they can exhibit “fear effects”, where they avoid humans, and the “human shield effect”, where wildlife are attracted to centers of human activity and use human presence as a buffer against predation. However the level of human disturbance that causes a detectable change in wildlife behavior remains unknown. Many disturbances that alter landscapes and modify wildlife habitat are expected to increase in frequency and severity with climate change, and post-disturbance successional patterns of wildlife communities remain poorly understood. In this thesis, I investigated the responses of wildlife to two types of disturbances: human activity (Chapter 2) and glacial recession (Chapter 3) in Glacier Bay National Park, Alaska (GLBA). GLBA is a remote park with relatively low but increasing levels of visitation, and it is centered around a marine fjord that is the product of the most rapid glacial recession in modern times. To understand the responses of brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*), and wolves (*Canis lupis*) to human activity, I used camera traps to document

wildlife activity and a paired-plot, crossover experimental design to manipulate human visitation during summers 2017 and 2018 ($n = 5$ pairs of sites). Single-season occupancy models and activity overlap analyses indicated that brown bears were unaffected by human use in GLBA, black bears exhibited fear effects temporally but the human shield effect spatially, moose utilized human presence as a shield temporally, and wolves exhibited fear effects temporally. Traditional occupancy models assume logit-linear relationships between predictor and response variables; however, visual inspection of the detection data showed a threshold in which detections did not exceed four per week for any species unless human activity was absent. The camera trap data was supplemented with small mammal trapping and vegetation surveys to investigate community-level successional patterns of mammals in GLBA and understand the roles of habitat and time-since-disturbance in shaping community assembly and diversity. Mammal communities in GLBA were more strongly influenced by time-since-disturbance than habitat, and dispersal ability had a strong influence on mammal colonization patterns, as indicated by both PERMANOVA and beta diversity analyses. My findings have several implications: first, despite low visitation to GLBA, I detected spatiotemporal responses of wildlife to human disturbance, indicating that the threshold level of human activity for sites to function as baseline controls in studies of anthropogenic impacts may be lower than those found in most protected areas. Additionally, these results support “land sparing” management techniques whereby visitors are concentrated in certain parts of protected areas to maintain spatial refugia for wildlife. Second, these results highlight the importance of incorporating landscape connectivity and dispersal ability metrics into wildlife conservation efforts following disturbances. Furthermore, caution should be used making inferences about changes in wildlife communities following disturbance based on changes in habitat, as my results indicate that wildlife and vegetation communities do

not respond to disturbance in the same way. This knowledge may improve predictions of mammalian community assembly following major disturbance events.

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CHAPTER 1

General Introduction

Wildlife have varying responses to disturbances depending on the duration, severity, and type of disturbance event. Some disturbances modify wildlife habitat, and can impact community assembly and patterns of diversity (Markovchick-Nicholls et al. 2008), while others can modify wildlife behavior. Human disturbance to wildlife often elicits a behavioral response (Gill et al. 2001), and while these behavioral responses are often measured in the short-term (Bateman and Fleming 2017), human disturbance to wildlife can have long-term consequences for wildlife populations (Gaynor et al. 2018). Alternatively, increasing climatic variability can trigger natural disturbances that modify wildlife habitats, and there is widespread agreement that climate change will influence the magnitude and frequency of these events (Easterling et al., 2000; Sergio et al., 2018). These disturbances are a fundamental process controlling diversity (Huston, 1994). Ultimately, both human disturbance and natural disturbance can have population-level consequences for wildlife, and as such, it is imperative to understand how biotic communities will respond.

Human disturbance can trigger two antithetical behavioral responses in wildlife: “fear effects”, where wildlife view humans as a “super predator” on the landscape, and a source predation risk (Frid and Dill 2002, Smith et al. 2017), and the “human shield effect”, where prey species use human presence as a buffer against predation (Sarmiento and Berger 2017). As public interest in nature-based recreation grows, it is important to understand how humans and wildlife will continue to coexist (Carter et al. 2012, Leung et al. 2018). In addition to serving as places that support outdoor recreation and biodiversity conservation, protected areas are also popular

venues for ecological research. National parks are often used as baseline “control” sites to evaluate anthropogenically caused ecological change outside of parks in the United States, particularly in regard to wildlife behavior (Arcese and Sinclair 1997, Sarmiento and Berger 2017). Although ecological processes within parks may have reduced human impacts (Leroux et al. 2010, Beissinger et al. 2017), many parks within the United States receive millions of visitors a year (National Park Service IRMA Portal, accessed 11/14/2017). Wildlife have demonstrated strong responses to people in these high-visitation national parks, calling into question their ability to serve as baseline controls (Sarmiento and Berger 2017).

To mitigate human disturbance impacts, managers of these spaces can adopt “land sparing” or “land sharing” strategies. Land sparing techniques concentrate human use in certain parts of protected areas to limit the areal extent of human impacts to the landscape (Cole 1992, Leung and Marion 1999). Alternatively, land sharing or visitor dispersal methods are sometimes used in areas of low human use such as Denali National Park and Preserve in Alaska, with the rationale that human impacts are sufficiently low that areas do not need to be “sacrificed” to maintain ecological integrity elsewhere (Leung and Marion 2000, Marion and Farrell 2002). However, the assumption that low levels of dispersed human activity has negligible impacts on wildlife has not been tested. Additionally, it is unknown if wildlife respond differently to human disturbance in national parks that are not as frequently visited, and whether there is a human visitation threshold for which wildlife begin to change their behaviors.

Protected areas such as national parks may have reduced human impacts compared to their non-protected counterparts, however climate change will impact landscapes regardless of whether an area is federally protected. As the frequency and intensity of natural disturbances increases with climate change, there is increased potential for these events to significantly reduce

wildlife community diversity. Understanding community succession is fundamental to the study of ecology (Cowles, 1901; Clements, 1916; Gleason, 1917; Cooper, 1913), however animal succession has not been as widely studied (Lessard, 2019). As such, habitat metrics are often used as a surrogate for changes in wildlife assemblages following disturbances (Barton et al., 2014). The importance of habitat suitability on establishment success of wildlife populations has been demonstrated in small mammal communities following fire (Monamy and Fox, 2010), however changes in wildlife communities may not directly track changes in vegetation if there are barriers to wildlife movement or if species have limited dispersal ability (Greve et al., 2005).

Impacts of disturbances on community assembly can strongly influence patterns of beta diversity (between-community diversity), which in turn can be influenced by dispersal rates (Vanschoenwinkel et al., 2013; Mutz et al., 2017). Beta diversity reflects two different biological phenomena, community nestedness and spatial species turnover (Baselga, 2010). Nestedness results from the sequential elimination or addition of species such that relatively species-poor assemblages are subsets of the richest assemblage (Han et al., 2018). Alternatively, spatial species turnover, or species replacement between sites, occurs when species in one site are substituted by different species in other sites. Understanding the relative contribution of both nestedness and turnover to overall beta diversity is a key component in community dynamics following disturbances (Svenning et al., 2011).

Glacier Bay National Park (GLBA) in Southeast Alaska represents a unique opportunity to study the impacts of both human and natural disturbances on wildlife communities. GLBA is a remote park with relatively low but increasing levels of visitation. Due to concerns about visitor impacts, park managers implemented a new tourism plan that allowed for the designation of “high-use” locations to concentrate human activity in specified areas and restrict human activity

in other areas. This new management plan provided the unique opportunity to experimentally manipulate visitation patterns and examine responses by wildlife. Additionally, GLBA has undergone the most rapid and extensive deglaciation in the world since the Little Ice Age (LIA; Connor et al. 2009). The 120km recession of Grand Pacific Glacier took place in less than 160 years (Fastie, 1995; Mann and Strevler, 2008), exposing several hundred square kilometers of glacial till and outwash to plant and animal colonization. Plant succession has been widely studied in GLBA, however the successional patterns of higher vertebrates has not been studied (Lewis 2012). Variation in habitat connectivity and seed sources has resulted in different patterns of plant succession between the west and east arms of the park (Buma et al., 2017). Thus, GLBA provides a unique opportunity to tease apart habitat from time-since-disturbance as drivers of community assembly, because these factors are not inherently correlated in GLBA as they often are in studies of succession.

The goal of this thesis is to address how large mammals (brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*), and wolves (*Canis lupus*)) respond to human activity in GLBA, and how the mammal community as a whole responds to glacial recession. I first assessed the spatiotemporal responses of bears, wolves and moose in GLBA to human activity using remote cameras. I expected moose, as a prey species, would demonstrate behavior synonymous with the human shield effect, as has been shown in other systems with higher human use (Thorsen 2016, Sarmiento and Berger 2017). Brown bears and wolves are apex predators, and as such I expected them to exhibit fear effect responses to humans. However, I expected black bears, as more of a mesopredator in GLBA, to potentially demonstrate the human shield effect if predation risk from brown bears is high.

To understand the successional patterns of terrestrial mammals in response to glacial

recession, I supplemented the camera trap data with small mammal trapping and vegetation surveys. I examined the relative importance of habitat and time-since-disturbance on both community assembly processes and beta diversity. If dispersal ability is a key process in vertebrate succession, then I expected time-since-disturbance should be more influential than habitat. In contrast, if filtering of species based on habitat requirements is the key process, then I expected habitat should be more influential. Additionally, I hypothesized that beta diversity of highly vagile mammals across sites would be lower than that of poor dispersers, through dispersal-driven homogenization (Vanschoenwinkel et al., 2013).

This work will shed light on the behavioral responses of wildlife to human disturbance, and determine whether spatiotemporal responses of wildlife can be documented in systems with low human use. If wildlife react to even low levels of human presence, it is quite possible that the desire of people to view and interact with wildlife in natural settings could ultimately reduce the possibility of those interactions. Therefore, these findings can be used to assist managers of protected areas in making decisions regarding visitor use and inform decisions on management techniques such as “land sparing” or “land sharing”. Additionally, as climate change threatens to increase the frequency and intensity of natural disturbances, these results can inform post-disturbance conservation efforts and contribute to understanding the mechanisms that drive whole-community responses of mammals to disturbance.

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CHAPTER 2

Spatiotemporal responses of wildlife to tourism in a low-visitation national park

ABSTRACT Protected areas such as national parks represent relatively untouched landscapes, and researchers often use highly visited parks as study systems to set baselines regarding wildlife behavior. However, the level of human disturbance that causes a detectable change in wildlife behavior remains unknown. In response to humans, wildlife can exhibit “fear effects”, where they avoid humans, as well as the “human shield effect”, where wildlife use humans as a buffer against predation. Here we investigated the spatiotemporal responses of brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*), and wolves (*Canis lupis*) to tourism in Glacier Bay National Park, Alaska (GLBA), a remote park with relatively low but increasing levels of visitation. We used camera traps to document wildlife activity and a paired-plot, crossover experimental design to manipulate human visitation during summers 2017 and 2018 ($n = 5$ pairs of sites). Single-season occupancy models and activity overlap analyses indicated that brown bears were unaffected by human use in GLBA, black bears exhibited fear effects temporally but the human shield effect spatially, moose utilized human presence as a shield temporally, and wolves exhibited fear effects temporally. Traditional occupancy models assume logit-linear relationships between predictor and response variables; however, visual inspection of the detection data showed a threshold in which detections did not exceed four per week for any species unless human activity was absent. GLBA is part of one of the world’s largest protected areas, and less than 40,000 on-land tourists visited the park in 2017. Despite this low visitation level, we detected spatiotemporal responses of wildlife to human disturbance. These results indicate the threshold level of human activity for sites to function as baseline controls in studies of anthropogenic impacts may be lower than those found in most protected

areas. Our findings support “land sparing” management techniques whereby visitors are concentrated in certain parts of protected areas to maintain spatial refugia for wildlife.

INTRODUCTION

Public interest in nature-based recreation is high and growing. Terrestrial protected areas around the world receive approximately 8 billion visitors per year (Balmford et al. 2015). While global protected area designations have increased steadily since 1990, with over 14% of the world designated as protected in 2016 (UNEP-WCMC and IUCN 2016), visitation rates are outpacing these expansions. Visitation to wilderness areas increased 17.7% between the years of 1999 and 2009 and is projected to increase by 24% by 2030 (White et al. 2016). Protected areas are a key component of global conservation strategies, and they are often dedicated to protecting biological diversity (Synge 1995). As such, it is important to understand how humans and wildlife will continue to coexist in these areas (Carter et al. 2012, Leung et al. 2018). World Heritage Sites, biosphere reserves, wilderness areas and national parks are key venues for nature-based recreation, and tourism to these areas can have a variety of environmental impacts. Increased visitation to these areas has increased the potential for interactions between humans and wildlife, and increased potential for disturbance to wildlife. Outdoor recreation is the fourth leading cause for decline of at-risk species in the United States (Czech et al. 2000) and in the more sparsely-populated Canada (Prugh et al. 2010), raising concerns about the sustainability of growth in recreation and nature-based tourism.

Some level of human impacts is inevitable in protected areas, and managers are tasked with providing meaningful experiences for visitors without compromising the environmental integrity of the protected area (UNEP-WCMC and IUCN 2016). To mitigate human disturbance impacts, managers of these spaces can adopt “land sparing” or “land sharing” strategies. Land

sparing techniques concentrate human use in certain parts of protected areas to limit the areal extent of human impacts to the landscape (Cole 1981, Cole 1992, Leung and Marion 1999), often concentrating use on the smallest number of frontcountry locations needed to accommodate visitors and has a long tradition of use in wilderness areas (Leung and Marion 2000).

Alternatively, land sharing or visitor dispersal methods are sometimes used in backcountry areas of low human use such as Denali National Park and Preserve in Alaska, with the rationale that human impacts are sufficiently low that areas do not need to be “sacrificed” to maintain ecological integrity elsewhere (Cole 1981, Leung and Marion 2000, Marion and Farrell 2002). However, the assumption that low levels of dispersed human activity has negligible impacts on wildlife has not been tested.

In addition to serving as places that support outdoor recreation and biodiversity conservation, protected areas are also popular venues for ecological research. National parks are often used as baseline “control” sites to evaluate anthropogenically caused ecological change outside of parks in the United States, particularly in regard to wildlife behavior (Arcese and Sinclair 1997, Berger 2007, Sarmiento and Berger 2017). Although ecological processes within parks may have reduced human impacts (Leroux et al. 2010, Beissinger et al. 2017), many parks within the United States receive millions of visitors a year (National Park Service IRMA Portal, accessed 11/14/2017). Wildlife have demonstrated strong responses to people in these high-visitation national parks, calling into question their ability to serve as baseline controls (Bruggeman et al. 2006, Berger 2007, Haroldson and Gunther 2013, Gunther et al. 2015, Sarmiento and Berger 2017). However, it is unknown if wildlife respond differently to human disturbance in national parks that are not as frequently visited, and whether there is a human visitation threshold for which wildlife begin to change their behaviors. If wildlife react to even

low levels of human presence, it is quite possible that the desire of people to view and interact with wildlife in natural settings could ultimately reduce the possibility of those interactions.

Wildlife can respond spatially and temporally to human disturbances in several ways. Both predators and prey may view humans as a “super predator” on the landscape, and a source predation risk (Frid and Dill 2002, Shannon et al. 2014, Clinchy et al. 2016, Smith et al. 2017). Human disturbance can cause short-term changes in wildlife behavior such as interruption of foraging and fleeing (Bateman and Fleming 2017). In the long term, increased human activity around wildlife can impact reproduction and survival due to decreased foraging time and increased stress levels, and can also cause displacement of animals, changes in breeding success, increased physiological and energetic stress, shifts in diel cycles, and even death (Anderson and Keith 1980, Boyle and Samson 1985, Taylor and Knight 2003, Monz et al. 2010, Gaynor et al. 2018). These non-consumptive effects of fear, or “fear effects,” can ultimately have a larger effect on populations than actual predation (Preisser et al. 2005, Ciuti et al. 2012, Bleicher 2017), and human disturbance is analogous to predation risk (Frid and Dill 2002). Alternatively, the “human shield effect” has been proposed as a way in which wildlife can respond to humans, where prey species use human presence as a buffer against predation (Berger 2007, Shannon et al. 2014, Sarmiento and Berger 2017). This response to humans can displace predators and prey and alter ecological interactions between them (Berger 2007, Hebblewhite and Merrill 2009, Sarmiento and Berger 2017). Human impacts on wildlife, whether manifesting in fear effects of the human shield effect, may be especially problematic for large mammals due to their large space requirements, low population densities, and low birth rates (George and Crooks 2006, Noss et al. 1996).

In this paper, we used remote cameras to quantify spatiotemporal activity patterns of large mammals in response to human activity in Glacier Bay National Park, Alaska (GLBA). GLBA provides a unique opportunity to study wildlife responses to relatively low levels of tourism and to evaluate potential thresholds of human disturbance in one of the most pristine World Heritage Sites. Despite relatively low visitation rates, the number of tourists visiting GLBA has almost doubled in the past 20 years (National Park Service IRMA Portal, accessed 10/5/2016). For example, shore excursions from tour vessels increased from 16 days in 2008 to 101 days in 2014 (NPS unpublished data). Due to concerns about visitor impacts, park managers implemented new tour vessel operating plans in 2016. These plans allowed for the designation of “high-use” locations to concentrate human activity in specified areas and restrict human activity in other areas. This new management plan provided the unique opportunity to experimentally manipulate visitation patterns and examine responses by wildlife.

We focused on four terrestrial mammal species: brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*), and wolves (*Canis lupus*). We hypothesized that moose, as a prey species, would demonstrate behavior synonymous with the human shield effect, as has been shown in other systems with higher human use (Hebblewhite et al. 2005, Thorsen 2016, Sarmiento and Berger 2017, Wakefield and Attum 2006, Waser et al. 2014, Shannon et al. 2014). As more of a mesopredator in the GLBA system, we expected black bears to respond similarly to moose if they are at risk of predation from the apex predators (brown bears and potentially wolves) in the park (MacHutchon et al. 1998). We hypothesized that these apex predators would exhibit fear effect responses to tourism, due to their history of persecution and hunting and previous studies that have found that large carnivores avoid humans (Gunther 1990 MacHutchon et al. 1998, Olson et al. 1998, Gibeau et al. 2002, Kaczensky et al. 2006, Shannon

et al. 2014, Smith et al. 2017). Alternatively, black bears in GLBA might respond similarly to brown bears and wolves if the risk of predation from human “super predators” outweighs the risk of predation from the apex predators in the park. Lastly, since tourism in GLBA is concentrated on shoreline areas of the park, we expected that if wildlife are in fact avoiding humans, there would be a displacement of wildlife to inland habitat while sites were in a high-use treatment.

STUDY AREA

Glacier Bay National Park and Preserve (GLBA) is a 13,000 km² portion of a 100,000 km² World Heritage Site (Figure 2.1). GLBA is comprised of marine fjords, mountains, glaciers and ice fields. A maritime climate dominates GLBA, with average summer temperatures between 10-15° C and annual average rainfall of 177 cm at the southern coastal end of the park, with conditions becoming much more extreme in the surrounding mountains.

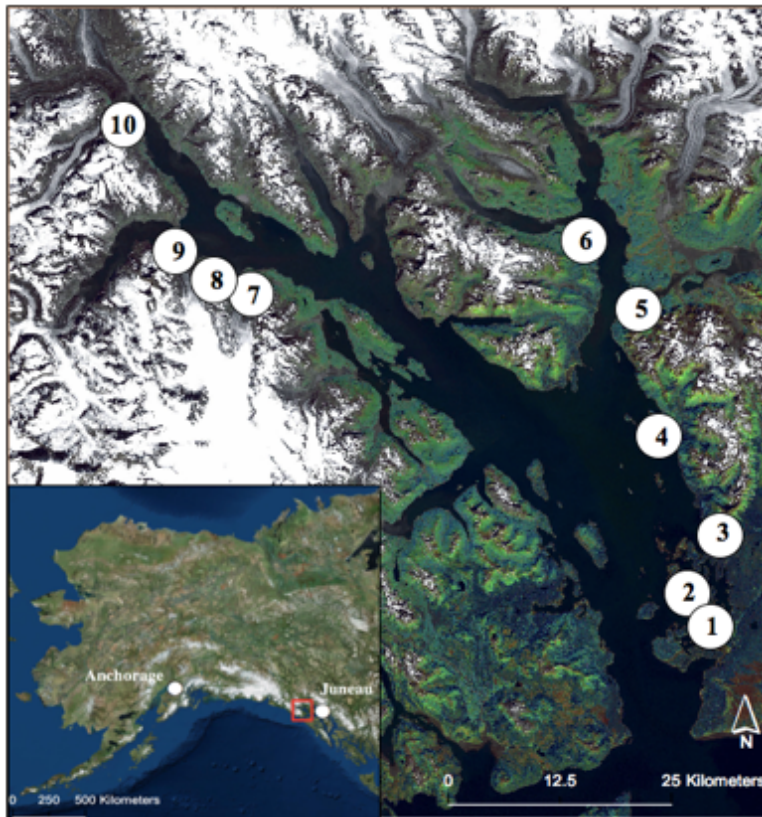


Figure 2.1: Map of location of Glacier Bay National Park, AK. White numbered circles represent study sites, described in Table 1.

GLBA is a product of the Little Ice Age (LIA) that reached a maximum around 1750 and was followed by a dramatic deglaciation over the past several hundred years (Connor et al. 2009). This retreat is the world's most rapid and extensive in modern times. A recession of 120 km took place in less than 160 years (Fastie 1995, Mann and Streveler 2008), exposing several hundred square kilometers of glacial till and outwash to plant and animal colonization. There are 29 known terrestrial mammalian species that have recolonized at least part of the park (Taylor 1984). In addition to the four large terrestrial mammalian species focused on in this study, GLBA is also home to wolverines (*Gulo gulo*), mountain goats (*Oreamnos americanus*), and coyotes (*Canis latrans*).

GLBA is the sixth largest national park by area (National Park Service IRMA Portal, accessed 2/17/2019), and there are no maintained trails or campgrounds outside of park headquarters. The only way to access GLBA is by boat or by plane, and 94% of all tourism to GLBA occurs on cruise ships where passengers never disembark. There are approximately 40,000 on-land tourists to GLBA per year. In 2018, 13,000 of those visited GLBA on tour vessels that drop visitors on shore for day hikes or kayak-based camping trips and the remainder of visitors either stayed within headquarters area or visited the backcountry by kayak or private vessel (National Park Service IRMA Portal, accessed 12/14/2018).

METHODS

Site Selection

We conducted this study during summers (June-August) in 2017 and 2018. We selected ten study sites across GLBA using several criteria. First, tour vessels needed to be willing to drop passengers off for shore excursions at one or both sites per pair. Second, GLBA managers needed to be willing to restrict use at one or both sites per pair either by closing each site to tour

vessels for half of the summer season or by switching drop-off points for campers and kayakers. And third, sites were paired together based on habitat similarity and spatial proximity.

Experimental Design

The basic sampling framework for the study was a crossover, paired-plot, two-factor design with five pairs of sites. The two factors were human use (high or low) and habitat (shore or inland). At three of the five pairs of sites, the human use treatment was swapped (i.e., “crossed over”) among sites mid-season. One site pair was visited by kayakers and two site pairs were visited by tour vessels (Table 2.1). The timing (early vs late summer) of the human use treatment was randomly determined for each pair and reversed in the second year to control for seasonal effects. In the remaining two pairs (Upper Tarr/Lamplugh and Bartlett Cove/Lester Island), it was not possible to swap the human use treatment among sites, so one site within each pair received the high-use treatment and one received the low-use treatment for the duration of the study. Upper Tarr was rarely used by tour vessels because it was difficult to anchor at, so this was a low-use site and Lamplugh received the high-use treatment in both years. Bartlett Cove contained park headquarters and could not be closed to human use, so this site received the high-use treatment and nearby Lester Island was a low-use site in both years (Table 2.1).

Camera Trapping

We installed four cameras (Reconyx HC600 Hyperfire Covert IR) at each of the ten study sites, for a total of 40 remote camera installations. Two cameras were installed in shoreline habitat and two cameras were installed in inland habitat. All cameras were approximately 0.5 km away from one another, forming as close to a square grid at each site as the landscape allowed. Cameras were set to take 3 photos every time they were triggered, with a “RapidFire” setting to reduce the time between photos to one second. Cameras were set up at a height of approximately

0.5 m above the ground. We placed cameras along game trails (where available), or in expected areas of wildlife concentration, to maximize detection probabilities. We checked the cameras approximately every 3 weeks throughout the field season to ensure cameras were working properly, download photograph data, and perform any required maintenance (Hernández-SaintMartín et al. 2013, Goad et al. 2014). We identified individuals detected to species (when possible) for each photo and processed photos using the Timelapse2 software (Greenberg and Godin 2015).

Table 2.1: Characteristics of experimental sites in Glacier Bay National Park. Site numbers, names, pairing information, average tree diameter at breast height (DBH), treatment designations, and total minutes of human activity are shown. “High” and “low” refer to human use treatment levels. Early 2017 and 2018 season was June 1 – June 14, and late 2017 and 2018 was June 15 – September 1. Human activity (minutes) was calculated by counting all humans detected in photos taken at each site and dividing by 60, since each photo represents one second. Site numbers correspond to Figure 1.

| Site # | Site Name | Early 2017 | Late 2017 | Early 2018 | Late 2018 | DBH (cm) | Human Activity (minutes) |
|--------|------------------|------------|-----------|------------|-----------|----------|--------------------------|
| 1 | Bartlett Cove | High | High | High | High | 47.1 | 4770.5 |
| 2 | Lester Island | Low | Low | Low | Low | 24.9 | 0.3 |
| 3 | Beartrack Cove | Low | High | High | Low | 32.4 | 37.1 |
| 4 | South Sandy Cove | High | Low | Low | High | 28.7 | 307.2 |
| 5 | Adams Inlet | High | Low | Low | High | 53.8 | 5.5 |
| 6 | Hunter Cove | Low | High | High | Low | 37.2 | 2.7 |
| 7 | Reid East | High | Low | Low | High | 0.0 | 98.1 |
| 8 | Reid West | Low | High | High | Low | 0.0 | 122.8 |
| 9 | Lamplugh | High | High | High | High | 0.0 | 282.6 |
| 10 | Upper Tarr | Low | Low | Low | Low | 0.0 | 0.5 |

Vegetation Surveys

To account for habitat differences that may have affected wildlife occupancy across sites of different ages since deglaciation, we collected information on the average diameter at breast

height (tree DBH) of trees at each site in 2018. We took four tree DBH measurements every 10m for a total of 40 measurements per site in the inland habitat.

Statistical Analysis

Temporal Activity Patterns

We assessed temporal activity patterns of each of the four focal species using the R (Version 1.1.463) package “Activity” (Version 1.1; Rowcliffe 2016). We screened photos first so that photographic events of the same species were considered independent events if they were separated by more than 30 minutes (Carter et al. 2012). We fit kernel density functions to temporal activity data, and the area under the distributions of these activity data provide information on the overall activity level of each species over the 24-hour diel cycle (Rowcliffe et al. 2014). We calculated the overlap of the activity patterns by comparing diel patterns in high-use vs low-use treatments for each focal species using von Mises kernel density functions with the package “Overlap” (Version 0.3.2; Meredith and Ridout 2017). Overlap coefficients ranged from 0-1, with 0 indicating no overlap and 1 indicating complete overlap. Thus, low overlap values indicate large differences in diel patterns between high and low human use treatments. To estimate confidence intervals of overlap coefficients, 10,000 smoothed bootstrap samples were generated for each species separately for high-use and low-use treatments. To determine if the activity patterns differed statistically among high-use versus low-use treatments, we performed a Watson’s Two-Sample Test of Homogeneity (hereafter Watson’s Test) on the circular time data for each species.

Spatial activity patterns

We examined spatial activity patterns using an occupancy modeling framework that estimated the probability of species occupancy while accounting for detection error, where

occupancy is defined as the probability that a randomly selected site contains at least one individual of a species (MacKenzie et al. 2006). Occupancy modeling uses repeat surveys at sites to estimate both the probability that a site is occupied by the focal species as well as the probability of detecting the species given it occurs there (MacKenzie et al. 2006). We partitioned detection histories into 7-day increments for each species (Rovero et al. 2014) using the package “camtrapR” (Version 0.99.9; Niedballa et al. 2017). We estimated the detection and occupancy probabilities of all species using single-season occupancy models utilizing these detection histories and site-level and observation-level covariates. Because the cameras were close to one another relative to the large home ranges of the target species, assumptions of independence were likely violated. To test for the potential effect of these violations on our parameter estimates, we included a random effect of the site in the top model for each species and examined the results. The significance of the human use related covariates did not change, and thus we used the results from models without any random effects for easy comparison and discussion using package “unmarked” (Version .12-0; Fiske and Chandler 2011).

We expected human use to affect detection probabilities rather than occupancy probabilities, because the relatively low levels of human use at GLBA even at high-use sites were unlikely to cause species to completely abandon sites. We expected habitat characteristics associated with the deglaciation history of sites to be the primary factor affecting occupancy probability, and consequently used average site tree DBH as the only covariate for occupancy.

We used a two-step model selection process to obtain the most parsimonious occupancy model for each species. First, we compared models with and without tree DBH as a covariate on occupancy, using a null (intercept-only) detection model. If the ΔAIC between the two models was less than or equal to 2, the intercept-only model was considered the more parsimonious

model (i.e. the model that best fits the data with the fewest parameters; Dingemanse et al. 2004), otherwise the model with the lowest overall AIC was chosen as the top model (Burnham and Anderson 2002). Second, we selected the best-supported detection model, using the best model for occupancy probability identified in step one. The following covariates of detection were tested: *HumanActivity* (see below; Table 2.2), *Habitat* (shore vs inland), *HumanUse* (Y or N for high-use or low-use), *Season* (early or late), and *Year* (2017 or 2018) (Table 2.2). For the black bear model, an additional covariate was included to test for potential avoidance of brown bears by black bears. *Brown*, the number of independent brown bear photos at each camera per week, was included in black bear models. We ran all possible additive models, and tested several 2-way interactions based on *a-priori* hypotheses. Interactions between *Habitat* and the two human use covariates (*HumanUse* and *HumanActivity*) tested the hypothesis that human use, which was generally concentrated along shores, would displace wildlife inland. To understand if detections were impacted by human use differentially among seasons or years, we included interactions between *HumanActivity* and *Season*, and *HumanActivity* and *Year*. Additionally, the interaction between *Brown* and *Habitat* was included to test for habitat-dependent responses of black bears to the presence of brown bears. We selected the top model for each species based on AICc, and if there were multiple top models within 2 Δ AICc of each other, the model with the fewest parameters was chosen as the top model (Supplementary Material A, Table S2.1). The total model set consisted of 210 models for brown bears and moose, and 878 models for black bears. Due to the relative sparseness of wolf detections, models with more than 5 parameters appeared to be over-parameterized, and as such only models with a maximum of 5 parameters were considered, including the same interactions as described above, leading to a total of 15 models for wolves.

Table 2.2: Description of covariates on detection and occupancy probabilities used in occupancy models. The “Brown” covariate was included in black bear models only.

| Covariate | Definition | Type | Range |
|----------------------|--|-------------|---------------|
| Occupancy (ψ) | | | |
| DBH | Average tree diameter at breast height (cm) | Continuous | 0.0 - 53.8 |
| Detection (p) | | | |
| Use | Site designated as a "high-use" area or not | Categorical | Y, N |
| Year | Which year data is from | Categorical | 2017, 2018 |
| Season | First half of summer season or second half of summer season. Corresponds to switching of treatment/control | Categorical | Early, Late |
| Habitat | Shore or inland | Categorical | Shore, Inland |
| HumanActivity | “Human minutes” of activity/week | Continuous | 0.0 – 180.5 |
| Brown | Number of independent brown bear photos per week | Integer | 0 - 8 |

Because substantial variation in the amount of human use was not accounted for by the binary human use management designation for each site, and because restrictions were not always adhered to, we calculated a continuous index of human use intensity based on the camera data. This *HumanActivity* covariate was calculated by summing the number of humans detected by each camera during each sampling week. Since each photo represented a second, the number of humans was then divided by 60, creating an index of the minutes of human activity per week at each camera station. Additionally, to determine the efficacy of the management designations, a paired t-test was conducted to compare *HumanActivity* levels across *HumanUse* treatments.

Threshold levels of human activity

Occupancy models assume logit-linear relationships between predictors and response variables, and could therefore not be used to identify threshold levels of human activity that altered wildlife detections. Likewise, statistical methods for threshold detection (e.g., broken-stick regression) were not possible due to the zero-inflated nature of the data (Toms and

Lesperance 2003). We therefore visually examined plots of weekly detection rates for each species in relation to the *HumanActivity* values at each camera station to identify potential thresholds of human activity that resulted in marked changes in detection rates. Because our aim was to identify a threshold value of human activity that altered wildlife behavior in a “pristine” system, we separated the data into Bartlett Cove and non-Bartlett Cove sites. Bartlett Cove, the park headquarters site, had significantly higher human minutes per week than any other site in the park, and therefore represents an area more typical of higher visitation national parks in the United States.

RESULTS

A total of 183,012 photos of humans and wildlife were taken, including 154,444 photos of humans (84% of which were taken at Bartlett Cove, the most heavily used site in the park), 5,860 photos of brown bears, 3,452 photos of black bears, 6,927 photos of moose, and 570 photos of wolves. Other species such as coyotes (*Canis latrans*), red squirrels (*Tamiasciurus hudsonicus*), North American porcupines (*Erethizon dorsatum*), hoary marmots (*Marmota caligata*), North American river otters (*Lontra canadensis*), wolverines (*Gulo gulo*), and several species of birds were also detected.

Temporal Activity Patterns

Human activity in GLBA was diurnal, with highest activity in the mid-afternoon. Estimates of temporal activity overlap between high and low human use treatments ranged from 0.64 – 0.87 among the four target species, with moose having the largest differences (i.e., lowest overlap) in temporal patterns (Table 1.3, Figure 2.2c). The differences in activity in areas with high-use compared to low-use were significant for black bears (Figure 2.2b; overlap = 0.87, 95% CI = 0.81-0.94, $p < 0.05$) and moose (Figure 2.2c; overlap = 0.64, 95% CI = 0.52-0.73, $p <$

0.001). Moose activity patterns shifted from largely crepuscular in areas of low human use to more uniform activity throughout the day in areas of high human use. Black bear activity decreased in the afternoon when human activity was at its highest, and increased in the late evening as human activity was declining. Similar to black bears, brown bears tended to shift their activity towards a peak later in the evening during the high human use treatment (Figure 2.2a). Likewise, wolves tended to decrease their activity during the high-use treatment, with activity dropping to zero during times of highest human activity and increasing as human activity declined (Figure 2.2d).

Table 2.3: Activity overlap estimates for each species during high versus low human use treatments. Data were pooled across sites ($n = 10$) and years ($n = 2$) within the high and low-use treatments. Total detections indicates how many detections of each species were used to calculate the overlap estimates and Watson's test statistic. * indicates statistical significance ($p < 0.05$).

Spatial activity patterns

| Species | Overlap Estimate | Watson's Test Statistic | P-value | Total Detections |
|------------|--------------------|-------------------------|-----------|------------------|
| Brown Bear | 0.85 (0.79 - 0.91) | 0.0774 | > 0.10 | 419 |
| Black Bear | 0.87 (0.81 - 0.94) | 0.1982 | < 0.05 * | 420 |
| Moose | 0.64 (0.52 - 0.73) | 0.8375 | < 0.001 * | 232 |
| Wolf | 0.68 (0.50 - 0.82) | 0.1113 | > 0.10 | 69 |

Occupancy probabilities ranged from 0.70 (brown bears) to 0.31 (wolves), and occupancy of black bears and moose increased with increasing tree DBH (Table 2.4, Supplementary Material B Table S2.2). Only the black bear model included significant human-use related covariates. Except for black bears, detection probabilities generally declined as the number of human photos per week increased, though these linear trends were not statistically significant (Figure 2.3). Both brown and black bears had a higher likelihood of being detected in 2018 than 2017. Detection probabilities of brown bears and wolves were higher in shore than inland

habitat, and probabilities of detecting brown bears and moose were higher in early summer than late summer (Table 2.4). Black bear detection increased as human minutes per week increased, but was higher in areas designated as low-use. Humans did not appear to displace any of the focal species from shore to inland habitat, as indicated by the lack of support for models with an interaction between human use and habitat covariates (Table 2.4).

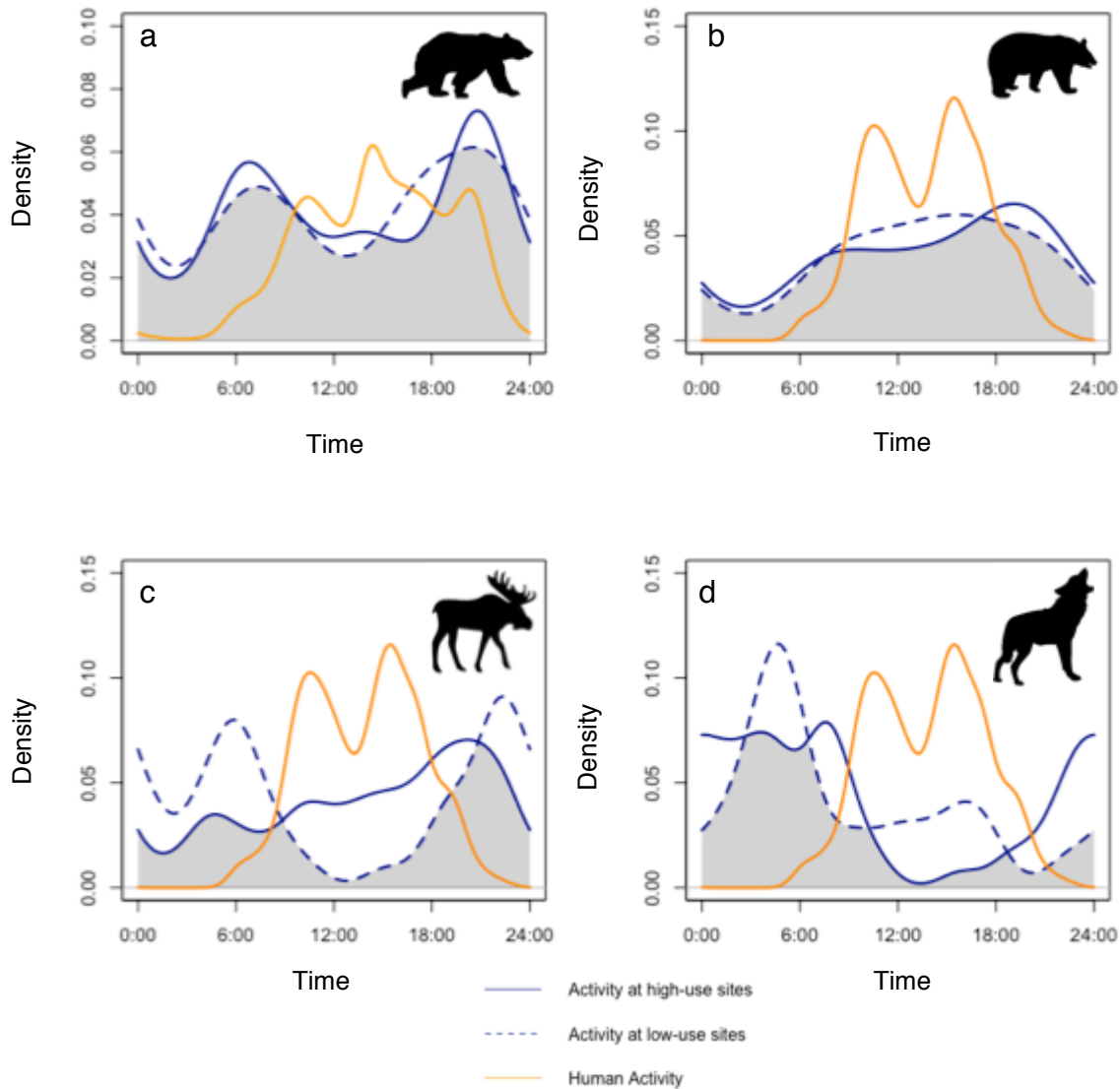


Figure 2.2: Temporal activity patterns of (a) brown bears, (b) black bears, (c) moose, and (d) wolves during high human use (dark blue dashed line) and low human use (dark blue line) treatments. Since not all wildlife species were detected at the same sites, human activity patterns (orange) were taken from the corresponding cameras that each species activity data was taken from.

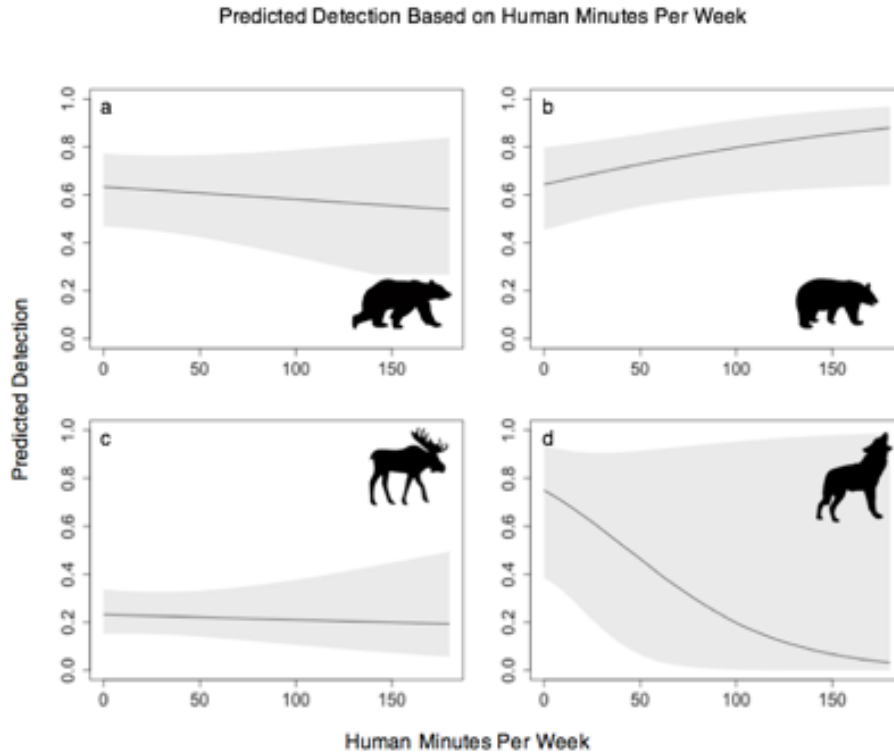


Figure 2.3: Predicted detection (and 95% confidence intervals) of brown bears (a), black bears (b), moose (c) and wolves (d) based on the number of human minutes per week. Only black bears significantly responded to this detection covariate.

The average number of human minutes per week at sites that were in a high-use treatment (mean = 9.655, SE = 1.189) was 24 times higher than sites that were in a low-use treatment (mean = 0.393, SE = 0.104), indicating that overall, the implementation of the high-use designation was successful (Figure 2.4; $t = 7.7$, $p < 0.001$). When excluding Bartlett Cove, which was the park headquarters site and an outlier, the average number of human minutes per week at the remaining high-use sites (mean = 1.421, SE = 0.189) was 3.6 times higher than at low-use sites. Two sites, South Sandy and Hunter Cove, had higher levels of human activity during the low human use treatment phase than the high human use treatment phase (Figure 2.4).

Table 2.4: Detection probabilities and 95% confidence intervals based on statistically significant covariates on detection from top model for each species. Occupancy probabilities and 95% confidence intervals were calculated based on either a null occupancy model (brown bear and wolf) or accounting for the impact of tree DBH (black bear and moose) on occupancy. Bolded detection probabilities indicate where an increase in detection was seen.

| Species | Factor | Coefficients | Occupancy (ψ) |
|------------|---------------------------|---------------------------|----------------------|
| Brown Bear | Habitat(Shore) | 0.49 (0.32 - 0.67) | 0.70 (0.60 - 0.78) |
| | Habitat(Inland) | 0.39 (0.25 - 0.54) | |
| | Year(2017) | 0.21 (0.15 - 0.30) | |
| | Year(2018) | 0.29 (0.20 - 0.41) | |
| | Season(Early) | 0.40 (0.30 - 0.50) | |
| | Season(Late) | 0.29 (0.20 - 0.41) | |
| Black Bear | Use(High) | 0.49 (0.29 - 0.69) | 0.40 (0.33 - 0.47) |
| | Use(Low) | 0.65 (0.49 - 0.78) | |
| | Year(2017) | 0.36 (0.22 - 0.52) | |
| | Year(2018) | 0.49 (0.29 - 0.69) | |
| | min(HumanActivity) | 0.48 (0.28 - 0.69) | |
| | max(HumanActivity) | 0.79 (0.54 - 0.92) | |
| | Season(Early) | 0.49 (0.29 - 0.69) | |
| | Season(Late) | 0.37 (0.17 - 0.62) | |
| Moose | Season(Early) | 0.29 (0.17 - 0.45) | 0.47 (0.37 - 0.56) |
| | Season(Late) | 0.19 (0.08 - 0.38) | |
| Wolf | Habitat(Shore) | 0.51 (0.29 - 0.72) | 0.31 (0.22 - 0.41) |
| | Habitat(Inland) | 0.247 (0.18 - 0.33) | |

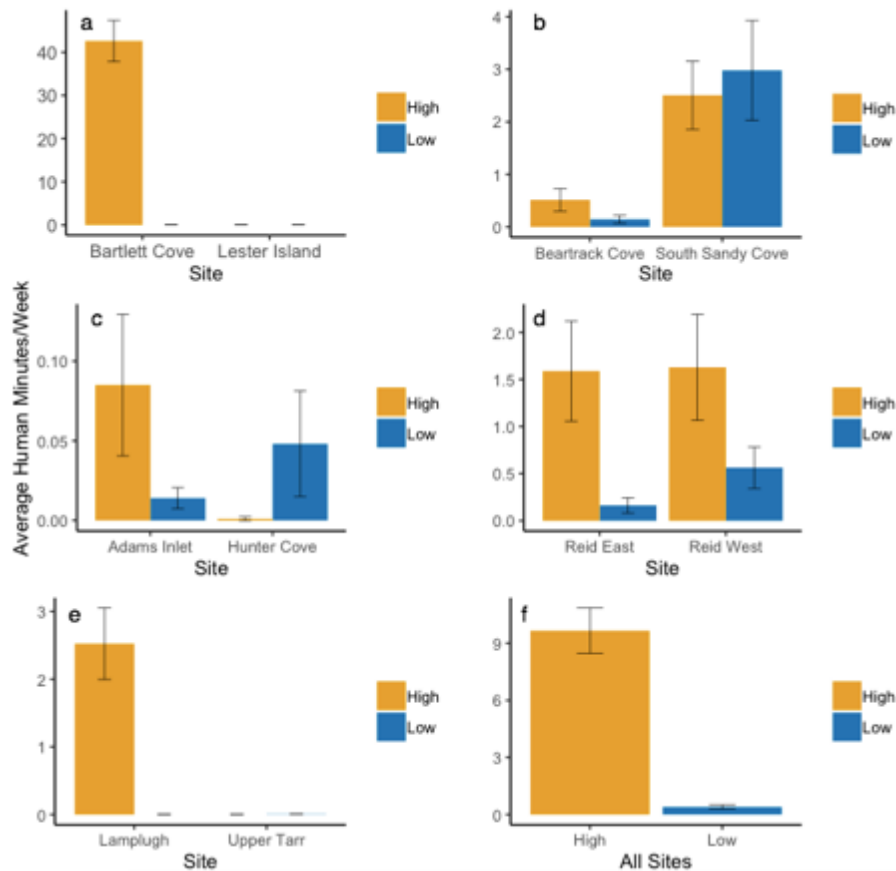


Figure 2.4: Average human minutes per week at (a) Bartlett Cove and Lester Island, (b) Beartrack Cove and South Sandy Cove, (c) Adams Inlet and Hunter Cove, (d) Reid East and Reid West, (e) Lamplugh and Upper Tarr, and (f) all sites combined when sites were in a high-use phase (orange), or low-use phase (blue). Error bars represent ± 1 SE.

Threshold Levels

The number of independent detections of each species ranged from 0-8 per week, and the level of human activity ranged from 0-181 minutes per week at each camera station (Figure 2.5). Detections of all species declined markedly as the level of human activity increased from 0-20 minutes per week (Figure 2.5). For all species, detections exceeded four per week only when there was no human activity at all. Wolves were not detected at any camera stations when human activity exceeded 20 minutes per week. Both species of bears showed some indication of

habituation to human presence, with moderate detection rates at the highest use Bartlett Cove site, whereas detections of moose were low and wolves were absent at this site (Figure 2.5).

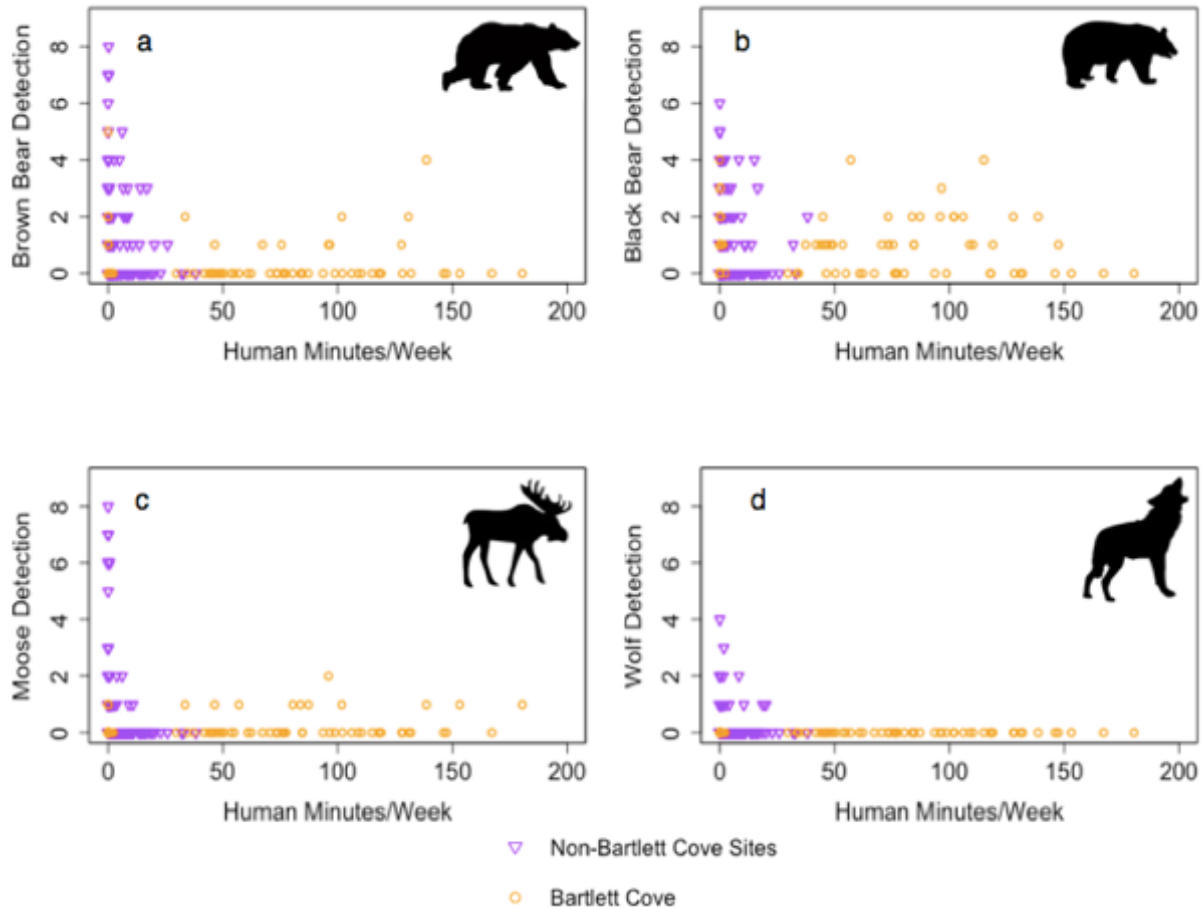


Figure 2.5: Influence of human activity on independent detection events of brown bears (a), black bears (a), moose (c), and wolves (d) per week at sites other than Bartlett Cove (purple) compared to Bartlett Cove (orange). Independent detection events were calculated by screening the remote camera data so that photographic events of the same species were considered independent events if they were separated by more than 30 minutes.

DISCUSSION

Wildlife responses to humans have been well documented in many systems around the world (e.g. Bruggeman et al. 2006, Berger 2007, Haroldson and Gunther 2013, Gunther et al. 2015, Sarmiento and Berger 2017). Protected areas are increasingly used to support such studies, as their landscapes are relatively untouched and populations of wildlife can exist with little

habitat disturbance (Stockwell et al. 1991, Borkowski et al. 2006, Bruggeman et al. 2006, Martin and Reale 2008, White et al. 2008, Longshore et al. 2013). Protected areas are essential for global conservation strategies, and tourism to these areas cultivates visitors' connections with the natural world that ultimately can promote conservation efforts (UNEP-WCMC and IUCN 2016). However, increased visitation to protected areas can be disruptive to wildlife. We have shown here that wildlife responses to humans are detectable even in a national park with few visitors, indicating that near complete restrictions on human activity in designated areas may be required for estimating true "baselines" regarding wildlife behavior and maintaining refuges where wildlife can persist without human impacts.

Of the four focal species in our study, wolves appear to be the most sensitive to human disturbance, avoiding humans during the midday hours and strongly avoiding areas of high human activity. While not statistically significant due to the low sample size of wolf detections, wolves shifted their activity patterns by 32% during high human use treatments (Figure 2d). Wolves are highly vagile, and while wolf harvest is not allowed in GLBA, negative experiences with humans outside of the park may cause them to be wary of humans inside the park. This is consistent with a study that found that wolf sightings decreased in both Yellowstone National Park and Denali National Park when wolves were harvested near park boundaries (Borg et al. 2016), and wolves have been shown to spatially avoid humans globally (Theuerkauf et al. 2003, Whittington et al. 2005, Kaartinen et al. 2005, Berger 2007, Karlsson et al. 2007, and Rogala et al. 2011). These non-consumptive impacts of humans on large carnivores like wolves can have cascading effects throughout ecosystems, likely due to top-down effects these animals have on their prey (Estes et al. 2011, Ripple et al. 2014, Kuijper et al. 2016). The absence of human related covariates in the top occupancy model for wolves does not necessarily indicate an

absence of human impact, because species that are most sensitive to humans may be the most difficult to demonstrate avoidance due to low detections (Gaynor et al. 2018). Wolves were not detected at all in the highest used site in GLBA (Figure 5d), which highlights their strong spatial avoidance of areas of high human activity. As such, we recommend that future studies examine detection data for nonlinearities in addition to conducting traditional occupancy modeling analyses.

Surprisingly, we did not detect a significant spatial or temporal response of brown bears to humans. Several studies have found that brown bears, especially males, avoid areas of high human use both spatially and temporally (Gibeau et al. 2002, Nevin and Gilbert 2005, Kaczensky, et al. 2006, Muhly et al. 2011, Oberosler et al. 2017). Lack of avoidance in our study may indicate that brown bears are habituated to people in GLBA. Wheat and Wilmers (2016) found that fear effects in brown bears were alleviated by habituation in southeast Alaska, while non-habituated bears showed fear-based avoidance behavior. Habituation of brown bears can lead to a reduction in escape responses (Smith et al. 2005, Geffroy et al. 2015), and brown bears can even habituate to olfactory, auditory and visual cues from humans (Nevin and Gilbert 2005). This is most likely to occur in protected areas, where the bears are protected from hunting and human activity is more controlled (Smith et al. 2005). Contrary to our wolf results, brown bears were detected at the highest used site in GLBA (Figure 2.5a), further indicating their potential habituation. Habituation may be a consequence of implementing land sparing management techniques and concentrating human use in certain parts of protected areas. This has been demonstrated in Denali National Park where visitor use is extremely concentrated in the frontcountry along the Denali Park road, and in Yellowstone and Grand Teton national parks where increasing levels of bear habituation in roadside habitat has been reported (Albert and

Bowyer 1991, Smith et al. 2005, Haroldson and Gunther 2013, Gunther et al. 2015). Managers of protected areas face the challenge of balancing the benefits of land sparing techniques with potential consequences of wildlife habituation, and more research is needed to better understand the level of human exposure at which wildlife habituation manifests.

Consistent with the human shield hypothesis, moose activity in GLBA shifted temporally to better align with human activity patterns during high-use treatments (Figure 2.2c), indicating that moose may have been using tourists as a temporal buffer against predation from bears and wolves. Similar temporal partitioning of ungulate activity was reported in Eurasian roe deer (*Capreolus capreolus*) (Thorsen 2016). Our results are in contrast to a meta-analysis that found significant increases in nocturnality in response to humans across a wide range of mammal species, which was particularly pronounced in herbivores (Gaynor et al. 2018). A temporal human shield is difficult to demonstrate using observational studies, because differences in temporal activity patterns between wildlife and humans or predators and prey may be due to natural differences in diel cycles rather than avoidance or attraction responses. Our experimental cross-over design removed the influence of potentially confounding site-specific effects and controlled for natural diel patterns, which allowed us to rigorously assess the influence of human activity on temporal activity patterns of wildlife. Additional experimental studies are needed to determine how widespread the use of humans as a temporal shield may be among prey species.

We found that moose did not use humans as a shield spatially, despite use of a temporal shield and in contrast to findings from other studies of ungulates such as elk (*Cervus elaphus*) (Hebblewhite et al. 2005, Rogala et al. 2011), moose (Stephens and Peterson 1984, Berger 2007), mountain goats (Sarmiento and Berger 2017), and mountain nyala (Atickem et al. 2014). As was the case for wolves in our study, detections of moose sharply declined at camera

sites when human activity levels increased above 15 minutes per week (Figure 2.5c). These contrasting patterns of temporal attraction and spatial avoidance may indicate substantial variation among individual moose in their responses to humans, whereby most individuals in low-use areas avoid humans, but those that do not may use their presence as a shield from predators. Over time, this process may lead to a habituated population, especially if increasing levels of human activity strengthen selection for bolder individuals. There was a slight increase in detection of moose at the highest use site in the park (Bartlett Cove), indicating potential habituation (Figure 5c). Individual variation in “boldness” or “shyness” in wildlife plays a large role in species’ abilities to cope with human disturbances (Sih et al. 2011), especially in protected areas where recurring benign encounters with humans can facilitate habituation (Thompson and Henderson 1998, Found and St. Claire 2016, Found 2019) and prey species may exploit these areas as predation refugia (Laundre et al. 2001). Individual variation in activity patterns of large mammals are rarely quantified, however, and these individual patterns could be correlated with boldness (Hertel et al. 2017). Individual adaptive behavioral strategies can have important implications for population persistence (Refsnider and Janzen 2012, Hertel et al. 2017), further highlighting the importance of understanding individual variation in response behavior. Analysis of individual variation in diel patterns and boldness behavior among individuals, facilitated by GPS tracking technology, would shed new light on the mechanisms by which wildlife responses to humans can change over time.

As with moose, the temporal and spatial responses of black bears to humans were opposing, but in the reverse direction: black bears avoided humans temporally and were positively associated with humans spatially, suggesting that black bears may seek spatial refuge from predation in GLBA. These contrasting results of both black bears and moose demonstrate

the importance of considering both spatial and temporal aspects of wildlife responses to disturbances. Bateman and Flemming (2017) found that only 5% of studies of wildlife and tourism had a spatial and temporal design, but our findings indicate that human impacts could be underestimated if spatial or temporal responses are not examined. While the *Brown* covariate was not included in the top black bear occupancy model, detection of black bears tended to decrease with increasing number of independent photos of brown bears, suggesting avoidance of brown bears by black bears may have motivated their use of humans as a shield. These findings are consistent with other studies that found that black bears attempt to avoid brown bears (Holm et al. 1999, Apps et al. 2006, Lewis 2012), and a study in coastal British Columbia found that black bears avoided areas with high brown bear occurrence and humans potentially offered a degree of protection from predation (MacHutchon et al. 1998). Additionally, visual inspection of detection data for black bears shows an increase in detections of black bears in the highest used site in the park (Figure 2.5b), potentially indicating a shift to habituation when exposed to more constant human activity. Black bears thus appeared to behave like mesopredators spatially, using humans as a shield to protect against predation, but their temporal avoidance of humans is more consistent with behavior of apex predators. Ayres et al. (1986), MacHutchon et al. (1998), and Reimchen (1998) similarly found that black bears that are typically diurnal may become nocturnal in response to humans.

The imperfect application of the human use treatment in this study highlights the challenge of using an experimental approach in wildlife studies. Most studies that investigate the response of wildlife to tourism are observational, and a unique strength of this study was the experimental manipulation of human use in GLBA with a crossover design. The ability to control tourism in a protected area is a powerful tool, but can be difficult to enforce even with

low human use as in GLBA. For example, there were contradictory findings within our spatial activity results for black bears resulting from imperfect application of the human-use treatment. While tour vessels were mandated by the park to follow the high-use designations laid out by this study, charter vessels do not fall under the same category and were not obliged to follow these designations. These are smaller vessels that operate in GLBA and also provide shore excursion opportunities for tourists. Charter vessel drop-offs at two of our sites (site 3 and 4) led to similar levels of human use during high and low-use treatments, and these sites were both frequented by black bears. When this was accounted for in the occupancy models for black bears, contradictory results were no longer detected, and detection of black bears increased with both increasing human activity, and in high-use areas (Appendix Table S2.4). Overall, however, human activity at high-use areas was more than three times higher than at low-use areas, illustrating that the management designation was generally successful (Figure 2.4).

We recommend that protected area managers take advantage of their ability to dictate closures to facilitate the use of an experimental approach in future studies. This would allow for research to be conducted to test the impacts of human activity on wildlife experimentally and would increase potential spatial refugia for wildlife to escape from human disturbance. These refugia can be important for wildlife, especially in systems that are consistently perturbed by human activity like many protected areas are. Spatial refugia can be very important for prey species (Sergio et al. 2003, Grassel et al. 2015), and can help stabilize predator-prey dynamics and enhance stability of a system (McNair 1986, Gonzalez-Olivares and Ramos-Jiliberto 2003, Goldberg et al. 2014). In protected areas where humans can act as “super predators”, these refugia could be important for all wildlife, as it’s been shown that animals often select protected microhabitats in areas of human disturbance (Dupke et a. 2016). This is especially true if human

use is relatively constant and intense and wildlife respond in ways consistent with the “risk disturbance hypothesis” (Frid and Dill 2002) where disturbance stimuli are analogous to predation risk. Creating spatial refugia by restricting visitor use to certain parts of protected areas, and redirecting it to other areas where potential impacts from visitors will be concentrated is a way in which national parks implement a “land sparing” strategy. The land sparing vs sharing debate is largely discussed in the context of agriculture and wildlife (Green et al. 2005, Fischer et al. 2008, Fisher et al. 2013), however the ideas behind the strategies can be applied in protected areas. The asymptotic relationship between human use and impact in protect areas implies that this concentration of visitor use to a limited number of sites ultimately results in lower overall impacts than a land sharing technique would produce (Leung and Marion 2000). While our study did not explicitly compare these strategies, our findings highlight that any amount of human activity can lead to a detectible response by wildlife. If protected area managers seek to provide refugia for wildlife with minimal impacts, and to maintain baseline controls that lack human impacts, our findings indicate that a land sparing strategy is needed.

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SUPPLEMENTARY MATERIAL A

Table S2.1: AIC table for top models for each species, including the number of parameters (K), AICc values, Δ AICc values, and AICc weight values. All models with a Δ AICc < 2 are shown. A “.” occupancy covariate indicates an intercept only model. Bolded models with a “*” indicate most parsimonious models based on Δ AIC and number of parameters.

| Model | K | AICc | Δ AICc | AICcWt |
|---|----------|-----------------|---------------|--------------|
| Brown Bears | | | | |
| $p(\text{Habitat} + \text{Season} + \text{Year}) \psi(.)$ * | 5 | 1047.767 | 0.000 | 0.031 |
| $p(\text{Use} + \text{Habitat} + \text{Season} + \text{Year}) \psi(.)$ | 6 | 1048.917 | 1.151 | 0.017 |
| $p(\text{Habitat} + \text{Season} + \text{HumanActivity} + \text{HumanActivity} * \text{Year}) \psi(.)$ | 7 | 1049.150 | 1.383 | 0.015 |
| $p(\text{Habitat} + \text{Season} + \text{Year} + \text{HumanActivity}) \psi(.)$ | 7 | 1049.178 | 1.383 | 0.015 |
| Black Bears | | | | |
| $p(\text{Use} + \text{Season} + \text{Year} + \text{HumanActivity}) \psi(\text{DBH})$ * | 7 | 715.629 | 0.000 | 0.013 |
| $p(\text{Use} + \text{Season} + \text{Year} + \text{HumanActivity} + \text{Brown}) \psi(\text{DBH})$ | 8 | 716.213 | 0.584 | 0.010 |
| $p(\text{Use} + \text{Season} + \text{Year} + \text{HumanActivity} + \text{HumanActivity} * \text{Season}) \psi(\text{DBH})$ | 8 | 715.052 | 1.423 | 0.007 |
| $p(\text{Use} + \text{Season} + \text{Year} + \text{HumanActivity} + \text{Brown} + \text{HumanActivity} * \text{Season}) \psi(\text{DBH})$ | 9 | 717.550 | 1.921 | 0.005 |
| Moose | | | | |
| $p(\text{Habitat} + \text{Season}) \psi(\text{DBH})$ | 5 | 675.212 | 0.000 | 0.032 |
| $p(\text{Season}) \psi(\text{DBH})$ | 4 | 675.438 | 0.225 | 0.028 |
| $p(\text{Habitat} + \text{Season} + \text{Year}) \psi(\text{DBH})$ | 6 | 676.156 | 0.943 | 0.020 |
| $p(\text{Habitat} + \text{Season} + \text{HumanActivity} + \text{HumanActivity} * \text{Habitat}) \psi(\text{DBH})$ | 7 | 676.219 | 1.006 | 0.019 |
| $p(\text{Season} + \text{Year}) \psi(\text{DBH})$ | 5 | 676.456 | 1.243 | 0.017 |
| $p(\text{Season} + \text{Year} + \text{HumanActivity} + \text{HumanActivity} * \text{Habitat}) \psi(\text{DBH})$ | 8 | 676.595 | 1.383 | 0.016 |
| Wolves | | | | |
| $p(\text{Habitat} + \text{Year}) \psi(.)$ | 4 | 374.32 | 0.000 | 0.351 |
| $p(\text{Use} + \text{Habitat}) \psi(.)$ | 4 | 375.06 | 0.730 | 0.243 |
| $p(\text{Habitat}) \psi(.)$ * | 3 | 375.62 | 1.290 | 0.184 |
| $p(\text{Habitat} + \text{HumanActivity}) \psi(.)$ | 4 | 376.16 | 1.840 | 0.140 |

Table S2.2: Top occupancy models for each species with estimates, standard errors and p-values of each covariate within the top occupancy model.

| Species | Process | Covariate | Estimate | SE | P-value |
|-------------|----------------|----------------|----------|--------|---------|
| Brown Bears | Occupancy | Intercept | 0.824 | 0.2120 | 0.0001 |
| | | Detection | | | |
| | Detection | Intercept | -0.854 | 0.2100 | <0.0001 |
| | | Habitat(Shore) | 0.447 | 0.1900 | 0.0188 |
| | | Season(Late) | -0.455 | 0.1780 | 0.0107 |
| | Year(2018) | 0.424 | 0.1820 | 0.0199 | |
| Black Bears | Occupancy | Intercept | -0.409 | 0.1790 | 0.0223 |
| | | DBH | 0.876 | 0.1890 | <0.0001 |
| | Detection | Intercept | 0.715 | 0.2471 | 0.0038 |
| | | Use(High) | -0.659 | 0.2321 | 0.0045 |
| | | Season(Late) | -0.502 | 0.2229 | 0.0242 |
| | | Year(2018) | 0.536 | 0.2193 | 0.0146 |
| | | HumanActivity | 0.169 | 0.0823 | 0.0400 |
| | | | | | |
| Moose | Occupancy | Intercept | -0.194 | 0.2150 | 0.3660 |
| | | DBH | 0.532 | 0.2050 | 0.0095 |
| | Detection | Intercept | -0.691 | 0.1500 | <.0001 |
| | | Season(Late) | -0.531 | 0.2840 | 0.0617 |
| Wolf | Occupancy | Intercept | -0.811 | 0.2660 | 0.0023 |
| | | Detection | | | |
| | | Intercept | -2.250 | 0.3440 | <0.0001 |
| | Habitat(Shore) | 1.130 | 0.3930 | 0.0039 | |

Table S2.3: Black bear top occupancy model re-ran with the human use designation (high vs low) switched for Beartrack Cove and Sandy Cove. The bolded row shows how the estimate switches from negative to positive when the model is re-ran, which remedies the contradictory results between the impact of human use designation and human activity found in the original black bear top model.

| Species | Process | Covariate | Estimate | SE | P-value |
|-------------|-----------|------------------|--------------|---------------|---------------|
| Black Bears | | | | | |
| | Occupancy | | | | |
| | | Intercept | -0.416 | 0.1780 | 0.0196 |
| | | DBH | 0.870 | 0.1880 | <0.0001 |
| | Detection | | | | |
| | | Intercept | 0.233 | 0.2428 | 0.3369 |
| | | Use(High) | 0.202 | 0.2301 | 0.3798 |
| | | Season(Late) | -0.446 | 0.2182 | 0.0409 |
| | | Year(2018) | 0.586 | 0.2167 | 0.0068 |
| | | HumanActivity | 0.067 | 0.0808 | 0.4085 |

CHAPTER 3

Successional patterns of terrestrial mammals following glacial recession

ABSTRACT: Disturbance is a key driver of community assembly and patterns of diversity. As climate change increases the frequency and severity of natural disturbances, it is important to understand how biotic communities will respond. While successional changes in vegetation have been well studied, post-disturbance successional patterns of wildlife communities remain poorly understood. Here, we investigated the roles of habitat and time-since-disturbance in shaping community assembly and the diversity of terrestrial mammals in Glacier Bay National Park, Alaska (GLBA), which has undergone the most rapid and extensive deglaciation in the world since the Little Ice Age. We used camera traps, small mammal trapping and vegetation surveys to investigate the patterns of mammalian succession following deglaciation during summers 2017 and 2018 ($n = 10$ sites). If environmental filtering is the dominant factor controlling community assembly following disturbance, we expected habitat characteristics to have the strongest impact. In contrast, if dispersal ability is the dominant factor, we expected time-since-disturbance to be the dominant driver of assembly and diversity patterns. Both PERMANOVA and beta diversity analyses indicated that mammal communities were more strongly influenced by time-since-disturbance than habitat. Thus, our findings indicate that dispersal abilities of mammals have a strong influence on colonization patterns, and mammalian succession does not necessarily track plant succession. Additionally, community nestedness in species with high dispersal ability was higher than low dispersal ability species, further highlighting the strong impact of vagility on mammal diversity patterns. Our results highlight the importance of incorporating landscape connectivity and dispersal ability metrics into wildlife conservation efforts

following disturbances. This knowledge may improve predictions of mammalian community assembly following major disturbance events.

INTRODUCTION

Disturbance is a fundamental process controlling diversity (Huston, 1979; Huston, 1994). Disturbances are defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment” (White and Pickett, 1985). Increasing climatic variability can trigger natural disturbances, and there is widespread agreement that climate change will increase the magnitude and frequency of these events (Easterling et al., 2000; Sergio et al., 2018). As such, it is imperative to understand how biotic communities respond to disturbances (Hu et al., 2013; Sergio et al., 2018). When the magnitude of disturbance events is so high that diversity of a region is reduced significantly, the starting point for community assembly processes is essentially reset (Turner et al., 1998). Understanding community succession is fundamental to the study of ecology (Cowles, 1901; Cowles, 1911; Clements, 1916; Gleason, 1917; Cooper, 1913), and studies can utilize these disturbances to investigate their impact on community assembly and diversity. There is a long history of research on vegetation succession, but animal succession has not been as widely studied (Monamy and Fox, 2010; Lessard, 2019).

The importance of habitat suitability for sustaining wildlife populations has been long recognized in ecology (Pickett and White, 1985; Sousa, 1984; Wood and del Moral, 1987). Habitat metrics are often used as a surrogate for changes in wildlife assemblages following disturbances (Barton et al., 2014), and models of wildlife distribution following disturbances often assume uniform rates of recolonization (Mutz et al., 2017). For example, the habitat accommodation model (HAM; Fox, 1982) of animal succession proposes that wildlife species

appear on a landscape undergoing successional change when the vegetation community reaches a threshold of habitat suitable for that species. This indicates that animal succession does not follow time-since-disturbance per se, but rather follows changes in vegetation (Fox et al., 2003). The HAM is built on the successional mechanisms of facilitation, tolerance and inhibition (Connell and Slatyer, 1977), and it has been used to demonstrate that small mammal succession was related to vegetation density rather than time-since-disturbance in fire-prone systems (Monamy and Fox, 2000; Monamy and Fox, 2010). However, changes in wildlife communities may not directly track changes in vegetation if there are barriers to wildlife movement or if species have limited dispersal ability (Greve et al., 2005). If dispersal ability is a key process in vertebrate succession, then time-since-disturbance should be more influential than habitat. In contrast, if filtering of species based on habitat requirements is the key process, then habitat should be more influential. Thus, quantifying the relative importance of these key factors is needed to gain a better understanding of processes driving post-disturbance wildlife community assembly.

Impacts of disturbances on community assembly can strongly influence patterns of beta diversity (between-community diversity). There are contrasting views as to how beta diversity is shaped by disturbances, however. Some studies have demonstrated that disturbances increase similarity between communities, reducing beta diversity (Inouye and Tilman, 1995; Chase, 2003a; Chase, 2007), while others have shown an increase in beta diversity following disturbance (Christensen and Peet, 1984; Vanschoenwinkel et al., 2013). Dispersal rates can influence the directional change of beta diversity following disturbances, and wildlife population persistence and community structure depends on the rate of recovery post-disturbance (Vanschoenwinkel et al., 2013; Myer et al., 2015; Mutz et al., 2017). Ultimately, beta diversity

reflects two different biological phenomena, community nestedness and spatial species turnover (Baselga, 2010). Nestedness results from the sequential elimination or addition of species such that relatively species-poor assemblages are subsets of the richest assemblage (Baselga and Orme, 2012; Han et al., 2018), and the extent of nestedness varies with dispersal ability (Lomolino, 1996; Greve et al., 2005). Alternatively, spatial species turnover, or species replacement between sites, occurs when species in one site are substituted by different species in other sites. Turnover reflects an ecological sorting mechanism whereby species are “filtered” by local environmental conditions (Svenning et al., 2011). Understanding the relative contribution of both nestedness and turnover to overall beta diversity is a key component in community dynamics following disturbances (Svenning et al., 2011).

Massive ice sheets have repeatedly advanced and retreated through history, having tremendous effects on landscapes and species composition, and glacial recession is a natural disturbance that is accelerating due to climate change. The exposure of new terrain following glacial recession facilitates plant and animal colonization (Barry, 2006), and many studies have examined the impact of deglaciation on plant community succession (Cooper, 1931; Cooper, 1939; Lawrence, 1958; Decker, 1966; Lawrence et al., 1967; Reiners et al., 1971; Lawrence, 1979). Svenning et al. (2011) investigated the impact of the Pleistocene glaciations on the beta diversity of mammals in Europe, but little is known about successional patterns of higher vertebrates in response to present-day glacial recession. In this paper, we used remote cameras, small mammal live-trapping, and vegetation surveys to investigate the roles of time-since-disturbance and habitat in determining successional patterns of terrestrial mammals in Glacier Bay National Park (GLBA) following glacial recession.

GLBA has undergone the most rapid and extensive deglaciation in the world since the

Little Ice Age (LIA; Kohls et al., 2003). Over the last 100 years, the chronosequence at GLBA has become one of the most intensely studied of its kind (Bormann and Sidle, 1990): soil development (Crocker and Major, 1955; Goldthwait et al., 1966), plant succession (Cooper, 1931; Copper, 1939; Lawrence, 1958; Lawrence et al., 1967; Reiners et al., 1971; Lawrence, 1979; Chapin et al., 1994), and stream successional patterns (Milner et al., 2000; Milner et al., 2007) have been widely studied in GLBA. Milner et al. (2000) found the colonization and succession of the fish community in GLBA were strongly related to stream age, and that the number of microcrustaceans and macroinvertebrate taxa, and juvenile fish abundance and diversity were significantly greater in older streams. The more rapid retreat of glaciers in the west arm of GLBA and variation in habitat connectivity and seed sources has resulted in different patterns of plant succession between the west and east arms (Buma et al., 2017). Thus, GLBA provides a unique opportunity to tease apart habitat from time-since-disturbance as drivers of community assembly, because these factors are not inherently correlated in GLBA as they often are in studies of succession.

If environmental filtering is the dominant driver of mammalian community assembly following disturbance, we expected assemblages to mirror successional patterns of the vegetation and for observed turnover to explain a larger proportion of total beta diversity than expected by random chance. If dispersal ability is instead the dominant driver, then we expected time-since-disturbance to have the strongest effects on species composition, and nestedness to explain a larger proportion of total beta diversity than expected. In addition, we expected that species with greater dispersal ability, such as large mammals, to have low beta diversity across GLBA through dispersal-driven homogenization (Vanschoenwinkel et al., 2013). Likewise, we expected the small mammal guild, which has relatively low dispersal ability, to have higher beta diversity.

STUDY AREA

Glacier Bay National Park and Preserve in southeast Alaska is a 100km long marine fjord surrounded by mountains, glaciers, ice fields, and rainforests (Figure 3.1). It has a maritime climate, with average summer temperatures between 10-15° C and annual average rainfall of 177 cm. The 120km recession of Grand Pacific Glacier in GLBA took place in less than 160 years (Fastie, 1995; Mann and Streveler, 2008), and when Grand Pacific reached Tlingit Point, it split into Grand Pacific Glacier and Muir Glacier (Figure 3.1), forming an east and west arm of the bay. Deglaciation allowed for the recolonization of the area by plants and animals, and there are 29 known terrestrial mammalian species that have recolonized at least part of the park (Taylor, 1984). Ten sites across GLBA were selected to span a gradient of time-since-deglaciation in both arms of the park (Figure 3.1). Sites needed to be accessible by boat, and habitat away from shore needed to be accessible by foot.

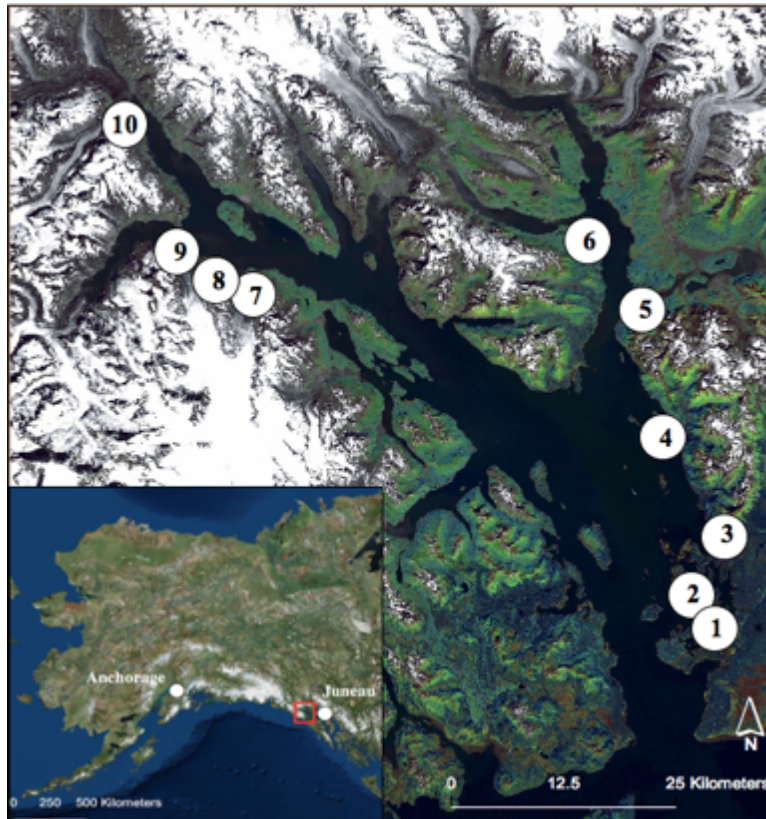


Figure 3.1: Location of Glacier Bay National Park, AK. White numbered circles represent study sites described in Table 1. The horizontally striped triangle represents Grand Pacific Glacier, the glacier that deglaciated sites 1-4 and 7-10, and the vertically striped triangle represents Muir Glacier, the glacier that deglaciated sites 5-6. The two glaciers split at Tlingit Point, represented by the star.

METHODS

Data collection

Vegetation surveys

We conducted vegetation surveys at the small mammal trapping grids in shore habitat and inland habitat at each site during 2018. Ten 1 m² plots were surveyed at each site, and plots were spaced approximately 10 m apart along the diagonal of the small mammal trapping grid (Figure S3.1). Overall configuration of the vegetation survey plots differed depending on accessibility of habitat. We recorded percent cover of understory vegetation and identified plants to species when possible, otherwise they were identified following Viereck et al. (1992).

Understory vegetation at each site was grouped into 7 categories: bare ground, low scrub, tall scrub, dwarf scrub, graminoid-herbaceous, forb-herbaceous and bryoid-herbaceous (Viereck et al. 1992), then we averaged percent cover for each category across all ten plots. We measured canopy cover in the inland habitat of each site by taking 4 densiometer readings per 1m² plot and averaging canopy cover at each site (n = 40 per site). We measured tree diameter at breast height (DBH) of the 4 closest trees to each plot, and average basal area (BA, m²) for each site was calculated by averaging all BA measurements for all trees surveyed at each site (n = 40 per site).

Small mammal trapping

We conducted small mammal trapping on two grids at each site using 50 large and 50 small folding Sherman traps (Model LFA; 3 x 3.5 x 9" and 2 x 2.5 x 6.5") per grid, with traps placed 10m apart in as close to a grid formation as the landscape allowed (Figure S3.1). Grids were approximately 0.5 km apart, and one grid was placed in inland habitat (approximately 0.5

km away from the shore) and one grid was placed in shore habitat at each site. Traps were baited using bird seed, oats, apples, dried mealworms and cotton batting. Trapping sessions lasted for three days and two nights, with traps left open and checked each morning and evening. Captured individuals were weighed, measured, identified to species and sex, and marked with a Sharpie on their back near the base of the tail, as well as the inside of the ear when possible. We calculated the Minimum Number Alive (MNA; Krebs, 1966) for each species as an index of population size and summed the MNA across both habitat types for each site to obtain a site-level estimate of species richness and diversity.

Camera trapping

We installed four cameras (Reconyx HC600 Hyperfire Covert IR) at each site, for a total of 40 remote camera installations. Two cameras were installed in shoreline habitat and two cameras were installed in inland habitat. All cameras were approximately 0.5 km away from one another, forming as close to a square grid at each site as the landscape allowed. Cameras were set to take 3 photos every time they were triggered, with a “RapidFire” setting to reduce the time between photos to one second. Cameras were set up at a height of approximately 0.5 m above the ground. We placed cameras along game trails (where available), or in expected areas of wildlife concentration, to maximize detection. We checked the cameras approximately every 3 weeks throughout the field season (June 1- September 1 of 2017 and 2018) to ensure cameras were working properly, download photograph data, and perform any required maintenance (Hernández-SaintMartín et al., 2013; Goad et al.; 2014).

We processed photos using the Timelapse2 software (Greenberg and Godin; 2015), identifying individuals detected to species for each photo. We screened photos to remove

photographic events of the same species at a camera that were taken less than 30 minutes apart (Carter, 2012). This was done for each camera at each site, then values of independent events for each species were summed between the four cameras to calculate species richness and diversity at each site.

Statistical analysis

Vegetation community analysis

To understand the structure of the vegetation communities, we focused on the data from the inland vegetation surveys. The shore habitat was subject to frequent disturbance via tidal fluctuations and was considered “edge” habitat, and therefore the inland habitat was more representative of the post-glacial vegetation community at each site. To identify potential successional stages, we performed an agglomerative hierarchical cluster analysis using Ward’s linkage in which observations were grouped to maximize similarity. The data were relativized by species maxima to allow for all species to contribute equally to differences between plots, and we used a Bray-Curtis distance measure. We used a Similarity Profile Analysis (SIMPROF; Clarke et al., 2008) in the R package “clustsig” (Whitaker and Christman, 2014; Version 1.1) to determine the number of significant clusters produced from the cluster analysis.

Principal Component Analysis and PERMANOVA

Because of the small sample size (10 sites), and the large number of potentially correlated age-related and habitat-related variables, we used Principal Component Analysis (PCA) to express these variables in a smaller number of uncorrelated dimensions variables (Table 3.1, Table 3.2). The PCA was performed on the correlation matrix of the variables, and we focused on the principal components that together explained more than 75% of the variance (Borcard et al., 2018). We then tested the influence of each selected principal component from the PCA on

the mammalian community as a whole, and their impact on good and poor dispersers (see below) using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). This procedure provides a multivariate equivalent to the F-ratio and a p-value based on permutations (Newman et al. 2014).

Table 3.1: Characteristics of site location for each site in GLBA. Site numbers correspond to Figure 1. *DistanceGlacier* represents the distance (km) to the glacier that deglaciated each site (Grand Pacific in the west arm, and Muir in the east arm; Figure 1). *DistanceMouth* represents the distance (km) of each site to the mouth of Glacier Bay. *Age* represents the year of site deglaciation determined from maps provided by the National Park Service.

| Site # | Site Name | Easting | Northing | DistanceGlacier | DistanceMouth | Age | Arm |
|--------|----------------|---------|----------|-----------------|---------------|------|-----|
| 1 | Bartlett Cove | 447413 | 6478484 | 72.42 | 13.36 | 1800 | E |
| 2 | Lester Island | 449123 | 6480711 | 69.54 | 15.60 | 1810 | E |
| 3 | Beartrack Cove | 451084 | 6495758 | 62.43 | 25.72 | 1830 | E |
| 4 | South Sandy | 443038 | 6509206 | 48.30 | 36.52 | 1860 | E |
| 5 | Adams Inlet | 439723 | 6524048 | 34.22 | 51.55 | 1900 | E |
| 6 | Hunter Cove | 434970 | 6531360 | 25.00 | 59.93 | 1900 | E |
| 7 | Reid East | 395729 | 6523717 | 27.56 | 71.35 | 1870 | W |
| 8 | Reid West | 394833 | 6525799 | 25.79 | 73.01 | 1870 | W |
| 9 | Lamplugh | 389140 | 6530393 | 20.09 | 79.47 | 1900 | W |
| 10 | Upper Tarr | 382799 | 6544135 | 4.56 | 94.20 | 1910 | W |

Table 3.2: Characteristics of habitat for each site in GLBA based on 10 vegetation plot surveys per site. Site numbers correspond to Figure 1 and Table 1. Percent cover of vegetation in 7 categories following Viereck et al. (1992) are listed, where BG = bare ground, LS = low scrub, DS = dwarf scrub, GH = graminoid-herbaceous, FH = forb-herbaceous, BH = bryoid-herbaceous, and TS = tall scrub. Total cover of each site, average basal area of trees and the standard deviation, and average canopy cover and standard deviation of each site are also listed.

| Site # | BG | LS | DS | GH | FH | BH | TS | TotalCover | MeanBA | CanopyCover |
|--------|------|------|------|------|------|------|-----|------------|--------------|---------------|
| 1 | 0 | 65.6 | 0 | 0.6 | 11 | 86.9 | 0 | 157.5 | 0.20 (0.16) | 89.73 (10.85) |
| 2 | 0 | 23.5 | 0 | 9.6 | 7.4 | 92.8 | 0.5 | 143 | 0.06 (0.07) | 90.85 (4.92) |
| 3 | 0 | 3.5 | 0 | 7.5 | 0 | 99.1 | 0 | 111.2 | 0.10 (0.08) | 90.30 (2.94) |
| 4 | 0 | 0 | 0 | 2.6 | 2.7 | 99.8 | 0 | 107.8 | 0.08 (0.06) | 94.49 (2.14) |
| 5 | 0 | 0 | 0 | 5 | 12.8 | 78.8 | 0 | 103.9 | 0.24 (0.11) | 90.51 (4.88) |
| 6 | 8 | 31.5 | 0 | 14.5 | 2.1 | 66.7 | 0 | 125.2 | 0.14 (0.15) | 86.56 (8.60) |
| 7 | 18 | 50.9 | 22 | 9 | 0 | 27.5 | 2.5 | 132.9 | 0.00 (0.00) | 0.00 (0.00) |
| 8 | 1 | 81 | 13.5 | 2.5 | 7.5 | 71 | 0 | 182.5 | 0.00 (0.00) | 0.00 (0.00) |
| 9 | 6 | 54.5 | 0 | 12.1 | 31.6 | 11.5 | 0 | 109.7 | 0.00 (0.00) | 0.00 (0.00) |
| 10 | 15.5 | 6 | 22.9 | 8.3 | 3.6 | 35.5 | 44 | 138.8 | 0.01 (0.002) | 95.97 (23.84) |

Mammal community analysis

Data from camera traps and small mammal traps were combined to analyze the mammal community as a whole at each of the 10 study sites. The data were relativized by species maxima and we used a Euclidean distance measure. To determine whether the mammal community composition matched vegetation community groupings, we conducted a cluster analysis on the mammal data using Ward's linkage and compared the dendrograms from the vegetation data and the mammal data. We used a tanglegram in package "dendextend" (Galili, 2015; Version 1.9.0) to determine if similar sites were grouping together in similar ways. If the vegetation and mammal communities followed the same successional patterns, the cluster dendrograms would be mirror images of each other. If they were different, the lines connecting equivalent nodes (sites) would become increasingly tangled.

We separated mammalian species into two dispersal ability categories: high dispersal ability (hereafter, "good dispersers") and low dispersal ability (hereafter, "poor dispersers") based on their body mass, as dispersal ability is proportional to body mass (Lindstedt et al., 1986; Table 3.3). We used body mass as a proxy for dispersal ability due to lack of information on dispersal distances for some of our study species. We ran a correlation between the log-transformed measures of body mass and home range size for each species (Jones et al. 2009) to determine how well body size correlates with movement ability, and found an R value of 0.90. Additionally, we examined how sensitive the dispersal results of all analyses were by varying the cutoff of body mass that dictated which species were considered good or poor dispersers from 10,000g to 200g, and the qualitative results were unchanged (Table S3.1). Thus, we used body mass for all further analyses, and species with an average body mass of greater than 8,000g were

categorized as good dispersers, and those with an average body mass of less than 8,000g were categorized as poor dispersers.

Table 3.3: Species scientific names, common names and average body mass for all mammals captured on cameras or in small mammal traps. Mammals were separated into two categories based on body mass: <8,000g (poor dispersers) and ≥8,000g (good dispersers). Average body mass for small mammals was calculated based on the species we caught, and average body mass for all other species was obtained from Jones et al. (2009). Across all sites, capture numbers are the minimum number alive from the small mammal trapping, and number of detections was calculated from the remote camera data.

| Scientific Name | Common Name | Capture Method | Body Mass (g) | Captures/ detections |
|--------------------------------|-------------------------|----------------|---------------|----------------------|
| Poor Dispersers | | | | |
| <i>Sorex cinereus</i> | Common Shrew | Live trap | 4 | 19 |
| <i>Sorex monticolus</i> | Montane Shrew | Live trap | 6 | 197 |
| <i>Microtus oeconomus</i> | Tundra Vole | Live trap | 17 | 7 |
| <i>Peromyscus keeni</i> | Keen's Mouse | Live trap | 22 | 31 |
| <i>Myodes rutilus</i> | Red-backed Vole | Live trap | 26 | 13 |
| <i>Microtus longicaudus</i> | Long-tailed Vole | Live trap | 37 | 8 |
| <i>Tamiasciurus hudsonicus</i> | Red Squirrel | Camera | 200 | 38 |
| <i>Martes americana</i> | American Marten | Camera | 874 | 10 |
| <i>Marmota caligata</i> | Marmot | Camera | 2254 | 113 |
| <i>Erethizon dorsatum</i> | Porcupine | Camera | 7420 | 270 |
| Good Dispersers | | | | |
| <i>Lontra canadensis</i> | River Otter | Camera | 8087 | 38 |
| <i>Canis latrans</i> | Coyote | Camera | 11,989 | 125 |
| <i>Gulo gulo</i> | Wolverine | Camera | 12,793 | 2 |
| <i>Canis lupus</i> | Wolf | Camera | 31,757 | 68 |
| <i>Odocoileus hemionus</i> | Sitka black-tailed deer | Camera | 84,561 | 10 |
| <i>Ursus americanus</i> | Black Bear | Camera | 196,288 | 429 |
| <i>Ursus arctos</i> | Brown Bear | Camera | 371,704 | 419 |
| <i>Alces alces</i> | Moose | Camera | 461,901 | 229 |

Beta diversity

We analyzed patterns of beta diversity using the R package “Betapart” (Baselga et al., 2018; Version 1.5.1). Calculating beta diversity using this method relies on the fact that neither

Simpson nor Sørensen dissimilarities account for nestedness, so the difference between the two is a measure of the nestedness component of beta diversity within the system (Baselga, 2010).

Overall beta diversity (Sørensen dissimilarity, β_{sor}), can be partitioned into Simpson dissimilarity (β_{sim}) or spatial turnover, and nestedness (β_{nes}) using the equation $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{nes}}$. The functions for each factor are:

$$\beta_{\text{sor}} = \frac{\max(b,c) + \min(b,c)}{2a + \min(b,c) + \max(b,c)}$$

$$\beta_{\text{nes}} = \frac{\max(b,c) - \min(b,c)}{2a + \min(b,c) + \max(b,c)} \times \frac{a}{a + \min(b,c)}$$

$$\beta_{\text{sim}} = \frac{\min(b,c)}{a + \min(b,c)}$$

where a is the number of species shared by two plots, and b and c are number of species in two different plots and larger values represent higher diversity.

We used multiple-site dissimilarity measures that account for compositional heterogeneity across multiple sites to calculate overall beta diversity of the terrestrial mammal community and estimate the contribution of its two components to the total amount of community-level heterogeneity (Baselga, 2010; Baselga and Orme, 2012). To understand if the observed beta diversity patterns deviate from the expectations of random assembly processes, we used a null modeling approach whereby we randomized species occurrence data across sites and recalculated beta diversity and its components using 1,000 iterations (Kraft et al, 2011). We compared the observed amount of turnover and nestedness to the null model expectations using the 95% confidence intervals generated from the resampling of expected beta diversity to assess significance. To understand the impact of dispersal ability on beta diversity, we calculated the overall beta diversity and its two components for good dispersers and for poor dispersers.

Lastly, to decompose the effects of spatial distance and environmental differences on the variation of community beta diversity across sites, we used a Mantel test to estimate the correlation between matrices of species composition dissimilarity across all sites with spatial and environmental distances. The spatial distance matrix was constructed by calculating the Euclidean distance between each pair of sites using the first principal component (time-since-disturbance metric, see Results) value of each site and the environmental distance matrices were constructed by calculating the Euclidean distance between each site based on values of the second and third principal components (habitat metrics, see Results). Mantel tests were also run separately for good and poor dispersers to understand if dispersal ability impacted the degree to which community dissimilarity correlated with spatial and environmental distance.

RESULTS

Vegetation community analysis

The cluster analysis of the vegetation community data yielded two distinct vegetation groups corresponding to the east and west arms of the park (Figure 3.2). One group consisted of only west arm sites that were characterized by low willow, bare ground, and dryas, and only one site within the west arm had black cottonwood trees (Site 10). The second group contained only east arm sites and were characterized by sites with sitka spruce, moss, black cottonwood, and western hemlock, and lacked early successional species such as dryas.

PCA Results

Based on the loadings, PC1 was best explained by time-since-deglaciation variables, while PC2 and PC3 were both highly associated with habitat characteristics. The PCA indicated a high level of correlation between *DistanceMouth*, *Northing*, and *Age* (Figure S3.2a-c; Table 3.2), and these three variables were all strongly negatively correlated with *DistanceGlacier* and

Easting. These variables were also highly associated with the first principal component (PC1), which explained 50.1% percent of the total variance, and the loadings indicated that *DistanceMouth* had the strongest influence on PC1 (Table 3.4). The second principal component, PC2, explained 18% of the variance, and habitat-related variables *TotalCover*, *LS* and *CanopyCover* were highly associated with this axis. The loadings indicated that PC2 was most strongly influenced by *LS*. The third principal component, PC3, explained 13.6% of the variance and was most strongly influenced by *FH*.

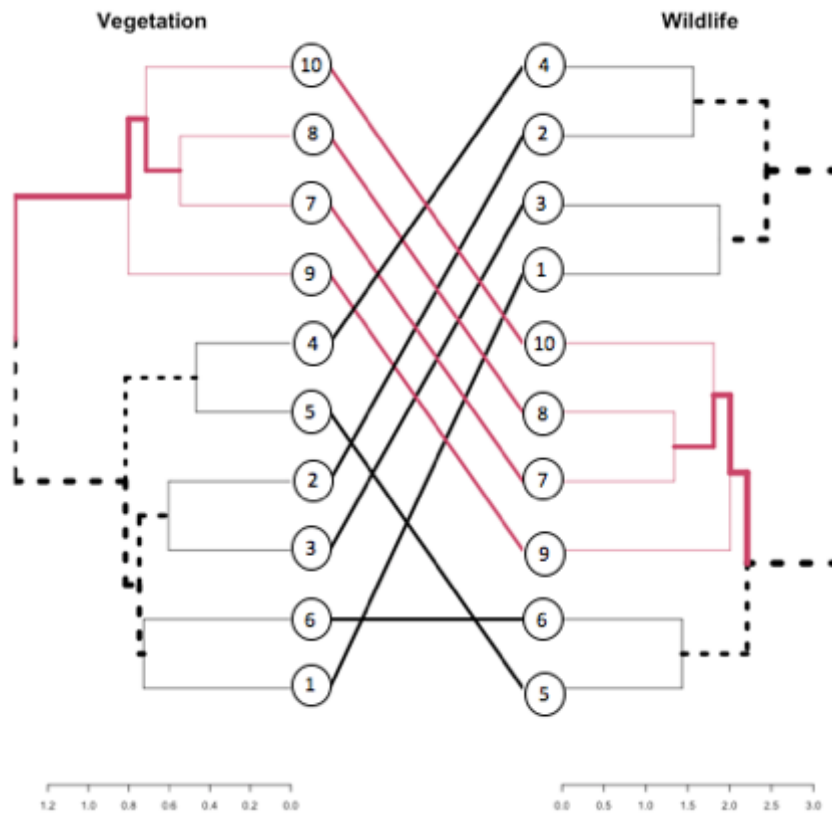


Figure 3.2: Results from the cluster analysis of vegetation and tanglegram comparing the clusters from the vegetation community to the clusters from the wildlife community. The vegetation cluster analysis yielded two significant groupings corresponding to sites in the east arm and west arm. The numbers represent sites described in Table 1, and sites are connected between the two dendrograms with a black or pink line. Pink lines indicate common sub-trees. Unique nodes are highlighted with dashed lines. Overall, vegetation clusters and wildlife clusters in the east arm differ. Sites 1-6 are east arm sites, and sites 7-10 are west arm.

Table 3.4: Loadings from the PCA for all age-related and habitat-related variables. Bolded numbers represent loadings > 0.30. PC1 was most strongly influenced by spatial variables (DistanceMouth) whereas PC2 and PC3 were influenced by habitat characteristics (LS and FH, respectively).

| Variable | PC1 | PC2 | PC3 |
|--------------------------|---------------|---------------|---------------|
| BG | -0.297 | -0.073 | -0.194 |
| LS | -0.081 | 0.553 | 0.117 |
| DS | -0.273 | 0.104 | -0.419 |
| GH | -0.154 | -0.218 | 0.243 |
| FH | -0.061 | 0.127 | 0.561 |
| BH | 0.327 | -0.058 | -0.183 |
| TS | -0.200 | -0.207 | -0.397 |
| TotalCover | -0.031 | 0.469 | -0.321 |
| MeanBA | 0.243 | -0.202 | 0.100 |
| CanopyCover | 0.215 | -0.394 | -0.239 |
| Easting | 0.348 | -0.147 | 0.011 |
| Northing | -0.322 | -0.189 | 0.069 |
| DistanceGlacier | 0.342 | 0.130 | -0.043 |
| DistanceMouth | -0.356 | -0.050 | 0.031 |
| Age | -0.286 | -0.276 | 0.173 |
| Total Variance Explained | 50.1% | 18.0% | 13.6% |

Mammal community analysis

Six species of small mammals were captured: Keen's mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudus*), northern red-backed voles (*Myodes rutilus*), tundra voles (*Microtus oeconomus*), montane shrews (*Sorex monticolus*), and common shrews (*Sorex cinereus*). There were a total of 284 captures of the 6 species, and we captured a minimum of 275 individuals, of which 72% (197 individuals) were montane shrews (Table 3.3). Our remote cameras detected 12 mammal species (Table 3.3): black bears (*Ursus americanus*), brown bears (*Ursus arctos*), moose (*Alces alces*), wolves (*Canis lupus*), coyotes (*Canis latrans*), American martens (*Martes flanaganensis*), hoary marmots (*Marmota flaviventris*), wolverines (*Gulo gulo*), red squirrels (*Tamiasciurus hudsonicus*), Sitka black-tailed deer (*Odocoileus hemionus*), North American porcupines (*Erethizon dorsatum*), and North American river otters (*Lontra*

62anadensis). There were a total of 1709 independent detections, and black bears were the most commonly detected (429 detections; Table 3.3), followed by brown bears (419) and porcupines (270).

Mammal community composition was closely tied to habitat in the west arm, but mammal and vegetation communities were not closely associated in the east arm (Figure 3.2). The PERMANOVAs indicated that time-since-deglaciation (PC1) explained 24% of the variation in the mammal community ($F_{1,8} = 2.55$, $p = 0.006$; Table 3.5), while habitat metrics (PC2 and PC3) explained 10% each ($F_{1,8} = 0.917$, $p = 0.50$, and $F_{1,8} = 0.911$, $p = 0.57$, respectively). Additionally, time-since-deglaciation (PC1) explained 27% of the variation in good dispersers and 22% of the variation in poor dispersers ($F_{1,8} = 3.033$, $p = 0.014$ and $F_{1,8} = 2.234$, $p = 0.022$, respectively; Table 3.5), while habitat metrics (PC2 and PC3) explained less than 13% of the variation in good and poor disperser communities each (Table 3.5).

The NMDS further indicated that mammal community assembly was impacted by dispersal ability. Good dispersers were associated with both high and low values of time-since-deglaciation (Figure 3.3), indicating they had a widespread distribution across sites of all ages. In contrast, poor dispersers were more commonly associated with intermediate to high values of time-since-deglaciation, indicating a concentration of those species at older sites. Overall, the horizontal spread of all species regardless of dispersal ability illustrates a stronger impact of time-since-deglaciation than habitat.

Table 3.5: Results from the PERMANOVAs testing the impact of PC1, PC2, and PC3 on all species, good dispersers, and poor dispersers. Degrees of freedom (Df), sum of squares (SumsOfSqs) R² values, F-statistics and p-values are shown. * indicates statistical significance (p < 0.05).

| | Df | SumOfSqs | R ² | F | P-Value |
|------------------------|----|-------------|----------------|---------|---------|
| All Species | | | | | |
| PC1 | 1 | 4.703320641 | 0.242037275 | 2.55461 | 0.006* |
| Residual | 8 | 14.72889552 | 0.757962725 | | |
| Total | 9 | 19.43221616 | 1 | | |
| PC2 | 1 | 1.997737388 | 0.102805433 | 0.91668 | 0.501 |
| Residual | 8 | 17.43447877 | 0.897194567 | | |
| Total | 9 | 19.43221616 | 1 | | |
| PC3 | 1 | 1.986137518 | 0.102208492 | 0.91075 | 0.572 |
| Residual | 8 | 17.44607864 | 0.897791508 | | |
| Total | 9 | 19.43221616 | 1 | | |
| Good Dispersers | | | | | |
| PC1 | 1 | 2.239559936 | 0.274890827 | 3.03282 | 0.014* |
| Residual | 8 | 5.907528719 | 0.725109173 | | |
| Total | 9 | 8.147088655 | 1 | | |
| PC2 | 1 | 0.545926309 | 0.06700876 | 0.57457 | 0.829 |
| Residual | 8 | 7.601162346 | 0.93299124 | | |
| Total | 9 | 8.147088655 | 1 | | |
| PC3 | 1 | 0.804362684 | 0.098730076 | 0.87636 | 0.609 |
| Residual | 8 | 7.342725971 | 0.901269924 | | |
| Total | 9 | 8.147088655 | 1 | | |
| Poor Dispersers | | | | | |
| PC1 | 1 | 2.463760705 | 0.218319262 | 2.23436 | 0.022* |
| Residual | 8 | 8.821366797 | 0.781680738 | | |
| Total | 9 | 11.2851275 | 1 | | |
| PC2 | 1 | 1.45181108 | 0.128648177 | 1.18114 | 0.296 |
| Residual | 8 | 9.833316422 | 0.871351823 | | |
| Total | 9 | 11.2851275 | 1 | | |
| PC3 | 1 | 1.181774835 | 0.104719671 | 0.93575 | 0.529 |
| Residual | 8 | 10.10335267 | 0.895280329 | | |
| Total | 9 | 11.2851275 | 1 | | |

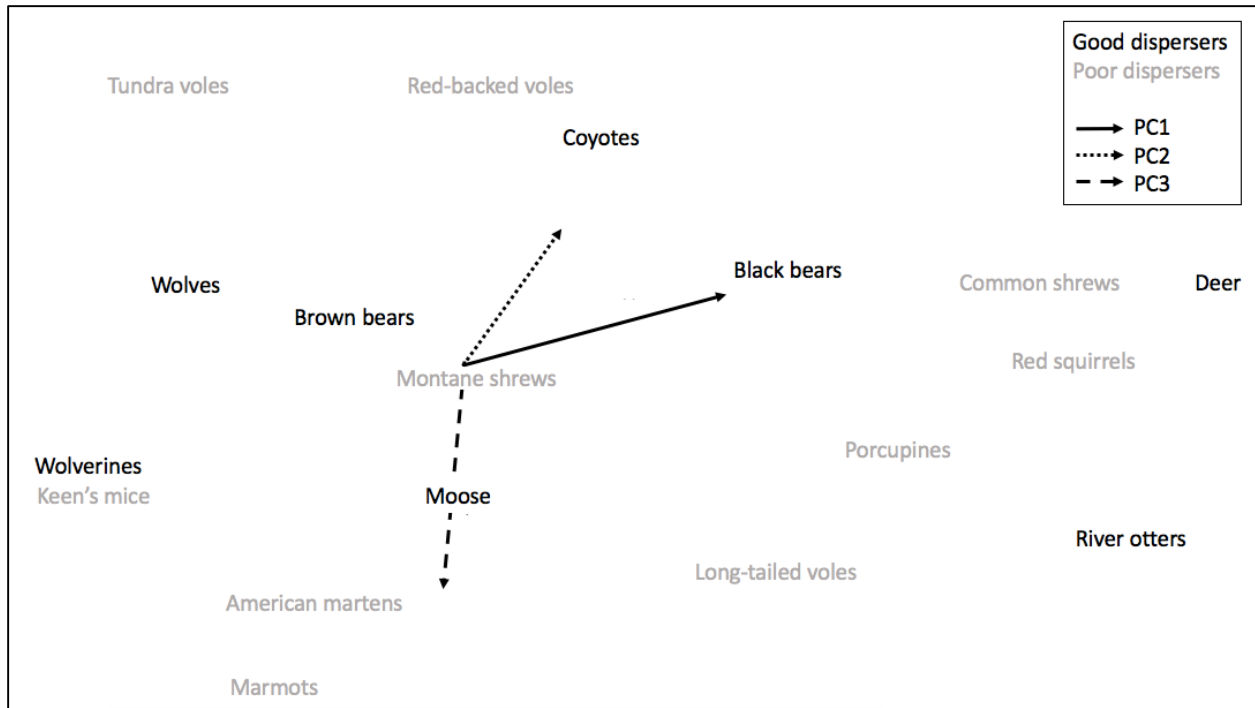


Figure 3.3: Results from the NMDS showing the location of highest relative species abundance in relation to the three principal components identified from the PCA. Grey species represent poor dispersers and black species represent good dispersers (based on body size). PC1 was most strongly associated with *DistanceMouth*, and thus best describes time-since-disturbance while PC2 and PC3 were both highly associated with habitat related variables (*LS* and *FH*, respectively).

Beta diversity

Beta diversity across all sites was explained primarily by turnover (Table 3.6), however while not statistically significant, nestedness tended to account for more of the total beta diversity and turnover for less of the total beta diversity than expected. Good dispersers had a lower overall beta diversity than poor dispersers (Table 3.6), and turnover and nestedness accounted for similar amounts of total beta diversity for good dispersers (55% turnover, 45% nestedness; Table 3.6, Figure 3.4). In contrast, turnover accounted for 90% of overall beta diversity in poor dispersers. Total beta diversity across all species and for both good and poor dispersers was positively correlated with time-since-deglaciation but uncorrelated with habitat (Table 3.7).

Table 3.6: Mammalian beta diversity calculations for all species, good dispersers, and poor dispersers, and expected beta diversity and its components. The expected beta diversity and its components are reported as averages with 95% confidence intervals and were calculated by randomizing species occurrence across sites 1,000 times and calculating an average value for turnover, nestedness and total beta diversity.

| Group | Turnover | Nested | Total |
|----------------------|---------------------|---------------------|-------|
| Observed All Species | | | |
| Value | 0.596 | 0.100 | 0.696 |
| Proportion | 0.856 | 0.144 | |
| Expected All Species | | | |
| Value | 0.619 (0.572-0.666) | 0.077 (0.030-0.124) | 0.696 |
| Proportion | 0.888 | 0.111 | |
| Good Dispersers | | | |
| Value | 0.315 | 0.257 | 0.571 |
| Proportion | 0.552 | 0.450 | |
| Poor Dispersers | | | |
| Value | 0.682 | 0.078 | 0.761 |
| Proportion | 0.896 | 0.102 | |

Table 3.7: Results from the Mantel tests investigating the correlation between total beta diversity and time-since-disturbance and habitat related variables across all sites in GLBA, for all mammals, for good dispersers, and for poor dispersers. Time is represented by the first principal component and habitat is represented by the second and third principal components of the PCA. The Pearson correlation coefficient (R) and p-value are shown for each component of beta diversity. * represent significant correlations.

| Group | Variable | R | P-Value |
|-----------------|----------------------|---------|---------|
| All GLBA | <i>PC1 (Time)</i> | 0.7519 | 0.002* |
| | <i>PC2 (Habitat)</i> | 0.0784 | 0.268 |
| | <i>PC3 (Habitat)</i> | 0.1143 | 0.223 |
| Good Dispersers | <i>PC1 (Time)</i> | 0.6443 | 0.001* |
| | <i>PC2 (Habitat)</i> | -0.0054 | 0.422 |
| | <i>PC3 (Habitat)</i> | -0.0800 | 0.588 |
| Poor Dispersers | <i>PC1 (Time)</i> | 0.6214 | 0.001* |
| | <i>PC2 (Habitat)</i> | 0.0660 | 0.283 |
| | <i>PC3 (Habitat)</i> | -0.2280 | 0.170 |

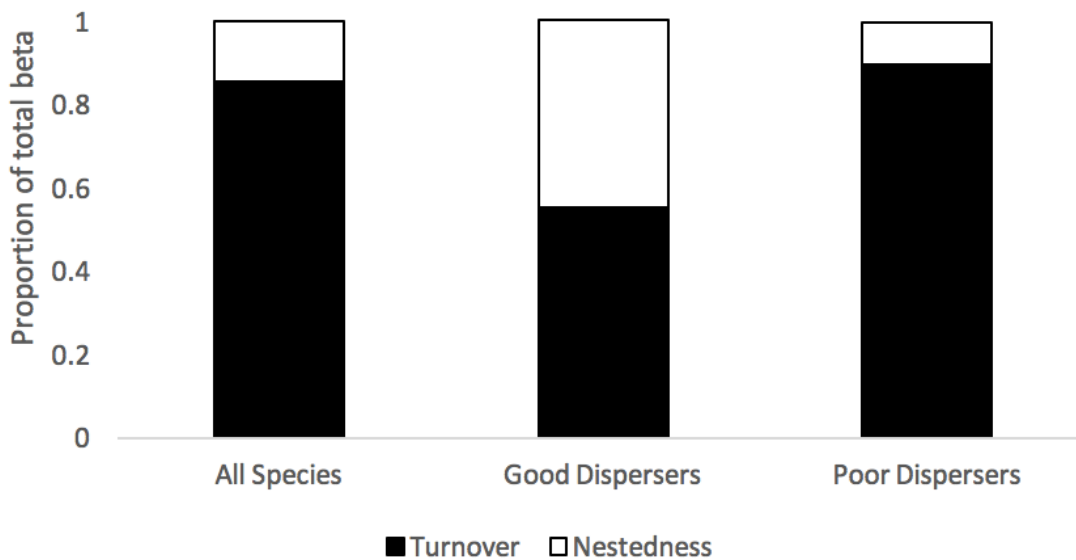


Figure 3.4: Proportion of total beta diversity explained by turnover and nestedness in all mammals across GLBA, and between good and poor dispersers.

DISCUSSION

Disturbances play a key role in shaping the structure and dynamics of natural systems (Sousa, 1984), but mechanisms driving whole-community responses of mammals to disturbance remain poorly understood (Fox, 1982; Monamy and Fox, 2000; Fox et al., 2003; Fontaine and Kennedy, 2012; McKelvey, 2015). Here, we show that mammal communities do not follow the same successional patterns as vegetation communities in response to glacial recession. Furthermore, while many studies have focused on the importance of habitat suitability in shaping wildlife community assembly following disturbances, we demonstrated that both community assemblage and beta diversity of mammals were impacted more by time-since-disturbance than habitat, and that dispersal ability was a strong determinant of both processes. Habitat metrics are widely used as surrogates for changes in wildlife communities following disturbances (Barton et al., 2014), however here we have shown that changes in wildlife communities do not directly track changes in vegetation communities. This highlights the importance of incorporating

landscape connectivity and dispersal ability metrics into wildlife conservation efforts following disturbances.

Variables associated with time-since-disturbance had a larger impact on the post-glacial mammal community assembly than habitat-related variables, which was contrary to prediction made by the habitat accommodation model in post-fire systems. It is generally difficult to separate habitat characteristics and time-since-disturbance in studies of community succession due to the inherent correlation between the two (Clements, 1916). However, GLBA provided a unique opportunity to differentiate them because there was variation in both factors across sites and lack of strong correlation between them, as indicated by the PCA. Time-since-disturbance may especially impact wildlife communities when there are barriers to wildlife movement that inhibit recolonization of disturbed areas even when suitable habitat is available. In GLBA, glacier covered mountains, ice fields, and marine fjords limit terrestrial connectivity, particularly in the west arm, where mountain peaks are generally steeper. The west arm of GLBA is dominated by the Fairweather mountain range and the Brady ice field, while the east arm of the park has low-lying mountains that have facilitated wildlife movement from eastern glacial refugia (Schoen and Albert, 2016). Therefore, even with good dispersal ability, the habitat accommodation model of animal succession may break down when physical barriers impede wildlife movement. Dispersal between patchy habitats via habitat connectivity features can have large impacts on the distribution of species and communities (Harrison, 1991; Hanski and Gilpin, 1997). If the isolation of patches in disturbed systems is an important limiting factor in colonizing success, incorporation of habitat linkages may be necessary in areas particularly prone to disturbances (Tucker, 2000). While many studies have found that the influence of patch isolation on community composition is small relative to habitat quality (Thomas et al., 2001;

Cunningham et al., 2005; Summerville et al., 2005; Grimbacher and Catterall, 2006), most of these studies have been conducted on insects. Further research is needed to understand the explicit role that habitat connectivity features and species traits play in community assembly and recolonization of disturbed landscapes by higher vertebrates.

As the frequency and intensity of natural disturbances increases and potentially produces disturbances that fragment landscapes, managers and conservationists face the challenge of mitigating the impact of dispersal barriers on wildlife recolonization. These factors also likely impact vegetation in GLBA, as our results indicate that plant communities in the east arm were different from those in the west arm (Figure 3.3). Most studies on plant succession in GLBA have focused on one arm of the park, and our results indicate that, as with wildlife, distance to seed sources and dispersal ability of plant species likely plays an important role in post-disturbance community assembly (Fastie, 1995). Our results indicate that there is still substantial variation in the mammal community unexplained by time-since-disturbance or habitat, however, and provides evidence that species can operate differently over the same set of sites (Pandit et al., 2009). The degree of habitat specialization may influence the development of biotic communities following disturbance, and often habitat generalists can outcompete habitat specialists in disturbed landscapes (Marvier et al., 2004). Assembly of habitat generalists have been shown to be governed by dispersal processes, and by environmental processes for specialists (Pandit et al., 2009), further highlighting the influence of dispersal ability on community assembly post-disturbance. Additionally, species interactions such as competition and facilitation may play a role in shaping mammal communities as they have been shown to in plants (Connell and Slatyer, 1977), and further research is needed to investigate the impact that additional species traits besides dispersal ability have on post-disturbance community assembly.

As with our community composition findings, patterns of total beta diversity were more strongly related to time-since-disturbance than habitat. Beta diversity across GLBA and between good and poor dispersers were positively correlated with time-since-disturbance rather than habitat (Table 3.7). Similar results were found in Svenning et al. (2011), where compositional variation in European mammal beta diversity accounted for by space was greater than that accounted for by environment. The increase of community dissimilarity with geographic distance, or distance decay, has long been recognized in ecology (Whittaker, 1975; Cody, 1985). Distance decay can result from a decrease in environmental similarity with increasing distance where the composition of communities is predictable from the environment given enough time, which separates species spatially based on different physiological requirements (Nekola and White, 2004; Calderón-Patrón et al., 2013). It can also be caused by dispersal from areas of origin or recolonization from refugia, and dispersal ability has been shown to impact distance decay (Tornero et al., 2018). Svenning et al. (1999) found that geographic processes such as dispersal contributed more to patterns of distance decay than environmental conditions alone, and in landscapes with more physical barriers to wildlife movement, similarity between communities decreases more abruptly (Calderón-Patrón et al., 2013). Our results support this, and indicate that dispersal may play a more important role in shaping distance decay patterns than habitat suitability. As such, our findings may help managers of protected areas such as GLBA anticipate post-glacial wildlife colonization patterns based on the composition of neighboring communities and landscape connectivity.

Habitat-based surrogates for changes in wildlife communities following disturbance are often used, and have been useful for understanding bird community recovery post-disturbance (Barton et al., 2014), however these surrogates may not be as useful for mammal communities,

as demonstrated here. While there is strong evidence for the response of wildlife to vegetation structure, the extent to which these habitat attributes are reflected in changes in wildlife communities is still relatively unknown because vegetation and wildlife can respond differently to disturbances (Barton et al., 2014). In addition to differences in responses to disturbances between wildlife and plant communities, dispersal ability can drive differences in responses within wildlife communities. Good dispersers in GLBA had lower beta diversity than poor dispersers, which has been widely supported in the literature (MacNally et al., 2004; Qian, 2009; Dobrovolski et al., 2012; Calderón-Patrón et al., 2013) and indicates a more widespread distribution of these species. Similarly, previous studies that have found that the degree of nestedness varies with dispersal ability (Lomolino, 1996; Greve et al., 2005), and our results suggest a trend towards a higher degree of nestedness than expected (Table 2.6), highlighting the influence of vagility on patterns of diversity. Turnover and nestedness components of beta diversity require antithetic conservation strategies (Baselga, 2010), and the higher proportion of total beta diversity explained by nestedness in large mammals that are particularly susceptible to disturbances (Noss et al., 1996) indicates that conservation efforts should prioritize a small number of the richest sites. Communities with a higher proportion of turnover require conservation strategies that prioritize many different sites, not necessarily the richest (Baselga 2010), highlight the importance of considering both aspects of beta diversity in post-disturbance conservation efforts.

Our study indicates that mammal communities do not respond to glacial recession in the same way as vegetation communities, and as such, caution should be used when using changes in habitat to make inferences about changes in wildlife communities following disturbance. This is particularly important when habitats are fragmented, and where dispersal limitations can play a

major role in determining community assembly processes. Species may be absent from areas following disturbance not because the habitat is not suitable at the site, but because individuals of that species have not yet arrived due to dispersal limitations or barriers to wildlife movement (Tilman, 1994). This limitation is an important factor for determining successional dynamics and community assembly and diversity patterns, and understanding how disturbance alters these processes is important as the nature of disturbances is altered by climate change. A large gap remains in understanding of how wildlife communities respond to disturbances other than fire, and few studies have extended beyond five years post-disturbance (McKelvey, 2015). To our knowledge, this is the first study to investigate the impacts of present-day glacial recession on the beta diversity and community assembly processes of terrestrial mammals. Additional research on wildlife community responses to disturbances such as glacial recession that will be influenced by climate change is needed to test the generality of our findings. While substituting space for time, as we have done here, has its share of critiques (Johnson and Miyanishi, 2008), it may be necessary when attempting to understand long-term disturbance-related impacts to wildlife communities (McKelvey, 2015).

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SUPPLEMENTARY MATERIAL B

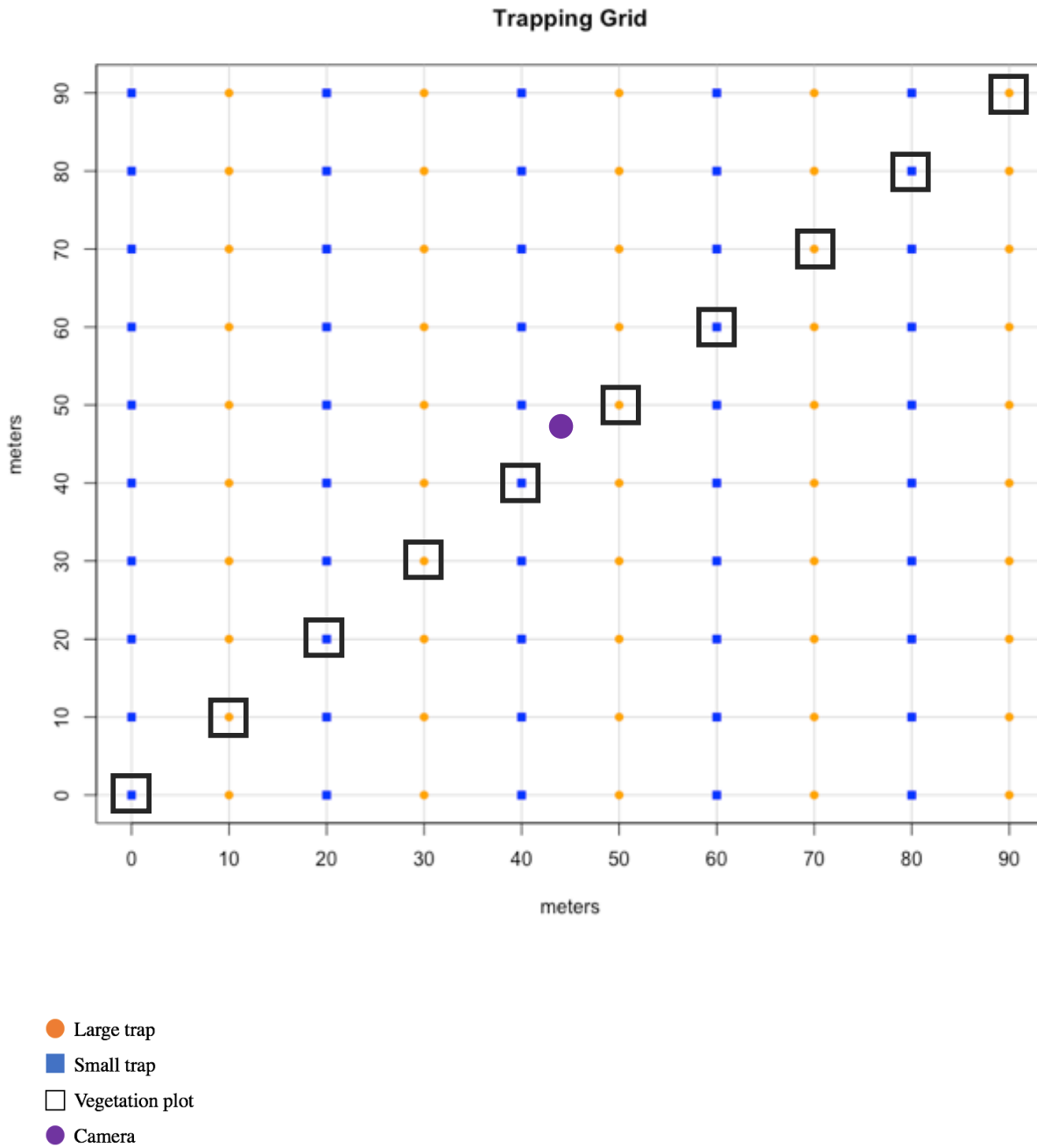


Figure S3.1: Diagram of the layout of a study site. Vegetation surveys occurred on the diagonal of the small mammal trapping grid, with the camera in the center. This diagram represents one of the two small mammal trapping grids placed at each site, and one of the two vegetation surveys. Four cameras were installed at each site, two of which did not have vegetation surveys or small mammal trapping grids placed at them.

Table S3.1: Sensitivity analysis of different body mass cutoffs for determining good and poor dispersers. Turnover, nestedness and total beta diversity are shown for each category within each cutoff group. Pearson correlation coefficients for the correlation between each category within each cutoff group and the first principal component (representing time-since-deglaciation; R1) and between each category and the second principal component (representing habitat; R2) are shown along with associated p-values. * indicates statistically significant correlations ($p < 0.05$).

| | Turnover | Nestedness | Total | R1 | P-value | R2 | P-value |
|-----------------|----------|------------|-------|--------|---------|---------|---------|
| 10,000 g | | | | | | | |
| Good Dispersers | 0.321 | 0.215 | 0.535 | 0.7008 | 0.004* | 0.0353 | 0.341 |
| Poor Dispersers | 0.676 | 0.093 | 0.768 | 0.6198 | 0.001* | 0.0093 | 0.438 |
| 800g | | | | | | | |
| Good Dispersers | 0.315 | 0.257 | 0.571 | 0.6443 | 0.001* | -0.0054 | 0.422 |
| Poor Dispersers | 0.682 | 0.078 | 0.761 | 0.6214 | 0.001* | 0.0660 | 0.283 |
| 500g | | | | | | | |
| Good Dispersers | 0.472 | 0.172 | 0.644 | 0.7575 | 0.001* | 0.0679 | 0.262 |
| Poor Dispersers | 0.676 | 0.076 | 0.751 | 0.5214 | 0.005* | 0.0393 | 0.359 |
| 200g | | | | | | | |
| Good Dispersers | 0.452 | 0.205 | 0.657 | 0.8049 | 0.001* | 0.0442 | 0.317 |
| Poor Dispersers | 0.706 | 0.044 | 0.750 | 0.3065 | 0.029* | 0.0571 | 0.321 |

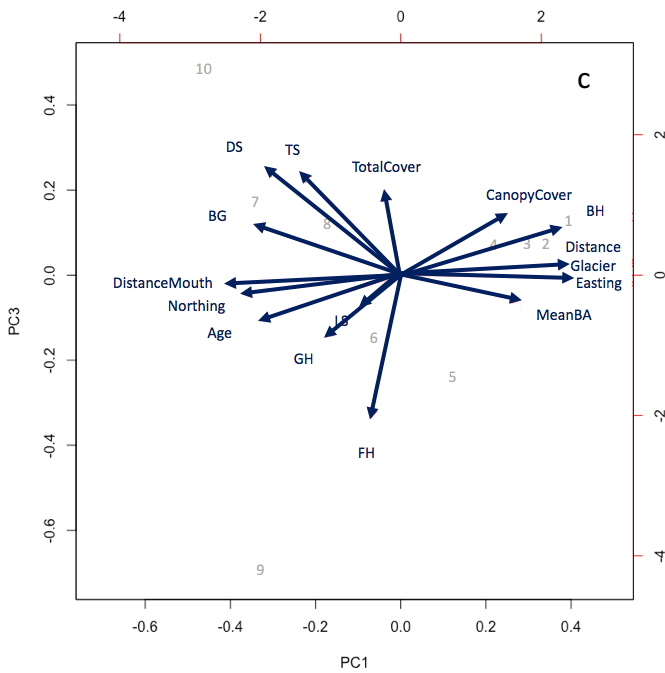
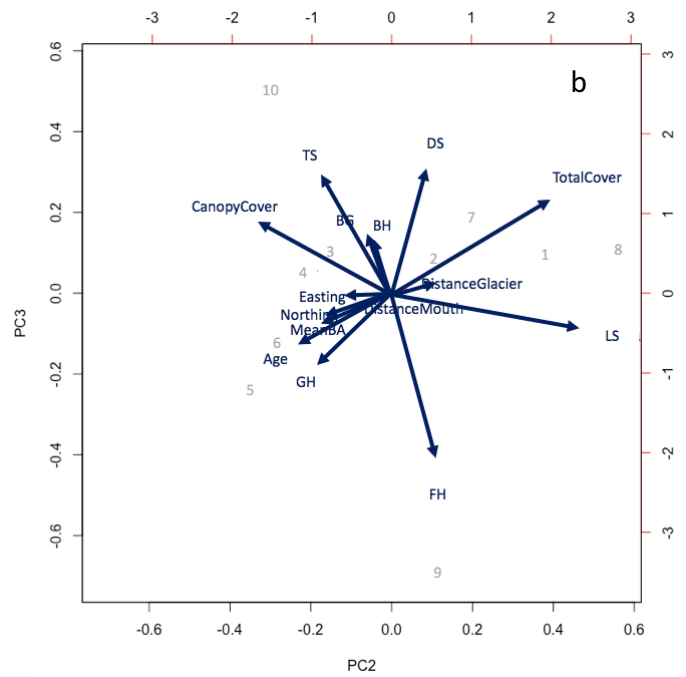
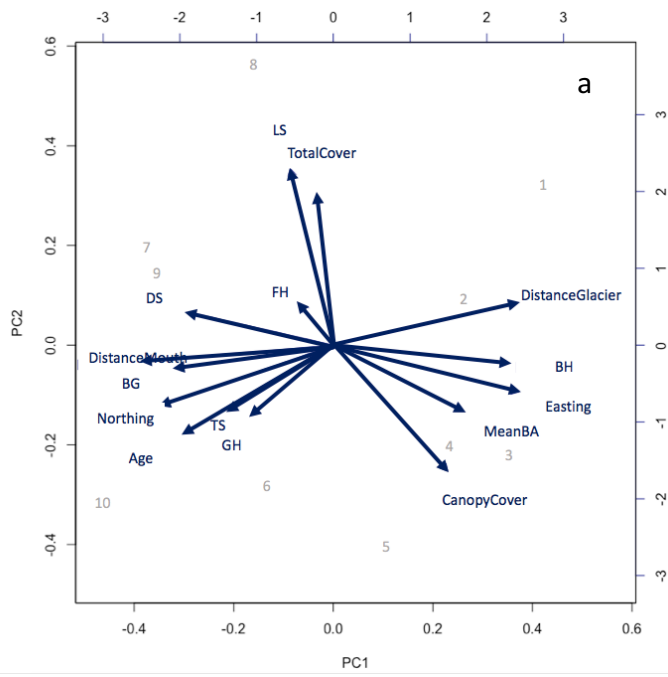


Figure S3.2: Results from the PCA of all variables showing (a) PC1 vs PC2, (b) PC2 vs PC3, and (c) PC1 vs PC3. PC1 explained 50.1% of the variation, PC2 explained 18%, and PC3 explained 13.6%. Vectors running parallel to axes indicate perfect correlation to that axis, while variables running perpendicular indicate that they are uncorrelated to the axis. Variables whose vectors are close to one another are strongly positively correlated, perpendicular indicates no correlation, and vectors pointing in opposite directions indicate strong negative correlation. Loadings are reported in Table 4 and numbers 1-10 correspond to site numbers (Table 3.1).

CHAPTER 4

General Conclusion

There are two broad types of disturbances that wildlife face, those that alter habitats, and those that alter wildlife behavior. Habitat-altering disturbance is a fundamental process controlling diversity (Huston, 1979; Huston, 1994), and as climate change influences the magnitude and frequency of these events, it's important to understand how biotic communities will respond. Additionally, human disturbance to wildlife will potentially increase as human visitation to protected areas increases world-wide, and managers of these areas must balance the desires of visitors to view wildlife with the needs of wildlife to exist in a space where disturbance from humans is minimized. Here, we studied the responses of wildlife to both human disturbance and natural disturbance. We detected significant responses of wildlife to humans in a system with very low human use, and showed that terrestrial mammal communities in GLBA do not necessarily follow the same successional patterns as vegetation following glacial recession, but instead are strongly impacted by time-since-disturbance.

Wildlife responses to humans have been well documented in many systems around the world (e.g. Bruggeman et al. 2006, Berger 2007, Haroldson and Gunther 2013, Gunther et al. 2015, Sarmiento and Berger 2017). We found that detections of brown bears, black bears, moose and wolves only exceeded four per week when there was no human activity at all, indicating that the threshold level of human activity for sites to function as baseline controls in studies of anthropogenic impacts may be lower than those found in most protected areas. If protected area managers seek to provide refugia for wildlife with minimal impacts, and to maintain baseline controls that lack human impacts, then our results support "land sparing" management strategies. Because management of protected areas is directly tied to management of human-wildlife

coexistence, understanding how visitors impact wildlife behavior can help to develop policies that provide visitors with viewing opportunities while also achieving wildlife conservation goals.

Individual variation in “boldness” or “shyness” in wildlife plays a large role in species’ abilities to cope with human disturbances (Sih et al. 2011), especially in protected areas where recurring benign encounters with humans can facilitate habitation (Thompson and Henderson 1998, Found and St. Claire 2016, Found 2019) and prey species may exploit these areas as predation refugia (Laundre et al. 2001). Individual variation in activity patterns of large mammals are rarely quantified, however, and these individual patterns could be correlated with boldness (Hertel et al. 2017). Our results indicate that some level of habituation at the highest visited site in GLBA may be taking place, however the use of technology that allows for the analysis of individual variation in diel patterns and boldness behavior among individuals, such as GPS tracking technology, would shed new light on the mechanisms by which wildlife responses to humans can change over time. Individual adaptive behavioral strategies can have important implications for population persistence (Refsnider and Janzen 2012, Hertel et al. 2017), further highlighting the importance of understanding individual variation in response behavior.

While the responses of wildlife to humans have been widely studied, less is understood about community level responses of wildlife to disturbance that alter habitats and landscapes (Fox, 1982; Monamy and Fox, 2000; Fox et al., 2003; Fontaine and Kennedy, 2012; McKelvey, 2015). Disturbances play a key role in shaping the spatial and temporal heterogeneity in the structure and dynamics of natural systems (Sousa, 1984), and disturbances such as fire, glacial recession, floods, and heat waves, are expected to increase in frequency and severity with climate change (Easterling et al., 2000; Sergio et al., 2018). We found that changes in wildlife communities do not directly track changes in vegetation communities, and demonstrated that

both community assemblage and beta diversity of mammals were impacted more by time-since-disturbance than habitat. Dispersal ability was a strong determinant of both processes, highlighting the importance of incorporating landscape connectivity and dispersal ability metrics into wildlife conservation efforts following disturbances.

Our study indicates that mammal communities do not respond to glacial recession in the same way as vegetation communities, and as such, caution should be used when using changes in habitat to make inferences about changes in wildlife communities following disturbance. This is particularly important when habitats are fragmented, and where dispersal limitations can play a major role in determining community assembly processes. Species may be absent from areas following disturbance not because the habitat is not suitable at the site, but because individuals of that species have not yet arrived due to dispersal limitations or barriers to wildlife movement (Tilman, 1994). This limitation is an important factor for determining successional dynamics and community assembly and diversity patterns, and understanding how disturbance alters these processes is important as the nature of disturbances is altered by climate change.

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