COMMON RAVEN RESOURCE SELECTION, DIET, AND BEHAVIOR AROUND A THREATENED SHOREBIRD

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A Thesis Presented to

The Faculty of California State Polytechnic University, Humboldt

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

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July 2024

ABSTRACT

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Human food subsidies have allowed populations of the common raven (*Corvus corax*) to expand and increase in density, especially in the western United States, which has amplified predation risk for other native species. Common ravens are well-documented nest predators of the federally threatened Western snowy plover (*Anarhynchus nivosus nivosus)* in Humboldt County, California; however, little is known about raven movement and foraging behavior in and around snowy plover habitat. Using GPS tracking and behavioral surveys, I examined movement and foraging behavior of beach-going ravens across snowy plover nesting habitat and I explored raven diet through stable isotope analyses. Beach-going ravens had a large average home range size of 141 km^2 and high variation between seasons and by age class, with larger movements observed in the non-breeding season and by sub-adult ravens. A Resource Selection Function revealed that ravens selected for snowy plover nesting areas and developed habitat, suggesting that ravens visiting snowy plover nesting areas are supported by human food sources in anthropogenic areas. Stable isotope diet analysis of tracked ravens revealed large variation between individuals at the trophic level and in overall diet composition. Ground-truthing of tracked raven locations revealed an abundance of both small and large-scale food resources throughout the study area, and observations of tagged ravens revealed territoriality of ravens at most snowy plover nesting beaches in the study area. Cumulatively, these results highlight the landscape-level features accessed by beach-going ravens and can inform management agencies on where to focus efforts for naturally managing raven populations.

ACKNOWLEDGEMENTS

A number of organizations and agencies helped make my project happen through providing access to data, resources, and financial assistance. First, I would like to say thank you for grant funds provided by the Bureau of Land Management, the Blake-Nuttall Fund, the Sea and Sage and North Cascades Audubon Societies, the California North Coast Chapter of The Wildlife Society, and the Association of Field Ornithologists. For financial support through scholarships, thank you to the Stanley and Lorene J. Harris Scholarship, the American Association of University Women, funders of the Bloom Hays Scholarship, Hegy Fellowship, Woolford Scholarship, Association of Environmental Professionals, HSU Dean and Alumni Scholarships, and the CSU Trustees Scholarship. Thanks also to the Wildlife Department at California State Parks, which assisted with project development, equipment use, and data sharing. Additionally, thank you to Krysta Rogers with California Department of Fish and Wildlife for testing ravens for Highly Pathogenic Avian Influenza and to National Park Service staff for helping mail ravens for necropsies. Thank you also to the Anthropology Department and to Dr. Marissa Ramsier, Professor and Department Chair in the Biological Anthropology Department for allowing me access to lab facilities to prepare feather samples for stable isotope analysis.

An incredible group of people also helped me start, continue, and complete this project including my advisor Dr. Barbara Clucas, my committee members Dr. Mark Colwell and Dr. Ho Yi Wan, my partner Jon, and my family. Thank you also to the undergraduate students and field assistants who helped conduct behavioral surveys and

whose curiosity, interest, and boundless love of ravens continues to remind me of why I am in this field of study.

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INTRODUCTION

Anthropogenic resources have the potential to impact natural ecosystems in a variety of ways, from altering animal behavior and demographics to modifying frequencies or types of interspecific interactions (Chace and Walsh 2006, Shochat et al. 2006). Food subsidies such as commercial and residential trash, roadkill, and agricultural feed often result from human development and activity and the effects of these subsidies can increase the density and reproductive success of generalist predators (Marzluff and Neatherlin 2006), with impacts to prey populations (Jimenez and Conover 2001). The common raven (*Corvus corax*; hereafter, raven) is a generalist predator ubiquitous where anthropogenic activity occurs, particularly because of human food subsidies (Kristan and Boarman 2004, Boarman et al. 2006, Harju et al. 2021) and, in some locations, the introduction of novel and previously unavailable nesting structures (Howe et al. 2014).

Human food subsidies have allowed populations of ravens to expand and increase in density, especially in the western United States (Harju et al. 2021). This increased abundance of human food has amplified predation risk for native birds, mammals, insects, reptiles, and amphibians through “spillover” predation, whereby prey in adjacent areas are decreased as a result of inflated predator populations in adjacent areas (Brunk et al. 2021), as well as “hyperpredation” in which predation pressure increases on typically non-target species as the predator’s population increases (Coates et al. 2021). Raven predation has been documented as impacting populations of ten sensitive, threatened, or endangered species within the United States including the Mojave desert tortoise

(*Gopherus agassizii*), California least tern (*Sternula antillarium browni*), Greater and Gunnison sage-grouse (*Centrocercus urophasianus* and *C. minimus*), Western snowy plover (*Anarhynchus nivosus nivosus*), marbled murrelet (*Brachyramphus marmoratus*), piping plover (*Charadrius melodus*), California condor (*Gymnogyps californianus*), greater sandhill crane (*Antigone canadensis tabida*), and San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*) (Coates et al. 2021, Harju et al. 2021). Importantly, ravens are likely impacting populations of common species as well, though common species and threats to their stability tend to be less well-studied (Andren 1992).

A variety of management strategies have been utilized to minimize raven predation on sensitive species, though many of these strategies show initial success then decreased impact over time as ravens habituate to the management strategy (summarized in USFWS 2023) (Appendix A). Some strategies have been successful on small geographic scales, typically too small to be ecologically relevant, some strategies are successful but are time or resource-intensive, highly invasive, and/or face public opposition, and other strategies have reduced effectiveness over time or can cause additional risks to sensitive species. Lethal removal, which is becoming increasingly common for managing ravens, is expensive (Harju et al. 2021), can lead to compensatory predation by other species, can face public opposition (Clucas 2021), and the lethal management of a native species is morally ambiguous (Marzluff et al. 2021). Additionally, lethal removal of ravens has never been evaluated as an isolated strategy (e.g., Conover and Roberts 2017) and typically needs to be performed annually as well as consistently throughout the year as new ravens take the place of removed individuals

(USDA Wildlife Services staff, personal comm.). Lethal removal does not address the causal factors of high raven abundance, instead acting as a temporary solution to a problem that requires a more holistic approach for long-term and large-scale effectiveness.

The Western snowy plover (hereafter, snowy plover) is a species of conservation concern threatened by raven egg and chick predation (Colwell et al. 2012; Colwell et al. 2019). This population which breeds along the Pacific coast of North America from Washington south to Baja California, is a federally threatened subspecies that nests semi-colonially on sparsely vegetated beaches and, less commonly, river gravel bars. Since being listed as threatened by the US Fish and Wildlife Service in 1993, extensive monitoring efforts have aimed to understand the causes of the snowy plover's population decline. Snowy plovers must contend with a variety of disturbances on Pacific Coast beaches including habitat loss to invasive plants, human development, and military operations, disturbance caused by humans, dogs, and off-highway vehicles, predation pressure from natural predators including raptors, skunks, coyotes, foxes, crows, and ravens, as well as rising sea levels and other negative impacts of climate change (Stenzel et al. 2023). Ongoing monitoring identifies ravens as the dominant nest predator of snowy plovers throughout their range (Strong et al. 2021). Ravens are thought to cue in on the movement of adult plovers on and off the nest to locate eggs, so as the amount of disturbance around plover nesting areas increases, the likelihood of a raven finding a plover nest also increases (Hardy and Colwell 2012).

In Humboldt County, California, the breeding population of plovers continues to fall below recovery goals (USFWS staff, personal comm.) with a breeding population of adults sustained by immigration from more productive areas, leading to this population being defined as a sink (Colwell et al. 2019). Extensive efforts in habitat restoration and protection, public outreach and education, and use of non-lethal predator management strategies have been utilized to improve snowy plover reproductive success (USFWS unpublished report) though a rich body of local research documents raven predation on plover eggs (and chicks, to a lesser extent) as the main barrier to plover breeding success and population recovery (Hardy and Colwell 2012; Feucht et al. 2019). Because of this, lethal removal of ravens was proposed in 2012, but public criticism prevented this strategy from moving past the proposal stage (Clucas 2021). While ongoing management efforts have been beneficial in promoting and restoring plover nesting activity and safeguarding nests from human disturbance, predation by ravens continues to be severe enough to offset all protective efforts (Feucht et al. 2019).

Snowy plover monitoring efforts in Humboldt County are extensive, with bi-annual population counts occurring at the peak of the breeding and wintering seasons and approximately twice-weekly productivity checks during the breeding season in all locations where breeding activity is occurring (Colwell et al. 2012, Raby 2018). In most nesting areas, adults and chicks receive unique color bands and individuals are monitored closely to determine reproductive success, movement, and survival of nests, adults, chicks, and fledglings. Habitat restoration involving the removal of invasive European beach grass (*Ammophila arenaria*), propagation of native dune species, and deposition of weathered oystershell to provide the sparse debris characteristic of preferred plover nesting habitat is carried out regularly at many sites, including two large habitat restoration areas (HRA) (approximately 20 hectares and 18 hectares in size) and six restored lagoon (3) and beach (3) sites (Leja 2015, personal comm. with CA State Parks and USFWS staff).

While ongoing monitoring and research continues to document ravens as a significant barrier to snowy plover recovery (e.g. Strong et al. 2021), no work to-date has focused on understanding the landscape-level resources utilized by ravens visiting snowy plover nesting beaches (similar work carried out for raven food subsidies and nesting structures related to conservation of Greater sage-grouse and desert tortoise is extensive, e.g., Coates et al. 2016). My study aims to address that gap in knowledge by identifying food and other resources utilized by beach-going ravens, especially sources of human food that can be mitigated by management agencies.

Using GPS units, stable isotope analyses, and behavioral surveys, I address three main objectives in this project. The first objective is to use GPS units to develop an understanding of where beach-going ravens are moving on the landscape and, specifically, where they are finding food. GPS data can identify many aspects of beach-going raven natural history, including core area and home range sizes, seasonal and demographic variation in movement, and, most importantly for this study, locations of food sources. Locations which are repeatedly visited could reveal human food sources agricultural or residential areas and identifying these areas can provide management agencies with regions, and potentially individuals, on which to focus outreach and education efforts. The second objective in this project is to use stable isotope analysis (SIA) to quantify raven diet, especially trophic level and variation between individuals and over time. Quantifying the diet of ravens using snowy plover nesting beaches will help understand the habitats and areas where ravens are accessing food resources. Finally, I am also using behavioral surveys to describe raven behavior on beaches as a means of informing snowy plover management strategies. Previous research has shown a negative correlation between raven density and snowy plover nest success (Burrell and Colwell 2012), so examining raven behavior on beaches to determine if behavior may provide additional insight into predation risk for snowy plover nests could prove useful.

Using these three approaches, I aim to better understand the causal factors of high raven abundance in coastal Humboldt County to inform management of ravens around snowy plover nesting areas. Importantly, results of this study will likely be applicable to additional species predated by ravens, especially other species associated with beach habitats including the California least tern and marbled murrelet, as well as unlisted species that ravens are known to predate heavily, such as nesting seabirds and waders (Kelly et al. 2005, Coates et al. 2021). Understanding raven movement patterns and core area sizes, their utilization of human food subsidies, diet, and how ravens use snowy plover nesting beaches can help identify the important sources of anthropogenic food ravens are accessing. In turn, this can inform management agencies of key areas to focus mitigation to decrease raven subsidies and allow raven populations to decrease closer to natural levels. This work will highlight the causal factors of high raven abundance locally with the intention of informing landscape-level mitigation efforts that benefit not just the sensitive species that ravens predate, but also the less well-studied common species likely impacted by inflated populations of this generalist predator.

STUDY AREA

Humboldt County is approximately 430 km north of San Francisco, California and has a Mediterranean climate with warm, wet winters and cool, dry summers. Average monthly temperatures on the coast range from 7.7 to 14.4 C and rainfall averages 0.09 meters per month (NOAA 2024). The study area consists of mostly flat land with small drainages entirely within 50 m of sea level. Many sources of fresh and salt water are present in the study area, as is extensive Coastal Redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forest and harvested timberland, agriculture (especially alfalfa and hay, small goat and cow dairies, and small vegetable farms), and forested public parks. Human development in the region is sparse and dispersed, with the urban centers of Eureka and Arcata having populations of 26,512 and 18,857, respectively (US Census Bureau 2024).

Raven captures and collection of feathers for stable isotope analysis were conducted on ten current or historic snowy plover nesting beaches. From south to north, these beaches include Centerville Beach, South Spit, North Spit, Ma-le'l Dunes, Mad River Beach, Clam Beach, Little River State Beach, Big Lagoon, Stone Lagoon, and Gold Bluffs Beach (Figure 1). Behavioral surveys occurred on 7 of these beaches (excluding Centerville, South Spit, and Gold Bluffs Beach). Most beaches in this study are managed or co-managed by public agencies including California State Parks, California Department of Fish and Wildlife, US Fish and Wildlife Service, Humboldt County Department of Parks and Recreation, and the Bureau of Land Management. Two sites are managed by nonprofit organizations, Friends of the Dunes and The Wildlands Conservancy, and both of these properties are either restored native dune habitat or are in transition towards becoming so.

Figure 1. Map of study area showing locations where ravens were tagged with GPS/GSM units and feathers were collected for stable isotope analysis (black circles and blue triangles) and where behavioral observations of ravens took place (blue triangles).

All beach sites consist of various amounts of habitat dominated by European beach grass (*Ammophila arenaria*) and patches of restored, native dune species such as coastal sand verbena (*Abronia latifolia),* Common yarrow (*Achillea millefolium)*, and Beach morning glory (*Calystegia soldanella*). Most foredune restoration was enacted explicitly to restore snowy plover nesting habitat and several beaches also undergo nearly annual deposition of weathered oyster shell by hand or tractor on top of expansive patches of open, dry sand to encourage plover nesting activities. The oyster shell mimics the sparse debris amongst which snowy plovers prefer to nest and is intended to provide more cryptic nesting habitat. This shell requires annual renewal because it typically gets buried by sand from higher winter tides. Some beaches are directly adjacent to developed urban centers, some are surrounded by agriculture, some are on spits bordered by ocean, bay, or wetlands, and others are bordered by extensive swaths of evergreen forest.

In October 2022, wild birds in the study area began testing positive for highly pathogenic avian influenza (HPAI H5N1), including ravens involved in this study (Appendix B) as well as Western snowy plovers (USFWS staff, personal comm.). This disease caused an unprecedented die-off in many populations of wild and domestic birds, and impacts of the outbreak on ravens and snowy plovers will be considered in the results and discussion sections. At the time of writing, this strain (H5N1) was still circulating along the Pacific Coast and continuing to pose a significant problem for wild birds and domestic poultry (Centers for Disease Control 2024).

METHODS

This study aims to understand the movement, diet, and behavior of ravens using snowy plover nesting beaches with three methods; 1) GPS/GSM units to track raven movement, 2) stable isotope analysis of raven feathers to compare diets, and 3) behavioral surveys of beach-going ravens to better understand behaviors associated with ravens present in snowy plover nesting habitat. Each strategy is addressed in a distinct section below.

GPS/GSM Data

To monitor the movement and resource use of beach-going ravens, I used two types of GPS/GSM units: ES-400 and ES-420 Evolution Series GPS loggers (Cellular Tracking Technologies, USA). These units collect data on location, turn angle, speed, and a relative activity index using satellites (GPS), then they transmit the data through cellular towers (GSM). Each unit has an on-board battery charged by a small solar panel on top of the unit and settings are programmable remotely through an online portal. Configuration settings were optimized for each individual raven based on maintaining a sufficient battery charge, which was impacted by factors such as feather coverage of the solar panel, geographical constraints impacting access to cellular towers, and mitigation of individual unit problems, such as broken battery thresholds that occurred on several units which required high collection rates to keep the battery charge low to avoid overheating the unit. Location collection settings ranged between every 15 minutes to every two hours and all units were programmed to collect data from nautical sunrise to nautical sunset and to relay data daily, typically at noon when the probability of clear connections with satellites was optimized. Additionally, one GPS/UHF unit (Ecotone Harrier) was used. This unit lacked a solar panel and collected data once an hour continuously until the battery died, relaying data to a pre-positioned base station.

All GPS units were field-tested to ensure proper function before deployment and to estimate accuracy and precision. During field trials, units were attached to a backpack and hiked on beaches and adjacent forested, urban, and agricultural habitats in the study area while a separate hand-held GPS unit was used to monitor location. The average latitudinal/longitudinal error of all units was less than 5 meters across all habitat types, but altitudinal accuracy was shown to be highly inaccurate so it was not used in subsequent analyses.

Raven capture and GPS attachment

I captured ravens using a remotely triggered net launcher that uses .22 caliber blanks to project a weighted 5-meter by 5-meter net on top a baited location. Grass and other lightweight materials were used to camouflage the net launcher, which was placed on the ground, and a small amount of food bait and food trash was placed two meters in front of the net launcher to lure in ravens. Most capture locations were parking lots with the baited area observable from inside a nearby vehicle, and the net was launched when the raven was in the proper location and no people, cars, or other species were within range. For non-parking lot locations, observations occurred from behind rocks or other features to remain out of site of the ravens.

Once captured, ravens were immediately removed from the net, placed in a cloth bag and weighed with a spring scale. I collected several morphometric measurements and if the bird was of sufficient weight such that added materials did not exceed 3% of the bird's body weight, I attached a GPS unit. Morphometric measurements included un-flattened wing chord, tail length, footpad length (distal tip of central toe to distal tip of hallux), culmen length (distal end of nares to tip of bill), tarsus length, visual checks for cloacal protuberances, brood patches, muscle, and fat, and visual assessments of feather fade and wear, molt limits in the flight feathers and coverts, eye color, and color of the inside of the mouth. I used feather wear, molt limits, and mouth color to determine bird age, with second-year (SY) birds having the presence of uniformly worn, brown feathers in the coverts and flight feathers plus a mostly pink mouth in January – June or exceptionally worn, brown flight feathers contrasting with glossy newly molted black feathers and some amount of pink in the mouth in July through December. Uniformly black, glossy feathers and little to no pink in the mouth indicated an after second year (ASY) bird. Hatch year (HY) birds were obviously identifiable by the presence of a gape (brightly colored skin on the outside of young birds' mouths), very pink inner mouths, and (anecdotally) incessant calling and movement during handling. While measurements were collected, a lightweight cloth bag was placed over the raven's head to limit visibility, which substantially calmed all birds during the handling process.

When breeding characteristics were not observed, five breast feathers were pulled for sex determination and sent to Animal Genetics Lab, LLC (Florida, USA). The distal ends of 1-3 tail feathers (typically right rectrix (RR)1, RR3, and RR5) were clipped from each raven for stable isotope analysis. GPS harnesses were hand-made from 3 mm Teflon ribbon (Bally Ribbon Mills, PA USA). GPS attachment involved using either a back-mounted harness, whereby the harness material crossed the bird's chest in an X-shape and the unit sat in the middle of the back below the nape, or a rump-mounted/leg-loop harness, whereby the harness straps on either side of the unit went around the inside of a leg, did not cross the body, and the unit sat centered on the bird's back above the uropygial gland above the tail (see Bedrosian and Craighead 2007 for more detail). Body feathers around the GPS unit were trimmed using small scissors and a 5 mm neoprene pad was glued on the underside of each unit to help raise the solar panel to access sunlight.

In addition to the GPS units, a standard butt-end United States Geological Survey (USGS) numeric band was placed on one leg and a purple aluminum band with a unique alpha-numeric combination secured with rivets was placed on the opposite leg. In 2023, ravens were also given a unique combination of colored plastic leg bands to ease field identification of individuals, as the purple metal bands were observed fading over time and were not easy to read in the field. Birds that were not of sufficient weight to receive a GPS unit were given a USGS metal band and, in 2023, also given unique combination of colored plastic leg bands.

<u>Analysis of GPS data</u>

In this analysis, home range is defined as the area regularly travelled by an individual to carry out normal activities excluding sallies and occasional explorations (Burt 1943), whereas core area is defined as that area within the home range with a higher intensity of use by individuals. In this project, I used each raven's innermost 95% of locations to define home ranges and the innermost 50% of locations was used to define core areas (Loretto et al. 2016). Home range and core area data were determined using data from the entire sampling duration for each individual raven, as well as by season, differentiating between the breeding season and the nonbreeding season. The breeding season was identified each year based on field observations of ravens carrying nesting material. Additionally, to address the possibility that the longer an individual is tracked, the larger its home range/core area might be, I also calculated home range and core area sizes for all ravens standardized for the shortest tracking duration observed in this study. I compared home range sizes by season to see if they were significantly larger in either the breeding season or the nonbreeding season using Welch's t-test. This test was selected because the sample sizes were unequal between the two seasonal groups and because there was some overlap between populations in each group, e.g., there was breeding and nonbreeding season data from some, but not all, ravens.

To understand raven space use across the landscape, I developed a Resource Selection Function (RSF) to evaluate the influence of a set of biologically relevant covariates on raven resource use. For the RSF, Minimum Convex Polygons (MCP) using the innermost 95% of GPS points for each raven were created and known raven location points within these areas were labelled as "use" locations. For each raven, a 5-meter buffer was created around all used locations within a raven's respective 95% MCP, all these buffered areas were removed from the MCP polygon, and from the remaining space, 10 times the number of used locations were randomly generated (ArcGIS Pro version 10.1). These random locations were labelled as “available”; since location data are not continuously collected for each raven, it cannot be stated with certainty that the randomly generated points were not, at some point, actually used by the ravens, thus they are “available” points, not “unused.”

The covariates evaluated in the candidate models included distance to major roads (speed limit ≥ 88.5 km per hour), distance to minor roads (speed limit < 88.5 km per hour), and distance to the following land cover types: low, medium, and high development, beach, evergreen forest, mixed forest, deciduous forest, emergent wetland, woody wetland, pasture, developed open space, and water. Values for road data were obtained from Humboldt County and Del Norte County websites and landcover data were obtained from the United States Geological Survey National Landcover Database (USGS NLCD) 2021 raster data. I evaluated the impact of landcover types at multiple spatial scales by first creating a binary raster of each landcover type in ArcGIS Pro, then I used a moving window in R (terra package, R version 4.2) to calculate the percentage of each landcover type in “windows” at each spatial scale. The spatial scales assessed include 30 m, 60 m, 90 m, 120 m, 150 m, 180 m, 210 m, 250 m, and 500 m moving windows.

To refine the number of covariates used in model development, univariate models were created for each landcover type at each spatial scale. The optimal spatial scale was identified as the model with the lowest AIC for each landcover type (with “use” as the response variable) and this optimal spatial scale was retained for each landcover type. Then univariate models were created to compare the “distance to” for each landcover type with the optimal spatial scale and retained the covariate with the lowest respective

AIC so that only one covariate for each landcover type was included in model development. Finally, univariate models with single variables were compared to broader groups and either the single variable or the grouped variable was selected for model development based on lowest respective AIC values. This singularity vs. broader grouping applied to roads (fast and/or slow), forest habitat (evergreen, mixed, and/or deciduous), wetland habitat (emergent herbaceous and/or woody), developed habitat (low, medium, and/or high), and agricultural habitat (cultivated crops and/or pasture). Once covariates were selected, a candidate model set of Generalized Linear Models (GLM) was developed with use as the response variable and a binomial distribution. A global model, null model, and models with covariates from agriculture, natural plant communities, and human features were developed (Webb et al. 2009, Coates et al. 2016). The model with the lowest AIC and highest weight was selected as the top model. Using values from the top model and raster data from covariates included in that model, a predictive map was generated in R using the "raster" package.

Night roost locations were identified using GPS locations collected at least 30 minutes after sunset or at least 30 minutes before sunrise. Previous research observing raven roost use found that ravens arrived at roost locations in the evenings over a period of an hour before sunset, departed roosts at dawn, with movement between roosts during the night occurring infrequently (Marzluff et al. 1996, Loretto et al. 2017, Engel et al. 1992). To identify night roost locations, points collected at least 30 minutes after sunset or at least 30 minutes before sunrise were selected as these locations serve as a moderately conservative analysis of raven night roost location. Unique roost locations were then defined as locations more than 100 m apart and the ArcGIS tool "Integrate" was used to collate points within a 50-m radius to a single location which fell in the middle of those points. Night roost data were summarized for each raven as the total number of unique roosts per individual utilized throughout the study and habitat data from the USGS NLCD 2021 landcover dataset was attached to night roost locations using the "Extract Values to Points" tool in ArcGIS Pro to calculate the number of night roost locations in each habitat type. It's important to highlight that night roost data were collected opportunistically and are not standardized for tracking duration or number of points per night.

Stable Isotope Analysis

Stable isotopes are discrete isotopes of elements defined by the number of neutrons in their nuclei. Stable isotopes do not degrade over time and they are conserved through the food web and are highly useful for investigating animal diet. Stable isotope analysis (SIA) involves quantifying the ratio of light to heavy stable isotopes in a tissue using the following formula, with results reported in parts per thousand or "per mil" (‰):

$$\delta X = \frac{ratio_{sample}}{ratio_{standard}} - 1$$

This formula can be read as the isotopic signature of an element X (δX) is equal to the ratio of heavy to light isotopes in the sampled tissue divided by the ratio of heavy to light isotopes in an internationally recognized standard reference material, minus one. For carbon, the standard reference material is Vienna PeeDee Belemnite (VPDB), for nitrogen it is atmospheric nitrogen (air), and for sulfur it is Vienna Canyon Diablo Troilite (VCDT).

For these three elements used in this project, the ratios of the isotopes ^{13}C to ^{12}C, ^{15}N to ^{14}N, and ^{34}S to ^{32}S were used in analyses. Carbon ($\delta\,^{13}C$) is conserved across the food web which makes it useful for looking at general diet composition. Nitrogen ($\delta\,^{15}N$) is useful for examining the trophic level of consumed items, with an increase or decrease of 2-3‰ $\delta\,^{15}N$ within a sample corresponding to an increase or decrease, respectively, in trophic level of diet items. Berries and seeds, for example, have a mean $\delta\,^{15}N$ signature of +0.10‰ whereas insects have a mean $\delta\,^{15}N$ signature of +3.20‰ and terrestrial meat from human food sources has a mean $\delta\,^{15}N$ signature of +5.20‰ (West et al. 2016) (these values may vary slightly by geographic location, but the relationship between values would be relatively consistent). Due to excretion in waste of lighter nitrogen isotopes, animals are typically enriched by 5‰ in nitrogen compared to their diets (Peterson and Fry 1987).

Finally, in the context of this research, sulfur ($\delta\,^{34}S$) is useful for differentiating marine vs. terrestrial origin of food sources due to the differing sulfuric content of the underlying geological processes of each, so it is useful for assessing whether ravens were eating predominantly food from marine or terrestrial origin. Similar to carbon, sulfur is conserved across the food web, so sulfur signatures of consumers generally reflect those of their prey. Terrestrial vegetation typically ranges between +2 to +6‰ $\delta\,^{34}S$ whereas marine vegetation has a much higher value and ranges from +17 to +21‰ $\delta\,^{34}S$ (Peterson and Fry 1987). Sulfur can also be useful in differentiating signatures of consumer from those of prey when nitrogen and carbon values are similar between the two (Connolly et al. 2004).

To conduct stable isotope analysis, 50 mm distal ends of rectrices were collected (cut) from each GPS-tagged raven during processing. Feathers, rather than blood, were selected for dietary analysis because their collection is less invasive and feathers are easier to store and prepare for analysis. Feathers reflect diet during the period in which they are grown (Hobson and Clark, 1992), with ravens' central tail feathers getting replaced in May, taking approximately two weeks to complete growth. Tail feathers are grown sequentially from R1 to R6 on both sides, with the outermost feathers (R6) typically replaced in October (Pyle 1987). Thus, by sampling the central tail feathers, I sampled the window of time most relevant for peak snowy plover breeding activity, allowing insight into raven diet during that crucial period of time relevant for snowy plover reproduction. For ravens captured at the beginning of the study, only one feather was sampled, typically the right central tail feather (RR1). In subsequent ravens, multiple feathers (typically RR1, RR3, and RR5) were sampled to quantify temporal diet variation. If a raven was captured during an active molt, additional feathers were sampled to capture interannual variation, e.g., both old and new feathers were sampled regardless of whether they were RR1, RR3, and RR5.

To prepare feathers for isotopic analysis, all samples were soaked in methanol for 24 hours, dried in an oven at 140 degrees F for 24 hours, cut into small pieces using scissors, weighed on a microbalance in disposable paper weigh boats, and encapsulated in 8.5 mm or 10 mm tin capsules at Cal Poly Humboldt's Anthropology Lab facilities.

Samples were prepared for sulfur analysis with a sample weight range of 2-3 micrograms and combined carbon and nitrogen analysis with a sample weight range of 1.5-3 mcg. Encapsulated samples were stored in a labelled 96-well plate in a humidity-controlled chamber to keep them dry until all samples were prepared, then they were mailed to the Stable Isotope Facility at University of California, Davis for analysis. Samples were analyzed for three stable isotopes: carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) at this facility, which uses a mass spectrometer to analyze the gases produced by samples as they are combusted and the ratio of heavy to light isotopes for each element are reported. Results are reported in relation to (e.g., higher or lower than) an internationally-recognized, constant standard reference material for each element.

Analysis of stable isotope data

Using $\delta^{13}C$ values to understand diet composition requires modeling for an omnivorous species such as the raven, which is beyond the scope of this thesis but will be investigated in subsequent analyses, so reporting of $\delta^{13}C$ here is simply descriptive. Values of $\delta^{15}N$ are compared directly with reference items from published literature to describe the trophic level at which sampled ravens were eating. Values of $\delta^{34}S$ are also compared directly with terrestrial and marine sources from published literature to identify broadly which ravens were eating food of terrestrial or marine origin. Raw values from these three isotopes are used in combination to make direct comparison and assess variation between individuals, within individuals over time, and between locations within the study area.

Behavioral Surveys

Behavioral surveys were conducted at 7 sites with current or historic snowy plover nesting activity: North Spit, Ma-le'l Dunes, Mad River Beach, Clam Beach, Little River State Beach, Big Lagoon (south), and Stone Lagoon (Figure 1). All sites are characterized as coastal beaches with extensive wave slopes and foredune covered by sparse shell, driftwood, and vegetation, which are representative of preferred nesting habitat for snowy plovers. Some sites are restored to native vegetation (Stone Lagoon, Big Lagoon), others contain large habitat restoration areas (Ma-le'l Dunes, Little River Beach), some are almost entirely unrestored invasive grasses (Clam Beach, North Spit), and one site consists of a naturally restored area maintained by tidal over wash (Mad River Beach). All sites except Mad River also include areas of dense vegetation in the back dune. Human use and impact at these 7 sites varies, with low impact sites characterized by low human visitation rates (Mad River Beach) and prohibition of all non-human animals (Big Lagoon, Stone Lagoon), moderately impacted sites characterized by heavier human use, allowance of voice-controlled or leashed dogs, and some horse use (Clam Beach, Little River, Ma-le'l Dunes), and high impact sites allowing motorized vehicles, dogs, horses, and fires on the beach (North Spit).

Behavioral surveys were performed during the plover breeding season from March to August, 2022 and March to August, 2023. Surveys at all sites were conducted twice a month until plover nesting began (April 11 in 2022 and April 20 in 2023), after which, surveys were performed weekly at all sites. Each week, the survey day of the week (Monday through Sunday) was selected randomly using a random number generator independently for all sites. Survey times were either morning (sunrise to 4 hours past sunrise) or afternoon (4 hours after sunrise to 2 hours before sunset). Initially, evening surveys (2 hours before sunset to sunset) were also performed, but no ravens were observed on beaches during evening surveys, so this time period was dropped after several weeks in 2022 and not used in 2023. Survey timing for the first survey at each site was selected randomly using a random number generator (1 or 2 corresponding with morning or evening) and subsequent surveys at each site alternated between the two time periods.

Surveys began from the same location for each site and each survey lasted approximately 1 hour. The surveys consisted of walking the survey route along the wave slope at all sites except Mad River, where surveys were stationary and conducted from a parking lot overlooking the beach. Focal sampling was conducted when at least one raven was present. To avoid observer bias in selecting ravens to observe, if more than one raven was present the surveyor counted the total number of ravens present and then used a random number generator to select a number within that range. The raven to be observed was selected from the group by counting from left to right, with the left-most raven being raven 1, and the randomly generated number being the raven that was observed. Surveys were conducted by pairs of trained field assistants, with one surveyor observing and the other recording data, or by myself or more experienced trained field assistants using an audio recorder. We recorded raven behavior every 30 seconds (2022) or every 10 seconds (2023) and observations lasted up to 10 minutes for an individual bird. If, after 10 minutes, additional ravens were still present, another observation followed on a different raven. Due to the variability in raven use of these 7 sites, surveys did not consistently cover the same distance. For example, if we surveyed five ravens at the start of the survey, less than 50 m may have been walked in an hour-long survey, whereas if no ravens were observed, more than 2 km could be surveyed over the same period of time.

We recorded 9 unique behaviors during focal individual surveys as well as “Out of Sight” and “Other” (Table 1). In addition to behaviors, we also recorded the total number of ravens present during each hour-long survey as a high count. This high count was conservative, e.g., if two ravens flew south then 3 ravens flew north twenty minutes later, the total raven count was 3, not 5. Weather data including temperature, wind direction and speed, visibility, and cloud cover was collected at the beginning and end of every survey and the total number of people and dogs present was also recorded.

Table 1. Names and brief descriptions of behavioral categories from surveys of Common ravens (*Corvus corax)* conducted on beaches in Humboldt County, California.

Behavior	Description
Exploring	Raven may handle items with its bill and/or feet but is not observed swallowing the item.
Flying	The raven is in flight.
Foraging	Raven is observed swallowing an item. Type of food (natural or anthropogenic) is noted as well.
Hopping	Raven is hopping – moving both legs synchronously.
Perching	Raven is perched on a log or branch or rock, etc. with its talons closed around the object and it is not exhibiting any other behavior (e.g., preening, socializing).
Preening	Raven is using bill to straigten and clean its feathers.
Social interaction	Raven is interacting with other animals by allopreening, sharing or begging for food, bowing, non-agonistic chasing, or aggressive acts such as chasing or harassing; may involve conspecifics or heterospecifics.
Standing	Not to be confused with perching, standing is usually at or near ground level and toes are flat (not wrapped around an object)
Walking	Raven is moving on the ground with legs alternating steps
Out of Sight	Raven is temporarily out of sight, for example because it walked behind a bush or small sand dune. If a bird is out of sight for more than three continuous observations the survey ends.
Other	Raven is exhibiting behaviors observed minimally, such as drinking water, caching food, digging in the sand, or coughing up a pellet.

We also recorded the habitat where ravens spent the majority of their time during the survey. Habitat types included wave slope (wet sand), wrack (materials left behind by most recent high tide), foredune (dry sand facing the ocean), back dune (dry sand facing away from ocean – often sparsely vegetated), vegetation, or air (if the observation occurred while the raven was flying). Several types of events were also tallied during each raven survey: calls, defecations, and bill wipes. After an observation was completed, the events were tallied as a rate of each event per minute based on the duration of the observation.

<u>Analysis of behavioral data</u>

I used a Mann-Whitney test to check for a difference in the number of ravens observed across all surveys at all sites between years. To determine whether results from that comparison were observable in other data, I performed the same test on an external dataset containing raven point count data provided by California State Parks. Briefly, these data were collected during instantaneous point counts of ravens within 500 m of the observer collected every twenty minutes during snowy plover monitoring surveys (see Lau 2015 for a more thorough description of these methods). For analysis of the CA State Parks data, surveys were used from the same time period as behavioral surveys from my research.

To test for differences in the percentage of time behaviors were exhibited based on location, I used an analysis of variance test (ANOVA). If the ANOVA test showed a significant difference ($\alpha < 0.05$), Tukey's Honestly Significant Difference (HSD) test was used to make pairwise comparisons between all locations to determine which locations differed in a statistically significant manner from each other.

A generalized linear model (GLM) was also developed to better understand raven behavior by site. To accomplish this, I first excluded surveys that were less than a minute in length. Then, multiple behaviors presumed to be associated with raven detection of snowy plover nests and chicks were combined into a single response variable called, collectively, "attentive" behaviors. These combined behaviors included foraging, exploring, perching, standing, and walking as these five behaviors represent ravens closely interacting with a site and could reasonably lead to a raven either finding a plover nest by chance or observing a plover moving on/off its nest (see Coates et al. 2021 for correlation between plover tracks leading to nests and plover movement on and off nests being positively associated with risk of raven nest predation). Behaviors excluded from this response variable were not likely to be correlated with ravens finding a plover nest and included preening, socializing, hopping, and flying as these behaviors involve a raven focusing its attention on itself, on other ravens, or on moving quickly, collectively termed "other" behaviors. While ravens can certainly forage while in flight, the behavior of "flying" was most often associated with continuous flight involving a raven leaving the surveyed location, often ending an individual survey, thus it was considered a behavior more closely associated with transit than foraging.

Once combined, behavioral data were arcsine transformed to generate a more normal distribution of the data. A list of 13 covariates were considered for model formation, including temporal variables (year, Julian date, survey start hour, total minutes surveyed), weather variables (temperature, wind direction, wind speed, and cloud cover), environmental covariates (survey location and habitat), and the number of ravens, humans, and dogs present during the survey. A correlation matrix was created (package "PerformanceAnalytics" in R, V. 4.1.2) to evaluate correlations between all continuous covariates, with a Pearson's correlation coefficient (r) greater than 0.6 being considered highly correlated and leading to one of the two variables being selected for removal from further analysis, after which the correlation matrix was re-run until all correlations were less than 0.6. Two pairs of variables were highly correlated; Julian date with temperature ($r = 0.65$) and total number of humans with total number of dogs ($r = 0.72$). The variable perceived to be more relevant to ravens from each of the two pairs was included; Julian date and total number of humans, while start temperature and total number of dogs were removed from subsequent analyses.

I generated a model selection table that included a null model, the global model, and all top models with a delta AICc < 2. Model evaluation was performed using model weight as well as AICc (Akaike's Information Criterion corrected for small sample sizes), with lower AICc indicating a better fit model (Burnham and Anderson, 2004). After running the model, coefficients were back-transformed.

Ethical Note: IACUC

All project methodologies and research were authorized under Institutional Animal Care and Use Committee (IACUC) protocol numbers 2021W4-A and 2021W20.

RESULTS

GPS Data

GPS units were attached to 22 ravens beginning on March 21, 2021 with the last ravens captured on September 1, 2023. This report includes data until January 25, 2024. Collection time periods for each raven ranged from 14 to 973 days (mean 292, SD 240.7) resulting in 85,006 unique GPS locations total. Most GPS units collected data hourly (n = 13), some units collected data every two hours (n = 2), and some units collected data every 30 minutes (n = 6) or 20 minutes (n = 1). Of the 22 tagged ravens, 15 were male, 6 were female, and 1 is unknown sex, 0 were captured as hatch-year birds (HY), 3 were captured as second-year (SY) birds, and 19 were captured as after second-year birds (ASY). Based on GPS data, behavioral observations, and 1 raven with a brood patch present during capture, 7 ravens were breeding birds since capture, 8 did not attempt to nest during the study period, 1 raven switched from non-breeding to breeding during the study, and 6 are unknown based on unavailability of data during the breeding season. Hereafter, breeding ravens are referred to as adults and nonbreeding ravens are called sub-adults, the latter of which includes ravens that are paired but not nesting as well as unpaired ravens. The date of capture/GPS unit deployment, duration of deployment, age and sex of individual, date of last data collection, and collection configuration are described for each raven in Appendix B.

Home ranges and territories

Mean home range and core area size, ranges, and standard deviations are shown below in Table 2 (more details are provided in Appendices C and D). Table 2 includes data from all ravens across all years (AY), differentiates data by season (breeding; BR vs. nonbreeding; NB), and the bottom row shows the same data adjusted for the shortest duration an individual raven was tracked; 14 days, which standardizes tracking duration for all ravens. The breeding season in 2021 was identified as March 1 – August 15, in 2022 as March 1 – August 15, and in 2023 as March 15 – August 15 based on field observations of the timing of ravens carrying structural nesting material indicating they were beginning nesting activities.

Table 2. Home range and core area size for GPS/GSM-tagged ravens. Data includes either all months across all years (AY), the breeding season only (BR), or the nonbreeding season only (NB).

Category	Average Home Range (MCP 95, km^2)	Range, SD (km^2)	Average Core Area (MCP 50, km^2)	Range, SD (km^2)
All data (n = 22)	141.35	2.95 – 1,334.54 (285.78)	10.11	0.21 – 31.77 (10.36)
Breeding season (n = 16)	46.85	1.01 – 114.13 (45.22)	8.00	0.13 – 45.09 (12.91)
Nonbreeding season (n = 18)	119.87	1.78 – 1,044.65 (256.77)	11.49	0.31 – 73.14 (17.81)
First 14 days (n = 22)	13.96	0.53 – 57.58 (16.38)	6.11	0.03 – 39.68 (11.82)

Overall, when examining data from all months and years for all ravens, there was large variation in the sizes of home ranges and core area between individuals, with the smallest raven home range being 2.95 km^2 and the largest being over 1,300 km^2, with an average size of 141.35 km^2 and a standard deviation of over 280 km^2. Core areas averaged 10.11 km^2 with a range of 0.21 – 31.77 km^2. When standardizing for temporal variation by using only the first 14 days of each raven's movement data, home range sizes were almost ten times smaller, averaging 13.96 km^2 and ranging between 0.53 – 57.58 km^2 and core areas averaged 40% smaller at 6.11 km^2 and ranged between 0.03 – 39.68 km^2. The standardized first 14-day home ranges and core area sizes also show variation between ravens (Appendix D). Some ravens' home ranges did not vary much when tracked for shorter periods of time, but most had larger home ranges in accordance with increased tracking duration. Within those ravens, some home ranges were between 2-20 times larger, but the most extreme ravens had home ranges 126 and 764 times larger. Pearson's correlation coefficient was used to determine whether tracking duration was correlated with home range or core area size, but neither were shown to be significantly correlated ($r = -0.239$ and $p = 0.285$ for home range, $r = -0.130$ and $p = 0.564$ for core area).

Separating movement data by season, when including all data for each raven, home ranges were almost three times larger in the nonbreeding season, averaging 119.87 km^2 compared to 46.85 km^2 in the breeding season, although this difference was not statistically significantly different (Welch's two sample t-test; $t = -1.186$, $p = 0.251$; Figure 2). Home range sizes across all years and seasons were roughly stratified by age class, with adults having smaller home ranges and sub-adults having larger home ranges (Appendices C and D), regardless of geographic location.

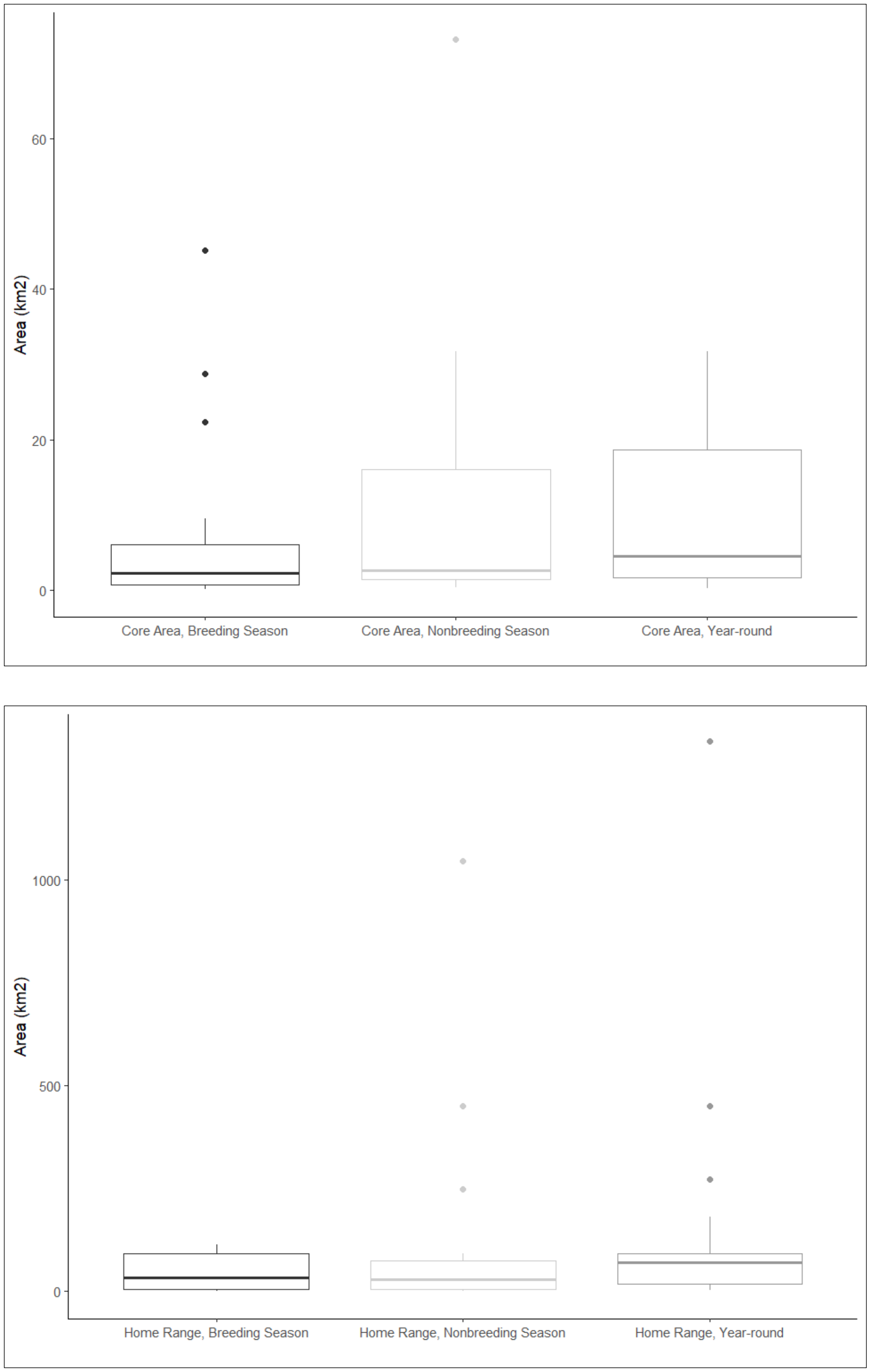


Figure 2. Boxplots showing the mean values, ranges, and outliers of raven home ranges (left) and territories (right) of GPS/GSM-tagged individual ravens.

Resource selection function

For this analysis, all data from all ravens was used until January 25, 2024 (Appendix B). The optimal spatial scales for each landscape variable were the following: 30 m for open water, woody wetland, shrub, barren ground/sand, emergent wetland, evergreen forest, developed open space, pasture, and deciduous forest, 60 m for crops, 120 m for grassland, and 180 m for mixed forest as well as low, medium, and high developed habitat. In developing a RSF, the correlation matrix revealed high correlations ($r > 0.7$) between two covariates, so one was excluded from subsequent analyses: distance to grassland habitat (highly correlated with distance to scrub, $r = 0.71$). The covariate selected for exclusion was presumed less important for raven ecology than that retained, and univariate models comparing grassland to scrub habitat produced a lower AIC for distance to scrub habitat. Distance to mixed forest and deciduous forest were both highly correlated with distance to evergreen forest ($r = 0.88$ and $r = 0.82$, respectively) so the three forest types were combined into a single distance to forest category. Similarly, distance to high, medium, and low developed habitats were strongly correlated with each other ($r = 0.72$ for medium and high, $r = 0.86$ for medium and low, $r = 0.61$ for low and high) so they were combined into a single covariate - distance to developed habitat. Univariate model selection based on lower AIC for the better model compared “distance to” versus the optimal spatial scale for each landcover type and resulted in covariates for distance to crops, distance to forest, and distance to barren land/sand being excluded from further analyses, with the optimal spatial scale for each respective covariate being retained instead, and vice versa for all other landcover types.

Crop habitat was ultimately removed from analysis as it was not present in most ravens' home ranges and it was minimally present on the landscape. A candidate set of 9 covariates were included in model development (Table 3). Continuous variables were centered and scaled to better compare relative influence of these variables on raven resource selection.

Table 3. Covariates examined in a Resource Selection Function developed to assess features important to raven resource selection.

"Distance to" Covariates	Optimal Scale Habitat Covariates
1. Distance to all roads	8. % evergreen forest (30 meters)
2. Distance to all development	9. % barren/sand (30 meters)
3. Distance to pasture/hay	
4. Distance to developed open space	
5. Distance to snowy plover nesting areas	
6. Distance to all wetland	
7. Distance to scrub	

I generated a candidate model dataset for a generalized linear model (GLM) with unique models representing anthropogenic features, natural plant communities, and agriculture (Webb et al. 2009) as well as a global model, a null model, and a model with only distance to snowy plover nesting habitat. Results are shown below (Table 4). The top model was identified by having the lowest respective AIC relative to other models (Table 5).

Table 4. Candidate model set of Generalized Linear Models (GLM).

Model ID	Covariates included	AIC	Model Weight
Global	All (1-9)	523858	1.0
Snowy plover	5	547485	0
Natural plant communities	6-9	547756	0
Agriculture and Anthropogenic	1-4	553523	0
Anthropogenic	1, 2, 4	554135	0
Agriculture	3	568844	0
Null model	None	569712	0

Table 5. Covariates and their respective influence on raven resource selection as defined by the top model. A positive value for a distance indicates a covariate was selected against by ravens, and vice versa, whereas positive values for percentages indicate attraction, and vice versa.

Features	Coefficient	Direction of Influence	Standard Error
Intercept	-2.718	NA	<0.01
% Barren/Sand	1.100	Attraction	<0.02
Distance to snowy plover nesting areas	-0.556	Attraction	<0.01
Distance to development	-0.570	Attraction	<0.02
Distance to scrub	-0.116	Attraction	<0.01
% Evergreen Forest	0.242	Attraction	<0.02
Distance to wetland	-0.582	Attraction	<0.01
Distance to developed open space	0.119	Avoidance	<0.01
Distance to pasture	0.189	Avoidance	<0.01
Distance to roads	0.025	Avoidance	<0.01

The equation for the top model from the GLM includes covariates and their respective attraction or avoidance values above in Table 5. For this top model, p-values for all covariates were <0.001 with standard error <0.02 for all variables. Interpreting the effect of “distance to” covariates in this model is counterintuitive in that a negative value for a “distance to” covariate indicates that ravens were selecting against greater distances. In other words, they are selecting for the covariate feature. Thus, negative values for “distance to” features indicate attraction whereas positive values indicate avoidance. The top model was the global model and the covariate with the strongest relationship with raven location use was barren land/sand which had a positive association with raven resource selection. It's important to again note here that ravens tracked in this study were captured at the beach, so results from this model are applicable to beach-going ravens. The second strongest relationship was distance to wetland habitat which was positively associated with raven resource use. Importantly, raven resource selection was also positively associated with snowy plover nesting areas. For the other covariates, raven resource selection was slightly positively associated with distance to developed areas, scrub habitat, and forest and slightly negatively associated with distance to developed open space, pasture, and roads, though the strength of the relationship with all avoided covariates is not strong.

The sign (negative or positive) for all covariates was the same across all models except distance to road and distance to pasture. The distance to road covariate was very slightly negatively associated with raven location in the top model (0.028) and positively associated with raven location in the combined agriculture and anthropogenic, agriculture-only, and anthropogenic-only models. Distance to pasture was selected against in the global model and the combined agriculture and anthropogenic model but when considered by itself in the agriculture-only model it was an attractive feature to ravens. A predictive map was generated using values and covariates from the top model to show the likelihood of resource use by beach-going ravens across the landscape is shown below, with likelihood of use denoted by color and quantified in the legend (Figure 3).

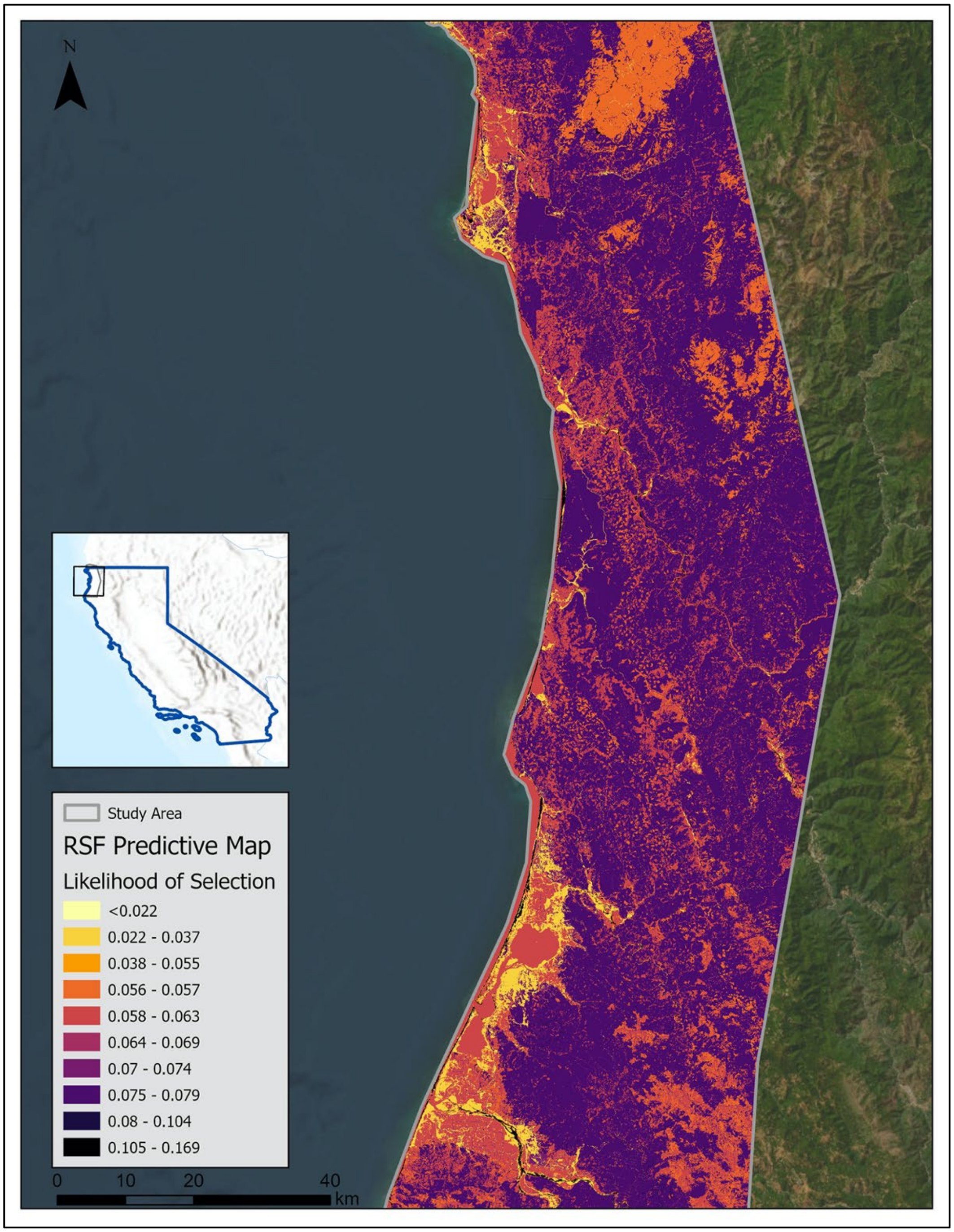


Figure 3. Predictive map showing the likelihood of beach-going ravens using resources across the landscape generated using values and covariates from the top Resource Selection model.

<u>Night roost locations</u>

In total, 6,074 night roost locations were identified for 20 ravens from 806 individual raven-nights, the range of night roost locations for ravens varied largely between 5 – 1147 locations with a large standard deviation of 354.3. The majority of all night roost locations were located in evergreen forest habitat (47.0%) and evergreen forest was the dominant night roost habitat type for 15 ravens. The second and third-most dominant habitat types were mixed forest (13.2%) and developed open space (12.6%) which were the dominant roosting habitat types for 1 and 2 individual ravens, respectively (Table 6). The dominant roosting habitat types for the remaining two ravens were emergent herbaceous wetland and pasture/hay, the latter of which likely consists of human structures such as barns within hay fields. Besides two ravens which were a known pair, none of the ravens from this study ever roosted in the same location on the same night as other tagged ravens. On a single occasion two different birds roosted approximately 200 meters from each other on the same night, but for the remaining 6,073 occasions, tagged raven night roost locations were geographically much further from each other. After collating points within 100 m of each other, the total number of unique roost locations decreased by 655 to 5,419 unique roost locations.

Table 6. Habitat type associated with raven roost location based on data from 20 ravens representing 6,419 unique roost locations. Habitat type data were obtained from USGS NLCD 2021 landcover.

Habitat Type	No. Roosts in each Habitat Type	No. Ravens roosting dominantly in each habitat type
Evergreen forest	2857	15
Mixed forest	801	1
Developed open space	763	2
Emergent herbaceous wetland	594	1
Developed – low intensity	275	0
Woody wetland	238	0
Shrub/scrub	216	0
Pasture/hay	121	1
Developed – medium intensity	80	0
Grassland/herbaceous	50	0
Barren land (rock, sand)	32	0
Open water*	20	0
Deciduous forest	16	0
Developed – high intensity	4	0

*The habitat type for 20 night roosts was identified as open water, which is certainly an unsuitable night roost location. Based on examination of these points comparing assigned landcover categories with 0.6 meter satellite imagery, in some cases the assignment of "water" as the habitat type is due to the large spatial resolution of the landcover data (30 by 30 meter resolution) misidentifying forest as water (n = 2), in some cases it is most likely GPS error (n = 3) based on repeated use of a location over multiple nights or within the same night for multiple hours, and some cases weren't able to differentiate between these two options (n = 13). In other cases it is likely due to the raven actually being located over water, indicating the raven either arrived at a roost >30 minutes after sunset or left a roost in the morning >30 minutes before sunrise (n = 2). Existing literature on raven night roost arrival and departure timing indicates infrequent outliers such as the arrival or departure of ravens to a roost exceptionally early or late (e.g., Marzluff et al. 1996, Engel et al 1992).

Stable Isotopes

In total, I collected 48 feathers from 17 individual ravens. Of these 17 individuals, 5 ravens had a single feather collected (typically R1, the central rectrix, grown during June of each year) and 12 ravens had more than 1 feather collected (typically R1, R3, and R5) (Appendix E). Of the sampled individuals, 6 ravens were captured during an active molt, so feathers grown in the current year and the previous year were present simultaneously, 2 ravens were recaptured after a complete molt cycle had taken place, and 4 ravens were recovered after a mortality event (all confirmed or suspected Highly Pathogenic Avian Influenza H5N1, see Discussion); additional feather samples were collected from all of these birds, thus data from multiple years was available for these ravens. There is some overlap in the preceding groups, and in total 7 ravens had feathers sampled representing two or more years (Appendix E).

The mean value for $\delta^{13}C$ for all ravens was -20.48‰ (SD of 2.01) with a range of -24.98 to -17.12‰ (Figure 4). The lowest carbon signatures were documented in a pair of birds that stayed predominantly in agricultural habitats (and have never been documented at the beach; ravens 1D and 1E). Higher carbon signatures did not obviously correlate with location or habitat types as indicated by the shapes, representing general geographic location, in Figures 4 and 5 being relatively mixed and not obviously segregated within the figure. For ravens with multiple feather samples tested, carbon signatures were relatively consistent for some individuals, as indicated by the tight grouping of points (Figures 4 and 5; ravens 1D, 1E, 2S, 53, and 72) but varied more in others, as indicated by the greater range between points for each raven (Figure 4; ravens 1B, 2M, 54, 71, 75, and 85). No obvious patterns based on age class or sex were apparent in values for carbon isotopes.

The mean value for $\delta^{15}N$ from all samples was 10.31‰ (SD of 1.66) with a range of 7.41 to 15.16‰ which represents a difference of three to four trophic levels within all samples (Figures 4 and 6). Three ravens, each with just a single feather sampled, had the three highest levels of nitrogen (ravens 97 followed by OK and 41) indicating that during the period in which the sampled feathers were grown, they were eating highest on the trophic level relative to all ravens within this sample. The two highest of these, 97 and OK, are two of the northern-most ravens with home ranges consisting of beach, forest, and minimal developed areas. The three southern-most ravens with home ranges largely consisting of agriculture had highly stable levels of nitrogen among their samples (ravens 1D, 1E, and 1B, all values within <1.0‰ of each other), which was also true for 53 but not true for any other raven with multiple samples. The individuals with the highest variation in $\delta^{15}N$ included raven 2M followed by raven 85 and raven 75. Both ravens 2M and 75 were unpaired sub-adults, while raven 85 was a nesting adult.

Finally, the mean value for $\delta^{34}S$ was 10.26‰ (SD of 3.84) with a wide range of 3.81 to 18.86‰. As with values for nitrogen, 97 and OK, the two northern-most captured ravens, had some of the higher values for sulfur but had only a single sample available for testing. Ravens 85, 54, and 41 also had some of the highest values for sulfur. The ravens with the two lowest values also had samples with mid-range and higher values, specifically raven 2M, with samples ranging from 3.81-14.09‰ and raven 2U with values ranging less drastically between 5.34-8.32‰, indicating flexibility in diet containing sulfur.

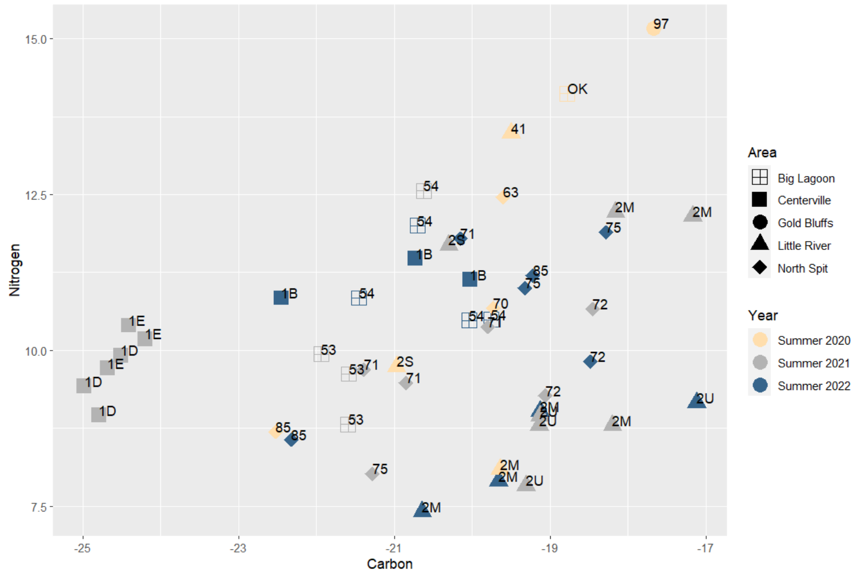


Figure 4. Scatterplot of carbon (δ13C) and nitrogen (δ15N) stable isotopes obtained from raven feather samples. Samples are labelled by the alphanumeric leg band of the raven from which they were collected and color and shape correspond to year and location.

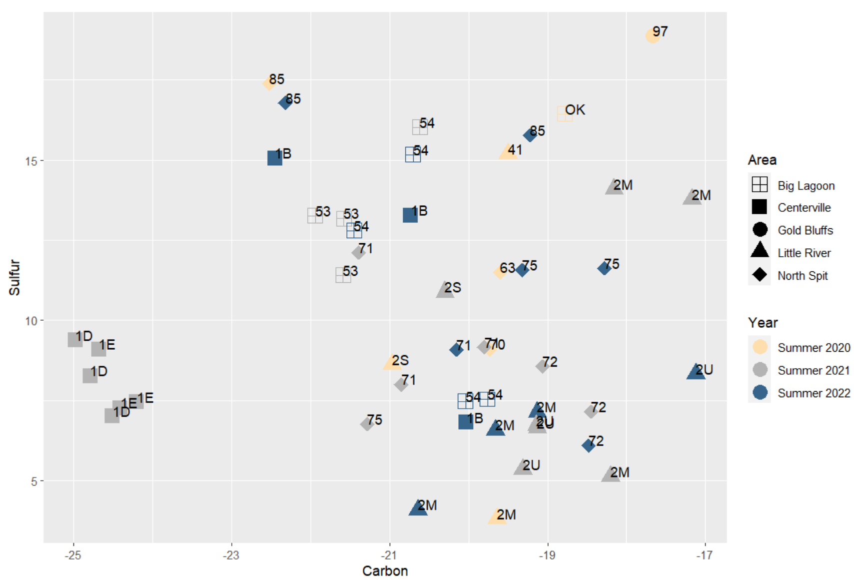


Figure 5. Scatterplot of carbon (δ13C) and sulfur (δ34S) stable isotopes obtained from raven feather samples. Samples are labelled by the alphanumeric leg band of the raven from which they were collected and color and shape correspond to year and location.

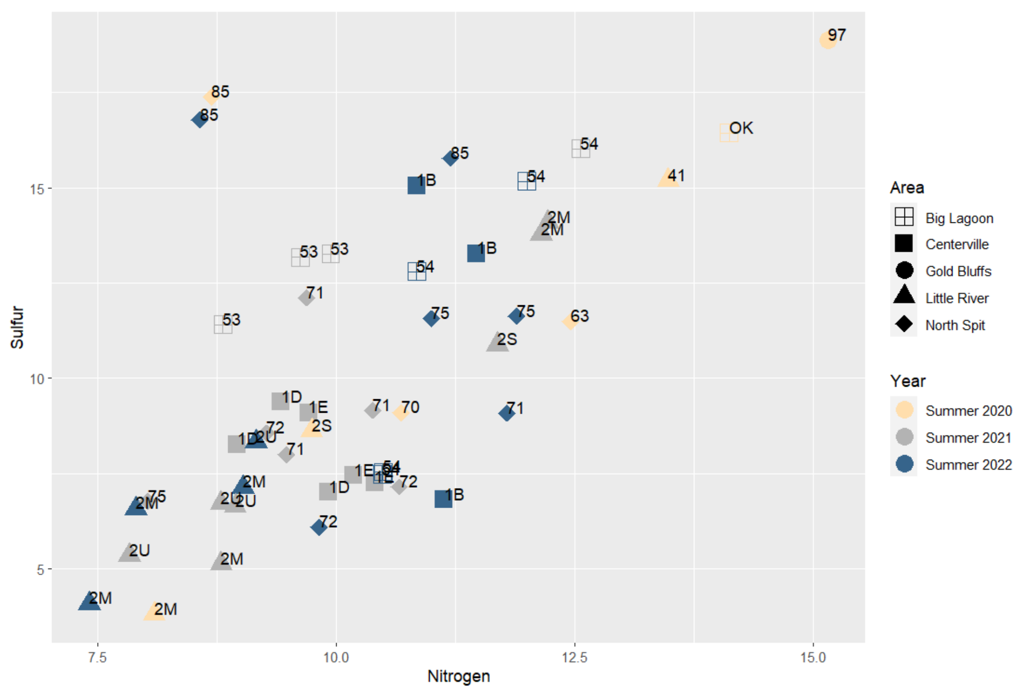


Figure 6. Scatterplot of sulfur (δ34S) and nitrogen (δ15N) stable isotopes obtained from raven feather samples. Samples are labelled by the alphanumeric leg band of the raven from which they were collected and color and shape correspond to year and location.

Behavioral Surveys

I completed a total of 122 behavioral surveys in 2022 and 122 surveys in 2023, with both years having approximately the same number of surveys at each of the 7 sites (in 2022 and 2023, respectively, from south to north: North Spit = 17 and 18 surveys, Ma-le'l Dunes = 19 and 20 surveys, Mad River = 19 and 14 surveys, Clam Beach = 15 and 17 surveys, Little River = 17 and 18 surveys, Big Lagoon = 17 and 18 surveys, and Stone Lagoon = 18 and 17 surveys). Variation between years was due to cancellations of surveys due to strong winds (> 5 on Beaufort scale) or heavy rain.

The average number of ravens and humans varied by location (Figure 7), with the highest numbers of ravens at Clam Beach (CB), Little River (LR), and Mad River (MR) and highest human activity at Clam Beach and Little River. Previous studies using similar methods at the same seven sites also showed these three locations to have higher raven activity than the other four locations, Big Lagoon (BL), Ma-le'l Dunes (MD), North Spit (NS), and Stone Lagoon (SL) (Colwell et al. 2009).

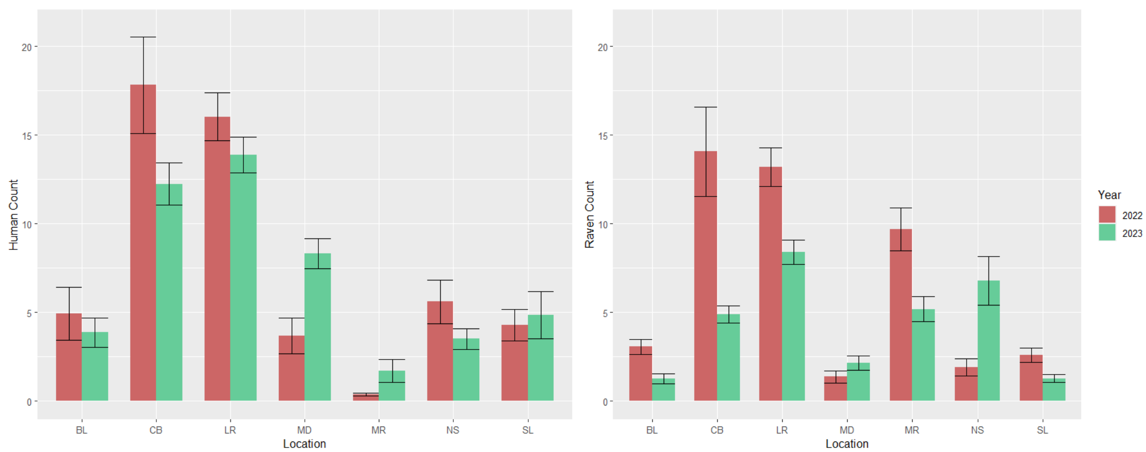


Figure 7. Mean count (+/- standard error) of humans (left) and ravens (right) at 7 surveyed locations comparing data from all surveys in 2022 (red bars) and 2023 (green bars).

Data from high counts revealed that the total number of ravens observed across all sites was significantly different between the two years, with a 50% reduction in the average number of ravens seen across all surveys between 2023 compared to 2022 (mean of 7.93 ravens per survey in 2022 and 4.75 in 2023; $W = 27097$, $p < 0.001$). The total number of people present during all surveys was not statistically different by year (mean of 7.55 humans in 2022 and 6.79 in 2023; $W = 7075$, $p = 0.574$) and the average number of dogs present during surveys also did not vary significant by year (mean of 2.44 dogs across all surveys in 2022 and 2.77 in 2023; $W = 6805$ $p = 0.268$), suggesting raven presence did not decrease because of a change in human presence. ANOVA results revealed that raven numbers differed significantly by survey location ($F = 23.5$, $df = 6$, $p < 0.001$), with Tukey's HSD test using pairwise comparisons revealing statistically significant differences between multiple pairs of locations (Table 6 below, all $p < 0.033$). Clam Beach, Mad River, and Little River each had a significantly higher mean number of ravens than Big Lagoon, Stone Lagoon, Ma-le'l Dunes, or North Spit, whereas the majority of relationships within those two groups did not show statistically significant differences in raven abundance. While ownership varies amongst the three beaches with the most ravens, these three beaches could, ecologically, be considered one contiguous stretch of beach, as Mad River in the south is separated from Clam Beach by only a river mouth and Clam Beach and Little River are contiguous. Sites with fewer ravens are more spread out to the north and south and don't share any geographic boundaries.

The ten categories of behavior used in behavioral surveys were grouped into four broader categories based on having similar biological function, especially in the context of being relevant to a raven finding a snowy plover nest in the area. These broad categories include locomotion (hopping, walking, and flying), observational (standing and perching), foraging/exploring, and other (preening, socializing, and other). The percentage of time ravens exhibited these behavioral categories varied minimally by location, though some sites had more noteworthy differences. Specifically, ravens, when present, spent a greater proportion of time foraging/exploring at Stone Lagoon and Clam

Beach compared to the five other locations, less time in locomotion behavior at North Spit and Ma-le'l Dunes compared to the other five locations, and more time in observational behaviors at Big Lagoon and Ma-le'l Dunes (Figure 8).

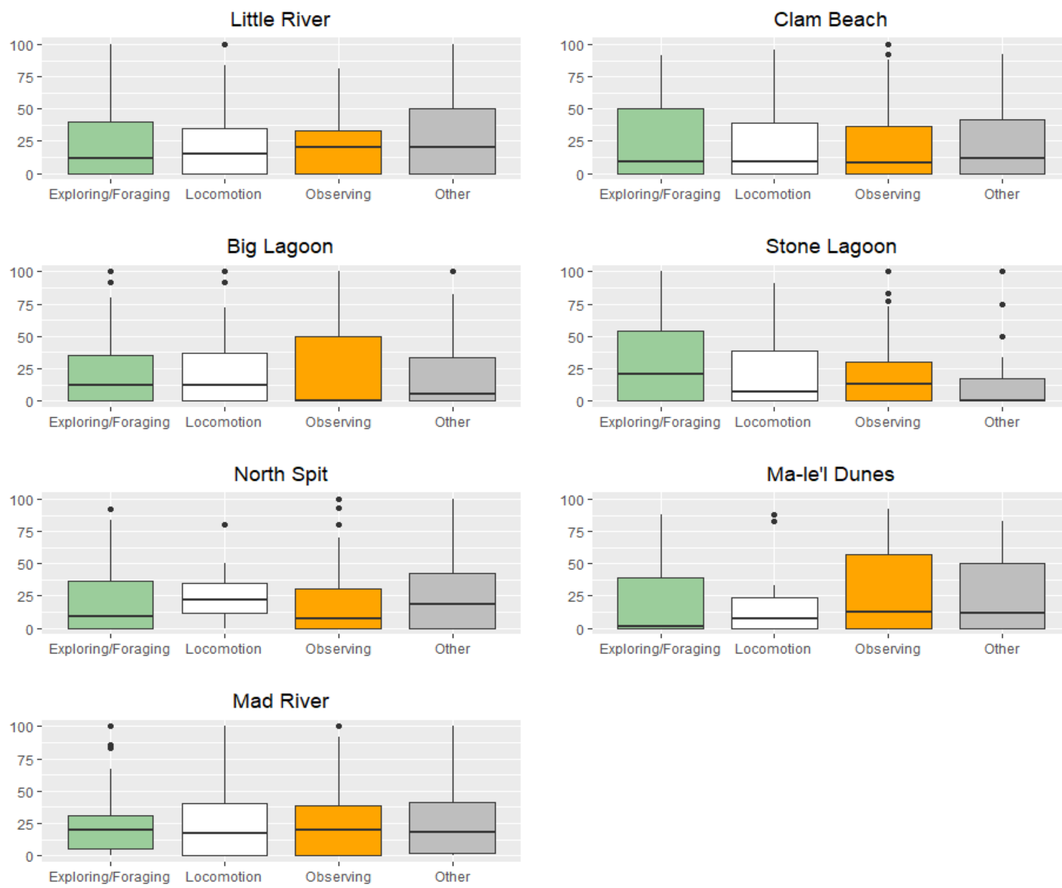


Figure 8. Boxplots summarizing the mean values, quartiles, and outliers of the frequencies of 4 categories of behaviors. Each box plot sequence represents one survey location.

GLM analyses based on models with percentage of time spent in "attentive" behavior as the response variable, which included behaviors that could be linked to ravens finding a plover nest if it is present, resulted in six top models within a delta AIC of ~2 (Table 7). The best model, indicated by the lowest AICc and highest model weight, includes a slightly positive relationship between the response variables and Julian date, length of observation, and total number of ravens observed, indicating that later in the season, when more ravens were present, and when observations occurred for a longer duration, the observed raven was more likely to exhibit behaviors related to a raven finding a snowy plover nest ("attentive" behavior). The model formula for the top model is as follows, with H being habitat type, JD being Julian date, LO being length of observation, R being total number of ravens, and W being wind direction:

$$Attentive\ behavior\ = 0.004 + H\ +\ 0.001(JD) + 0.002(LO) + 0.001(R) + W$$

The top three models have a combined weight of 0.74 and have only minor differences in their covariates; the top model does not include cloud cover and the third-best model includes an interaction between cloud cover and Julian date. Only one of the top models (Mod.5 which carried 9% of the weight) included the covariate "survey timing", which represents differences between a morning or afternoon survey, suggesting that time of day is not a significant variable in explaining raven behavior. The same is true for Year, which was present in Mod.4 only, which carried 9% of the weight, suggesting that raven behavior was not significantly impacted by year.

Table 7. GLM model selection results with percentage of time ravens spent exhibiting behaviors related to finding a snowy plover nest as the response variable.

	Intercept	Cloud Cover	Habitat	Julian Date	Survey Timing	Obs. Length	Total Ravens	Wind Dir.	Year	Cloud Cover * Julian Date	df	logLik	AICc	Delta	Model Weight
Top Model	0.004	NA	+	<0.001	NA	0.002	<0.001	+	NA	NA	20	-59.62	163.25	0.00	0.27
Mod.2	0.003	<0.001	+	<0.001	NA	0.002	<0.001	+	NA	NA	21	-58.40	163.29	0.05	0.26
Mod.3	-0.012	0.004	+	<0.001	NA	0.002	<0.001	+	NA	< -0.001	22	-57.41	163.76	0.52	0.21
Mod.4	0.726	NA	+	<0.001	NA	0.002	<0.001	+	-0.001	NA	21	-59.48	165.37	2.12	0.09
Mod.5	0.002	<0.001	+	<0.001	+	0.002	<0.001	+	NA	NA	22	-58.28	165.50	2.26	0.09
Mod.6	-0.017	0.007	+	<0.001	NA	0.002	NA	+	NA	< -0.001	21	-59.55	165.58	2.33	0.08

Finally, correlations were examined between raven behavior and rate of raven predation on snowy plover nests. To accomplish this, data on snowy plover nest fate were compiled for all 7 sites where behavioral surveys occurred from agency surveyor data for 2022 and 2023. These values tracked plover nest fate with nests either described as hatched or failed with cause of failure documented when possible. From this dataset, rates of raven predation on plover nests were calculated based on the total number of nests documented as predated by ravens divided by the total number of nests with a known fate. This dataset consisted of 5 sites that had plover nesting activity in 2022 and /or 2023 (Big Lagoon, n = 20, Little River, n = 1; Mad River, n = 14; North Spit, n = 13; and Stone Lagoon, n = 11). A Pearson's correlation test was run in R using the corrplot package and attentive behavior was found to be strongly positively correlated with occurrence of plover nest predation by ravens ($r = 0.73$, $p = 0.027$), whereas no significant correlation was found between raven predation on plover nests and any single other behavior or locomotive behaviors combined (flying and hopping).

Avian Influenza

In total, 7 GPS-tagged ravens died in a 3-month period, with 3 testing positive for Highly Pathogenic strain of Avian Influenza (HPAI) H5N1, 2 being too degraded to test, and 2 not found despite numerous attempts to locate GPS units or carcasses. One additional raven was strongly suspected to have died from HPAI due to the sudden disappearance of this territorial bird, although the GPS unit battery on this bird had died so the suspicion could not be confirmed with GPS data or recovery of the carcass. Of the

6 recovered ravens, 4 were recovered due to observations of GPS locations indicating mortality and 2 were recovered opportunistically from reports by community members. Of these latter two ravens, one raven's GPS unit battery had died over a year prior and the other raven's GPS unit had malfunctioned less than two weeks prior. For the 2 ravens with active GPS units that were not recovered but strongly presumed to have died, movement data mirrored the unique and severe reduction in movement observed in the confirmed HPAI positive ravens. One of these ravens is likely in the waters of Humboldt Bay and the other one was in dense forest, with repeated visits unable to locate the individual. It's important to note that without direct observations of the cause of mortality or extensive (and expensive) necropsies it's impossible to know for certain whether HPAI killed the ravens that tested positive or if they were simply carrying the disease. However, the unprecedented decrease in movement shown by the HPAI positive GPS-tagged ravens 1-2 weeks before their deaths and the extreme emaciation of all ravens is nearly unequivocal evidence that the disease contributed significantly, if not directly, to these deaths, in addition to research documenting corvids as dying from HPAI H5N1 (e.g., Tanimura 2006).

DISCUSSION

Results of this study show several important behavioral and ecological aspects of ravens in the study area relevant to understanding ravens generally as well as how they relate to snowy plovers. One major finding from this research is the high variability in raven home range size shown by GPS data, with beach-going ravens regularly travelling several kilometers inland and using a variety of anthropogenic features. A second major finding based on modeling with a RSF was revealing that within the study area, snowy plover nesting areas and beach habitat were two of the three covariates with the strongest relationship associated with raven resource use, both as attractive features. A third major finding from the research was documenting with point count data that raven abundance was shown to vary among sites and coupled with GPS-tagged ravens, that raven abundance significantly decreased (by 50%) in 2023 compared to 2022, coinciding with the arrival of HPAI H5N1.

Home Ranges and Territories

Results of GPS data analysis revealed that home ranges averaged 141.35 km^2 with a range of 2.95 – 1,334.54 km^2 while core areas averaged 10.11 km^2 and ranged from 0.21 – 31.77 km^2. These values include all data from all ravens with tracking durations that also ranged broadly based on GPS unit function, and though correlational tests between tracking duration and home range or core area sizes were not statistically significant, most ravens had larger home ranges when considering more than just the first

14 days of data. Regardless of the approach used, the large variation in raven home range size, especially when mapped over the landscape, highlights the resources accessed by marked ravens using snowy plover nesting areas, and from a management perspective elucidates the extent and diversity of features a landscape-level raven management strategy would need to address. The exploratory aspect of this project which involved following up with repeatedly visited locations also revealed that beach-going ravens, especially those tagged at or near Little River, also spent time at the common murre nesting colonies off Trinidad, potentially predating common murre nests as raven predation of those colonies is a known issue (D. Barton, personal communication). This highlights how the ravens using snowy plover nesting areas are also likely impacting other species.

Resource Selection Function

The resource selection function developed with data from 22 ravens showed that tagged individuals positively selected for beaches and snowy plover nesting areas as well as high, medium, and low developed areas. Ravens also selected for scrub habitat and evergreen forest, but they selected against all other natural habitat types examined in the model as well as roads and pasture. It's important to note that capture methods for this study focused on ravens near the beach accessing human food in parking lots almost exclusively, so the sampled population may not be a perfect representation of the entire population in the study area. However, GPS data and numerous and regular observations of ravens on the beaches showed that the sampled population was using snowy plover nesting habitat, thus the capture techniques effectively monitored at least part of the target population of ravens.

When developing the RSF, univariate models were created to identify the optimal spatial scale for each habitat covariate. The smallest scale of 30 m^2 was optimal for most landcover types, but ravens are likely capable of selecting for features at finer resolutions than this due to their high intelligence, strong memory, and sociality enabling them to identify small-scale resources. Due to the coarse resolution of spatial data, some habitat information is lost from the study area, so future investigations may benefit from finer scale resolution covariate data which would more accurately reflect the study area and potentially more precisely capture raven resource selection, at least for some resource types. This is especially relevant for ravens with small home ranges such as ravens 2S, 41, and 1E who all have core areas smaller than the smallest spatial scale examined. Interestingly, no existing literature was found that uses landscape data with a spatial scale finer than 30 m^2, but most research utilizing multiple spatial scales was also carried out in less urban areas with a likely lower density of ravens (e.g., Mueller et al. 2009, Coates et al. 2016) or in more homogenous habitat types such as redwood forest (Scarpignato and George 2013) or sage-steppe habitat (Bui et al. 2010, Howe et al. 2014, Coates et al. 2016).

Also important for the RSF and understanding raven resource use is that the GPS/GSM units used in this project were not able to differentiate raven activity at each location, so for each location, it cannot be discerned whether a raven was on the ground using the landscape or in the air flying over, which may be important for understanding whether features are attractive to ravens for use or for movement. While "speed" is frequently calculated to discern movement from use in location data, it is typically calculated as the distance between two points divided by amount of time between location collection. Ravens can cover large distances relatively quickly and can also double back in their movements in short periods of time, so speed was not considered to be an accurate metric of resource use.

Night Roosts

Collection of night roost data in this project was opportunistic, but these opportunistic points revealed 5,419 unique night roost locations within the project area, predominantly in evergreen forest habitat, which is still useful in understanding that ravens in this study moved their night roost locations frequently. Due to the opportunistic nature of night roost data collection and the sampling methodologies which targeted beach-going ravens and likely favored territorial individuals, the night roost dataset was limited in inference to the sampled population of ravens rather than ravens as whole in the study area. However, exploratory analyses of the data are still highly useful in better understanding night roost behavior within the project area, especially as it relates to the ravens using snowy plover nesting areas and specifically in identifying a large number of unique night roost locations and demonstrating that most ravens frequently switch night roost locations between nights and occasionally within nights. Previous research in the northeastern U.S. found raven roosts to be ephemeral and transitory, typically in response to food availability (Heinrich et al. 1994, Marzluff et al. 1996), and further study on the plasticity of raven night roost selection in the project area could prove interesting in understanding whether night roost selection is impacted by proximity to ephemeral food resources such as marine mammal carcasses or seasonal sand crab eggs, how night roost behavior might be impacted by the stability of many human food resources in the study area, and if night roost selection varies amongst adult and subadult ravens or by season.

Night roost disturbance has not previously been effectively used as a management strategy for discouraging raven presence in an area (Marchand et al. 2018, USFWS 2023), and due to the large number of roosts in this study area and frequent night roost movement within and between nights, it is also unlikely that roost disturbance would be an effective management strategy locally. Additionally, there were never documented instances of tagged ravens roosting together, so any targeted night roost hazing strategy would likely need to access much of the study area to be effective. While inferences here are based on a limited dataset, it is possible that night roosts in this study area are composed of a small number of ravens.

Stable Isotope Analysis

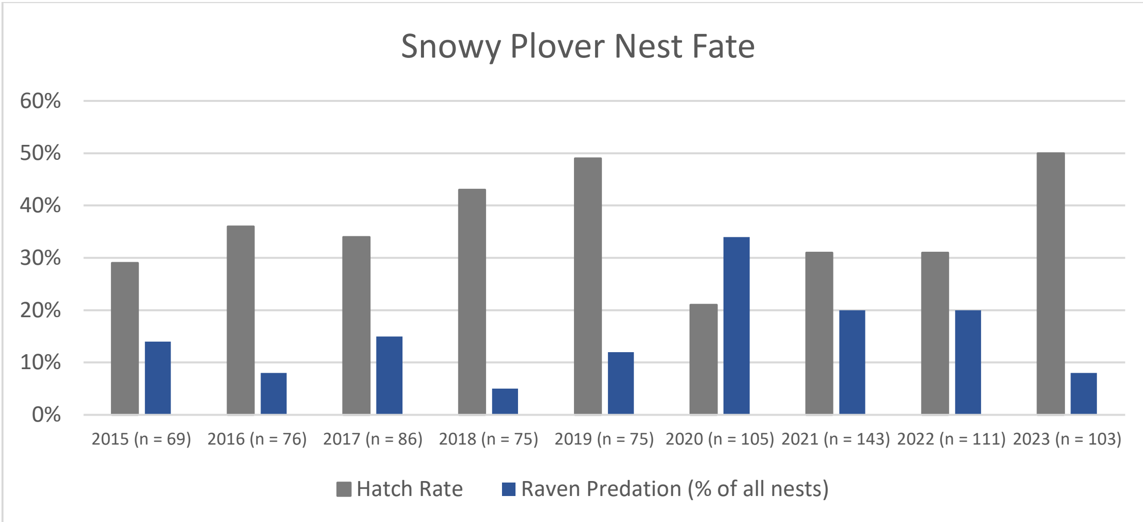
The examination of carbon, nitrogen, and sulfur isotopes in this study population revealed interesting variation between and within individuals, with some individuals showing consistent values of one or more isotopes over time while others had some temporal diversity, and between individuals all isotopes were fairly spread out, indicating a variety of diet compositions within this population. Perhaps because the sample size for SIA was small, no obvious pattern emerged by geographic location, which has been shown in other studies. For example, Harju et al. (2021) found raven chick diets examined through stable isotope analysis reflected proximity/density of sage grouse leks, with chicks closer to leks having a higher percentage of sage grouse in their diets. In addition, no correlation was found in this study between age or breeding status and diet, but the variation between and within individual ravens in this study on its own is interesting and warrants further study. Mixed modeling, especially of carbon isotopes and all isotopes combined, is anticipated in the future and will better pinpoint exact diet content (e.g. Harju et al. 2021 or West et al. 2016).

Avian Influenza as a Natural Removal Experiment

Three datasets were available to document raven mortality after the 2022 arrival of HPAI H5N1: GPS-tagged raven movement data, raven behavioral surveys, and California State Parks point count data. These three datasets all showed statistically significant declines of around 50% in raven abundance, either in the raw data (GPS-tagged population) or mean number of ravens detected per survey. On beaches, this decrease was not coincident with a decrease in humans or dogs, which highlights how humans and their associated activities, e.g., provision of food resources in parking lots and day use areas, was not correlated with the decrease in ravens, suggesting that something other than human activity is responsible for the decrease in ravens. This population decline and documented loss of territorial ravens from snowy plover nesting habitat provided a natural removal experiment, offering a way to assess the impact of lethal raven removal on beaches where that management strategy is not practiced. Based on observations of territoriality and nesting activity in tagged ravens, there were four beaches where known territorial ravens were 'removed' (Big Lagoon North and South, North Spit, and Ma-le'l Dunes) and one beach where a tagged territorial raven remained (Mad River Beach). Interestingly, this raven at Mad River Beach was observed attempting to predate a snowy plover chick in 2023.

Based on anecdotal observations performed while recovering dead ravens, newly vacant territories were occupied within two weeks, indicated by territorial displays and calls of new, untagged raven pairs. Behavioral surveys which began in March 2023 further confirmed that all newly available beaches were occupied by the beginning of the snowy plover breeding season. While mortality from HPAI mimics lethal removal in that beach-going ravens were removed, in some locations it's possible that the previous year's fledglings were still present based on the presence of small groups of young ravens spending a lot of time in the area used by fledglings accompanied by tagged adults the previous season. Additionally, the newly arrived ravens who established territories could have come from anywhere, e.g., they could have had territories adjacent to the beach the previous year and made forays to the beach on occasion, demonstrating it cannot be assumed that the new ravens were unfamiliar with their new territories. Another important difference between HPAI and lethal raven removal conducted for management is the timing of the removal: avian influenza killed ravens in the fall and winter, which allowed time for new ravens to occupy the vacant territories, whereas lethal raven removal performed for WSP conservation typically begins at the start of the breeding season. This latter strategy maximizes the likelihood that territorial ravens are removed and that territories remain unoccupied throughout the breeding season. Finally, and perhaps most importantly, HPAI killed ravens across the landscape, including inland (e.g., Ringenberg et al. 2023), whereas lethal removal for snowy plover management would only target beach-going ravens. It's therefore likely incorrect to presume that lethally removing ravens for snowy plover management would have the same impact as HPAI, since targeted removal from beaches may lead to rapid occupation by new ravens, as was observed in this study.

Hatch rate of snowy plover nests increased from 31% in 2022 to 50% in 2023 and raven predation of all nests fell from 20% in 2022 to 8% in 2023 (USFWS unpublished data; Figure 9). Raven predation fluctuates annually, with data from 2015 – 2023 showing ravens responsible for between 5-34% of predation events, and 2023 raven predation was tied for the second-lowest on record (USFWS unpublished data). The decrease observed in 2023 cannot be called unprecedented, thus it is difficult to directly link ravens removed by HPAI to an increase in plover nesting success (especially in light of the fact that HPAI did not remove *all* territorial ravens in snowy plover nesting habitat) and due to the use of mini-exclosures around most snowy plover nests on California State Parks property in 2023.



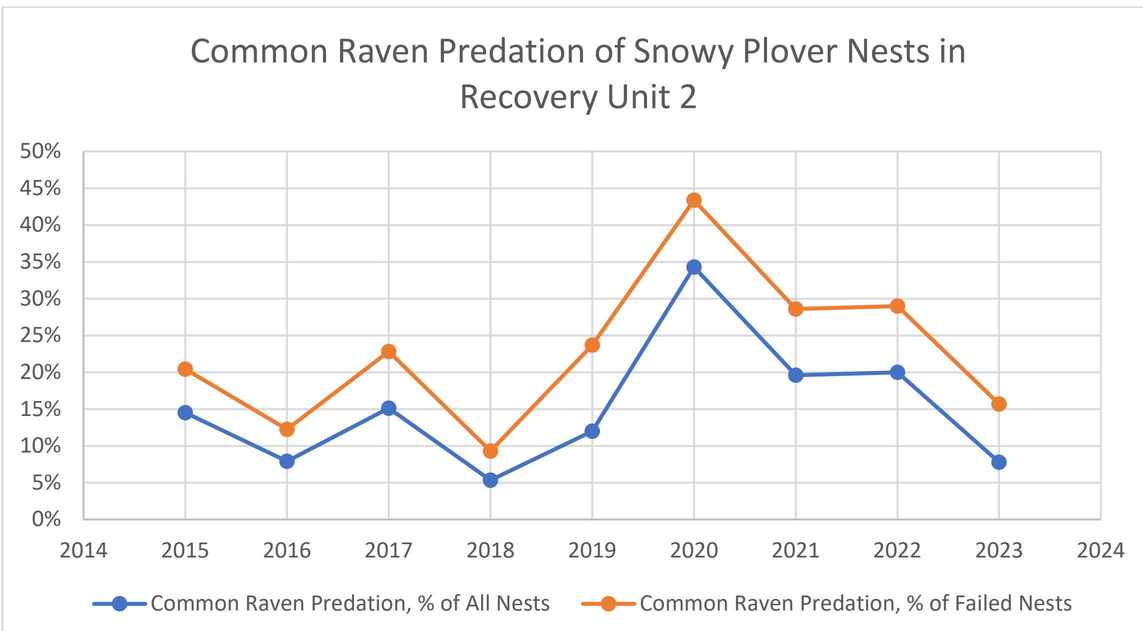


Figure 9. Snowy plover nest fate and raven predation of snowy plover nests in Recovery Unit 2 from 2015 to 2023. Data in this figure were collected by California State Parks Recovery Unit 2 on their beaches in Mendocino, Humboldt, and Del Norte Counties.

It is important to highlight a few features of the snowy plover monitoring dataset in regards to understanding raven predation: while snowy plover surveyors are trained in locating and monitoring nests, detection is imperfect, thus some nests may fail but be undocumented (USFWS, personal communication). When a monitored nest does fail it is frequently difficult to identify the cause of failure, for example because sand is coarse which makes tracking difficult and nest surveys are not performed every day, so weather variables like wind can distort evidence of the cause of failure over time. In data gathered between 2015-2023, the species responsible for predation could not be identified 22% of the time. One study which aimed, in part, to address the imperfect detection of cause of predation used video cameras to monitor the fate of snowy plover nests (Burrell and Colwell 2012). In this study, ravens predated 70% of nests though independently, snowy plover monitors described 77% of these as having an unknown cause of failure, indicating that ravens may be responsible for much more snowy plover nest failure than monitoring can attribute (Burrell and Colwell 2012).

RECOMMENDATIONS

Types and Locations of Human Food Subsidies

One major goal of this research was to understand the anthropogenic resources, especially food subsidies, that beach-going ravens are utilizing. Knowledge of these food resources can be used to inform management agencies about the landscape-level resources ravens access to develop an improved understanding of causal factors contributing to high raven abundance within the study area. Locations of food resources were identified by monitoring GPS data then visiting sites or using aerial imagery to identify food sources. Many unique locations of food subsidies were also obtained opportunistically through conversations with community members or scouting for locations to capture ravens. This list and map of anthropogenic food subsidies is certainly not exhaustive as many food resources are ephemeral, but it provides some baseline data useful in a landscape context (Figure 10).

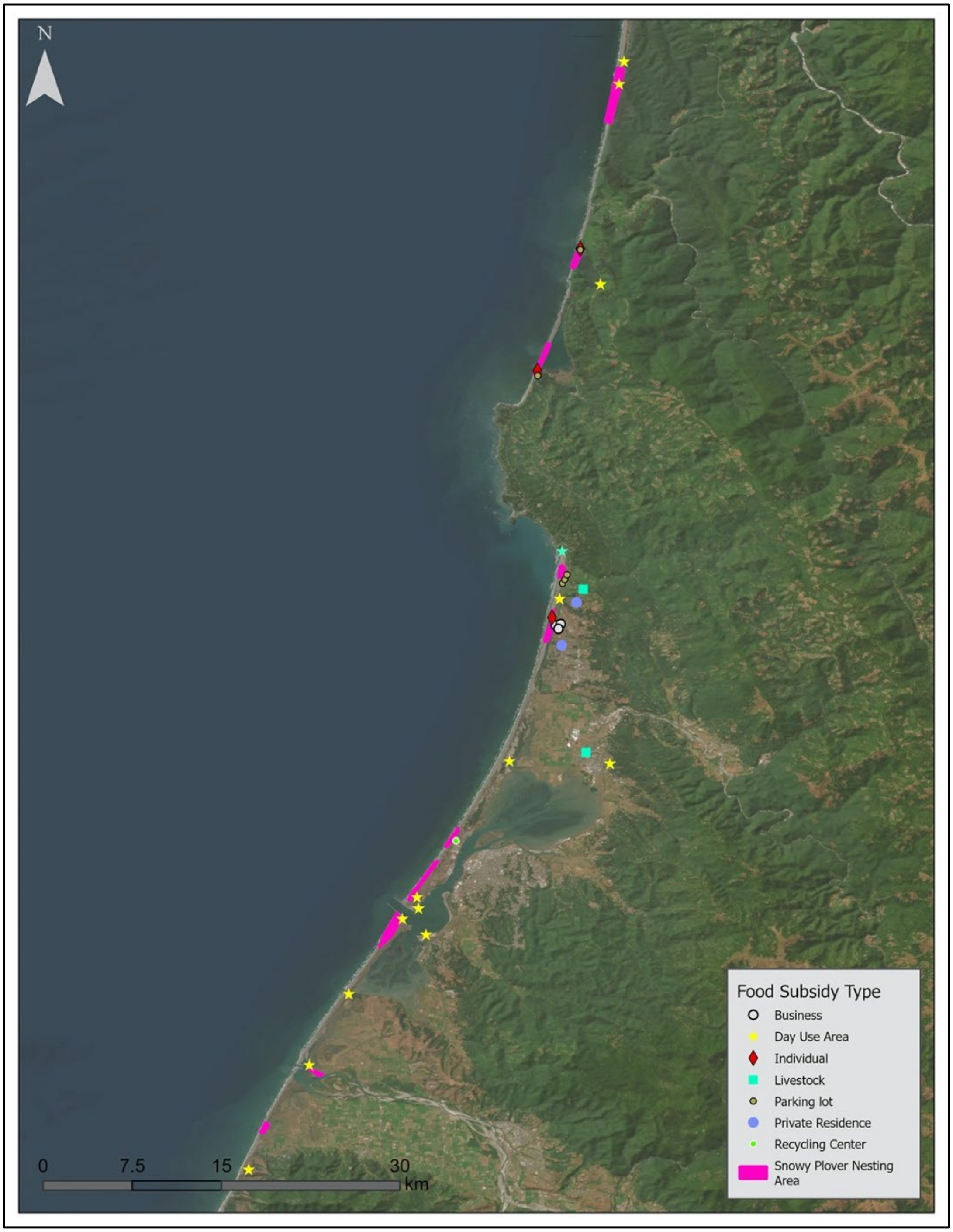


Figure 10. Locations and type of food subsidies identified opportunistically, based on repeated visitation by tagged ravens, and through behavioral observations throughout this study.

Raven management techniques for snowy plovers and other species have been proposed and evaluated for decades in both peer-reviewed and grey literature (Appendix A). Of these strategies, few have aimed to address the causal factor of high raven abundance: human food subsidies. Locations where ravens accessed anthropogenic food resources identified in this study included private and public businesses, day use and picnic areas, individuals feeding ravens in public locations, livestock carcasses and feed operations, parking lots, private residences, and recycling centers. Some of these sites are observable from well-trafficked roads while others are on private land hidden largely from public view and would not have been identifiable without GPS-tagged raven data. Food resources associated with individuals and private residences, which represent observations of individual people feeding ravens either on public land or at their homes, highlight the importance of public outreach and education to address individuals who feed ravens intentionally.

After numerous conversations with individuals who intentionally feed ravens, it became clear that many of these people have a strong emotional bond with ravens, which indicates that certain outreach strategies would likely be more effective than others (e.g., conveying the information that congregating ravens by intentional feeding leads to increased risk of disease transmission vs. informing people that feeding ravens is illegal). Conversely, other conversations showed that providing information on how problematic ravens can be and how human activity subsidizes them changes the habits of some people, e.g., an individual who put her compost outside for ravens to dispose of started disposing of it in another way. The abundance of Day Use Areas on the landscape and observations of ravens repeatedly using them emphasizes the importance of educational signage and trash receptacles at these facilities (e.g., Brunk et al. 2021). Livestock operations either find ravens to be a nuisance due to consumption of feed intended for livestock and/or property destruction or they utilize ravens for disposing of carcasses, so future collaboration approaches with livestock operations will be contingent upon the ways ravens use these operations to access food, but outreach and education can be used to find solutions to problem ravens and less ecologically harmful means of carcass disposal.

These landscape approaches can serve as a long-term alternative to another raven management approach under consideration: lethal removal. Lethal removal does not address the causal factors of high raven abundance and instead, functions as a temporary fix for a problem that requires a more holistic approach for long-term and large-scale effectiveness. Lethal removal, which is becoming increasingly common for managing ravens in areas where sensitive species nest and breed, is expensive (Harju et al. 2021) and can lead to compensatory predation by other species. For example, Bodey et al. (2009) found that removal of hooded crows correlated with a significant increase in predation by common raven predation on artificial nests, suggesting that the presence on one predator kept another in check. Lethal removal can also face public opposition (Clucas 2021), which can be a significant barrier if a public agency or public-facing organization wants to use the strategy. Additionally, the lethal management of a native species is morally ambiguous (Marzluff et al. 2021), has never been evaluated for effectiveness specifically for ravens as an isolated strategy (e.g., Conover and Roberts

2017) and typically needs to be practiced every year as well as consistently throughout the year as new ravens take the place of removed individuals (USDA Wildlife Services staff, personal comm.). Finally, a landscape-level approach to raven management will benefit all the species impacted by overpopulation of this generalist predator, whereas targeted management in one landscape would only benefit one or a few species.

LITERATURE CITED

Andren, H. (1992). Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology, 73(3),* 794-804.

Bedrosian, B., & Craighead, D. (2007). Evaluation of techniques for attaching transmitters to common raven nestlings. *Northwestern Naturalist, 88(1),* 1-6.

Brinkman, M. P., Garcelon, D. K., & Colwell, M. A. (2018). Evaluating the efficacy of carbachol at reducing corvid predation on artificial nests. *Wildlife Society Bulletin, 42(1),* 84-93.

Boarman, W. I., Patten, M. A., Camp, R. J., & Collis, S. J. (2006). Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. *Journal of Arid Environments, 67*, 248-261.

Bodey, T. W., McDonald, R. A., & Bearhop, S. (2009). Mesopredators constrain a top predator: competitive release of ravens after culling crows. *Biology Letters, 5(5),* 617-620.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research, 33(2),* 261-304. https://doi.org/10.1177/0049124104268644

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of mammalogy, 24(3)*, 346-352.

Burrell, N. S., & Colwell, M. A. (2012). Direct and indirect evidence that productivity of Snowy Plovers Charadrius nivosus varies with occurrence of a nest predator. *Wildfowl, 62(62),* 204-223.

Brunk, K.M., West, E H., Peery, M.Z., & Pidgeon, A. M. (2021). Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas. *Biological Conservation* 256:109081.

Bui, T. V. D., Marzluff, J. M., & Bedrosian, B. (2010). Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. *The Condor, 112(1),* 65-78.

Centers for Disease Control and Prevention. (2024, February 21). H5N1 bird flu: Current situation summary. Centers for Disease Control and Prevention. https://www.cdc.gov/flu/avianflu/avian-flu-summary.htm

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landscape and urban planning, 74(1),* 46-69.

Clucas, B. (2021). Human dimensions of predator management for threatened western snowy plovers. *Wader Study, 128(1),* 1-9.

Coates, P. S., Brussee, B. E., Howe, K. B., Gustafson, K. B., Casazza, M. L., & Delehanty, D. J. (2016). Landscape characteristics and livestock presence influence common ravens: relevance to greater sage-grouse conservation. *Ecosphere, 7(2),* e01203.

Coates, P. S., Webb, W. C., Dettenmaier, S. J., Harju, S. M., & Delehanty, D. J. (2021). Synthesis of nest predation impacts of common ravens on sensitive avian species. *Human–Wildlife Interactions, 15(3),* 11.

Colwell, M.A., T.L. George, and R.T Golightly. (2009). A predator management strategy to address corvid impacts on productivity of Snowy Plovers (Charadrius alexandrinus) and Marbled Murrelets (Brachyramphus marmoratus) in coastal northern California. Final Report submitted to U.S. Fish and Wildlife Service, Arcata, CA. 115 pp.

Colwell, M. A., Lau, M. J., Feucht, E. J., & Pohlman, J. J. (2019). Corvids and humans create ecological traps in otherwise suitable snowy plover habitat. *Wader Study*, *126*(3), 178-189.

Connolly, R. M., Guest, M. A., Melville, A. J., & Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia, 138,* 161-167.

Conover, M. R., & Roberts, A. J. (2017). Predators, predator removal, and sage-grouse: A review. *The Journal of wildlife management, 81(1),* 7-15.

Dinsmore, S. J., Lauten, D. J., Castelein, K. A., Gaines, E. P., & Stern, M. A. (2014). Predator exclosures, predator removal, and habitat improvement increase nest success of Snowy Plovers in Oregon, USA. *The Condor: Ornithological Applications, 116(4),* 619-628.

Dwyer, J. F., Leiker, D. L., & King, S. N. (2015). Testing nest deterrents for Chihuahuan ravens on H-frame transmission structures. *Wildlife Society Bulletin, 39(3),* 603-609.

Engel, K. A., Young, L. S., Steenhof, K., Roppe, J. A., & Kochert, M. N. (1992). Communal roosting of common ravens in southwestern Idaho. *The Wilson Bulletin*, 105-121.

Feucht, E.J., M.A. Colwell, K.M. Raby, J.A. Windsor, and S.E. McAllister. 2019. Final Report: 2019 Western Snowy Plover Breeding in Coastal Northern California, Recovery Unit 2. Unpublished report submitted to U.S. Fish and Wildlife Service, Arcata Field Office.

Gibble, C. M., Neuman, K. K., & Beck, J. (2021). Demography, morphometrics, and stomach contents of common ravens examined as a result of controlled take. *Human–Wildlife Interactions, 15(3),* 15.

Hardy, M. A., & Colwell, M. A. (2008). The impact of predator exclosures on Snowy Plover nesting success: a seven-year study. *Wader Study Group Bulletin, 115(3),* 161-166.

Hardy, M. A., & Colwell, M. A. (2012). Factors influencing Snowy Plover nest survival on ocean-fronting beaches in coastal northern California. *Waterbirds, 35(4),* 503-656.

Harju, S. M., Coates, P. S., Dettenmaier, S. J., Dinkins, J. B., Jackson, P. J., & Chenaille, M. P. (2021). Estimating trends of common raven populations in North America, 1966–2018. *Human–Wildlife Interactions, 15(3),* 5.

Heinrich, B. (1994). Does the early Common Raven get (and show) the meat?. *The Auk, 111(3),* 764-769.

Hobson, K. A., & Clark, R. G. (1992). Assessing avian diets using stable isotopes I: turnover of 13C in tissues. *The Condor, 94(1),* 181-188.

Howe, K. B., Coates, P. S., & Delehanty, D. J. (2014). Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem. *The Condor: Ornithological Applications, 116(1),* 35-49.

Kelly, J. P., Etienne, K. L., & Roth, J. E. (2005). Factors influencing the nest predatory behaviors of Common Ravens in heronries. *The Condor, 107(2),* 402-415.

Kristan III, W. B., Boarman, W. I., & Crayon, J. J. (2004). Diet composition of common ravens across the urban-wildland interface of the West Mojave Desert. *Wildlife Society Bulletin, 32(1),* 244-253.

Lau, M. J. (2015). Geospatial modeling of Common Raven activity in Snowy Plover habitats in coastal northern California. MSc thesis, Humboldt State University, USA.

Leja, S.D. 2015. Habitat selection and response to restoration by breeding Western Snowy Plovers in coastal northern California. MSc thesis, Humboldt State University, USA.

Loretto, M. C., Schuster, R., & Bugnyar, T. (2016). GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps. *Current Zoology, 62(4),* 337-344.

Loretto, M. C., Schuster, R., Itty, C., Marchand, P., Genero, F., & Bugnyar, T. (2017). Fission-fusion dynamics over large distances in raven non-breeders. *Scientific Reports, 7(1),* 380.

Marchand, P., Loretto, M. C., Henry, P. Y., Duriez, O., Jiguet, F., Bugnyar, T., & Itty, C. (2018). Relocations and one-time disturbance fail to sustainably disperse non-breeding common ravens Corvus corax due to homing behaviour and extensive home ranges. *European journal of wildlife research, 64,* 1-13.

Marzluff, J. M., Loretto, M. C., Ho, C. K., Coleman, G. W., & Restani, M. (2021). Thinking like a raven: restoring integrity, stability, and beauty to western ecosystems. *Human–Wildlife Interactions, 15(3),* 516-533.

Marzluff, J. M., & Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological conservation, 130(2),* 301-314.

Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Raven roosts are mobile information centres. *Animal Behaviour, 51(1),* 89-103.

Mueller, T., Selva, N., Pugacewicz, E., & Prins, E. (2009). Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist. *Ecography, 32(2),* 345-353.

National Oceanic and Atmospheric Administration (NOAA). 2024. National Weather Service Forecast Office. Accessed 21 May 2024.

Peebles, L. W., & Conover, M. R. (2016). Effectiveness of the toxicant DRC-1339 in reducing populations of common ravens in Wyoming. *Wildlife Society Bulletin, 40(2),* 281-287.

Peterson, S. A., & Colwell, M. A. (2014). Experimental evidence that scare tactics and effigies reduce corvid occurrence. *Northwestern Naturalist, 95(2),* 103-112.

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual review of ecology and systematics, 18(1),* 293-320.

Pyle, P. (1987). Identification guide to North American passerines: a compendium of information on identifying, ageing, and sexing passerines in the hand. Slate Creek Press.

Raby, K. M. (2018). Western snowy plover nest survival in Humboldt County, California. MSc thesis, Humboldt State University, USA.

Ringenberg, J. M., Weir, K., Humberg, L., Voglewede, C., Oswald, M., Root, J. J., Dilione, K., Casey, E., Milleson, M., Linder, M., & Lenoch, J. (2023). Prevalence of Avian Influenza Virus in Synanthropic Birds Associated with an Outbreak of Highly Pathogenic Strain EA/AM H5N1. *bioRxiv,* 2023-11.

Sanchez, C. A., Brussee, B. E., Coates, P. S., Holcomb, K. L., Harju, S. M., Shields, T. A., Vaughn, M., Prochazka, B. G., Mathews, S. R., Cornell, S., Olson, C. V., & Delehanty, D. J. (2021). Efficacy of manipulating reproduction of common ravens to conserve sensitive prey species: three case studies. *Human–Wildlife Interactions, 15(3),* 21.

Scarpignato, A. L., & George, T. L. (2013). Space use by Common Ravens in Marbled Murrelet nesting habitat in northern California. *Journal of Field Ornithology, 84(2),* 147-159.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in ecology & evolution, 21(4),* 186-191

Stenzel, L. E., Hudgens, B. R., Page, G. W., Neuman, K. K., Palkovic, A. L., Erbes, J. L., Eyster, C. R., Ramer, B. A., & George, D. E. (2023). Climate change consequences for differential adult survival and the mating system of a temperate breeding shorebird. *Ecosphere, 14(7),* e4608.

Strong, C., Neumann, K. K., Hutchinson, J. L., Miller, J. K., Clark, A. L., Chang, L., ... & Wooten, T. (2021). Common raven impacts on nesting western snowy plovers:

integrating management to facilitate species recovery. *Human-Wildlife Interactions, 15(3),* 465.

Tanimura, N., Tsukamoto, K., Okamatsu, M., Mase, M., Imada, T., Nakamura, K., ... & Imai, K. (2006). Pathology of fatal highly pathogenic H5N1 avian influenza virus infection in large-billed crows (Corvus macrorhynchos) during the 2004 outbreak in Japan. *Veterinary Pathology, 43(4),* 500-509.

US Census Bureau. 2024. Arcata and Eureka Population, 2020. Prepared by QuickFacts. Retrieved from https://www.census.gov/quickfacts/

U.S. Fish and Wildlife Service, Division of Migratory Birds Management (USFWS) (2023). Management of Conflicts Associated with Common Ravens in the United States: A Technical Review of the Issues, 2023. U.S. Fish and Wildlife Service Migratory Bird Program Division of Bird Conservation, Permits, and Regulations Branch of Bird Conservation.

Webb, W. C., Boarman, W. I., & Rotenberry, J. T. (2009). Movements of juvenile common ravens in an arid landscape. *The Journal of Wildlife Management, 73(1),* 72-81.

Webb, W. C., Marzluff, J. M., & Hepinstall-Cymerman, J. (2012). Differences in space use by common ravens in relation to sex, breeding status, and kinship. *The Condor, 114(3),* 584-594.

West, E. H., Henry, W. R., Goldenberg, W., & Peery, M. Z. (2016). Influence of food subsidies on the foraging ecology of a synanthropic species in protected areas. *Ecosphere, 7(10),* e01532.

APPENDICES

Appendix A. List of management techniques for addressing common ravens as a problematic predator of sensitive species.

Strategy	Description	Results	Source
Subsidy denial/removal	Removal of access to food or other subsidies, e.g., removal of roadkill or dead livestock or closing off access to feed or trash	Highly effective when used but often difficult to practice	SOURCE
Nest exclosures	An exclosure is placed directly around the nest of the protected species, preventing raven access	Mixed; in some areas led to higher adult mortality and nest abandonment, in other areas was successful	Hardy and Colwell 2008
Hazing through sound or visual clues	Use of loud noises and lights, including propane cannons, flashing lights, lasers, and pyrotechnics to deter or disperse ravens	Initially successful, but ravens habituate to nonlethal hazing. Powerful and randomly enacted lasers, however, have been showing extreme success at dispersing then deterring ravens from food subsidy sites in the Mojave.	Currylow et al. 2021
Effigies	Taxidermy ravens positioned to be obviously dead, effigies are positioned around the area to be protected	Successful on a small scale (~50m radius), not reasonable for intended protected species	Peterson and Colwell, 2014
Nest deterrence	Erecting structures to prevent ravens from nesting in particular areas, e.g., on power poles or structures	For specific locations this can be effective, but ravens will likely find another location to nest	Dwyer et al. 2015
Conditioned taste aversion	Use of non-lethal decoy eggs painted to look like eggs of the protected species, consumption causes vomiting which ravens avoid in the future	Ineffective in the long-term; ravens learned to differentiate the fake eggs	Brinkman et al. 2018
Egg addling	Oil is sprayed on raven eggs, preventing them from hatching but raven adults continued to incubate	Successfully prevents egg hatching and keeps nesting pair tending nest	Sanchez et al. 2021

Strategy	Description	Results	Source
Egg/Nest removal	Raven eggs are removed and/or nest is destroyed	Stops reproduction but if done early in nesting season, further nesting attempts elsewhere are likely	Sanchez et al. 2021
Lethal removal: avicide	DRC 1339, only permitted users are USDA APHIS staff	Can effectively target problem individuals*, but not effective on the population level**	*Dinsmore et al. 2014 **Peebles and Conover 2016
Lethal removal: shooting	Shooting ravens using firearms	Effective at removing ravens but over time, ravens start to associate the person and/or vehicle with the shooting. Challenging to carry out in most public locations.	Gibble et al. 2021

Appendix B. Date of capture/GPS attachment, duration of time tracked, and morphometric data from ravens involved in this study. BR represents the breeding season and NB represents the nonbreeding season.

Raven ID	Date of Capture	Duration of Data (days)	Frequency of Collection (minutes)	Age	Sex	Nesting Status
2M	04/25/21●	535	30	ASY	M	N
70	05/12/21●	500	60	ASY	M	B
63	05/18/21!	148	60	ASY	M	N
OK	05/21/21!	36	60	ASY	M	Y
41	05/26/21*	973	120	ASY	M	Y
85	06/14/21●	510	60	ASY	F	Y
97	06/15/21!	327	60	ASY	M	Y
54	7/05/21●	498	60	ASY	M	N
2S	7/28/21**	406	60	ASY	F	Y
71	2/18/22●	284	30	ASY	M	Y
2U	5/30/22●*	45	60	SY	F	N
1D	6/05/22**	230	60	ASY	F	N
1E	6/05/22*	598	30	ASY	M	N
53	7/15/22●	28	30	ASY	F	Y
75	8/23/22*	519	30	SY	F	N
72	8/23/22●	82	60	SY	M	N
1B	10/20/22**	14	120	ASY	U	U
92	4/05/23!	116	30	ASY	M	U
GS:YK	9/01/23*	145	20	ASY	M	TBD
bs40	9/01/23*	145	60	ASY	M	TBD
OHys	9/01/23*	145	60	ASY	M	TBD
64gs	9/01/23*	145	60	ASY	M	TBD

*denotes ravens with GPS/GMS units that are still active
**denotes ravens with GPS/GSM units that broke or had batteries depleted during the study
• denotes ravens which were confirmed or strongly suspected to have died from HPAI
! denotes a raven with an inactive GPS unit, no longer present in its core area, with an unknown fate

Appendix C. Home range and core area sizes (all in km^2) for ravens monitored in this study (n = 22). Data is shown from all months/all years (AY), the breeding season only (BR), and outside the breeding season only (NB).

Raven ID	Home Range Size, AY	Core Area Size, AY	Home Range Size, BR	Core Area Size, BR	Home Range Size, NB	Core Area Size, NB
41	15.68	0.23	6.18	0.14	1.78	0.31
53	5.22	1.11	5.22	1.11	NA	NA
54	1334.54	21.41	3.24	0.49	1044.65	73.14
63	91.49	4.41	106.86	4.86	6.46	1.43
70	106.15	11.98	105.88	9.47	45.28	12.48
71	62.86	2.81	52.33	3.30	10.32	2.42
72	76.28	16.79	NA	NA	74.58	17.27
75	271.78	25.82	114.13	45.09	247.57	19.35
85	39.47	1.57	14.10	0.66	32.78	1.98
92	69.09	4.54	69.09	4.54	NA	NA
97	180.08	3.95	95.18	3.86	4.58	1.60
1B	26.93	19.25	NA	NA	26.93	19.25
1D	12.48	2.13	6.81	1.14	4.94	2.00
1E	4.04	0.75	4.81	0.78	2.72	0.71
2M	88.87	28.59	89.51	28.77	5.78	1.25
2S	2.95	0.21	1.01	0.15	2.87	0.34
64gs	91.32	2.86	NA	NA	91.32	2.86
2U	72.07	22.29	72.07	22.29	NA	NA
bs40	33.55	7.97	NA	NA	33.55	7.97
gsyk	450.23	10.75	NA	NA	450.23	10.75
OHys	71.36	31.77	NA	NA	71.36	31.77
OK	3.21	1.31	3.21	1.31	NA	NA

Appendix D. Home range and core area sizes (all in km^2) for ravens monitored in this study (n = 22) accounting for differences based on tracking duration. Data are shown from only the first 14 days of tracking for each raven.

Raven ID	Tracking Duration	Home Range Size	Core Area Size	HR total / HR14*	CA total / CA 14*
41	973	1.27	0.03	12.38	8.14
53	28	10.21	1.06	0.51	1.05
54	498	1.74	0.38	764.97	55.82
63	148	5.41	0.44	16.90	10.08
70	500	2.65	0.41	40.09	29.16
71	284	31.08	5.97	2.02	0.47
72	82	33.41	4.68	2.28	3.59
75	519	12.84	7.39	21.17	3.49
85	510	0.66	0.07	59.64	23.38
92	116	19.94	2.97	3.46	1.53
97	327	5.28	0.74	34.12	5.35
1B	14	26.93	19.25	1.00	1.00
1D	230	5.50	0.88	2.27	2.42
1E	598	4.26	0.88	0.95	0.86
2M	535	57.58	37.54	1.54	0.76
2S	406	0.53	0.08	5.55	2.55
64gs	145	5.74	0.31	15.92	9.13
2U	45	48.13	39.68	1.50	0.56
bs40	145	8.02	0.38	4.18	21.24
gsyk	145	3.57	0.21	126.05	50.76
OHys	145	19.25	9.86	3.71	3.22
OK	36	3.15	1.18	1.02	1.11

*Home range (HR) data and Core area (CA) data from the entire tracking duration for each raven (total) is divided by the HR and CA sizes from just the first 14 days to show the difference in size, respectively, for each raven.

Appendix E. Stable isotope results, with sampled feathers identified by side of the body (R – right, L – left), feather type (P – primary, R – rectrix), and feather number (Pyle 1987).

Raven ID	Feather Sampled	Time Period Represented	$\delta^{34}S_{VCDT}$ (‰)	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)
1B	RR1	May, 2022	6.81	-20.03	11.13
1B	RR3	June, 2022	13.27	-20.73	11.47
1B	RR5	July, 2022	15.05	-22.45	10.84
1D	RR1	May, 2021	9.38	-24.98	9.42
1D	RR3	June, 2021	8.27	-24.79	8.96
1D	RR5	July, 2021	7.01	-24.51	9.92
1E	RR1	May, 2021	9.10	-24.68	9.71
1E	RR3	June, 2021	7.26	-24.41	10.40
1E	RR5	July, 2021	7.45	-24.20	10.18
(2M)	RR1_11-22	May 2022	6.58	-19.66	7.90
(2M)	RR1_NEW	May 2021	5.13	-18.20	8.79
(2M)	RR1_OLD	May 2020	3.81	-19.64	8.09
(2M)	RR3_11-22	June 2022	4.09	-20.64	7.41
(2M)	RR3	June 2020	13.77	-17.17	12.15
(2M)	RR5_11-22	July 2022	7.14	-19.13	9.02
(2M)	RR5	July 2020	14.09	-18.16	12.22
(2S)	R1	May 2021*	10.88	-20.30	11.69
(2S)	R3_OLD	June 2020	8.62	-20.97	9.74
(2U)	LP16	October 2022	8.32	-17.12	9.16
(2U)	RR1	May 2021	6.72	-19.14	8.79
(2U)	RR3	June 2021	6.64	-19.13	8.94
(2U)	RR5	July 2021	5.34	-19.31	7.83
41	R1	May 2020	15.19	-19.50	13.48
53	RR2	May/June 2021	11.41	-21.59	8.81
53	RR4	July 2021	13.17	-21.58	9.62
53	RR5	July 2021	13.26	-21.94	9.94
(54)	2021	Summer 2020 or 2021	16.02	-20.62	12.56
(54)	RR1_11-22	May 2022	12.80	-21.45	10.84
(54)	RR3_11-22	June 2022	7.47	-20.04	10.48
(54)	RR3-2_11-22	June 2022 (duplicate)	7.54	-19.76	10.49
(54)	RR5_11-22	July 2022	15.16	-20.70	12.00
63	Rectrix	Summer 2020	11.49	-19.60	12.46
70	Rectrix	Summer 2020	9.10	-19.73	10.68
(71)	RR1	May 2021	12.11	-21.39	9.69
(71)	RR2_NEW	May 2022*	9.09	-20.15	11.79
(71)	RR3	June 2021	8.00	-20.85	9.48
(71)	RR6	August/September 2021	9.16	-19.80	10.38

Raven ID	Feather Sampled	Time Period Represented	$\delta^{34}S_{VCDT}$ (‰)	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)
(72)	LP1	May 2021	7.15	-18.45	10.66
(72)	new	Summer 2022*	6.09	-18.48	9.82
(72)	RR6	August/September 2021	8.56	-19.06	9.27
(75)	RR1	May 2022*	11.56	-19.32	11.00
(75)	RR3	June 2022*	11.62	-18.28	11.89
(75)	RR6	August/September 2021	6.76	-21.28	8.02
85	2021	Summer 2020	17.37	-22.52	8.69
85	LR1_2022	May 2022	16.78	-22.32	8.57
85	LR4	August 2022	15.77	-19.22	11.20
97	97	Summer 2020	18.86	-17.67	15.16
OK	RP7	July 2020	16.44	-18.78	14.12

*An asterisk after the date indicates that the growth period for a feather was known based on the feather still growing in when sampled, otherwise all growth periods are estimated based on the molt cycle of the species (Pyle 1987)
() around the Raven ID indicates that a raven had feathers sampled representing two or more years.

Appendix F. Results of Tukey's HSD test comparing mean number of ravens observed by location during all behavioral surveys in 2022 and 2023. Significant differences between sites have been highlighted in gray and have a p-value below 0.05.

Pairwise Comparison	Difference	Lower	Upper	Adjusted p-value
Clam Beach-Big Lagoon	6.312	2.517	10.106	<0.001
Little River-Big Lagoon	8.819	5.360	12.277	<0.001
Mad River-Big Lagoon	5.799	2.173	9.425	<0.001
Ma-le'l Dunes-Big Lagoon	-0.418	-4.404	3.567	0.999
North Spit-Big Lagoon	2.649	-1.277	6.575	0.322
Stone Lagoon-Big Lagoon	-0.298	-4.350	3.753	0.999
Little River-Clam Beach	2.507	-0.778	5.792	0.185
Mad River-Clam Beach	-0.513	-3.974	2.949	0.999
Ma-le'l Dunes-Clam Beach	-6.730	-10.566	-2.894	<0.001
North Spit-Clam Beach	-3.663	-7.438	0.112	0.033
Stone Lagoon-Clam Beach	-6.610	-10.515	-2.706	<0.001
Mad River-Little River	-3.020	-6.109	0.069	0.031
Ma-le'l Dunes-Little River	-9.237	-12.741	-5.733	<0.001
North Spit-Little River	-6.170	-9.607	-2.733	<0.001
Stone Lagoon-Little River	-9.117	-12.696	-5.538	<0.001
Ma-le'l Dunes-Mad River	-6.217	-9.887	-2.548	<0.001
North Spit-Mad River	-3.150	-6.755	0.455	0.079
Stone Lagoon-Mad River	-6.098	-9.838	-2.357	<0.001
North Spit- Ma-le'l Dunes	3.067	-0.899	7.034	0.172
Stone Lagoon- Ma-le'l Dunes	0.120	-3.970	4.210	0.999
Stone Lagoon-North Spit	-2.947	-6.980	1.085	0.229
Clam Beach-Big Lagoon	6.312	2.517	10.106	<0.001