# WINTER SANDPIPER COMMUNITIES ON HUMBOLDT BAY: HIGH-TIDE ROOST USE AND HABITAT FEATURES THAT INFLUENCE ROOST SITE SELECTION

By

Chelsea Polevy

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

Committee Membership
Dr. Mark Colwell, Committee Chair
Dr. Jeff Black, Committee Member
Dr. Matthew Johnson, Committee Member
Dr. Erin Kelly, Graduate Coordinator

May 2022

# ABSTRACT

## WINTER SANDIPIER COMMUNITIES ON HUMBOLDT BAY: HIGH-TIDE ROOST USE AND HABITAT FEATURES THAT INFLUENCE ROOST SITE SELECTION

Chelsea Polevy

Roosts, locations at which birds and other animals come together to rest and preen while remaining vigilant for predators, are a common facet of the nonbreeding biology of many shorebirds. Roosts fall on a continuum from traditional to ephemeral; traditional roosts are used consistently by the same individuals, whereas ephemeral roosts are used inconsistently and may be used only once or a few times. Studies show that roost habitat preference is the result of an individual shorebird's attempt to optimize the costs and benefits associated with time constraints, energetic demands, and danger risks as they relate to overall fitness.

In this study, I evaluated roost site availability for a population of calidridine sandpipers wintering in Humboldt Bay, California along with the habitat characteristics that influence occurrence at roost sites. I organized a team of observers to conduct coordinated high-tide surveys of Humboldt Bay once per month from November 2018 through February 2019. My dataset included 129,196 observations of sandpipers at 104 roost sites throughout the bay.

My findings revealed that sandpipers occupied a large number of roost sites in diverse habitats. Sandpipers used a majority of these roosts infrequently, suggesting that suitable roosting habitat is readily available and that individuals have many options when choosing roost sites throughout Humboldt Bay. In addition, habitat features influenced distribution among roosts, as individuals selected roost sites with landscape characteristics that balanced competing needs associated with time and energy constraints while minimizing risk of danger posed by predators. Because roosts differ in terms of quality of habitat, there is likely a minimum distribution of ideal roost habitat needed to maintain wintering sandpiper populations throughout Humboldt Bay.

# ACKNOWLEDGEMENTS

I would like to thank Audubon California, the California Department of Fish and Wildlife, the March Conservation Fund, and the Sequoia Park Zoo Conservation Fund – this project was made possible by their financial support. Thank you to my advisor, Dr. Mark Colwell, for your guidance throughout this process. I truly appreciate both your patience and persistence as I worked on the majority of this project remotely. My professors, most notably Dr. Jim Graham and Dr. Andre Buccheister, provided considerable insight on my spatial and statistical analyses. Daniel Orr kindly produced Figure 1, and Khara Strum and Anna Weinstein provided additional project support.

Thank you to the surveyors who worked through rain and shine to provide continuous counts of shorebirds across Humboldt Bay. This thesis project (and the entire Humboldt Bay Shorebird Survey Project) would not have been possible without your unwavering commitment. Mario Balitbit, Jayde Blair, Aren Der-Gevorgian, Lizzie Feucht, David Fix, Rob Fowler, Gary Friedrichsen, Gina Graziano, Sarah Hoepfner, Alex Jamal, Deven Kammerichs-Berke, Tony Kurz, Fanter Lane, Matt Lau, Hannah LeWinter, Sharmaine Lindahl, Eric Nelson, Angela Petrice, Jeremy Pohlman, Jude Power, Katie Raby, James Ray, Kurt Roblek, Casey Ryan, Keith Slauson, Carol Wilson, Steve Wilson, and Justin Windsor – you are all incredibly talented ornithologists whom I admire.

Thank you to the wildlife graduate students at Humboldt State University, my friends and roommates in Arcata, and my friends all across the country – you provided invaluable support and encouragement through the many highs and lows associated with

the thesis writing process. I would specifically like to thank my best friend and fellow graduate student Mollie O’Brien for reading many iterations of this paper and providing insightful feedback. Finally, thanks a million to my parents, brother, and grandparents for always believing in me and for supporting my passion for wildlife conservation. I love you endlessly!

# TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# LIST OF APPENDICES

# INTRODUCTION

Group living is common in the animal kingdom (Krause and Ruxton 2002). Diverse taxa, including primates (Richner and Heeb 1996), butterflies (Finkbeiner et al. 2012), bats (Lewis 1995), and birds (Eiserer 1984), self-organize into aggregations (Parrish and Edelstein-Keshet 1999) to accrue benefits such as attracting mates (Stamps 1988), finding shelter (Mysterud and Østbye 1999), reducing energetic costs (Fish 1995), finding food (Pitcher et al. 1982), and avoiding predation (Abrahams and Colgan 1985). These benefits are most evident during periods of nonbreeding, when finding food and avoiding predation are the strongest selective forces shaping behavior (Colwell 2010).

Roosts, locations at which multiple individuals coalesce to rest and preen while remaining vigilant for predators, are a common facet of the nonbreeding biology of many birds (Eiserer 1984, Colwell 2010). In coastal regions, shorebirds (i.e., sandpipers, plovers, and other groups) are prompted by regular inundation from rising tides to move from their feeding grounds to roosts (Hartwick and Blaylock 1979, Kelly and Cogswell 1979, Myers 1984). At roosts, individuals spend time resting, preening, and occasionally foraging while remaining vigilant for predators (Colwell et al. 2003, Conklin and Colwell 2007).

Birds roost communally to gain three major benefits. First, individuals may acquire information on the location of ephemeral food sources (Ward and Zahavi 1973, Beauchamp 1999). The information center hypothesis (Ward and Zahavi 1973) states that roosts facilitate information transfer among individuals regarding the location of unpredictable food resources, with naïve individuals following successful companions to productive foraging areas. Second, roosts reduce energetic demands of thermoregulation by facilitating huddling and providing shelter from wind (Du Plessis et al. 1994, Beauchamp 1999). Finally, communal roosting serves to protect birds from predation through mechanisms similar to flocking (Elgar 1989). By joining a flock, an individual enhances vigilance and spreads its risk among others (Stinson 1980, Elgar 1989). Moreover, predators may become confused and may risk injury when attacking individuals in flocks (Myers 1984). These antipredator benefits are substantiated by the negative relationship between shorebird flock size and predation risk (Roberts 1996, Lilleyman et al. 2016).

Shorebird roosts fall on a continuum from traditional to ephemeral (Colwell et al. 2003). Traditional roosts are used consistently by the same individuals; ephemeral roosts are used inconsistently and may be used only once or a few times (Colwell et al. 2003). At the individual level, some studies show that wintering shorebirds display roost-site fidelity over intervals spanning days (Warnock and Takekawa 1996) to years (Rehfisch et al. 1996, 2003). By contrast, other studies suggest that individuals move frequently among roosts (Colwell et al. 2003, Conklin et al. 2008, Peters and Otis 2007). Studies of roost use at the population level reveal more consistent use of traditional roosts. For instance, populations of shorebirds in the U.K. have been observed using the same roost sites for decades (Burton et al. 1996, Rehfisch et al. 1996, 2003).

Shorebird roosts occur at locations within coastal habitats such as atop saltmarshes (Conklin and Colwell 2007), on unvegetated sandy beaches (Myers 1984), or on constructed structures such as jetties (Burton et al. 1996). Though roosting behavior is most often observed on a terrestrial landscape, shorebirds occasionally form aerial roosts (Dekker 1998). Large groups of shorebirds in-flight may occur when they are forced off terrestrial roosts due to disturbance by humans or predators (Dekker 1998, Hötker 2000, Conklin and Colwell 2007, Dekker et al. 2011).

Terrestrial roosts are features of the landscape that possess particular attributes that attract shorebirds (Zharikov and Milton 2009). These attributes are associated with an individual bird's ability to manage three critical factors: time, energy, and danger (Colwell 2010). In other words, roost habitat preference is the result of an individual's attempt to optimize the costs and benefits associated with time constraints, energetic demands, and danger risks as they relate to the individual's overall fitness. Table 1 provides a summary of literature on roost habitat preferences organized around these three concepts.

Table 1. Examples of studies detailing the variables that influence quality of roost sites as they relate to the concepts of time, energy, and danger.

| **Roost Characteristic** | **Findings** | **Reference** |
|---|---|---|
| ***Time/Energy*** | | |
| Proximity to foraging areas | Dunlin (*Calidris alpina*) in Alaska selected major diurnal roost sites adjacent to intertidal foraging habitat. | Handel and Gill 1992 |
| | In Portugal's Tagus Estuary, density of *C. alpina* at feeding habitat declined significantly as distance the nearest roost increased. | Dias et al. 2006 |
| | Bar-tailed Godwits (*Limosa lapponica*) and Eastern Curlews (*Numenius madagascariensis*) wintering in Australia selected roost habitats adjacent to foraging areas. | Zharikov and Milton 2009 |

| **Roost Characteristic** | **Findings** | **Reference** |
|---|---|---|
| ***Energy*** | | |
| Protection from inclement weather | During a period of cold weather in South Africa, Cattle Egrets (*Bubulcus ibis*) moved from traditional tree roosts to nearby branches overhanging a factory roof that provided warmth. | Siegfried 1971 |
| | In pine woods, European Starlings (*Sturnus vulgaris*) selected roost sites where wind velocity was lower and air temperature was higher. | Kelty and Lustick 1977 |
| | In Alaska, during a period of steady 25-30 kilometer per hour (km/h) winds, the number of roosting *C. alpina* decreased significantly at a roost site that offered minimal protection from winds. | Handel and Gill 1992 |
| | For eight species of shorebirds wintering on the coast of South Carolina, daily roost use was influenced primarily by wind speed and shelter from wind. | Peters and Otis 2007 |
| ***Danger*** | | |
| Openness of habitat | In a study of five species of shorebirds in New South Wales, 83% of roosts were at least 30 meters (m) from trees that were 5 m tall and 90% were further than 10 m from trees and bushes that were 2 m tall. Only 2% of roosts were within 10 m of trees over 5 m tall. | Lawler 1996 |
| | On the Wadden Sea, *C. alpina* exhibited aerial roosting due to the presence of raptors and tall trees and the absence of unvegetated roosting areas. | Hötker 2000 |
| | *C. tenuirostris* and *C. canutus* in Australia selected nighttime roosts that were presumably safe because they were far from tall cover. | Rogers et al. 2006 |
| | Calidridine sandpipers wintering in Australia were more abundant at roosts with greater viewsheds and thus greater perceived safety. | Zharikov and Milton 2009 |
| Distance from human activity | A 57% decline in the total number of shorebirds roosting on the Dee estuary between 1975 and 1985 was determined to be a consequence of increased levels of disturbance from dogs, horseback riders, and walkers. | Mitchell et al. 1988 |

| Roost Characteristic | Findings | Reference |
|---|---|---|
| | Human disturbance negatively affected the frequency with which Semipalmated Sandpipers (*C. pusilla*), Sanderlings (*C. alba*), and Ruddy Turnstones (*Arenaria interpres*) preferred roost habitats on sandy beaches in Massachusetts. | Pfister et al. 1992 |
| | During summer migration along the Long Island Sound, shorebirds were observed roosting on sandbars instead of habitat on the mainland as a means of decreasing anthropogenic disturbance. | Placyk and Harrington 2004 |
| | Dowitchers (*Limnodromus sp.*) in South Carolina appeared to track daily human disturbance, avoiding prospective roosts when boat activity was high within 100 m of the roost. | Peters and Otis 2007 |

Roost site selection is significant from the perspective of time and energy together, as shorebirds must allocate a portion of their daily time and energy budgets to traveling between roost sites and foraging sites (Colwell 2010). In coastal regions, foraging habitat is available for a limited time within a 24-hour cycle (Van Gils et al. 2006). Most tidally influenced areas experience a mixed semidiurnal tidal pattern with two unequal high tides and two unequal low tides per day. Neap tides of low amplitude move slowly and may not fully inundate tidal flats during high tide, thus providing foraging habitat for longer periods of time. Spring tides of extreme amplitude move quickly and fully inundate tidal flats during high tide. Because of these variations in tide cycles, shorebirds experience time and habitat restrictions with regard to foraging. Moreover, individuals must weigh the energetic costs of traveling to and from high-quality areas versus low-quality areas. Van Gils et al. (2006), who studied foraging patterns of Red Knots (*C. canutus*) in the Wadden Sea, found that individuals travel past foraging sites that offer low prey densities in order to reach sites that offer high prey densities, proving that individuals trade off energy intake rates against travel costs.

In addition to balancing time constraints and energetic demands, avoiding disturbance (both natural and anthropogenic) is one of the strongest forces shaping roost habitat selection in shorebirds (Weatherhead 1983, Luís et al. 2001, Rogers 2003, Rosa et al. 2006). Disturbance exacerbates energetic costs of movement, increases risk of predation, and restricts access to high-quality foraging habitat (Bechet et al. 2004, Peters and Otis 2007). Moreover, as predators such as raptors likely recognize roost sites, it is possible that the best an individual can do to evade predation is to join a flock whenever it roosts (Colwell 2010). Page and Whitacre (1975) estimated that raptors killed 21% of Dunlin, 14% of Sanderling, 12% of Least Sandpipers (*C. minutilla*), and 8% Western Sandpipers (*C. mauri*) wintering in Bolinas Lagoon, California, and concluded that predation was the driving force in flocking among these shorebirds. Handel and Gill (1992), who studied roosting behavior of Dunlin the Yukon-Kuskokwim Delta, Alaska, concluded that the risk of predation strongly influenced roosting behavior in that 42% of all flocks were disturbed by predators.

Roost quality is affected by a number of habitat features related to human disturbance and predation risks. Roosts occur in areas that are comparatively open, meaning they are free of structures, vegetation, and landscape features that may obstruct an individual’s viewscape. Open habitats allow individuals to scan their surroundings for danger, detect potential predators at great distances, and escape quickly and easily (Straw and Saintilan 2006). Shorebirds will choose to roost in areas close to tall vegetation or structures that obscure their view only when they have no alternative (Straw and Saintilan 2006).

Little is known about the influence of habitat characteristics on roost site selection in shorebirds wintering in Humboldt Bay, California USA. (Conklin and Colwell 2007). I aimed to evaluate roost use in the context of habitat variables linked with an individual's ability to manage time constraints, energetic demands, and danger risks. Based on literature review, I identified seven variables as physical descriptors of roosting habitat with the potential to influence shorebird abundance and distribution in Humboldt Bay (Table 2). I predicted that shorebirds select roost habitat that is: 1) far from human activity, 2) far from visual obstruction, 3) far from tall, wide obstructions, 4) gradual in slope, 5) high atop the landscape, 6) high above the average high tide level, and 7) close to foraging habitat.

Table 2. Predictor variables, descriptions, and expected effects.

| Variable | Description | Expected Effect |
|---|---|---|
| Exposure to human activity | Distance to nearest road or trail, indexed according to perceived level of danger | Shorebirds will select roost habitat far from human activity to minimize danger |
| Distance to cover | Distance to nearest obstruction (i.e. shrub, tree, building, jetty, levee, or other human-made structure) | Shorebirds will select roost habitat far from visual obstruction to minimize danger |
| Extent of cover | Height of nearest obstruction multiplied by width of nearest obstruction | Shorebirds will select roost habitat far from tall, wide obstructions to minimize danger |
| Slope | Steepness (0-90 degrees) | Shorebirds will select roost habitat with gradual slopes to minimize danger |
| Topographic position | Elevation of roost site relative to the surrounding topography | Shorebirds will select roost habitat high on the landscape to minimize danger |
| Height above tide | Height above average high tide level | Shorebirds will select roost habitat high above the average high tide level to minimize danger |
| Distance to foraging habitat | Distance to nearest high-elevation tidal flat | Shorebirds will select roost habitat close to foraging habitat to minimize time/energy expenditure |

# METHODS

## Study Area

Humboldt Bay is one of the largest estuaries on the Pacific coast of North America. In California, it is second only to San Francisco Bay in size (Barnhart et al. 1992). Humboldt Bay is an important location along the Pacific Americas Flyway and is recognized as a site of Hemispheric Importance by the Western Hemispheric Shorebird Reserve Network (WHSRN) based on estimates of shorebird abundance collected during this study (Colwell and Feucht 2018, Colwell et al. 2019, Colwell et al. 2020). These estimates reveal that the bay is utilized by approximately 176,000, 54,000, and 622,000 individuals of 31 species in the summer/fall, winter, and spring, respectively (Colwell et al. 2020). Humboldt Bay is valuable to shorebirds because it supports diverse habitats, including intertidal mudflats, sandy beaches, rock jetties, freshwater wetlands, and riverine systems that offer an abundance of foraging opportunities year-round (Colwell 1994, Colwell and Feucht 2018).

Humboldt Bay consists of two large basins, Arcata Bay and South Bay, connected by a shipping channel that leads to the Pacific Ocean (Figure 1; Mathis et al. 2006). The bay exhibits a mixed semidiurnal tidal pattern. During low tides, approximately 61 km$^2$ of intertidal habitat is exposed (Barnhart et al. 1992), which consists of a diversity of sediment types ranging from fine silt to coarse sand (Danufsky and Colwell 2003) along with dense strands of eelgrass (Colwell and Feucht 2018). Low tide provides a prime opportunity for shorebirds to forage on an assortment of invertebrate species, including small crustaceans, polychaetes, and bivalves (Barnhart et al. 1992). At high tide, shorebirds roost around the perimeter of the bay or forage in seasonal wetlands within fields and pastures (Colwell et al. 2003, Conklin and Colwell 2007, Conklin et al. 2008, Colwell et al. 2020).

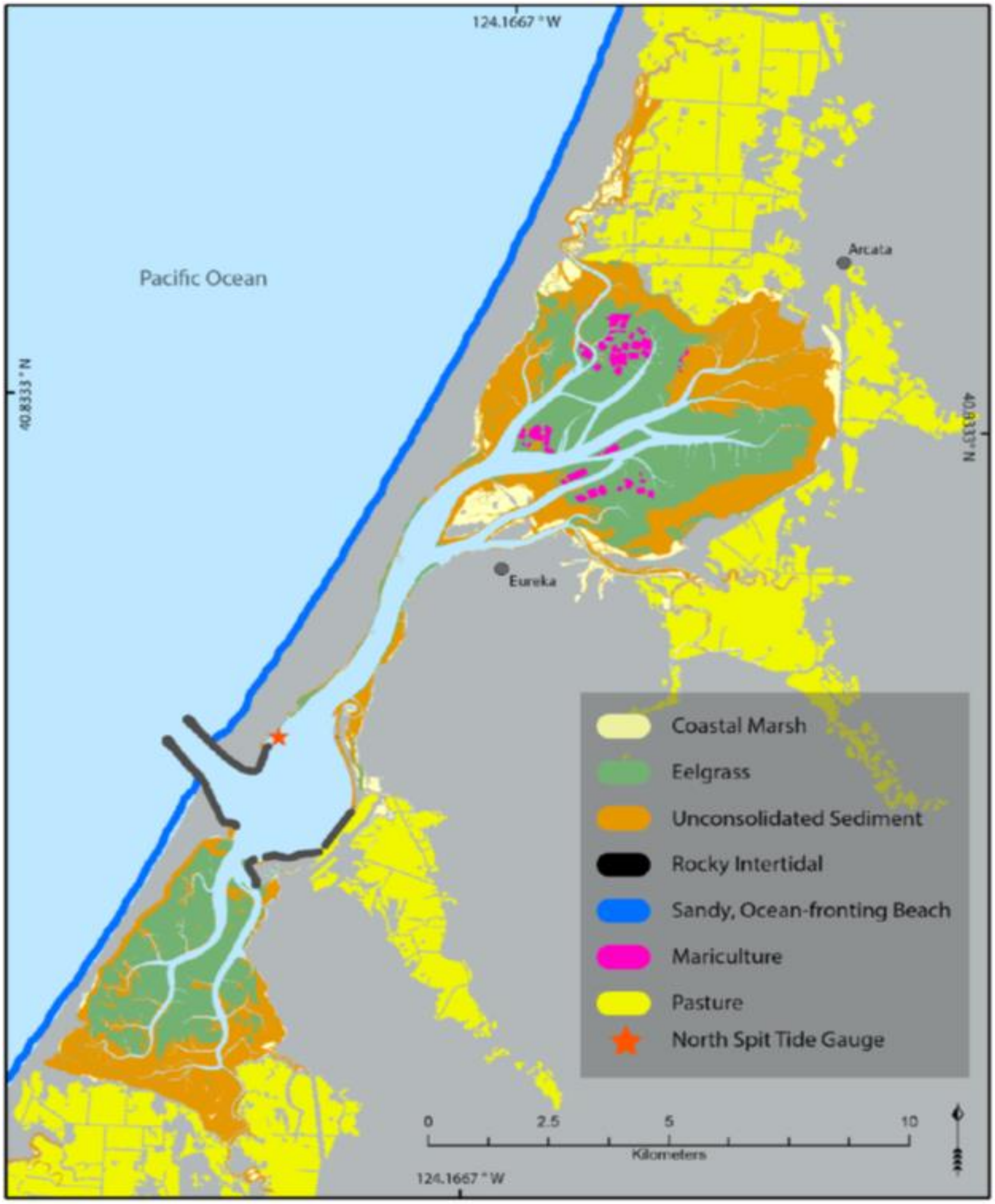

Figure 1. Major habitat types supporting shorebirds in Humboldt Bay, California, USA (Colwell et al. 2019).

## Survey Methods

For the purpose of this study, I divided Humboldt Bay into 15 survey areas that included the perimeter of the bay, ocean-fronting beaches, and adjacent pasture lands. Habitat types consist of outer beaches and bay shores, jetties and breakwaters, wharfs, pier pilings and other exposed human-made structures, islands, slough channels and mouths, river and creek mouths, tidally influenced saltmarshes, levee-protected ponds and mudflats, agricultural fields and pastures, and ephemeral wetlands (Figure 1). See Colwell et al. (2018, 2019, and 2020) for details.

Surveyor recruitment, training, and deployment occurred prior to the start of the first survey (Colwell et al. 2018, 2019, 2020). Observers conducted four coordinated surveys of Humboldt Bay once per month from November 2018 through February 2019. Survey methods adhered to the 2018 Program for Regional and International Shorebird Monitoring (PRISM), which provides guidelines for designing and implementing nonbreeding shorebird monitoring programs and projects (PRISM 2018). Surveys took place within the three-hour window bracketing diurnal high tide as indicated by the tide gauge located near the north jetty of Humboldt Bay (Figure 1). This followed the protocol used to survey shorebirds during spring migration (Colwell and Feucht 2018). Table 3 provides dates, high tides, and time intervals for the four winter surveys.

Table 3. Winter schedule for the Humboldt Bay shorebird survey project.

| Date | Tide Height (m) | Start Time | High Tide Time | End Time |
|---|---|---|---|---|
| 4 Nov 2018 | 2.16 | 0748 | 0918 | 1048 |
| 9 Dec 2018 | 2.17 | 1048 | 1218 | 1348 |
| 20 Jan 2019 | 2.53 | 0856 | 1026 | 1156 |
| 17 Feb 2019 | 2.47 | 0752 | 0922 | 1052 |

Project coordinators assigned observers to survey a single geographic area through which they walked, drove, or boated for approximately three hours while recording all observations and estimates of shorebirds along the way. Surveyors traveled each route in a predetermined way, as outlined by a detailed route description, in order to maximize efficiency and minimize the risk of double-counting birds. Colwell et al. (2018, 2019, 2020) provides further details. After each survey, observers collated data to include a count or estimate of abundance for each species encountered in chronological order. Observers associated these counts or estimates with roost boundary locations that they mapped on high resolution images of the survey area. In instances where observers could not identify birds to species due to similarities in nonbreeding plumage and/or impaired viewing conditions, they reported group totals for unidentified calidridine sandpipers (*Calidris spp*.) as “peeps.”

Conditions varied across the four observation dates (Table 3). Specifically, precipitation and abnormally high tides during the January and February surveys inundated intertidal habitats, which forced large numbers of shorebirds into pasture lands adjacent to the bay. Observed behavior in pastures on these survey dates included both roosting and foraging. As such, for the purpose of this study, I have defined roosts as aggregations of one or more shorebirds at high tide that were observed resting, preening, or foraging.

## Data Summary

### Response variables

I focused analyses on *C. alpina*, *C. minutilla*, *C. mauri*, and unidentified peeps; these taxa comprised approximately 70% of total observations. Three additional calidridine species accounted for 1% of total observations and 18 species of large-bodied shorebirds accounted for 29% of total observations; see Colwell et al. (2020) for details. I excluded the few additional calidridine species from analyses because they were rarely observed. I excluded the large-bodied species from analyses because they differ in behavior and habitat preferences from those of small taxa. Studies of interspecific variation in responses to human disturbance, for instance, show that larger species have greater flight initiation distances than smaller species (Blumstein et al. 2005). My final dataset included observations of 38,521 *C. alpina* (30% of total observations), 26,486 *C. minutilla* (20% of total observations), 15,232 *C. mauri* (12% of total observations), and 48,957 peeps (38% of total observations) for a total of 129,196 observations at 104 roost sites throughout Humboldt Bay between November 2018 and February 2019 (see Appendix A for a list of total observations per roost site and survey date). I used ArcMap (Environmental Systems Research Institute, Inc., Redlands, California, USA, Version 10.6.1) to digitize roost site boundaries, which observers recorded on Google Earth images at the time of each survey. I plotted geometric polygons of roost locations over a base-map (Figure 2 and Figure 3) and recorded species counts in each roost polygons' attribute table.

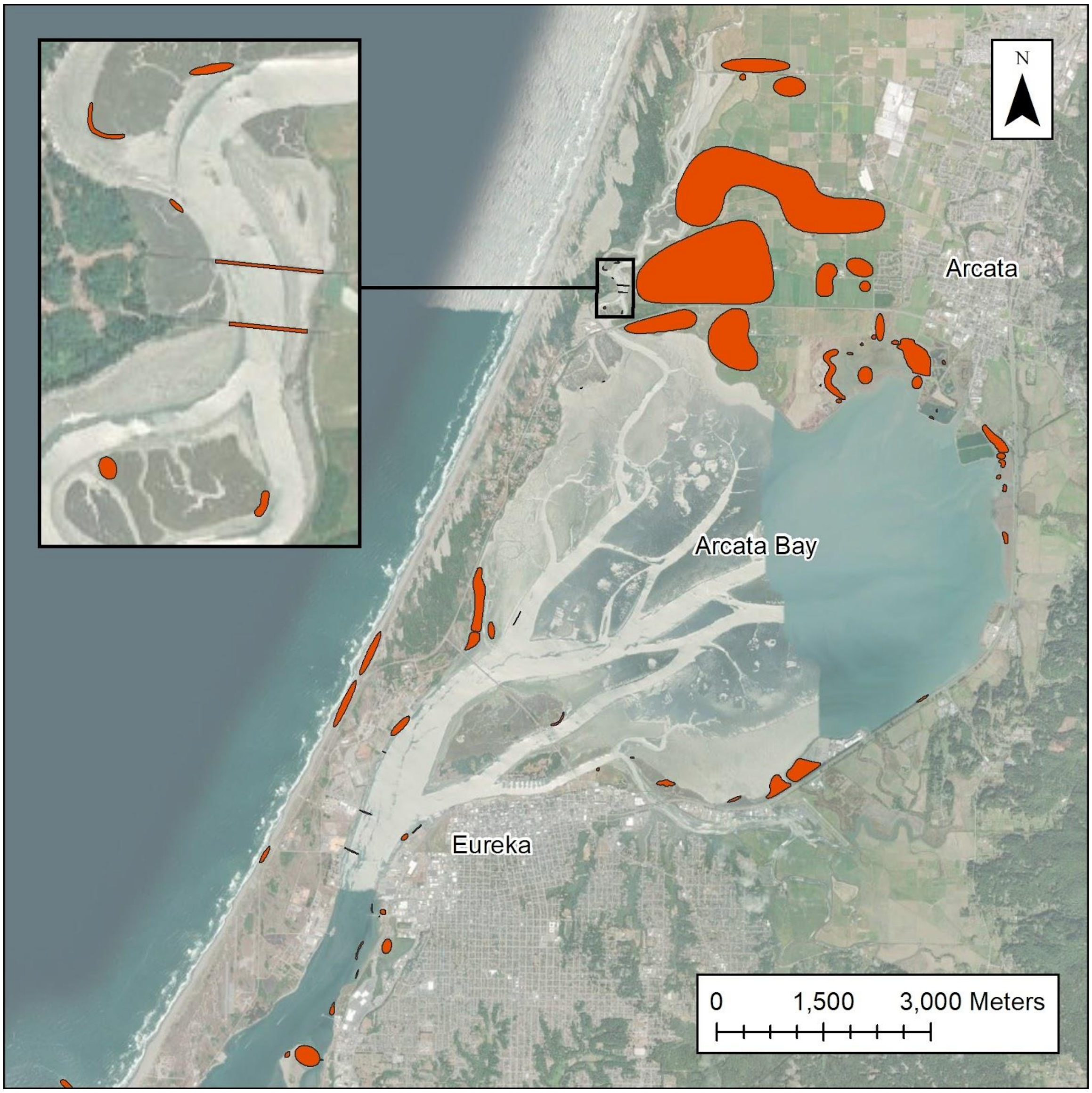

Figure 2. Spatial distribution of study species (*C. alpina*, *C. mauri*, *C. minutilla*, and *C. spp.*) observed at roost sites throughout Arcata Bay during the winter 2018-2019 shorebird surveys.

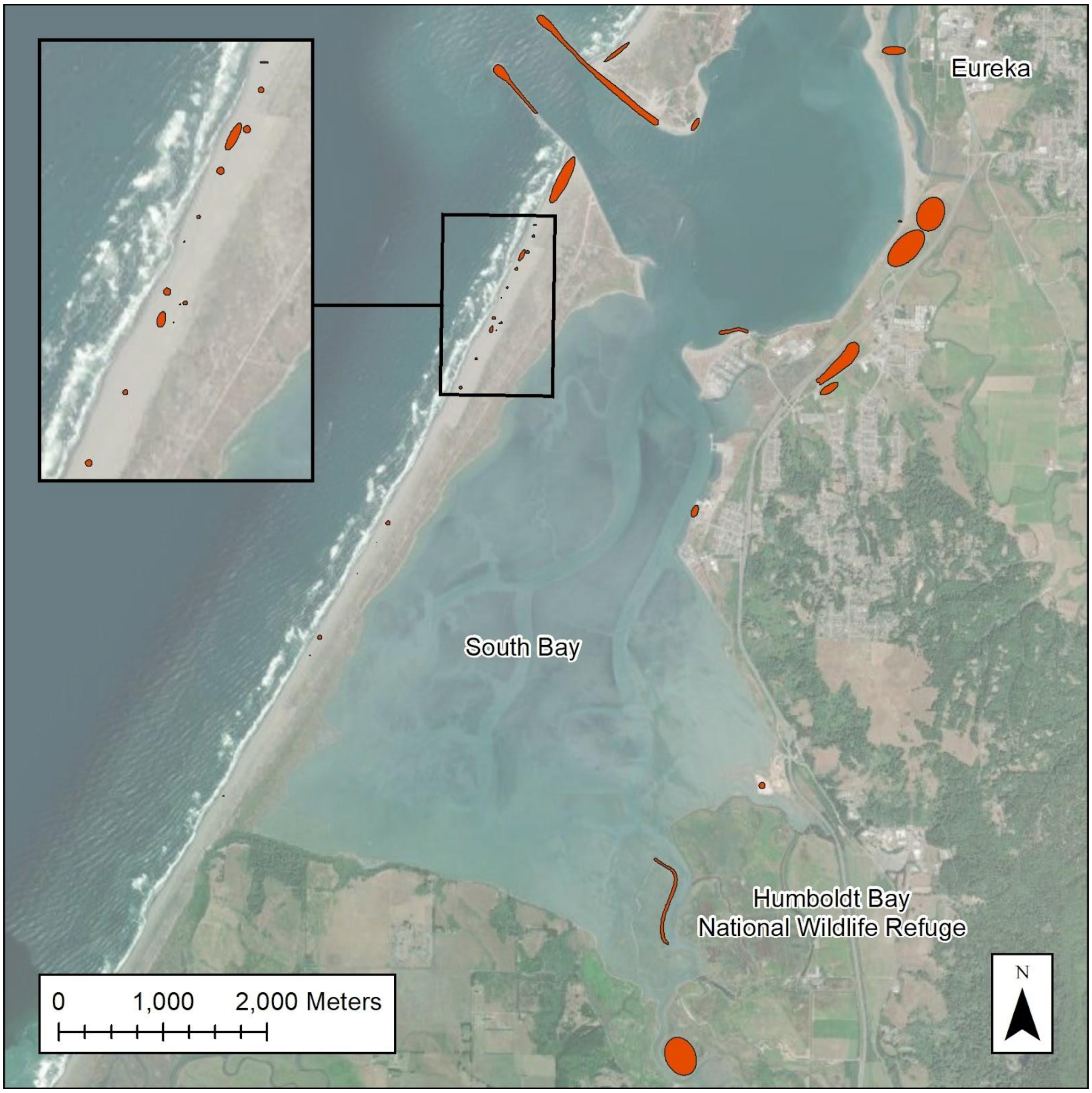

Figure 3. Spatial distribution of study species (*C. alpina*, *C. mauri*, *C. minutilla*, and *C. spp*.) observed at roost sites throughout South Bay during the winter 2018-2019 shorebird surveys.

Predictor variables

I selected a set of seven predictor variables pertaining to time constraints, energetic demands, and danger risks that have the potential to influence shorebird abundance and distribution at roosts (Table 4).

Table 4. Predictor variables, names of variables as they appear in the logistic regression models, sources from which variable data was acquired, year and spatial resolution of data, and notes on methods used for data preparation and extraction.

| Predictor Variable | Name in Model | Units | Source | Year | Resolution | Notes |
|---|---|---|---|---|---|---|
| Exposure to human activity | exp_to_human | m (indexed) | Humboldt County GIS Roadway Centerline shapefile | 2021 | - | See Appendix B |
| Distance to cover | dist_to_cover | m | Canopy height model (CHM) | 2019 | 1 m | CHM derived from LiDAR data using the Raster Calculator tool in ArcMap |
| Extent of cover | ext_of_cover | m | CHM | 2019 | 1 m | - |
| Slope | slope | Degrees (0-90) | Digital surface model (DSM) | 2019 | 1 m | DSM derived from LiDAR data using the Raster Calculator tool in ArcMap |
| Topographic position | TPI | Indexed | DSM | 2019 | 1 m | - |
| Height above tide | ht_abv_tide | m | DSM | 2019 | 1 m | - |
| Distance to foraging habitat | dist_to_foraging | m | DSM and field observations | Multiple | 1 m | - |

I measured predictor variables using spatial analysis tools in ArcMap. For roost sites smaller than 25 $m^2$, I measured variables from each roost's centroid. For roost sites larger than 25 $m^2$, I extracted randomly generated points within each roost polygon and averaged these points for each roost. The number of randomly generated points within roost polygons ranged from two points within a 27 $m^2$ polygon (the smallest observed roost polygon over 25 $m^2$) to 103 points within a 1.85 $km^2$ polygon (the largest observed roost polygon). I chose to measure habitat variables from centroid locations and randomly generated points within roost boundaries rather than from roost edges because studies have shown that birds compete for central positions within roosts in order to increase thermoregulation and reduce risk of predation (Calf et al. 2002, McGowan et al. 2006).

I calculated exposure to human activity using Humboldt County Highways and Roads vector data (Von Dohlen 2021) and indexed this variable according to perceived level of danger (Appendix B). I evaluated danger based on knowledge of both amount and frequency of human activity near roost sites (Luís et al. 2001) and generated index values ranging from 1 (least dangerous) to 4 (most dangerous). I chose to adopt a small scale of index values in order to reduce potential subjectivity (Luís et al. 2001). I assigned a value of 1 to quiet roads considered least dangerous, including walking trails in remote areas (e.g. trails at the Humboldt Bay National Wildlife Refuge), private drives, and dirt roads. I assigned a value of 2 to roads considered mildly dangerous, including paved roads in quiet neighborhoods (e.g. roads south of Eureka). I assigned a value of 3 to roads considered moderately dangerous, including paved roads with average traffic and walking/biking trails in busy neighborhoods (e.g. Eureka Waterfront Trail). I assigned a value of 4 to highly-trafficked roads considered most dangerous, including highways, paved roads in downtown Eureka, and walking/biking trails at the Arcata Marsh. I multiplied these perceived danger values by distance from roost to nearest road in order to quantify exposure to human activity.

I measured distance to cover and extent of cover using ArcMap base-map imagery and a canopy height model (CHM), which represents the height of vegetation, buildings, and other human-made structures above the underlying ground elevation. To create the CHM, I used the Raster Calculator tool in ArcMap’s Spatial Analyst Extension to extract the differences between the first returns and last returns of 1-m resolution remotely sensed Light Detection and Ranging (LiDAR) data acquired in 2019 (OCM Partners 2021). To calculate distance to cover, I used the Euclidean Distance tool to measure distance from each roost site to the nearest obstruction with a height of at least 1 m. I chose an obstruction threshold of 1 m as this has the potential to conceal raptors and has been used as a threshold in previous studies on the effects of cover in avian predator-prey relationships (Lazarus and Symonds 1992, Pomeroy et al. 2006). After identifying obstructive cover nearest each roost, I quantified the extent of that cover object, defined as the product of cover height by cover width. I extracted cover height from the CHM raster and measured cover width at the object’s widest point using ArcMap’s Measure tool.

I derived slope, topographic position, and height above tide from a digital surface model (DSM), which captures the elevation of both natural topography such as bare ground and vegetation and artificial environmental features such as buildings and pier pilings. The DSM uses the Raster Calculator tool in ArcMap's Spatial Analyst Extension to extract the first returns of 1-m resolution LiDAR data (OCM Partners 2021). I measured slope in degrees (from 0 to 90) using the Slope tool in ArcMap's Spatial Analyst Extension. To quantify topographic position, I calculated a topographic position index (TPI) whereby positive index values represent locations that are higher than their average surroundings (e.g. ridges) and negative index values represent locations that are lower than their average surroundings (e.g. valleys). I extracted the TPI from the DSM raster by comparing each cell's slope value to the mean slope of its neighbors (in 10-m increments) using the TPI tool in ArcMap's Topography Toolbox Extension. To calculate height above the average high tide level, I converted the DSM's original geodetic datum, North American Vertical Datum of 1988 (NAVD 88), to a tidal datum, Mean Sea Level (MSL). I then subtracted the average high tide height across all four winter survey dates (2.30 m) from the MSL value at each roost location.

I quantified distance to foraging habitat by identifying high elevation tidal flats using a combination of DSM elevation measurements and field observations of foraging locations throughout Humboldt Bay. I used the Near tool in ArcMap's Analysis Toolbox to calculate distance from roost site to foraging habitat.

## Data Analysis

To evaluate the effects of time, energy, and danger on roost habitat selection, I created resource selection functions (RSFs) by measuring and comparing predictor variables identified at used roost locations to those identified at available (i.e. random) roost locations (Manly et al. 2002). I derived used and available locations from the spatial scale corresponding to the second order of habitat selection (Johnson 1980), which I refer to as the home range scale. The home range scale consisted of the area encompassed by all 15 winter survey routes (Colwell and Feucht 2018, Colwell et al. 2019, Colwell et al. 2020).

I followed a Design 1 study as defined by Thomas and Taylor (2006), meaning I evaluated data at the population level. Because shorebirds are highly gregarious, I considered a roost “used” if at least two individuals of a species occurred at a site (Zharikov and Multion 2009) during at least one of the four winter surveys. I coded used/available values as 1/0, respectively. I classified used locations as roosts occupied by at least one calidridine species. I classified available locations as randomly sampled roosts within suitable habitat using the Create Random Points tool in ArcMap’s Data Management Toolbox. I made the number of available roosts equal to the number of used roosts within each of the 15 survey boundaries; for instance, observers identified six roosts within the Jacoby Creek survey boundary and I randomly generated six available roosts within the Jacoby Creek survey boundary. My final dataset included 104 used roost locations and 104 available roost locations throughout 62.95 km$^2$ of suitable habitat around Humboldt Bay (Figure 4 and Figure 5Figure 5).

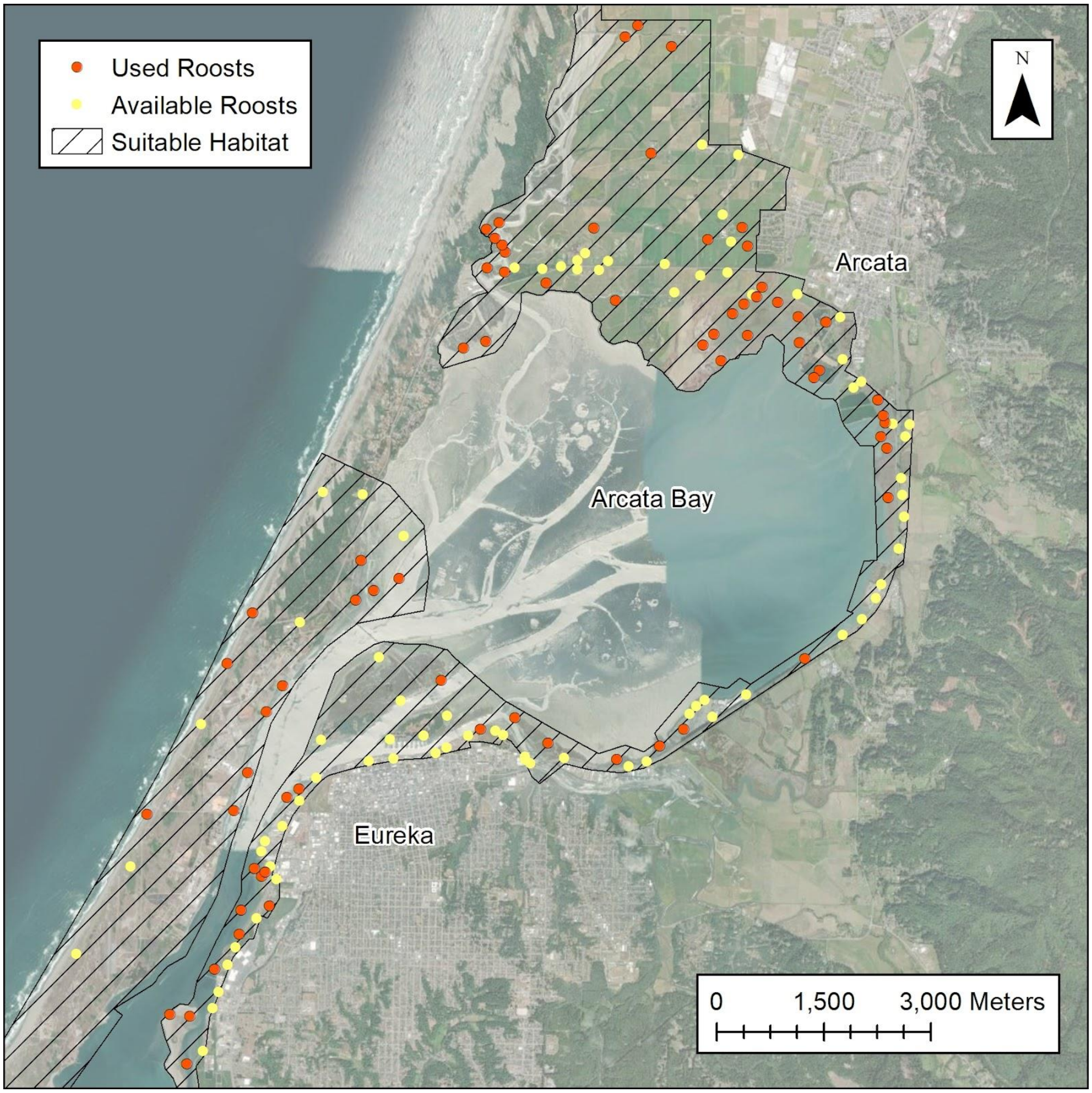

Figure 4. Centroids of used and available roost locations throughout Arcata Bay at the second-order scale of habitat selection, defined as the area encompassed by all 15 winter survey routes (i.e. “suitable habitat”).

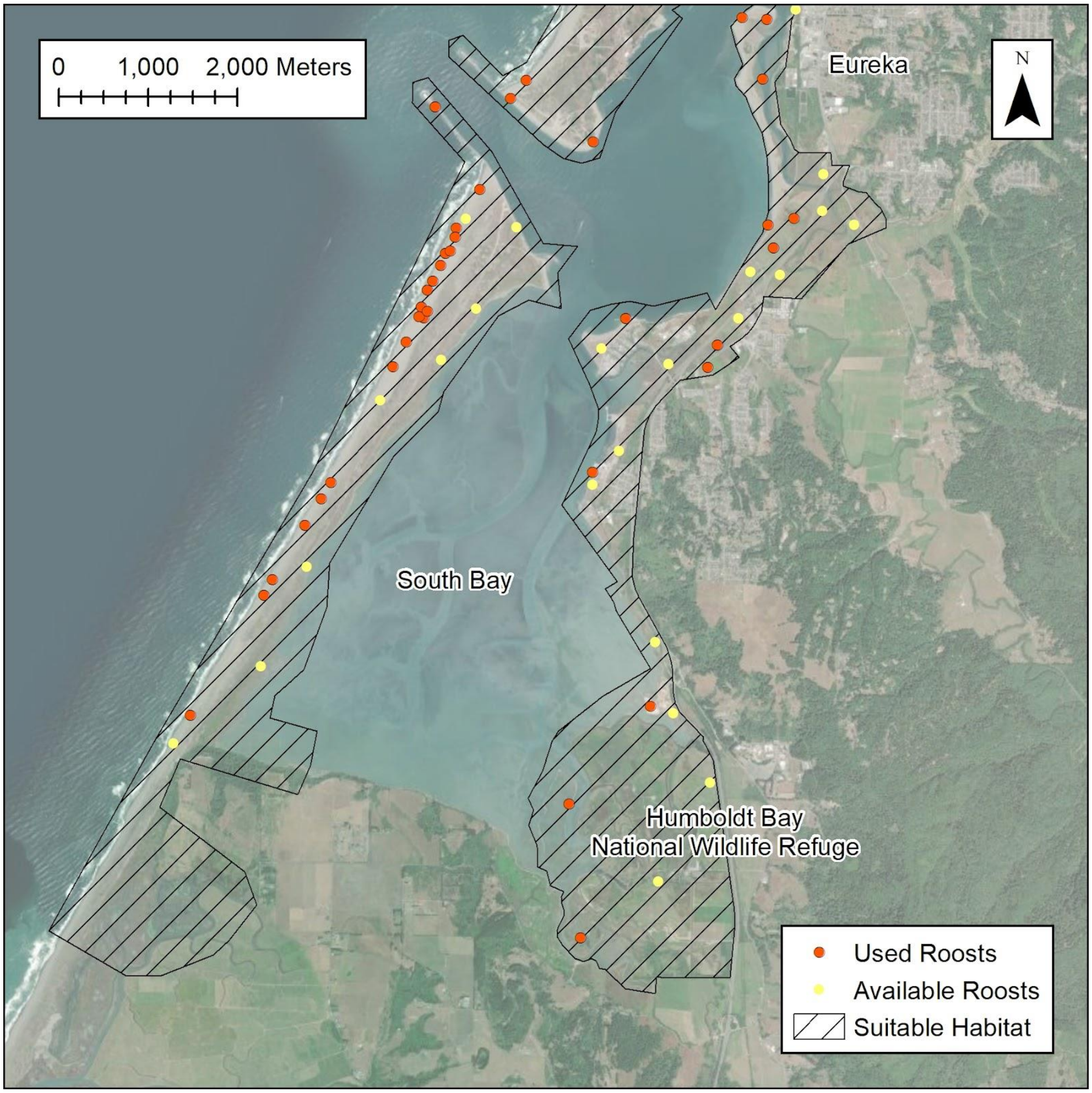

Figure 5. Centroids of used and available roost locations throughout South Bay at the second-order scale of habitat selection, defined as the area encompassed by all 15 winter survey routes (i.e. "suitable habitat").

A preliminary review of field data collected during the winter 2018-19 survey period revealed that sandpipers used most roosts infrequently and only a few roosts consistently (Figure 6 and Figure 7). As such, in order to evaluate the contribution of habitat variables to variation in roost use, I also thought it important to model shorebird incidence at roost sites. I defined incidence as the proportion of total surveys conducted in which at least two individuals occurred at a roost site. I assigned used roosts incidence values ranging from 0.25 (shorebird presence during one of four surveys) to 1 (shorebird presence during all four surveys) and I assigned available roosts incidence values of 0. I used logistic regression to conduct the same analysis with the same predictors as with my used/available RSFs, this time accounting for incidence.

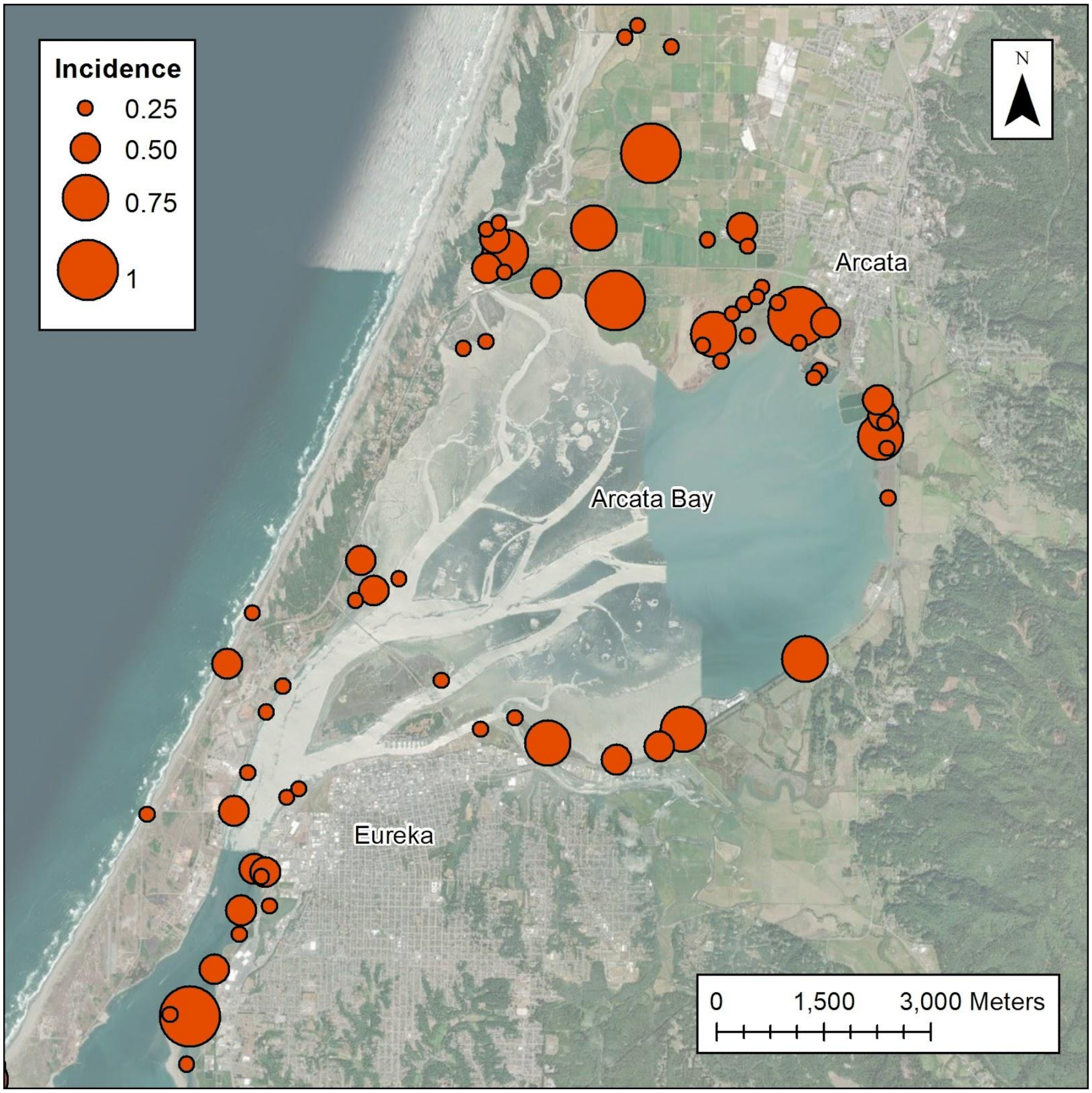

Figure 6. Sandpiper incidence at roost sites throughout Arcata Bay. An incidence value of 0.25 represents a roost that was occupied during one of four winter surveys, while an incidence value of 1 represents a roost that was occupied during all four winter surveys.

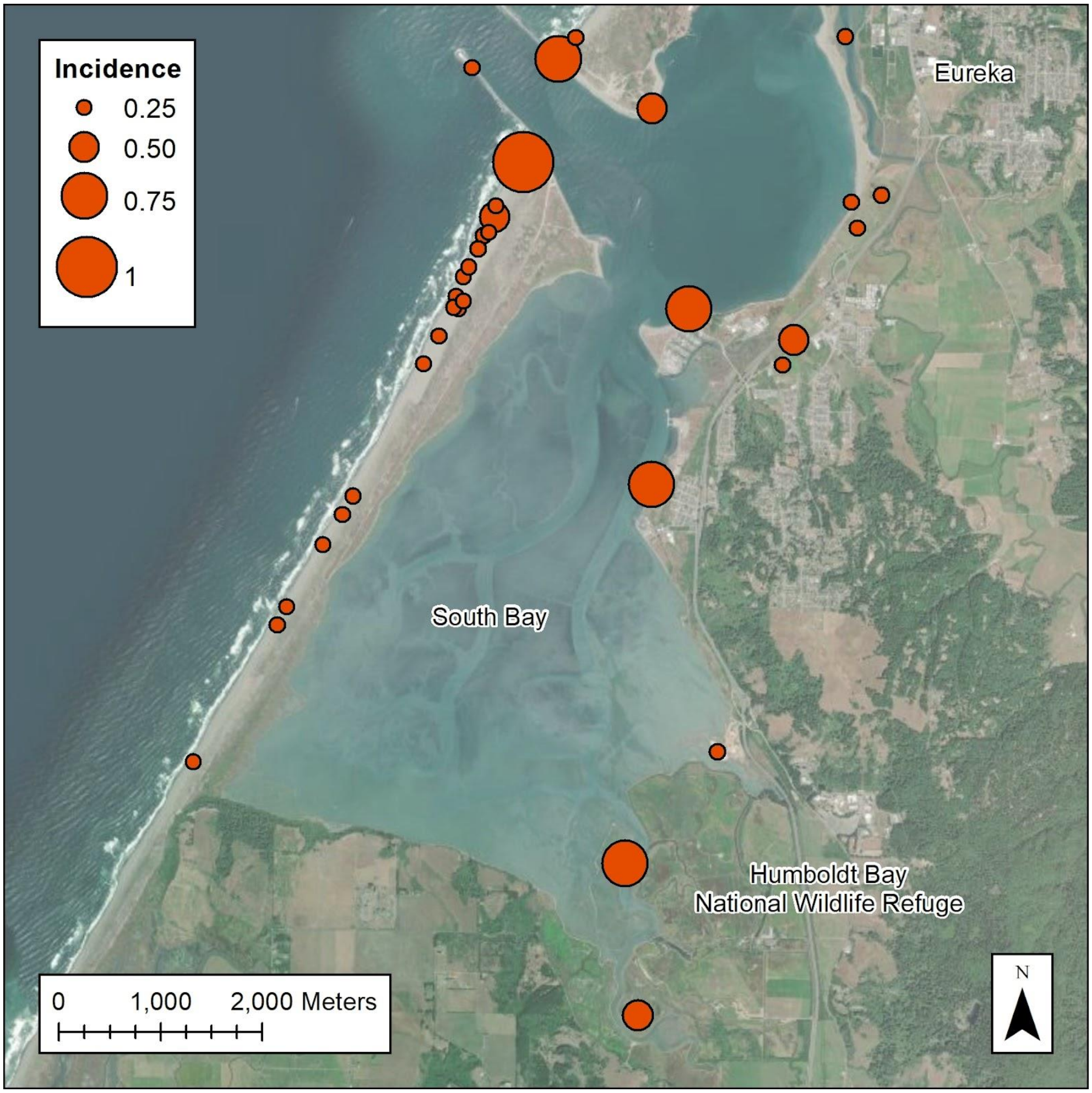

Figure 7. Sandpiper incidence at roost sites throughout South Bay. An incidence value of 0.25 represents a roost that was occupied during one of four winter surveys, while an incidence value of 1 represents a roost that was occupied during all four winter surveys.

To estimate response coefficients for each predictor variable, I produced RSFs by creating logistic regression models with binomial distributions and logit link functions in Program R (R Core Team 2020). In an RSF framework, habitat selection can be evaluated using logistic regression functions that estimate relative probability of use for each resource unit (Manly et al. 2002, Johnson et al. 2006). Prior to modeling, I performed data exploration as a means of identifying outliers, collinearity, and relationships between predictor and response variables (Zuur et al. 2009). I identified potential outliers among predictors, but chose to keep all data points in my model because I have a small dataset ($n = 208$). I tested for associations between predictors and found no collinearity ($r < 0.60$). I then performed a logarithmic (base 10) transformation on predictor variables that violated assumptions of normality in order to linearize the relationships between predictors and response.

Initially, I generated seven logistic regression models containing a single predictor in each model to inform variable selection for multiple logistic regression models and to prevent overfitting (Slinker and Glantz 2008). I removed insignificant predictors (i.e. $p$-value > 0.50) from consideration for multiple regression models. Next, I generated sets of multiple logistic regression models containing the same variables included as fixed effects but different two-way interaction terms. I modeled interactions based on biological knowledge (Zuur et al. 2009); it is plausible that the relationship between the response (roost use or roost availability) and one predictor may depend on another predictor for multiple sets of variables. To prevent overfitting, I omitted insignificant interactions and interactions that were significant (i.e. $p$-values < 0.05) when their corresponding individual predictors were insignificant (Zuur et al. 2009). I used these results to determine which interactions, if any, to retain in my candidate models (Zuur et al. 2009). I generated a candidate set of 64 multiple logistic regression models with six predictors included as fixed effects for both used/available models (Appendix C) and incidence models (Table 13 in Appendix D). I used the MuMIn package in Program R to rank models and obtain model weights based on Akaike's information criterion scores adjusted for small sample size (AICc; Burnham and Anderson 2002, Burnham et al. 2011).

Because model selection results did not yield a single optimal model for either my used/available RSF or my incidence RSF, I utilized multi-model inference (Symonds and Mousalli 2011) to generate parameter estimates and produce predictive models. To perform multi-model inference, I averaged the highest-ranking models and produced parameter estimates derived from the weighted averages of these models. I examined 95% CIs of parameter coefficients, dropped the predictors for which coefficients overlapped zero (Boyce et al. 2002), and re-ran my final models with a reduced set of predictor variables. Finally, to evaluate model performance, I employed a binning method and performed a Hosmer-Lemeshow goodness of fit test (Fagerland and Hosmer 2013).

# RESULTS

## Variation in Roost Use

Of the 104 observed roosts, sandpipers used 67 roost (64%) during one of four surveys, 21 roosts (20%) during two of four surveys, 11 roosts (11%) during three of four surveys, and five roosts (5%) during all four surveys (Figure 8).

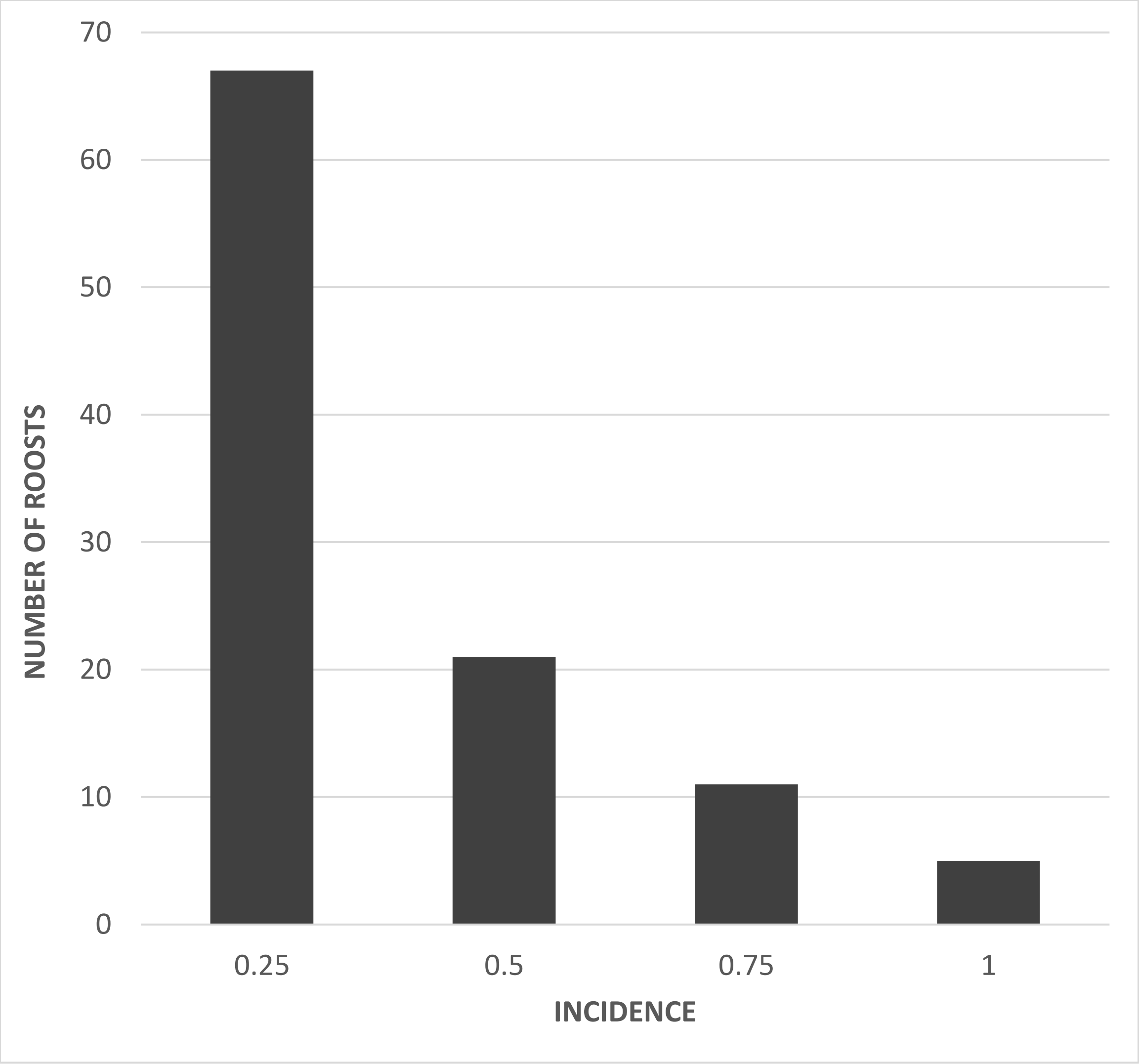

Figure 8. Sandpiper incidence at 104 roost locations observed throughout Humboldt Bay during the 2018-19 winter survey period. Incidence is defined as the proportion of total surveys in which at least two sandpipers occupied a roost site.

Total abundance at roost sites ranged across several orders of magnitude, from two birds at multiple roost sites to 38,817 birds at roost no. 71 (Figure 9; see also Appendix ). Roost use was fairly concentrated: 24% of total observations (31,298 sandpipers) were recorded at roosts occupied during one or two surveys, while 76% of total observations (97,898 sandpipers) were recorded at roosts occupied during three or four surveys. These findings reveal a positive relationship between total abundance and incidence at roost sites; as total abundance increases, incidence increases ($y = 6.7384x – 7.7477$; $R^2 = 0.38$). Though most roosts identified over the course of my study were used infrequently, the vast majority of sandpipers occupied a small number of roost sites consistently.

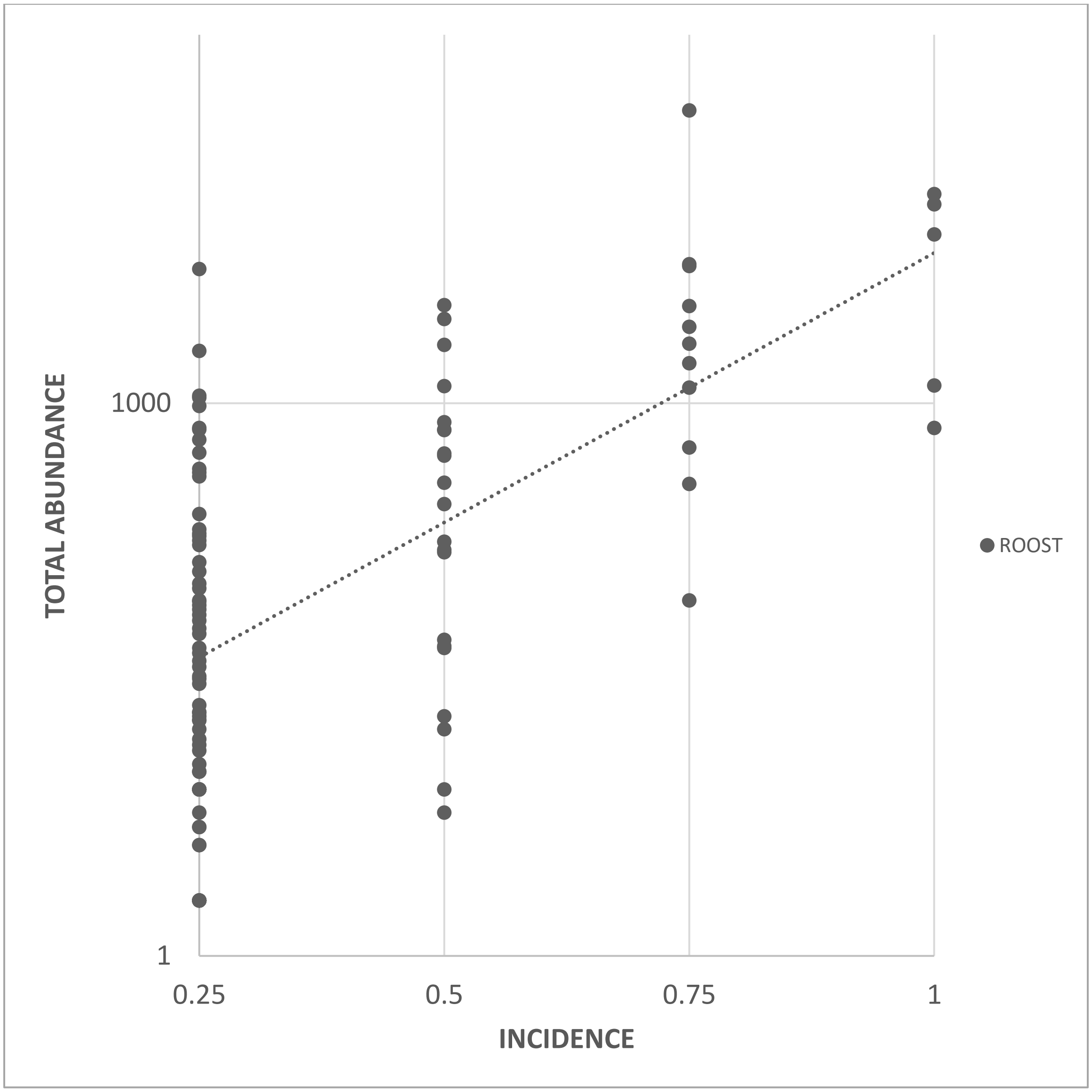

Figure 9. Relationship between total shorebird abundance and incidence at 104 roost sites throughout Humboldt Bay during the 2018-19 winter survey period, displayed at the logarithmic (base 10) scale. The dashed line represents the slope.

## Habitat Characteristics of Roosts

Univariate analyses (Table 5) indicated significant differences between used and available roost sites for six of seven variables. Exposure to human activity, distance to cover, extent of cover, slope, topographic position, and distance to foraging habitat were statistically significant (i.e. *p*-value < 0.05) and were subsequently retained for multiple regression models. I eliminated height above high tide from multivariate models due to the absence of a significant relationship in univariate analysis and the broad overlap in range of values between used available roosts.

Table 5. Mean, standard error (SE), and range values of predictor variables at used roosts (*n* = 104) and available roosts (*n* = 104) throughout Humboldt Bay, California. *P*-values were derived from used/available univariate logistic regression models.

| **Variable** | **Used Mean** | **Used SE** | **Used Range** | **Available Mean** | **Available SE** | **Available Range** | **P-value** |
|---|---|---|---|---|---|---|---|
| Exposure to human activity (m, indexed) | 445 | 50 | 0 - 2655 | 237 | 29 | 13 - 1709 | 0.0160 |
| Distance to cover (m) | 115 | 15 | 1 - 1202 | 42 | 4 | 1 - 227 | 0.000002 |
| Extent of cover (m) | 172 | 48 | 2 - 684 | 261 | 37 | 7 - 2335 | 0.000000184 |
| Slope (degrees) | 17.30 | 1.40 | 0.66 - 69.12 | 10.81 | 1.51 | 0.33 - 77.52 | 0.000000254 |
| Topographic position (indexed) | 0.90 | 0.23 | -2.47 - 11.16 | -0.71 | 0.19 | -7.48 - 7.18 | 0.0000303 |
| Height above tide (m)[1] | 1.80 | 0.16 | -0.74 - 6.24 | 1.70 | 0.14 | -0.62 - 8.47 | 0.328 |
| Distance to foraging habitat (m) | 728 | 68 | 0 - 2806 | 986 | 78 | 23 - 3280 | 0.00585 |

[1] The parameter was eliminated from consideration for multiple logistic regression because its *p*-value > 0.05.

The highest-ranking used/available RSF included a set of five predictors: distance to cover, extent of cover, slope, topographic position, and distance to foraging habitat. However, model selection results did not yield a single optimal model with a significantly low AICc score or an Akaike weight ($w_i$) greater than 0.80. Instead, three models (Table 6) with ΔAICc values less than six were considered competitive; I used these models to perform multi-model inference. Together, the three highest-ranking models constitute 97% of the cumulative model weight.

Table 6. Top model selection results of used/available models evaluating roost habitat selection of small calidridine shorebirds wintering in Humboldt Bay, California. Degrees of freedom (df), log likelihood (LogLik), AICc, ΔAICc, and $w_i$ are compared. See Appendix C for a full list of model selection results.

| Model Rank | Model Description | df | LogLik | AICc | ΔAICc | $w_i$ | Acc $w_i$ |
|---|---|---|---|---|---|---|---|
| 1 | distance to cover + extent of cover + slope + topographic position + distance to foraging habitat | 6 | -73.74 | 159.93 | 0.00 | 0.63 | 0.63 |
| 2 | exposure to human activity + distance to cover + extent of cover + slope + topographic position + distance to foraging habitat | 7 | -73.50 | 161.62 | 1.69 | 0.27 | 0.90 |
| 3 | distance to cover + extent of cover + slope + topographic position | 5 | -77.07 | 164.47 | 4.54 | 0.07 | 0.97 |

Parameter estimates (Table 7), odds ratios (ORs; Figure 10), and response plots (Figure 11) reveal that relative probability of sandpiper roost use in Humboldt Bay, California increased as distance to cover, slope, and topographic position increased. Conversely, relative probability of roost use decreased as extent of cover and distance to foraging habitat decreased.

Table 7. Estimated regression parameters, adjusted SE values, 95% CIs, and relative importance (w+) of variables in predicting roost habitat selection of small calidridine shorebirds wintering in Humboldt Bay, California, averaged based on the three highest-ranking used/available models.

| | **Estimate** | **Adjusted SE** | **95% CI** | **w+** |
|---|---|---|---|---|
| (Intercept) | -0.34904 | 1.68321 | -3.6480678 - 2.9499858 | - |
| Exposure to human activity[1] | 0.08557 | 0.27450 | -0.5750975 - 1.1854203 | 0.28 |
| Distance to cover | 2.48461 | 0.52160 | 1.4622947 - 3.5069206 | 1.00 |
| Extent of cover | -1.65980 | 0.32734 | -2.3013766 - (-1.0182220) | 1.00 |
| Slope | 1.69708 | 0.51329 | 0.6910515 - 2.7031138 | 1.00 |
| Topographic position | 0.53104 | 0.17347 | 0.1910461 - 0.8710403 | 1.00 |
| Distance to foraging habitat | -0.95798 | 0.47899 | -1.8521697 - (-0.2024553) | 0.93 |

[1] The parameter was dropped from the final model because its 95% CI overlaps zero.

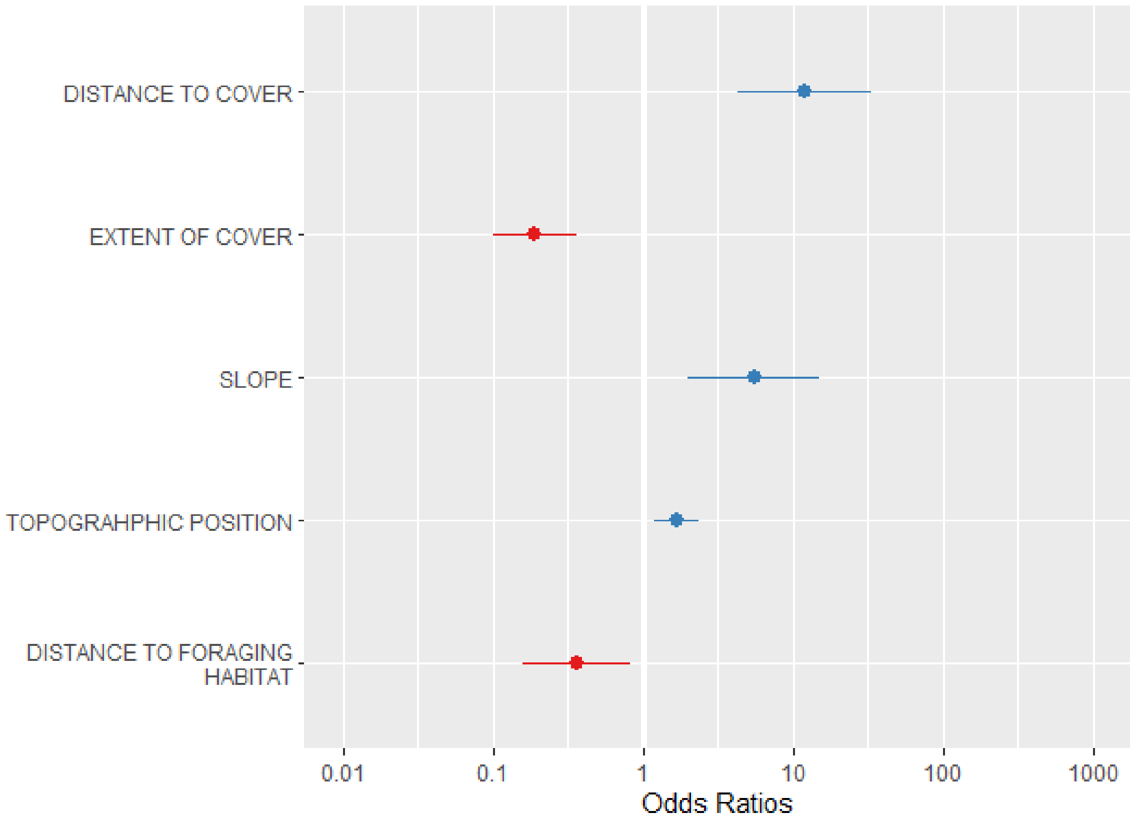

Figure 10. ORs representing the strength of the association between each predictor variable and sandpiper roost use in Humboldt Bay, California. Values above 1

(blue) and below 1 (red) represent positive and negative effects, respectively. Horizontal lines represent 95% CIs.

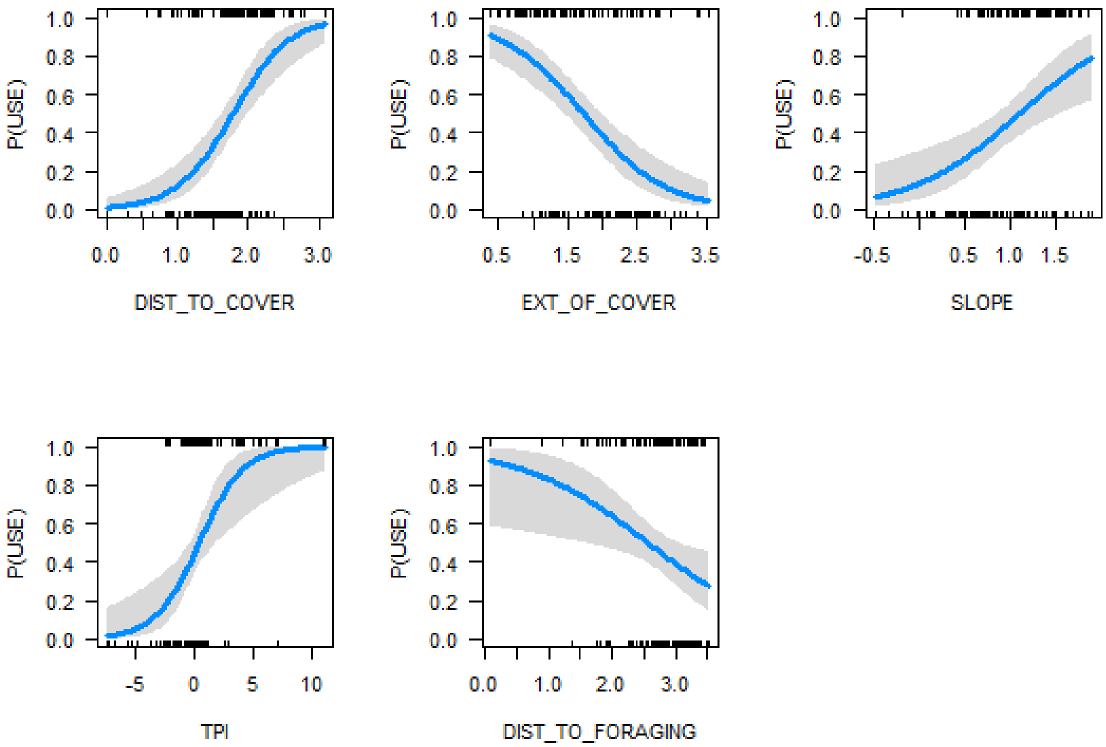

Figure 11. Response plots displaying the effects of each individual habitat predictor variable on the probability of shorebird roost use in Humboldt Bay, California. Blue lines represent expected values, gray bands represent 95% CIs, and black tick marks indicate approximate locations of positive and negative residuals.

To evaluate top model performance, I employed a binning method and performed a Hosmer-Lemeshow goodness of fit test (Fagerland and Hosmer 2013). I divided my dataset of 208 roosts into 15 bins, computed the number of used roosts and total roosts within each bin, and computed the mean predicted probability within each bin. I then plotted observed proportions against predicted probabilities (Figure 12; Pearson’s r =

0.93). I calculated a non-significant *p*-value of 0.4323, indicating no evidence that the observed and expected frequencies differ (i.e. evidence of good fit).

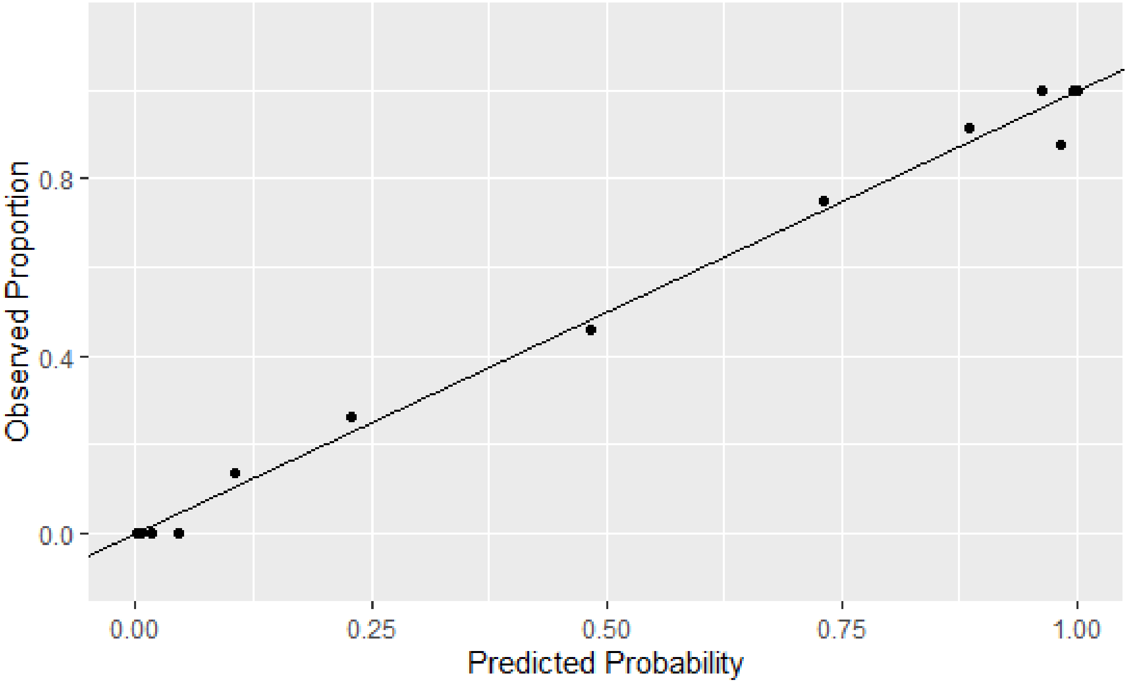

Figure 12. Binned predicted probabilities and observed proportions for the highest-ranking used/available RSF detailing sandpiper roost use in Humboldt Bay, California. The trend line passing through most of these intervals confirms that the variation from the expected is not excessive.

In order to properly interpret the biological significance of my final used/available RSF, I back-transformed all previously log-transformed predictors and derived OR values. Adjusted for the effects of all other predictors, for every 1 m increase in distance to cover, the odds of sandpiper roost use increased by 1.65%. For every 1 $m^2$ increase in extent of cover (i.e. 1 m increase in cover width and 1 m increase in cover height), the odds of roost use decreased by 0.13%. For every 1 degree increase in slope, the odds of roost use increased by 2.26%. For every 1 unit (i.e. 10 m) increase in topographic position, the odds of roost use increased by 51.02%. For every 1 m increase in distance to foraging habitat, the odds of roost use decreased by 0.03%.

I obtained nearly identical results for both my used/available models and my incidence models; however, distance to foraging habitat proved insignificant in my final incidence model. Appendix D contains incidence model results, including a list of top models, estimated regression parameters, ORs, and a full list of models considered in the selection process.

# DISCUSSION

In this study, I evaluated roost site selection for a population of calidridine sandpipers wintering in Humboldt Bay, California along with the habitat characteristics that influence occurrence at roost sites. Several findings and conservation implications emerged from this study. First, sandpipers occupied a large number of roosts (*n* = 104) in diverse habitats. Sandpipers used a majority of these roost sites (84%) infrequently. Moreover, sandpipers concentrated at a small number of these roosts, with 97,898 observations (76% of total abundance observations) occurring at just 16% of roost sites. My findings suggest that the majority of roosts in Humboldt Bay are used infrequently. In addition, sandpipers selected roost sites with habitat characteristics that balanced competing needs associated with time and energy constraints while minimizing risk of danger posed by predators. Roost occurred in locations that differed from random (i.e. available) locations and correlated with habitat variables suggesting that individuals selected habitats far from visual obstruction, far from expansive cover, steep in slope, atop higher ground, and close to foraging habitat.

## Roost Site Selection in Response to Habitat Variables Associated with Predation

As compared with random sites, sandpipers were more likely to roost at sites farther from obstructive edges and farther from extensive cover (i.e., vegetation, buildings, levees, and jetties greater than 1 m high and 1 m wide). These results parallel other studies concluding that shorebirds select habitat far from cover that may obscure their view of approaching predators. For instance, Pomeroy et al. (2006), who studied foraging *C. mauri* at a stopover site in British Columbia, built an obstructive 1-m high by 20-m long fence and found that individuals avoided foraging near obstructive cover and instead foraged in open areas with no obstructions. Yasué (2006), who studied foraging site selection at a migration stopover site in British Columbia, found that shorebirds chose sites far from forest cover in order to reduce predation risk.

Slope (i.e. steepness) at roost habitats correlated positively with roost use, which was opposite my prediction. I had inferred that roost sites with little to no slope provide 360-degree fields of view and therefore enhance cumulative vigilance at roost sites. However, a review of raw data revealed a trend of biological significance: all roosts with steep slopes > 30 degrees were located atop human-made structures such as north and south jetties, water pipes located along Mad River Slough, and pier pilings located adjacent to industrial properties in Eureka. Although these sites have steep slopes, they are located far from tall cover and thus provide clear viewscapes for collective groups of roosting shorebirds.

I predicted that roost use would increase as height above the average high tide level increased; however, height above tide was an insignificant predictor in my models. Given the exceptionally high tides that occurred during the survey periods (Table 3), I included height above tide in my models as a physical factor affecting the availability of roosts around the bay. The absence of relationship between tide height and roost use may be attributed to the simple fact that lower-elevation habitats were inundated and unavailable to roosting shorebirds; as such, my habitat analysis was restricted to exceptionally high-tide roost habitats by default. Had I incorporated a wider range of tide heights into the winter surveys, observers may have identified more roosts overall and my statistical analysis may have revealed a relationship between height above tide and roost use.

Topographic position, defined as the elevation of the roost site relative to its surrounding topography, was a significant predictor of roost use. As topographic position increased (i.e. as roost sites became more ridge-like), roost use increased. This result supports previous studies concluding that shorebirds select open roost habitats that allow for vigilance (Lawler 1996, Hötker 2000, Rogers et al. 2006, Zharikov and Milton 2009; see Table 1).

Though I focused specifically on the habitat characteristics associated with shorebird vigilance and predator avoidance, there are many field methods that may better quantify the significance of safety from predation, including data on actual disturbance and/or predation rates. For example, Rosa et al. (2006), who found that shorebirds in Portugal’s Tagus Estuary preferred to roost in mudflats rather than saltpans due to decreased predator pressure, observed the number of raptors flying over each roost, the number of alarm flights that occurred at each roost, and the proportion of time that individuals displayed vigilance.

### Roost Site Selection in Response to Habitat Variables Associated with Time Constraints and Energetic Demands

Distance to foraging habitat, the single predictor associated with the influence of time constraints and energetic demands on roost habitat selection, proved significant in my used/available model but not in my incidence model. This finding suggests that distance to foraging habitat is less important in selection of roosting habitat in Humboldt Bay as compared with other predictor variables, which may be due to the bay's small size or to the limited spatial extent of my study area.

My results support previous studies highlighting the significance of time and energy expenditure in relation to travel between roosts and foraging areas. For instance, Zharikov and Milton (2009) found that proximity to foraging habitat was the most common positive predictor of roost site selection in seven of 11 shorebird species wintering in eastern Australia and attributed this finding to the importance of low commuting costs. In another study in the Dutch Wadden Sea, van Gils et al. (2006) found that *C. canutus* knowledgeable about the quality of each foraging location within their environment most often chose roost sites closest to high-quality feeding grounds. Individuals uncertain about the quality of foraging locations, however, most often chose random roost sites.

As with all organisms, shorebirds expend more energy when traveling farther distances for longer periods of time. Foraging sites in Humboldt Bay (approximately 61 $km^2$) are relatively close together in comparison to, say, foraging sites in the Dutch Wadden Sea (approximately 500 $km^2$; Lodder et al. 2019). As such, distance to foraging habitat may have a greater influence on roost site selection in areas where distances between roosts and tidal flats are farther and trade-offs between time minimization and energy maximization are more significant. Moreover, the absence of relationship between distance to foraging habitat and incidence at roosts may be attributed to the fact that prey availability and intake rates differ between foraging sites. Studies have shown that individuals weigh the costs and benefits of traveling to and from high-quality foraging areas versus low-quality foraging areas (Swennen 1984, van Gils et al. 2006). As such, future studies of roost habitat selection in sandpipers wintering in Humboldt Bay should consider forage quality in addition to forage availability.

### Roost Site Selection in Response to Habitat Variables Associated with Human Disturbance

Though I predicted that roost use would increase as exposure to human activity increased, exposure to human activity was not a significant predictor of roost use in my models. While some studies highlight a relationship between roost site selection and anthropogenic disturbance (Mitchell et al. 1988, Pfister et al. 1992, Placyk and Harrington 2004, Peters and Otis 2007; see Table 1), others draw the opposite conclusion. Conklin and Colwell (2007) studied consistency of roost use of *C. alpina* wintering in Humboldt Bay and found that individuals fled roost sites upon detection of avian predators but not upon detection of humans. Yasué (2006), who studied the effect of human presence on shorebird habitat choice, also found that humans did not displace shorebirds; instead, shorebirds chose habitat farther from forest cover as a means of avoiding predation risk. As such, it is possible that exposure to human activity was an insignificant predictor in my statistical models because the danger posed by humans is far less than the danger posed by predators in Humboldt Bay.

In addition to the biological factors that may explain the lack of relationship between human activity and roost habitat selection, it is possible that my quantifications of physical habitat features did not accurately characterize human activity and, hence, disturbance. I indexed disturbance at each road and trail around Humboldt Bay according to perceived level of danger (see Appendix B); however, it was difficult to score each attribute objectively. The effect of anthropogenic disturbance depends on the amount and frequency of human activity in an area (Luís et al. 2001), and I could only make an educated guess about characteristic human behaviors at each location. Burger (1981), who studied the effects of human activity on birds at a coastal bay in New York, concluded that fast-paced human activities such as jogging caused birds to flee, whereas leisurely activities such as birdwatching and clamming did not. As such, future studies of habitat selection in shorebirds in Humboldt Bay should consider incorporating real-time observations of shorebirds' responses to human activity.

## Limitations

It is possible that observers misidentified species and/or miscounted individuals moving between habitats, particularly during the January and February surveys dates when precipitation compromised quality of observations. In order to eliminate error associated with miscounting shorebirds during these large-scale protocol surveys, I utilized used/available and incidence data as opposed to count data in my statistical analyses. While used/available modeling is useful in a wide variety of contexts, it also contains inherent biases. Used/available RSFs, by nature, equate the presence of a single individual at a used site to the presence of tens, hundreds, or thousands of individuals at a used site. From a conservation and habitat management perspective, roost sites with the capacity to hold many shorebirds should be prioritized over roost sites with the capacity to hold few shorebirds. I attempted to resolve this issue by modeling incidence data in conjunction with used/available data. However, while modeling incidence is important from the perspective of frequency of roost use, it still does not adequately account for sheer numbers of birds using roost sites. Because shorebird abundance at roosts varied over several orders of magnitude, it is important that similar studies of roost use in Humboldt Bay incorporate count data into their statistical methods.

It is also important to note that measurements of predictors are imprecise due to the large size of many roost sites. As detailed in my methods, I measured habitat variables at small roosts (i.e. those smaller than 25 $m^2$) from each roost's centroid and at large roosts (i.e. those larger than 25 $m^2$) from randomly generated points within each roost; I then averaged the measurements of predictors for each large roost. So, for instance, although the slope at one end of a 40 $m^2$ roost was five degrees and the slope at the other end of the roost was 45 degrees, I produced a single (average) measurement of this predictor. As such, a significant limitation of my study is that calculations of habitat variables are approximate.

## Conservation Implications

My research revealed that an abundant assemblage of sandpipers use Humboldt Bay to varying extents throughout the winter. Of the 104 observed roosts, sandpipers used 84% infrequently and 16% frequently. My findings corroborate other studies suggesting that presence at roost sites varies (Rehfisch et al. 1996, Peters and Otis 2007, Zharikov and Milton 2009) and that individuals wintering in Humboldt Bay move regularly among roosts (Colwell et al. 2003, Conklin and Colwell 2007, Conklin et al. 2008). This variation in frequency of roost use suggests that suitable roosting habitat is readily available and that sandpipers have many options when choosing roost locations throughout Humboldt Bay.

Variation in frequency of roost use also suggests that roost quality differs throughout Humboldt Bay, and my research revealed that habitat features influence distribution among roosts. Individuals used roost sites near foraging habitat, which suggests that roost site selection is influenced by time spent in transit and the energetic costs of travel. Most significantly, individuals used roost sites far from visual obstruction, far from expansive cover, steep in slope, and atop higher ground, which suggests that roost site selection is influenced by predation risk.

Because roosts differ in terms of quality of habitat, there is likely a minimum distribution of ideal roost habitat needed to maintain wintering sandpiper populations throughout the bay. This means that the alteration or destruction of roost habitats will negatively affect sandpiper distributions throughout Humboldt Bay. Any efforts to restore or enhance habitat for the preservation of shorebird species should consider the importance of maintaining a diverse network of roost habitats that decrease risk of predation and provide easy access to foraging areas. Future studies aimed at improving our understanding of roost quality throughout the bay should evaluate additional factors affecting roost site selection (e.g. environmental conditions) and should incorporate real-time observations of shorebirds’ responses to human activity and predator pressure.

# LITERATURE CITED

Abrahams, M. V., and Colgan, P. W. (1985). Risk of predation, hydrodynamic efficiency, and their influence on school structure. Environmental Biology of Fishes 13: 195-202.

Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J., Clark, J. A., and Ireland, P. L. (2003). Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. Biological Conservation 114: 127-141.

Barnhart, R. A., Boyd, M. J., and Pequegnat, J. E. (1992). The ecology of Humboldt Bay, California: an estuarine profile. United States Fish and Wildlife Service, Washington, D.C.

Beauchamp, G. (1999). The evolution of communal roosting in birds: origin and secondary losses. Behavioral Ecology 10: 675-687.

Beauchamp, G. (2010). Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. Ethology, 116(7): 645-652.

Bechet, A., Giroux, J. F., and Gauthier, G. (2004). The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology, 41: 689-700.

Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A., and Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. Journal of Applied Ecology, 42: 943-953.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K.A. (2002). Evaluating resource selection functions. Ecological Modelling, 157: 281-300.

Burger, J. (1981). The effect of human activity on birds at a coastal bay. Biological Conservation, 21: 231-241.

Burnham, K. P., and Anderson, D. R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed.). Springer, New York, New York, USA.

Burnham, K. P., Anderson, D. R., and Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology, some background, observations, and comparisons. Behavioral Ecology and Sociobiology, 65: 23-25.

Burton, N. H. K., Evans, P. R., and Robinson, M. A. (1996). Effects on shorebird numbers of disturbance, the loss of a roost site and its replacement by an artificial island at Hartlepool, Cleveland. Biological Conservation, 77(2-3): 193-201.

Calf, K., Adams, N., and Slotow, R. (2002). Dominance and huddling behaviour in bronze mannikin *Lonchura cucullata* flocks. Ibis, 144: 488-493.

Colwell, M. A. (1994). Shorebirds of Humboldt Bay, California: abundance estimates and conservation implications. Western Birds, 25: 137-145.

Colwell, M. A. (2010). Shorebird Ecology, Conservation, and Management. University of California Press, Berkeley, California, USA.

Colwell, M. A., Danufsky, T., Fox-Fernandez, N., Roth, J. E., and Conklin, J. R. (2003). Variation in shorebird use of diurnal high-tide roosts: How consistently are roosts used? Waterbirds, 26: 484-493.

Colwell, M. A., and Feucht, E. J. (2018). Humboldt Bay, California is more important to spring migrating shorebirds than previously recognized. Wader Study, 125: 135-141.

Colwell, M. A., Feucht, L. J., and Polevy, C. A. (2019). Winter abundance of shorebirds on Humboldt Bay, California, USA. Wader Study, 126(2): 116-124.

Colwell, M. A., Polevy, C., and LeWinter, H. (2020). Humboldt Bay, California, USA hosts a globally important shorebird community year-round. Wader Study, 127(3): 228-235.

Conklin, J. R., and Colwell, M. A. (2007). Diurnal and nocturnal roost site fidelity of Dunlin (*Calidris alpina*) at Humboldt Bay, California. Auk, 124: 677–689.

Conklin, J. R., Colwell, M. A., and Fox-Fernandez, N. W. (2008). High variation in roost use by Dunlin wintering in California: Implications for habitat limitation. Bird Conservation International, 18: 275-291.

Danufsky, T., and Colwell, M. A. (2003). Winter shorebird communities and tidal flat characteristics at Humboldt Bay, California. Condor, 105: 117-129.

Dekker, D. (1998). Over-ocean flocking by Dunlins, *Calidris alpine*, and the effects of raptor predation at Boundary Bay, British Columbia. Canadian Field-Naturalist, 112: 694-697.

Dekker, D., Dekker, I., Christie, D., and Ydenberg, R. (2011). Do staging Semipalmated Sandpipers spend the high-tide period in flight over the ocean to avoid falcon attacks along the shore? Waterbirds, 34: 195-210.

Dias, M. P., Granadeiro, J. P., Lecoq, M., Santos, C. D., and Palmeirim, J. M. (2006). Distance to high-tide roosts constrains the use of foraging areas by dunlins: implications for the management of estuarine wetlands. Biological Conservation, 131: 446-452.

Du Plessis, M. A., Weathers, W. W., and Koenig, W. D. (1994). Energetic benefits of communal roosting by acorn woodpeckers during the non-breeding season. Auk, 96: 631-637.

Eiserer, L. A. (1984). Communal roosting in birds. Bird Behavior, 5(2-3): 61-80.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biological Reviews, 64: 13-33.

Fagerland, M. W. and Hosmer, D. W. (2013). A goodness-of-fit test for the proportional odds regression model. Statistics in Medicine, 32: 2235-2249.

Finkbeiner, S. D., Briscoe, A. D., and Reed, R. D. (2012). The benefit of being a social butterfly: communal roosting deters predation. Proceedings of the Royal Society of London B: Biological Sciences, 279: 2769–2776.

Fish, F. E. (1995). Kinematics of ducklings swimming in formation: consequences of position. Journal of Experimental Zoology, 273: 1-11.

Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G., Triplet, P., le V. dit Durell, S. E. A., and McGrorty, S. (2004). When enough is not enough: shorebirds and shellfishing. Proceedings of the Royal Society of London B: Biological Sciences, 271: 233-237.

Handel, C. M., and Gill, R. E. (1992). Roosting behavior of premigratory dunlins (*Calidris alpina*). Auk, 109: 57-72.

Hartwick, E. B., and Blaylock, W. (1979). Winter ecology of a Black Oystercatcher population. Studies in Avian Biology, 2: 207-215.

Hötker, H. (2000). When do Dunlins spend high tide in flight? Waterbirds, 23: 482-485.

Iwamura, T., Possingham, H. P., Chadès, I., Minton, C., Murray, N. J., Rogers, D. I., Treml, E. A., and Fuller, R. A. (2013). Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society of London B: Biological Sciences, 280.

Johnson, C. J., Nelson, S. E., Merrill, E. H., McDonald, T. L., and Boyce, M. S. (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management, 70: 347-357.

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology, 61(1): 65-71.

Kelly, P. R., and Cogswell, H. L. (1979). Movements and habitat use by wintering populations of Willets and Marbled Godwits. Studies in Avian Biology, 2: 69-82.

Kelty, M. P., and Lustick, S. I. (1977). Energetics of the starling *Sturnus vulgaris* in a pinewood. Ecology, 58: 1181.

Krause, J., and Ruxton, G. D. (2002). Living in groups. Oxford University Press, Oxford, England.

Lawler, W. (1996). Guidelines for Management of Migratory Shorebird Habitat in Southern East Coast Estuaries, Australia [Master of Resource Science thesis]. University of New England, Armidale, New South Wales, Australia.

Lazarus, J., and Symonds, M. (1992). Contrasting the effects of protective and obstructive cover on avian vigilance. Animal Behavior, 43: 519-521.

Lewis, S. E. (1995). Roost Fidelity of Bats: A Review. Journal of Mammalogy, 76(2): 481-496.

Lilleyman, A., Franklin, D. C., Szabo, J. K., and Lawes, M. J. (2016). Behavioural responses of migratory shorebirds to disturbance at high-tide roosts. Emu, 116: 111-118.

Lodder, Q. J., Wang, Z. B., Elias, E. P., van der Spek, A. J., de Looff, H., and Townend, I. H. (2019). Future response of the Wadden Sea tidal basins to relative sea-level rise—An aggregated modelling approach. Water, 11(10): 2198.

Luís, A., Goss-Custard, J. D., and Moreira, M. H. (2001). A method for assessing the quality of roosts used by waders during high tide. Wader Study Group Bulletin, 96: 71-74.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2002). Introduction to resource selection studies. In Resource selection by animals: statistical analysis and design for field studies (pp. 1-15). Kluwer, Boston, Massachusetts, USA.

Masero, J. A., Pérez-Hurtado, A., Castro, M., and Arroyo, G. M. (2000). Complementary use of intertidal mudflats and adjacent salinas by foraging waders. Ardea, 88: 177-191.

Mathis, R. L., Colwell, M. A., Leeman, L. W., and Leeman, T. S. (2006). Long-billed Curlew distributions in intertidal habitats: scale-dependent patterns. Western Birds, 37: 156-168.

McGowan, A., Sharp, S. P., Simeoni, M., and Hatchwell, B. J. (2006). Competing for positions in the communal roosts of long-tailed tits. Animal Behavior, 72: 1035-1043.

Mitchell, J. R., Moser, M. E., and Kirby, J. S. (1988). Declines in midwinter counts of waders roosting on the Dee estuary. Bird Study, 35(3): 191-198.

Myers, J. P. (1984). Spacing behavior of nonbreeding shorebirds. In Behavior of marine animals (Vol. 6, pp. 271-321). Plenum Press, New York, New York, USA.

Mysterud, A., and Østbye, E. (1999). Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography. Wildlife Society Bulletin, 27(2): 385-394.

Northern Hydrology and Engineering (NHE). (2014). Estimates of local or relative sea level rise for Humboldt Bay region. Accessed at: https://humboldtbay.org/

OCM Partners. (2021). 2019 Lidar: City of Eureka, California. National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information. Accessed at: https://www.fisheries.noaa.gov/inport/item/59069

Page, G., and Whitacre, D. F. (1975). Raptor predation on wintering shorebirds. The Condor, 77: 73-83.

Parrish, J., and Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science, 284(5411): 99-101.

Peters, K. A., and Otis, D. L. (2007). Shorebird roost-site selection at two temporal scales: Is human disturbance a factor? Journal of Applied Ecology, 44: 196-209.

Pfister, C., Harrington, B. A., and Lavine, M. (1992). The impact of human disturbance on shorebirds at a migration staging area. Biological Conservation, 60: 115-126.

Piersma, T., Gill, R. E., de Goeij, P., Dekinga, A., Shepherd, M. L., Ruthrauff, D., and Tibbitts, L. (2006). Shorebird avoidance of nearshore feeding and roosting areas at night correlates with presence of a nocturnal avian predator. Wader Study Group Bulletin, 109: 73-76.

Pitcher, T. J., Magurran, A. E., and Winfield, I. J. (1982). Fish in larger shoals find food faster. Behavioral Ecology, 10: 149-151.

Placyk, J. S., and Harrington, B. A. (2004). Prey abundance and habitat use by migratory shorebirds at coastal stopover sites in Connecticut. Journal of Field Ornithology, 75: 223-231.

Pomeroy, A. C., Butler, R. B., and Ydenberg, R. C. (2006). Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. Behavioral Ecology, 17: 1041-1045.

Program for Regional and International Shorebird Monitoring (PRISM). (2018). Standards for Monitoring Nonbreeding Shorebirds in the Western Hemisphere. Accessed at: https://www.shorebirdplan.org/science/program-for-regional-andinternational-shorebird-monitoring/

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed at: http://www.R-project.org/

Rehfisch, M. M., Clark, N. A., Langston, R. H. W., and Greenwood, J. J. D. G. (1996). A guide to the provisions of refuges for waders: an analysis of 30 years of ringing from the Wash, England. Journal of Applied Ecology, 33: 673-687.

Rehfisch, M. M., Insley, H., and Swann, B. (2003). Fidelity of overwintering shorebirds to roosts on the Moray Basin, Scotland: implications for predicting impacts of habitat loss. Ardea, 91: 53-70.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology, 86: 2805-2814.

Richner, H., and Heeb, P. (1996). Communal life: honest signaling and the recruitment center hypothesis. Behavioral Ecology, 7(1): 115-118.

Roberts, G. (1996). Why individual vigilance declines as group size increases. Animal Behavior, 51: 1077-1086.

Rogers, D. I. (2003). High-tide roost choice by coastal waders. Wader Study Group Bulletin, 100: 73-79.

Rogers, D. I., Piersma, T., and Hassell, C. J. (2006). Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. Biological Conservation, 133: 225-235.

Rosa, S., Encarnação, A. L., Granadeiro, J. P., and Palmeirim, J. M. (2006). High water roost selection by waders: maximizing feeding opportunities or avoiding predation? Ibis, 148: 88-97.

Senner, S. E., Andres, B. A., and Gates, H. R. (Eds.). (2016). Pacific Americas shorebird conservation strategy. National Audubon Society, New York, New York, USA. Accessed at: http://www.shorebirdplan.org

Siegfried, W. R. (1971). Communal roosting of the cattle egret. Transactions of the Royal Society of South Africa, 39(4): 419-443.

Slinker, B. K., and Glantz, S. A. (2008) Multiple linear regression: Accounting for multiple simultaneous determinants of a continuous dependent variable. Circulation, 117(13): 1732-1737.

Smit, C., and Visser, G. M. (1993). Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. Wader Study Group Bulletin, 68: 6-19.

Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. The American Naturalist, 131(3): 329-347.

Stinson, C. H. (1980). Flocking and predator avoidance: Models of flocking and observations on the spatial dispersion of foraging winter shorebirds (Charadrii). Oikos, 34: 35-43.

Straw, P., and Saintilan, N. (2006). Loss of shorebird habitat as a result of mangrove incursion due to sea-level rise and urbanization. In G. C. Boere, C. A. Galbraith, and D. A. Stroud (Eds.), Waterbirds Around the World (pp. 717-720). The Stationery Office, Edinburgh, UK.

Swennen, C. (1984). Differences in quality of roosting oystercatchers. In P. R. Evans, J. D. Goss-Custard, and W. G. Hale (Eds.), Coastal waders and wildfowl in winter (pp. 177-189). Cambridge University Press, Cambridge, UK.

Symonds, M. R. E., and Mousalli, A. (2011). A brief guide to model selection, multimodal inference and model averaging in behavioral ecology using Akaike’s information criterion. Behavioral Ecology and Sociobiology, 65: 13-21.

Thomas, D. L., and Taylor, E. J. (2006). Study designs and tests for comparing resource use and availability II. The Journal of Wildlife Management, 70(2): 324-336.

Thorne, K. M., Dugger, B. D., Buffington, K. J., Freeman, C. M., Janousek, C. N., Powelson, K. W., Gutenspergen, G. R., and Takekawa, J. Y. (2015). Marshes to mudflats: sea-level rise effects on tidal marshes along a latitudinal gradient in the Pacific Northwest [Open-File Report 2015–1204]. U.S. Department of the Interior, Geological Survey, Sacramento, California, USA.

van Gils, J. A., Spaans, B., Dekinga, A., and Piersman, T. (2006). Foraging in a tidally structured environment by Red Knots (*Calidris canutus*): Ideal, but not free. Ecology, 87: 1189-1202.

von Dohlen, J. (2021, March). Humboldt County Highways and Roads. Humboldt County Planning and Building Department. Accessed at: https://humboldtgov.org/276/GIS-Data-Download

Ward, P., and Zahavi, A. (1973). The importance of certain assemblages of birds as ‘information- centres’ for food-finding. Ibis, 115: 517-534.

Warnock, S. E., and Takekawa, J. Y. (1996). Wintering site fidelity and movement patterns of western sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis, 138: 160-167.

Weatherhead, P. (1983). Two Principal Strategies in Avian Communal Roosts. The American Naturalist, 121(2): 237-243.

Yasué, M. (2006). Environmental factors and spatial scale influence shorebirds’ responses to human disturbance. Biological Conservation, 128: 47-54.

Yasué, M., Quinn, J. L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshank. Functional Ecology, 17: 727-736.

Zharikov, Y., and Milton, D. (2009). Valuing coastal habitats: Predicting high-tide roosts of non-breeding migratory shorebirds from landscape composition. Emu, 109: 107-120.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). Mixed Effects Models and Extensions in Ecology with R. Springer, New York, New York, USA.

# APPENDIX A

Table 8. Roost sites, XY coordinates of roost centroids, and raw totals of calidridine sandpipers identified during the four winter 2018-2019 shorebird surveys.

| **Roost No.** | **X COORDS** | **Y COORDS** | **4 Nov 2018** | **9 Dec 2018** | **20 Jan 2019** | **17 Feb 2019** | **Total/Roost** |
|---|---|---|---|---|---|---|---|
| 1 | -124.0841567 | 40.84894893 | 965 | 0 | 0 | 0 | 965 |
| 2 | -124.2569553 | 40.72368006 | 0 | 84 | 0 | 0 | 84 |
| 3 | -124.2590968 | 40.7210032 | 0 | 420 | 0 | 0 | 420 |
| 4 | -124.26436 | 40.71381999 | 0 | 190 | 0 | 0 | 190 |
| 5 | -124.2739099 | 40.7015959 | 0 | 15 | 0 | 0 | 15 |
| 6 | -124.2394963 | 40.7513032 | 0 | 105 | 0 | 0 | 105 |
| 7 | -124.2432074 | 40.74497846 | 0 | 8 | 0 | 0 | 8 |
| 8 | -124.243403 | 40.7427603 | 0 | 41 | 0 | 0 | 41 |
| 9 | -124.2437031 | 40.74213251 | 0 | 32 | 0 | 0 | 32 |
| 10 | -124.2234005 | 40.69315221 | 415 | 2454 | 500 | 0 | 3369 |
| 11 | -124.2128234 | 40.70315486 | 0 | 170 | 0 | 0 | 170 |
| 12 | -124.2045424 | 40.73978905 | 394 | 320 | 0 | 0 | 714 |
| 13 | -124.1881431 | 40.79159082 | 4 | 16 | 0 | 0 | 20 |
| 14 | -124.1868989 | 40.7906126 | 0 | 2 | 0 | 0 | 2 |
| 15 | -124.1902842 | 40.78628629 | 327 | 392 | 0 | 0 | 719 |
| 16 | -124.1980455 | 40.75203989 | 0 | 8 | 0 | 0 | 8 |
| 17 | -124.1451799 | 40.81112919 | 0 | 20 | 0 | 0 | 20 |
| 18 | -124.1048489 | 40.86593922 | 0 | 540 | 0 | 0 | 540 |
| 19 | -124.1022725 | 40.86403942 | 0 | 180 | 0 | 0 | 180 |
| 20 | -124.094132 | 40.86160729 | 0 | 21 | 0 | 27 | 48 |
| 21 | -124.0951907 | 40.85550174 | 0 | 56 | 0 | 0 | 56 |
| 22 | -124.1115381 | 40.85656215 | 0 | 634 | 0 | 0 | 634 |
| 23 | -124.1097687 | 40.86255649 | 0 | 5 | 0 | 0 | 5 |
| 24 | -124.1071807 | 40.85984996 | 0 | 1100 | 0 | 0 | 1100 |
| 25 | -124.128232 | 40.89736 | 0 | 8 | 0 | 0 | 8 |
| 26 | -124.1478361 | 40.86743946 | 0 | 23 | 0 | 0 | 23 |
| 27 | -124.2324933 | 40.76444588 | 0 | 44 | 36 | 5 | 85 |
| 28 | -124.2409226 | 40.74868018 | 720 | 0 | 0 | 0 | 720 |
| 29 | -124.2425124 | 40.7635193 | 66 | 0 | 0 | 0 | 66 |
| 30 | -124.2168111 | 40.7423901 | 80 | 1550 | 0 | 19 | 1649 |
| 31 | -124.1856041 | 40.78686568 | 4 | 0 | 0 | 0 | 4 |
| 32 | -124.1905127 | 40.78327872 | 37 | 0 | 0 | 0 | 37 |
| 33 | -124.1985484 | 40.77283962 | 242 | 476 | 2 | 15 | 735 |
| 34 | -124.199001 | 40.76678548 | 45 | 0 | 0 | 0 | 45 |
| 35 | -124.1574683 | 40.81572117 | 400 | 0 | 0 | 0 | 400 |
| 36 | -124.1828813 | 40.80068445 | 4 | 0 | 0 | 0 | 4 |
| 37 | -124.1209662 | 40.80774426 | 1050 | 1025 | 0 | 0 | 2075 |
| 38 | -124.1169872 | 40.80991846 | 970 | 1130 | 0 | 4 | 2104 |
| 39 | -124.0843939 | 40.8498647 | 176 | 0 | 2 | 0 | 178 |

| Roost No. | X COORDS | Y COORDS | 4 Nov 2018 | 9 Dec 2018 | 20 Jan 2019 | 17 Feb 2019 | Total/Roost |
|---|---|---|---|---|---|---|---|
| 40 | -124.0834908 | 40.83954247 | 5345 | 0 | 0 | 0 | 5345 |
| 41 | -124.0985528 | 40.8590291 | 440 | 0 | 0 | 0 | 440 |
| 42 | -124.0960566 | 40.85458867 | 137 | 0 | 0 | 0 | 137 |
| 43 | -124.1078416 | 40.86377169 | 1920 | 0 | 0 | 0 | 1920 |
| 44 | -124.1058308 | 40.86470638 | 71 | 0 | 0 | 0 | 71 |
| 45 | -124.1544583 | 40.85778288 | 2 | 0 | 0 | 0 | 2 |
| 46 | -124.1508075 | 40.85861339 | 4 | 0 | 0 | 0 | 4 |
| 47 | -124.1509236 | 40.87283898 | 14 | 0 | 0 | 0 | 14 |
| 48 | -124.1488065 | 40.87366965 | 735 | 0 | 0 | 0 | 735 |
| 49 | -124.2061082 | 40.79824225 | 99 | 0 | 0 | 0 | 99 |
| 50 | -124.1931194 | 40.81747191 | 277 | 6 | 0 | 0 | 283 |
| 51 | -124.1890194 | 40.82389313 | 1075 | 0 | 0 | 0 | 1075 |
| 52 | -124.2018892 | 40.77298553 | 2 | 0 | 0 | 0 | 2 |
| 53 | -124.1408591 | 40.86616076 | 101 | 0 | 0 | 3300 | 3401 |
| 54 | -124.1074294 | 40.87109167 | 0 | 0 | 0 | 2 | 2 |
| 55 | -124.1261345 | 40.8988532 | 0 | 0 | 0 | 30 | 30 |
| 56 | -124.1945643 | 40.75271362 | 0 | 0 | 0 | 10 | 10 |
| 57 | -124.0853567 | 40.85183798 | 0 | 1157 | 0 | 83 | 1240 |
| 58 | -124.0847644 | 40.84719237 | 3000 | 2350 | 0 | 326 | 5676 |
| 59 | -124.0837338 | 40.84579255 | 0 | 0 | 0 | 10 | 10 |
| 60 | -124.2058097 | 40.73752365 | 0 | 0 | 0 | 207 | 207 |
| 61 | -124.1477324 | 40.86996841 | 5 | 2500 | 0 | 97 | 2602 |
| 62 | -124.2396338 | 40.75033312 | 0 | 0 | 122 | 33 | 155 |
| 63 | -124.2402974 | 40.74894359 | 0 | 0 | 0 | 122 | 122 |
| 64 | -124.2415238 | 40.74747649 | 0 | 0 | 0 | 19 | 19 |
| 65 | -124.2440141 | 40.74320712 | 0 | 0 | 0 | 4 | 4 |
| 66 | -124.2442778 | 40.74222706 | 0 | 0 | 0 | 21 | 21 |
| 67 | -124.2459534 | 40.73965868 | 0 | 0 | 0 | 33 | 33 |
| 68 | -124.2476616 | 40.73716143 | 0 | 0 | 0 | 5 | 5 |
| 69 | -124.255706 | 40.7253714 | 0 | 0 | 0 | 11 | 11 |
| 70 | -124.2632718 | 40.71542129 | 0 | 0 | 0 | 2 | 2 |
| 71 | -124.1330976 | 40.87314543 | 0 | 8284 | 20506 | 10027 | 38817 |
| 72 | -124.1139972 | 40.87186801 | 0 | 0 | 197 | 0 | 197 |
| 73 | -124.1204375 | 40.89622322 | 0 | 0 | 8 | 0 | 8 |
| 74 | -124.1146285 | 40.85849713 | 0 | 0 | 13 | 0 | 13 |
| 75 | -124.1711111 | 40.83071379 | 0 | 0 | 528 | 5 | 533 |
| 76 | -124.1719496 | 40.82570353 | 0 | 0 | 250 | 0 | 250 |
| 77 | -124.1972915 | 40.74973236 | 0 | 0 | 60 | 0 | 60 |
| 78 | -124.2304926 | 40.76631615 | 0 | 0 | 6 | 0 | 6 |
| 79 | -124.2425461 | 40.74584728 | 0 | 0 | 80 | 0 | 80 |
| 80 | -124.2431665 | 40.74280885 | 0 | 0 | 17 | 0 | 17 |
| 81 | -124.1083375 | 40.87347405 | 0 | 48 | 0 | 2 | 50 |
| 82 | -124.1494702 | 40.87170832 | 460 | 330 | 0 | 0 | 790 |
| 83 | -124.1507715 | 40.86795776 | 2 | 7 | 0 | 0 | 9 |

| **Roost No.** | **X COORDS** | **Y COORDS** | **4 Nov 2018** | **9 Dec 2018** | **20 Jan 2019** | **17 Feb 2019** | **Total/Roost** |
|---|---|---|---|---|---|---|---|
| 84 | -124.0988088 | 40.86223233 | 3210 | 4895 | 120 | 13 | 8238 |
| 85 | -124.0970095 | 40.81905717 | 0 | 180 | 165 | 20 | 365 |
| 86 | -124.1280963 | 40.80603168 | 0 | 4 | 0 | 366 | 370 |
| 87 | -124.1395434 | 40.80793967 | 435 | 700 | 0 | 82 | 1217 |
| 88 | -124.1508363 | 40.80959053 | 0 | 0 | 0 | 21 | 21 |
| 89 | -124.1689197 | 40.82697862 | 0 | 35 | 0 | 17 | 52 |
| 90 | -124.164692 | 40.82854253 | 8 | 0 | 0 | 0 | 8 |
| 91 | -124.1808718 | 40.80174783 | 0 | 76 | 0 | 0 | 76 |
| 92 | -124.1863164 | 40.79118317 | 0 | 0 | 6 | 12 | 18 |
| 93 | -124.1945128 | 40.77876507 | 47 | 0 | 0 | 0 | 47 |
| 94 | -124.2208887 | 40.72676438 | 156 | 4 | 0 | 0 | 160 |
| 95 | -124.2216417 | 40.6796697 | 0 | 168 | 264 | 143 | 575 |
| 96 | -124.2364303 | 40.75523152 | 415 | 2453 | 0 | 0 | 2868 |
| 97 | -124.2214399 | 40.76017263 | 181 | 288 | 653 | 127 | 1249 |
| 98 | -124.1293226 | 40.86399827 | 2 | 0 | 0 | 4 | 6 |
| 99 | -124.1128098 | 40.85994972 | 594 | 716 | 3917 | 8419 | 13646 |
| 100 | -124.1236443 | 40.88268799 | 4181 | 1085 | 282 | 0 | 5548 |
| 101 | -124.1838747 | 40.81474023 | 77 | 35 | 741 | 11170 | 12023 |
| 102 | -124.1865259 | 40.81143254 | 85 | 0 | 0 | 0 | 85 |
| 103 | -124.1894337 | 40.80373216 | 0 | 19 | 0 | 0 | 19 |
| 104 | -124.1917193 | 40.79885005 | 500 | 20 | 0 | 0 | 520 |
| **Total/ Survey** | | | 29479 | 36429 | 28475 | 34813 | - |

# APPENDIX B

Table 9. Roads within the study area located in proximity to used roost sites, road classifications, and values indexed according to perceived level of danger (1 = least dangerous, 2 = mildly dangerous, 3 = moderately dangerous, and 4 = most dangerous).

| Road Name | Classification | Danger Index |
|---|---|---|
| 1st Street | Paved road | 4 |
| A Street | Paved road | 3 |
| Bayside Cutoff Road | Paved road | 2 |
| Bay School Road | Paved road | 3 |
| Bay Street | Paved road | 2 |
| Broadway Street | Paved road | 2 |
| Buhne Drive | Paved road | 3 |
| Bunker Road | Paved road | 2 |
| C Street | Paved road | 2 |
| Dolly Vardon Road | Paved road | 2 |
| Dunes Trail | Walking trail | 2 |
| Elk River Road | Paved road | 1 |
| Felt Street | Paved road | 3 |
| Foster Avenue | Paved road | 3 |
| Front Street | Paved road | 4 |
| Hikshari' Trail | Walking/biking trail | 3 |
| Hilfiker Lane | Paved road | 2 |
| Hookton Road | Paved road | 1 |
| Howell Street | Paved road | 2 |
| Humboldt Bay Trail North | Walking/biking trail | 3 |
| Humboldt Hill Road | Paved road | 3 |
| Indianola Cutoff Road | Paved road | 2 |
| Jackson Ranch Road | Paved road | 2 |
| Lanphere Road | Paved road | 3 |
| Lincoln Road | Paved road | 2 |
| Marilann Court | Paved road | 3 |
| Marina Way | Paved road | 3 |
| Moxon Lane | Paved road | 2 |
| New Navy Base Road | Paved road | 2 |
| Old Samoa Road | Paved road | 3 |
| Peninsula Drive | Paved road | 2 |
| Pound Road | Paved road | 2 |

| **Road Name** | **Classification** | **Danger Index** |
|---|---|---|
| Purdue Drive | Paved road | 3 |
| Railroad Avenue | Paved road | 2 |
| Ranch Road | Dirt road | 1 |
| Route 101 | Highway | 4 |
| Route 225 | Paved road | 4 |
| Seidel Road | Paved road | 2 |
| South Broadway Street | Paved road | 3 |
| South G Street | Paved road | 3 |
| South I Street | Paved road | 3 |
| South Jetty Road | Paved road | 2 |
| Startare Drive | Paved road | 3 |
| Tooby Road | Paved road | 1 |
| Unnamed (at Humboldt Bay National Wildlife Refuge) | Dirt road | 1 |
| Unnamed (at Humboldt Bay National Wildlife Refuge) | Walking trail | 1 |
| Unnamed (off Vance Avenue) | Dirt road | 1 |
| Unnamed (on private property) | Dirt road | 1 |
| Unnamed (trail at Arcata Marsh) | Walking/biking trail | 4 |
| Vaissade Road | Paved road | 3 |
| Vance Avenue | Paved road | 3 |
| V Street | Paved road | 3 |
| Waterfront Trail | Walking/biking trail | 3 |
| West 14th Street | Paved road | 3 |
| West Del Norte Street | Paved road | 3 |
| West Waterfront Drive | Paved road | 3 |

# APPENDIX C

Table 10. List of 64 used/available multiple logistic regression models considered in the model selection process. Degrees of freedom (df), log likelihood (LogLik), AICc, ΔAICc, and $w_i$ are compared. Values are rounded to the nearest hundredth.

| **Model Rank** | **Intercept** | **exp to human** | **dist to cover** | **ext of cover** | **slope** | **TPI** | **dist to foraging** | **df** | **logLik** | **AICc** | **ΔAICc** | **$w_i$** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.02 | - | -2.51 | 1.68 | -1.69 | -0.53 | 1.01 | 6 | -73.74 | 159.93 | 0.00 | 0.63 |
| 2 | 0.55 | -0.31 | -2.44 | 1.64 | -1.71 | -0.52 | 1.06 | 7 | -73.50 | 161.62 | 1.69 | 0.27 |
| 3 | 2.71 | - | -2.38 | 1.60 | -1.73 | -0.54 | - | 5 | -77.07 | 164.47 | 4.54 | 0.07 |
| 4 | 3.05 | -0.16 | -2.33 | 1.58 | -1.74 | -0.54 | - | 6 | -77.00 | 166.46 | 6.53 | 0.02 |
| 5 | -2.15 | - | -2.33 | 1.75 | - | -0.61 | 1.08 | 5 | -80.02 | 170.37 | 10.44 | 0.00 |
| 6 | -1.92 | -0.14 | -2.29 | 1.74 | - | -0.60 | 1.09 | 6 | -79.97 | 172.39 | 12.46 | 0.00 |
| 7 | 0.59 | - | -2.57 | 1.52 | -1.91 | - | 1.02 | 5 | -81.64 | 173.61 | 13.68 | 0.00 |
| 8 | 1.15 | -0.32 | -2.48 | 1.49 | -1.94 | - | 1.06 | 6 | -81.34 | 175.14 | 15.21 | 0.00 |
| 9 | 0.70 | - | -2.21 | 1.70 | - | -0.62 | - | 4 | -84.05 | 176.31 | 16.38 | 0.00 |
| 10 | 0.83 | -0.07 | -2.19 | 1.69 | - | -0.62 | - | 5 | -84.03 | 178.39 | 18.46 | 0.00 |
| 11 | 3.37 | - | -2.47 | 1.45 | -1.96 | - | - | 4 | -85.15 | 178.52 | 18.59 | 0.00 |
| 12 | 3.78 | -0.20 | -2.41 | 1.43 | -1.97 | - | - | 5 | -85.02 | 180.37 | 20.44 | 0.00 |
| 13 | -1.66 | -0.82 | - | 1.25 | -1.48 | -0.52 | 0.97 | 6 | -87.41 | 187.28 | 27.34 | 0.00 |
| 14 | -3.41 | - | - | 1.30 | -1.41 | -0.56 | 0.87 | 5 | -89.62 | 189.57 | 29.64 | 0.00 |
| 15 | 3.61 | -0.76 | -1.77 | - | -1.85 | -0.43 | 0.98 | 6 | -89.39 | 191.24 | 31.31 | 0.00 |
| 16 | 0.86 | -0.69 | - | 1.20 | -1.54 | -0.56 | - | 5 | -90.63 | 191.58 | 31.64 | 0.00 |
| 17 | -2.02 | - | -2.40 | 1.62 | - | - | 1.13 | 4 | -92.18 | 192.58 | 32.65 | 0.00 |
| 18 | -0.85 | - | - | 1.25 | -1.49 | -0.60 | - | 4 | -92.31 | 192.84 | 32.91 | 0.00 |
| 19 | 2.28 | - | -1.87 | - | -1.75 | -0.43 | 0.88 | 5 | -91.32 | 192.96 | 33.03 | 0.00 |
| 20 | -1.81 | -0.13 | -2.36 | 1.61 | - | - | 1.14 | 5 | -92.13 | 194.58 | 34.65 | 0.00 |
| 21 | 5.76 | -0.61 | -1.63 | - | -1.85 | -0.42 | - | 5 | -93.20 | 196.73 | 36.80 | 0.00 |
| 22 | 4.49 | - | -1.74 | - | -1.78 | -0.43 | - | 4 | -94.55 | 197.32 | 37.39 | 0.00 |
| 23 | -3.66 | -0.68 | - | 1.38 | - | -0.59 | 1.02 | 5 | -93.66 | 197.65 | 37.72 | 0.00 |

| **Model Rank** | **Intercept** | **exp to human** | **dist to cover** | **ext of cover** | **slope** | **TPI** | **dist to foraging** | **df** | **logLik** | **AICc** | **$\Delta$AICc** | **$w_i$** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24 | -5.08 | - | - | 1.41 | - | -0.61 | 0.95 | 4 | -95.37 | 198.96 | 39.03 | 0.00 |
| 25 | 1.07 | - | -2.32 | 1.55 | - | - | - | 3 | -96.88 | 199.89 | 39.96 | 0.00 |
| 26 | 1.19 | -0.06 | -2.30 | 1.54 | - | - | - | 4 | -96.87 | 201.95 | 42.02 | 0.00 |
| 27 | 4.06 | -0.70 | -1.90 | - | -2.08 | - | 0.96 | 5 | -96.21 | 202.74 | 42.81 | 0.00 |
| 28 | -0.97 | -0.58 | - | 1.32 | - | -0.62 | - | 4 | -97.62 | 203.45 | 43.52 | 0.00 |
| 29 | -2.35 | - | - | 1.35 | - | -0.64 | - | 3 | -98.94 | 204.01 | 44.08 | 0.00 |
| 30 | 2.81 | - | -2.00 | - | -1.99 | - | 0.87 | 4 | -98.02 | 204.26 | 44.32 | 0.00 |
| 31 | -1.17 | -0.87 | - | 1.12 | -1.76 | - | 1.03 | 5 | -97.40 | 205.13 | 45.19 | 0.00 |
| 32 | 6.26 | -0.58 | -1.81 | - | -2.08 | - | - | 4 | -100.00 | 208.21 | 48.28 | 0.00 |
| 33 | 5.06 | - | -1.91 | - | -2.02 | - | - | 3 | -101.31 | 208.76 | 48.82 | 0.00 |
| 34 | 1.53 | -1.02 | - | - | -1.71 | -0.44 | 0.86 | 5 | -99.27 | 208.87 | 48.94 | 0.00 |
| 35 | -3.04 | - | - | 1.17 | -1.67 | - | 0.93 | 4 | -100.37 | 208.95 | 49.02 | 0.00 |
| 36 | 1.20 | -0.54 | -1.60 | - | - | -0.52 | 0.99 | 5 | -99.70 | 209.72 | 49.79 | 0.00 |
| 37 | 0.30 | - | -1.71 | - | - | -0.52 | 0.94 | 4 | -100.81 | 209.83 | 49.89 | 0.00 |
| 38 | 1.51 | -0.75 | - | 1.07 | -1.81 | - | - | 4 | -101.38 | 210.98 | 51.05 | 0.00 |
| 39 | 3.65 | -0.89 | - | - | -1.74 | -0.46 | - | 4 | -102.35 | 212.92 | 52.99 | 0.00 |
| 40 | -0.37 | - | - | 1.13 | -1.74 | - | - | 3 | -103.74 | 213.61 | 53.68 | 0.00 |
| 41 | -0.51 | - | - | - | -1.61 | -0.46 | 0.73 | 4 | -103.26 | 214.74 | 54.81 | 0.00 |
| 42 | 2.64 | - | -1.57 | - | - | -0.52 | - | 3 | -104.98 | 216.09 | 56.16 | 0.00 |
| 43 | 3.45 | -0.43 | -1.47 | - | - | -0.52 | - | 4 | -104.22 | 216.66 | 56.73 | 0.00 |
| 44 | 1.53 | - | - | - | -1.65 | -0.48 | - | 3 | -105.68 | 217.50 | 57.56 | 0.00 |
| 45 | 1.69 | -1.01 | - | - | -1.99 | - | 0.91 | 4 | -108.14 | 224.49 | 64.55 | 0.00 |
| 46 | -3.73 | -0.69 | - | 1.28 | - | - | 1.09 | 4 | -108.74 | 225.70 | 65.77 | 0.00 |
| 47 | -0.39 | -0.84 | - | - | - | -0.52 | 0.86 | 4 | -109.20 | 226.62 | 66.69 | 0.00 |
| 48 | -5.14 | - | - | 1.31 | - | - | 1.03 | 3 | -110.93 | 227.98 | 68.05 | 0.00 |
| 49 | 3.99 | -0.91 | - | - | -2.01 | - | - | 3 | -111.71 | 229.56 | 69.63 | 0.00 |
| 50 | -2.08 | - | - | - | - | -0.53 | 0.78 | 3 | -112.34 | 230.82 | 70.89 | 0.00 |
| 51 | -0.38 | - | - | - | -1.88 | - | 0.79 | 3 | -112.63 | 231.39 | 71.46 | 0.00 |

| Model Rank | Intercept | exp to human | dist to cover | ext of cover | slope | TPI | dist to foraging | df | logLik | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 52 | 0.61 | - | -1.91 | - | - | - | 0.94 | 3 | -112.91 | 231.95 | 72.02 | 0.00 |
| 53 | 1.76 | -0.74 | - | - | - | -0.54 | - | 3 | -113.02 | 232.17 | 72.23 | 0.00 |
| 54 | 1.35 | -0.45 | -1.81 | - | - | - | 0.98 | 4 | -112.02 | 232.25 | 72.32 | 0.00 |
| 55 | -0.80 | -0.60 | - | 1.22 | - | - | - | 3 | -113.96 | 234.05 | 74.12 | 0.00 |
| 56 | 0.07 | - | - | - | - | -0.54 | - | 2 | -115.66 | 235.38 | 75.44 | 0.00 |
| 57 | 1.83 | - | - | - | -1.92 | - | - | 2 | -115.67 | 235.40 | 75.46 | 0.00 |
| 58 | -2.21 | - | - | 1.25 | - | - | - | 2 | -115.67 | 235.41 | 75.48 | 0.00 |
| 59 | 3.02 | - | -1.81 | - | - | - | - | 2 | -117.44 | 238.94 | 79.01 | 0.00 |
| 60 | 3.70 | -0.36 | -1.72 | - | - | - | - | 3 | -116.82 | 239.78 | 79.85 | 0.00 |
| 61 | -0.61 | -0.81 | - | - | - | - | 0.91 | 3 | -124.59 | 255.31 | 95.38 | 0.00 |
| 62 | -2.25 | - | - | - | - | - | 0.84 | 2 | -128.08 | 260.22 | 100.28 | 0.00 |
| 63 | 1.70 | -0.73 | - | - | - | - | - | 2 | -129.31 | 262.68 | 102.75 | 0.00 |
| 64 | 0.05 | - | - | - | - | - | - | 1 | -132.33 | 266.67 | 106.74 | 0.00 |

# APPENDIX D

Table 11. Top model selection results of incidence models evaluating roost habitat selection of small calidridine shorebirds wintering in Humboldt Bay, California. Degrees of freedom (df), log likelihood (LogLik), AICc, ΔAICc, and $w_i$ are compared. See

Table 13 for a full list of model selection results.

| Model Rank | Model Description | df | LogLik | AICc | ΔAICc | $w_i$ | Acc $w_i$ |
|---|---|---|---|---|---|---|---|
| 1 | distance to cover + extent of cover + slope + topographic position + distance to foraging habitat | 6 | -186.05 | 384.56 | 0.00 | 0.32 | 0.32 |
| 2 | distance to cover + extent of cover + slope + topographic position | 5 | -187.32 | 384.96 | 0.39 | 0.26 | 0.58 |
| 3 | exposure to human activity + distance to cover + extent of cover + slope + topographic position + distance to foraging habitat | 7 | -185.69 | 385.99 | 1.43 | 0.16 | 0.74 |
| 4 | exposure to human activity + distance to cover + extent of cover + slope + topographic position | 6 | -186.94 | 386.34 | 1.77 | 0.13 | 0.87 |
| 5 | distance to cover + extent of cover + slope + distance to foraging habitat | 5 | -189.10 | 388.53 | 3.96 | 0.04 | 0.91 |
| 6 | distance to cover + extent of cover + slope | 4 | -190.54 | 389.3 | 4.73 | 0.03 | 0.94 |
| 7 | exposure to human activity + distance to cover + extent of cover + slope + distance to foraging habitat | 6 | -188.75 | 389.97 | 5.4 | 0.02 | 0.96 |

Table 12. Estimated regression parameters, adjusted standard error (SE) values, 95% CIs, and relative importance (w+) of variables in predicting roost habitat selection of small calidridine shorebirds wintering in Humboldt Bay, California, averaged based on the seven highest-ranking incidence models.

| | **Estimate** | **Adjusted SE** | **95% CI** | **w+** |
|---|---|---|---|---|
| (Intercept) | -2.81153 | 0.78258 | -4.3453593 - (-1.27770680) | - |
| Exposure to human activity[1] | -0.05567 | 0.14113 | -0.5736543 - 0.2262658 | 0.32 |
| Distance to cover | 1.11893 | 0.23104 | 0.661103 - 1.57175745 | 1.00 |
| Extent of cover | -0.53953 | 0.14288 | -0.8195761 - (-0.25949039) | 1.00 |
| Slope | 0.81719 | 0.26383 | 0.3001009 - 1.33428272 | 1.00 |
| Topographic position | 0.09567 | 0.05188 | 0.0213539 - 0.19097037 | 0.90 |
| Distance to foraging habitat[1] | -0.15559 | 0.18891 | -0.06159445 - 0.22626258 | 0.56 |

[1] The parameter was dropped from the final model because its 95% CI overlaps zero.

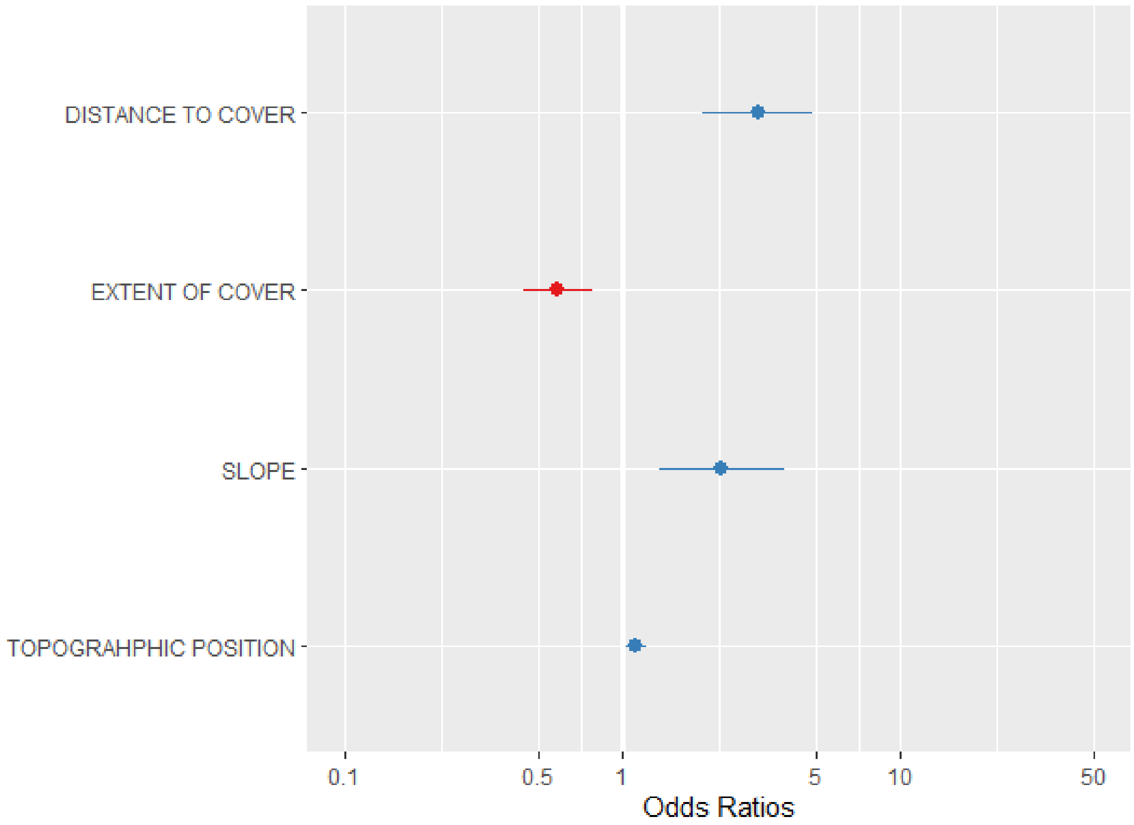

Figure 13. ORs representing the strength of the association between each predictor variable and sandpiper incidence at roosts in Humboldt Bay, California. Values

above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Horizontal lines represent 95% CIs.

Table 13. List of 64 incidence multiple logistic regression models considered in the model selection process. Degrees of freedom (df), log likelihood (LogLik), AICc, ΔAICc, and $w_i$ are compared. Values are rounded to the nearest hundredth.

| **Model Rank** | **Intercept** | **exp to human** | **dist to cover** | **ext of cover** | **slope** | **TPI** | **dist to foraging** | **df** | **logLik** | **AICc** | **ΔAICc** | **$w_i$** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | -2.55 | - | 1.09 | -0.54 | 0.79 | 0.10 | -0.28 | 6 | -186.05 | 384.56 | 0.00 | 0.32 |
| 2 | -3.29 | - | 1.08 | -0.53 | 0.8 | 0.11 | - | 5 | -187.32 | 384.96 | 0.39 | 0.26 |
| 3 | -2.23 | -0.17 | 1.16 | -0.56 | 0.77 | 0.11 | -0.27 | 7 | -185.69 | 385.99 | 1.43 | 0.16 |
| 4 | -2.96 | -0.18 | 1.15 | -0.55 | 0.78 | 0.11 | - | 6 | -186.94 | 386.34 | 1.77 | 0.13 |
| 5 | -2.93 | - | 1.18 | -0.51 | 1.06 | - | -0.29 | 5 | -189.10 | 388.53 | 3.96 | 0.04 |
| 6 | -3.72 | - | 1.17 | -0.50 | 1.08 | - | - | 4 | -190.54 | 389.30 | 4.73 | 0.03 |
| 7 | -2.62 | -0.17 | 1.24 | -0.53 | 1.04 | - | -0.29 | 6 | -188.75 | 389.97 | 5.40 | 0.02 |
| 8 | -3.40 | -0.17 | 1.23 | -0.52 | 1.06 | - | - | 5 | -190.18 | 390.67 | 6.11 | 0.02 |
| 9 | -1.62 | - | 1.09 | -0.61 | - | 0.17 | -0.30 | 5 | -191.27 | 392.86 | 8.30 | 0.01 |
| 10 | -2.41 | - | 1.09 | -0.61 | - | 0.17 | - | 4 | -192.71 | 393.63 | 9.06 | 0.00 |
| 11 | -1.22 | -0.23 | 1.18 | -0.63 | - | 0.17 | -0.29 | 6 | -190.64 | 393.73 | 9.17 | 0.00 |
| 12 | -1.99 | -0.23 | 1.18 | -0.63 | - | 0.17 | - | 5 | -192.05 | 394.42 | 9.86 | 0.00 |
| 13 | -3.45 | - | 0.98 | - | 0.93 | 0.09 | -0.26 | 5 | -193.67 | 397.67 | 13.11 | 0.00 |
| 14 | -4.16 | - | 0.98 | - | 0.95 | 0.09 | - | 4 | -194.73 | 397.68 | 13.11 | 0.00 |
| 15 | -4.06 | -0.06 | 1.00 | - | 0.94 | 0.09 | - | 5 | -194.69 | 399.70 | 15.13 | 0.00 |
| 16 | -3.37 | -0.05 | 1.00 | - | 0.92 | 0.09 | -0.25 | 6 | -193.64 | 399.73 | 15.17 | 0.00 |
| 17 | -3.77 | - | 1.07 | - | 1.15 | - | -0.27 | 4 | -196.09 | 400.39 | 15.83 | 0.00 |
| 18 | -4.51 | - | 1.07 | - | 1.18 | - | - | 3 | -197.27 | 400.66 | 16.10 | 0.00 |
| 19 | -3.70 | -0.05 | 1.09 | - | 1.15 | - | -0.27 | 5 | -196.06 | 402.45 | 17.88 | 0.00 |
| 20 | -4.42 | -0.06 | 1.09 | - | 1.18 | - | - | 4 | -197.23 | 402.67 | 18.10 | 0.00 |
| 21 | -1.68 | - | 1.23 | -0.59 | - | - | -0.34 | 4 | -200.45 | 409.11 | 24.55 | 0.00 |
| 22 | -1.26 | -0.24 | 1.32 | -0.62 | - | - | -0.34 | 5 | -199.76 | 409.84 | 25.28 | 0.00 |
| 23 | -1.55 | - | - | -0.45 | 0.76 | 0.14 | - | 4 | -200.94 | 410.10 | 25.54 | 0.00 |
| 24 | -0.88 | - | - | -0.45 | 0.74 | 0.14 | -0.24 | 5 | -199.89 | 410.10 | 25.54 | 0.00 |
| 25 | -2.42 | - | 0.98 | - | - | 0.17 | -0.31 | 4 | -201.34 | 410.89 | 26.33 | 0.00 |
| 26 | -2.58 | - | 1.23 | -0.59 | - | - | - | 3 | -202.44 | 411.01 | 26.44 | 0.00 |

| Model Rank | Intercept | exp to human | dist to cover | ext of cover | slope | TPI | dist to foraging | df | logLik | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | -1.34 | 0.18 | - | -0.43 | 0.77 | 0.13 | -0.25 | 6 | -199.42 | 411.29 | 26.72 | 0.00 |
| 28 | -2.01 | 0.18 | - | -0.43 | 0.79 | 0.14 | - | 5 | -200.51 | 411.35 | 26.78 | 0.00 |
| 29 | -2.13 | -0.25 | 1.32 | -0.62 | - | - | - | 4 | -201.69 | 411.59 | 27.03 | 0.00 |
| 30 | -3.26 | - | 0.98 | - | - | 0.17 | - | 3 | -202.82 | 411.77 | 27.21 | 0.00 |
| 31 | -2.26 | -0.10 | 1.02 | - | - | 0.17 | -0.30 | 5 | -201.20 | 412.73 | 28.16 | 0.00 |
| 32 | -3.07 | -0.12 | 1.03 | - | - | 0.17 | - | 4 | -202.65 | 413.52 | 28.96 | 0.00 |
| 33 | 0.06 | - | - | -0.52 | - | 0.20 | -0.28 | 4 | -205.02 | 418.26 | 33.69 | 0.00 |
| 34 | -0.67 | - | - | -0.53 | - | 0.20 | - | 3 | -206.39 | 418.90 | 34.34 | 0.00 |
| 35 | -2.45 | - | - | - | 0.9 | 0.13 | - | 3 | -206.47 | 419.06 | 34.50 | 0.00 |
| 36 | -1.76 | - | - | - | 0.87 | 0.13 | -0.24 | 4 | -205.42 | 419.06 | 34.50 | 0.00 |
| 37 | -2.36 | 0.26 | - | - | 0.9 | 0.12 | -0.25 | 5 | -204.47 | 419.27 | 34.71 | 0.00 |
| 38 | -3.05 | 0.25 | - | - | 0.93 | 0.12 | - | 4 | -205.57 | 419.35 | 34.78 | 0.00 |
| 39 | -1.18 | - | - | -0.41 | 1.07 | - | -0.25 | 4 | -205.67 | 419.56 | 35.00 | 0.00 |
| 40 | -1.89 | - | - | -0.41 | 1.1 | - | - | 3 | -206.84 | 419.81 | 35.25 | 0.00 |
| 41 | -0.23 | 0.12 | - | -0.51 | - | 0.20 | -0.28 | 5 | -204.81 | 419.94 | 35.37 | 0.00 |
| 42 | -1.73 | 0.22 | - | -0.39 | 1.09 | - | -0.26 | 5 | -204.97 | 420.26 | 35.69 | 0.00 |
| 43 | -0.95 | 0.11 | - | -0.52 | - | 0.20 | - | 4 | -206.20 | 420.62 | 36.05 | 0.00 |
| 44 | -2.44 | 0.21 | - | -0.39 | 1.12 | - | - | 4 | -206.21 | 420.63 | 36.07 | 0.00 |
| 45 | -2.67 | 0.30 | - | - | 1.19 | - | -0.26 | 4 | -209.25 | 426.71 | 42.14 | 0.00 |
| 46 | -2.51 | - | 1.15 | - | - | - | -0.35 | 3 | -210.46 | 427.05 | 42.49 | 0.00 |
| 47 | -3.39 | 0.29 | - | - | 1.23 | - | - | 3 | -210.46 | 427.05 | 42.49 | 0.00 |
| 48 | -2.00 | - | - | - | 1.18 | - | -0.25 | 3 | -210.55 | 427.22 | 42.66 | 0.00 |
| 49 | -2.71 | - | - | - | 1.21 | - | - | 2 | -211.67 | 427.41 | 42.85 | 0.00 |
| 50 | -2.37 | -0.09 | 1.18 | - | - | - | -0.35 | 4 | -210.35 | 428.92 | 44.36 | 0.00 |
| 51 | -3.48 | - | 1.16 | - | - | - | - | 2 | -212.55 | 429.16 | 44.60 | 0.00 |
| 52 | -3.30 | -0.11 | 1.20 | - | - | - | - | 3 | -212.40 | 430.93 | 46.36 | 0.00 |
| 53 | -0.74 | - | - | - | - | 0.20 | -0.31 | 3 | -212.91 | 431.94 | 47.38 | 0.00 |
| 54 | -1.18 | 0.20 | - | - | - | 0.20 | -0.32 | 4 | -212.34 | 432.90 | 48.34 | 0.00 |

| **Model Rank** | **Intercept** | **exp to human** | **dist to cover** | **ext of cover** | **slope** | **TPI** | **dist to foraging** | **df** | **logLik** | **AICc** | **ΔAICc** | **$w_i$** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 55 | -1.59 | - | - | - | - | 0.20 | - | 2 | -214.58 | 433.22 | 48.66 | 0.00 |
| 56 | -2.03 | 0.19 | - | - | - | 0.20 | - | 3 | -214.05 | 434.23 | 49.67 | 0.00 |
| 57 | 0.28 | - | - | -0.52 | - | - | -0.32 | 3 | -218.46 | 443.04 | 58.48 | 0.00 |
| 58 | -0.09 | 0.15 | - | -0.50 | - | - | -0.33 | 4 | -218.13 | 444.47 | 59.91 | 0.00 |
| 59 | -0.57 | - | - | -0.54 | - | - | - | 2 | -220.34 | 444.74 | 60.18 | 0.00 |
| 60 | -0.91 | 0.14 | - | -0.52 | - | - | - | 3 | -220.08 | 446.30 | 61.73 | 0.00 |
| 61 | -0.51 | - | - | - | - | - | -0.36 | 2 | -226.83 | 457.73 | 73.16 | 0.00 |
| 62 | -1.09 | 0.26 | - | - | - | - | -0.37 | 3 | -225.83 | 457.80 | 73.23 | 0.00 |
| 63 | -1.49 | - | - | - | - | - | - | 1 | -229.21 | 460.44 | 75.88 | 0.00 |
| 64 | -2.07 | 0.25 | - | - | - | - | - | 2 | -228.32 | 460.70 | 76.14 | 0.00 |