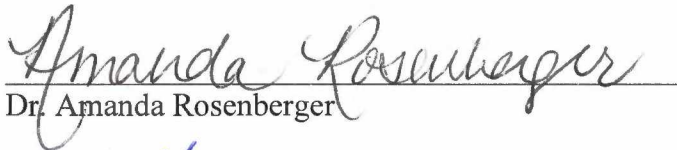


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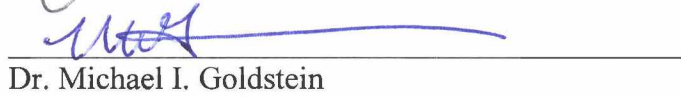
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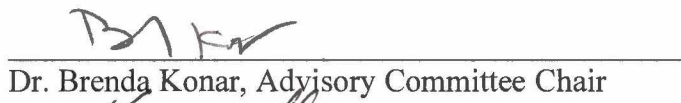
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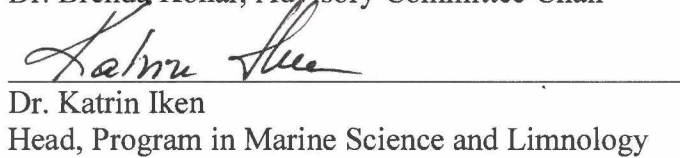
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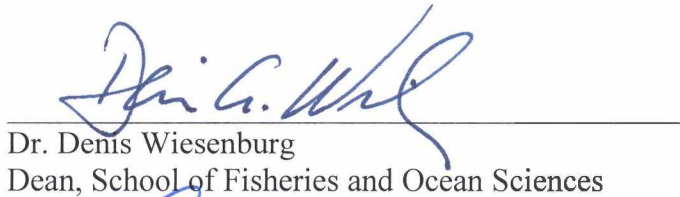


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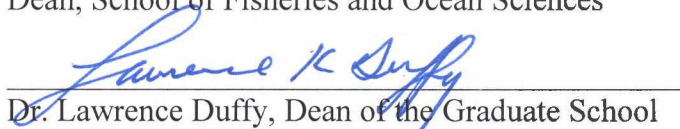


Dr. Katrin Iken
Head, Program in Marine Science and Limnology

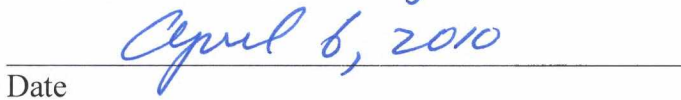
APPROVED:



Dr. Denis Wiesenburg
Dean, School of Fisheries and Ocean Sciences



Dr. Lawrence Duffy, Dean of the Graduate School



Date

HABITAT CHARACTERISTICS OF BLACK OYSTERCATCHER BREEDING
TERRITORIES

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Brooke A. McFarland, B. S.

Fairbanks, Alaska

May 2010

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Abstract

Habitat use in birds is often related to forage resources and predation avoidance. The large, long-lived black oystercatcher is a shorebird that defends a composite breeding territory for foraging in the intertidal zone and nesting in the immediate upland. Predation on young is a major source of mortality for many bird species, including black oystercatcher. As these are long-lived birds with many reproductive opportunities, adult survival, associated with forage resources, is expected to be more important in habitat use than less-predictable breeding success. To identify which factors most influence black oystercatcher breeding territory use, logistic regression models were developed and tested in south-central Alaska and tested in southeast Alaska. Intertidal community composition was sampled at a subset of sites. All known breeding sites in Kenai Fjords National Park and western Prince William Sound, plus sites in southeast Alaska, were matched with available breeding sites based on substrate and exposure classifications. Two factors related to predation avoidance, greater distance to vegetation and isolation from the mainland, were the most important variables in habitat models. Intertidal community composition did not vary between known breeding and available breeding sites. This suggests black oystercatchers choose breeding territories that reduce predation risk, contrary to expectations.

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INTRODUCTION

Habitat use studies are frequently applied to identify species requirements for positive fitness and to target critical areas for management (e.g. Greenberg et al. 1995, Petit 2000, Åberg et al. 2003, Kelly et al. 2008, Eglinton et al. 2009). In most studies, individuals are assumed to accurately recognize and select the most suitable habitat (Fretwell and Lucas 1970, Fretwell 1972), reflecting the process of natural selection (Clark and Shutler 1999). During the breeding season, habitat features are particularly critical in determining positive fitness. Two factors that influence habitat selection in breeding birds are forage resource availability (see review by Martin 1987) and predation (e.g. Baines 1990, Martin 1993, Johannsen 2001, Fontaine and Martin 2006), both of which can affect breeding success.

Foraging theory predicts that individuals will choose to forage in patches and on prey that are the most profitable (Pulliam 1974, Meire 1996); however, a number of constraints may affect the validity of this prediction. Such constraints include lack of fitness optimization and trade-offs with other unknown factors affecting fitness. Perfect knowledge, the assumption that individuals understand the surrounding habitat and its fitness value, if untrue, leads to an undermatching of high-quality patches and reduced fitness (Zimmerman et al. 2003, Shochat et al. 2004). Avian species, however, are likely to have extensive knowledge of their surroundings due to their mobility (Kristan 2007). Other factors may affect the ability of birds to use the best foraging sites, including incubation demands, which limit shorebirds' ability to access to the intertidal zone during low tide (Purdy and Miller 1988) and nest attendance requirements, which reduce time

available for travel to high quality forage sites (Charassin et al. 1998, Weimerskirch et al. 2001). These restrictions can lead to lower adult body condition and may eventually require a trade-off between maintaining a healthy condition and meeting the needs of growing chicks (Martin 1987).

Additionally, predation risk may affect the use of optimal foraging sites, both directly and indirectly. Offspring mortality due to predation is the major source of nest failure for many bird species (Martin and Roper 1988). Other costs of brood loss include brood replacement (Magnhagen 1991), increased energy store investment (Jonsson 1997), and vigilance (Lima and Dill 1990). When predation risk is known, birds can alter their choice of breeding territories to lower that risk (Suhonen et al. 1994). Birds may reduce activity at the nest site when predation risk is high by increasing nest attendance bout length (Fontaine and Martin 2006). Decreasing activity decreases detection of the nest site by predators, but also reduces parental body condition due to loss of foraging time (Smith et al. 1997).

Forage availability and predation risk may affect the breeding territory selection by black oystercatchers (*Haematopus bachmani*), large shorebirds that inhabit the rocky coast of the eastern North Pacific. It is particularly vital to understand territory selection in Alaska, where over 60% of the world population of these birds breed and where they are listed as a species of high concern due to a small global population and potential threats during the breeding season (USSCP 2004, Alaska Shorebird Group 2008). Black oystercatchers are also considered a Species at Risk (Stenhouse and Senner 2005), an

Alaska Region Sensitive Species (USDA Forest Service 2009) and a Management Indicator Species in the Chugach National Forest (USDA Forest Service 2002).

When breeding, black oystercatchers defend a composite territory of the intertidal zone for foraging and the area immediately upland for nesting (Andres and Falxa 1995). In birds such as oystercatchers, the benefits of territoriality are reduced with unstable food resources (Barlow 1993), but benefits are greatest when resources are moderately spatially clumped and highly predictable (Clark and Shutler 1999, Maher and Lott 2000). Territoriality can also act as a settlement cue for conspecifics, signaling when resources are fully used (Maher and Lott 2000).

Forage resources important to black oystercatchers include limpets, chitons, and mussels (Hartwick 1976, Andres and Falxa 1995, Hazlitt et al. 2002) and, in Prince William Sound in south-central Alaska, clams and barnacles (Andres 1998). As an apex predator, black oystercatchers themselves can impact the intertidal community composition at these territories. Predation by black oystercatchers has altered limpet microdistribution, and therefore algal cover, in Oregon (Frank 1982), Washington (Wootton 1995) and California (Lindberg et al. 1987). Conversely, where black oystercatchers are absent, intertidal grazers have reduced algal communities (Kurle et al. 2008).

Both small- and large-scale factors other than predation may also affect intertidal community composition at black oystercatcher breeding sites over space and through time (Menge 1995, Stanley 2008). Large-scale sources of variation include climate and ocean circulation (e.g. Stephenson and Stephenson 1949), which affect distribution limits

and dispersion of planktonic larvae. As many sessile intertidal invertebrates have a planktonic larval stage, these large-scale processes affect intertidal community composition and therefore forage resources available for black oystercatchers. Local-scale variation in intertidal composition is influenced by microclimate (e.g. Somero 2002), disturbance regimes (Carroll and Highsmith 1996), and positive interactions when neighboring organisms reduce environmental stress (Bertness and Leonard 1997). Environmental factors, such as substrate heterogeneity, have been found to affect intertidal species richness at large-scales and the biomass of sessile organisms at a local scale (Archambault and Bourget 1996).

Although black oystercatchers defend a composite territory including adjacent nesting and foraging sites, these birds may forage up to 1.5 km from their nest site (Andres and Falxa 1995). Distance to foraging sites may be inversely proportional to breeding success. In other oystercatcher species, the use of remote foraging locations is associated with decreased provisioning rates (American oystercatchers [*Haematopus palliatus*] Nol 1989 and European oystercatchers [*Haematopus ostralegus*] Ens et al. 1992). Increased chick predation has been reported during parental trips to remote foraging locations (Andres and Falxa 1995). To mitigate these predation losses, black oystercatchers employ biparental care and have cryptic coloration of eggs (Webster 1941).

To maximize lifetime reproductive success, a long-lived species such as the black oystercatcher could be expected to use habitat in a manner that reflects the importance of maintaining parental body condition. Avoiding predation on young is less predictable

(Williams 1966, Hirshfield and Tinkle 1975, Oro et al. 1999, but see Oro and Furness 2002). The goal of this project was to identify which primary factors, forage availability or predation avoidance, determined the suitability of coastal habitat for black oystercatcher breeding. A comparative approach between breeding sites and available breeding sites was used to determine whether habitat characteristics associated with forage resources more accurately identified use than did habitat characteristics associated with predation avoidance. Models were developed and tested based on a suite of habitat variables relating to these factors, with the best-fitting models further evaluated in a separate region to identify the transferability, and therefore generality, of these results. Refinement of these models through identification and analysis of a posteriori models were applied to these regions. Multi-dimensional scaling analysis was performed on intertidal biological communities at a subset of sites for forage differences.

STUDY AREAS

From July to September 2007, field data were collected in two geographic areas in south-central Alaska: Kenai Fjords National Park (KEFJ) and western Prince William Sound (PWS). A priori models were evaluated using these data. New data were collected from June to July 2008 in KEFJ and southeast Alaska (SEAK) to verify models and identify transferability of these models (Figure 1).

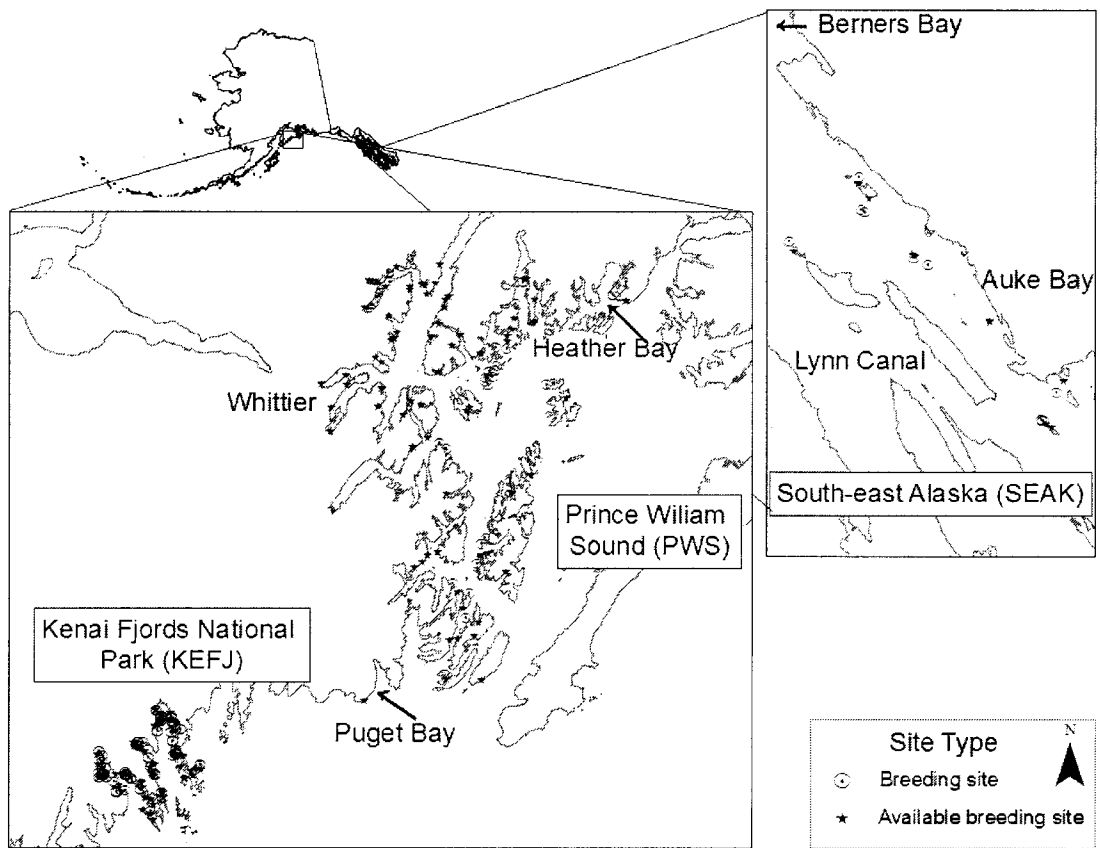


Figure 1. Study site locations. Black oystercatcher breeding and available breeding site locations in Kenai Fjords National Park (KEFJ; including all sites plus verification sites; total $n = 144$), Prince William Sound (PWS) ($n = 166$) and southeast Alaska (SEAK) ($n = 20$).

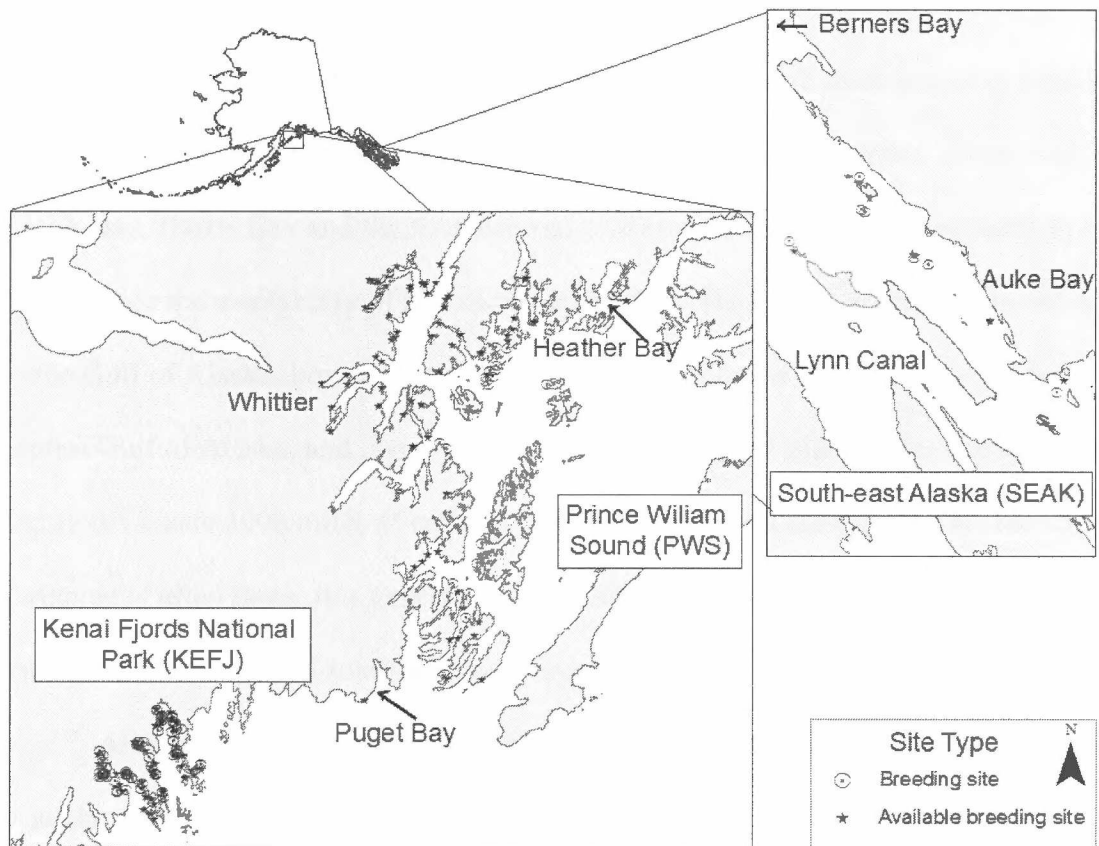


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KEFJ is located on the southeastern coast of the Kenai Peninsula. The Park encompasses more than 400 miles of coastline punctuated with short gravel or boulder beaches and longer gravel moraines exposed after recent glacial retreats. Three bays, Aialik Bay, Harris Bay and the southern end of Resurrection Bay, were included in this study due to the availability of historical survey data. These bays are relatively exposed to the Gulf of Alaska; however, many of the numerous coves are sheltered. PWS is in the central Gulf of Alaska, and is relatively protected by barrier islands. Numerous islands and fjords create 3000 miles of coastline. Islets are common close to shore, and while the shoreline is often steep, it is generally less so than KEFJ. Sites stretched from Whittier east to Heather Bay, and south to Puget Bay.

All known breeding sites in KEFJ and PWS were matched with randomly selected available breeding sites based on location, substrate, and exposure. KEFJ was treated as one location, and PWS, due to its large area, was divided into five equal blocks (50 km x 50 km), to create northern, central and southern sections. Sixty-five known breeding sites were matched with 65 available breeding sites in KEFJ, and 83 known breeding sites were matched with 83 available breeding sites in PWS.

Sites in SEAK were situated in the sheltered inland waters of the 90 mile long Lynn Canal between Auke Bay and Berners Bay. In this region, a mix of steep, rocky islands and gently-sloping gravel and sand islands are typically further from shore than in the other study areas. Ten known breeding sites matched with 10 available breeding sites in SEAK.

METHODS

Substrate and exposure were defined by the ShoreZone classification shoreline GIS layer in KEFJ (Coastal and Ocean Resources, Inc., Sidney, BC, Canada), and by the National Oceanic and Atmospheric Administration's (NOAA) Environmental Sensitivity Index (ESI) in PWS and SEAK (<http://nosdataexplorer.noaa.gov/nosdataexplorer/explorer.jsp>). ShoreZone classifications are more precise than ESI classifications; however, not all data were available in the ShoreZone database for all regions at the time of study. The National Park Service in KEFJ (Morse et al. 2006, NPS unpubl. data) and the Forest Service in PWS (Poe et al. 2009) identified black oystercatcher breeding locations from yearly boat based surveys. Additionally, the Forest Service (M. Goldstein, unpubl. data) located breeding sites in SEAK from a single survey in June 2008.

Remotely-sensed Data

Remotely-sensed habitat data were used to model known black oystercatcher breeding sites compared to available breeding sites. These data included habitat variables related to forage availability and predation risk. Forage availability habitat variables included aspect, modified effective fetch, slope, distance to freshwater, sea-surface temperature, chlorophyll a concentration and distances to kelp, eelgrass and blue mussel beds. A single predation avoidance habitat variable, isolation from the mainland, was included.

Aspect is an indicator of solar radiation at a site, which affects the microclimate and, in turn, the body temperature of intertidal organisms (Helmuth 2002), algal and vegetation growth, and persistence of snow in the spring. Aspect was obtained from 1:63360 scale NPS coastline GIS data

(http://www.nps.gov/gis/data_info/park_gisdata/ak.htm), and cosine transformed. Modified effective fetch, a quantitative measure of exposure (Howes et al. 1994), was calculated from the NPS coastline mapping data. Slope, related to the area available for forage, was calculated from a digital elevation model of the state of Alaska (<http://ned.usgs.gov/>) at a resolution of 60 m x 60 m. Another habitat variable, distance to freshwater, has the potential to affect the black oystercatcher as these birds occasionally drink freshwater; additionally freshwater runoff can alter coastal salinities and therefore intertidal community composition (Hohenlohe 2003). Distances from sites to mapped freshwater sources were identified utilizing the revised USGS Hydrography dataset (<http://nhd.usgs.gov/>) at a scale of 1:63360. Sea-surface temperature and chlorophyll a concentration are associated with the productivity of the nearshore (e. g. Wieters 2005), which can influence the productivity of the intertidal zone. Weekly sea-surface temperature from March to September, spanning the period from greatest mixing to greatest stratification (Vaughan et al. 2001) was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite at a resolution of 1 km, as were summer chlorophyll a concentrations (<http://www.gina.alaska.edu/data/gina-modis-images/>). Other factors affecting intertidal communities include kelp and eelgrass (*Zostera marina*) beds, as these enhance settlement of mussels (Reusch 1998) and recycle and export nutrients (Duggins et al. 1989). These distances, as well as that to blue mussel (*Mytilus edulis*) beds, a common forage species, were available through the ShoreZone database (<http://www.fakr.noaa.gov/maps/szintro.htm>) for KEFJ only at a resolution of 10 m. Sites

separated from the mainland at mean high water were classified as isolated, which lowers predation risk (Vermeer et al. 1992).

Field Data

Known breeding sites, along with matched available breeding sites, were randomly chosen using Hawth's tools (<http://spatialecology.com>) in ArcView for field data collection. Substrate composition was verified in situ. Black oystercatchers were not found breeding at any available breeding sites.

Field data included habitat variables related to forage availability and predation risk. Forage availability habitat variables included distance to freshwater, tidal width, and rugosity. Predation avoidance habitat variables included distance to vegetation and isolation. Distances were taken using a Yardage Pro Scout laser range finder (Bushnell, Overland Park, KS). Distances >500 m were recorded as 500 m. Other field-only habitat variables collected were: tidal width (the distance from the supralittoral to the zero-tidal height at the center of the site) and rugosity (a measure of surface complexity, with higher rugosity providing a greater area for settlement of sessile invertebrates at more complex sites). Rugosity was assessed along the full length of each transect at the high-, mid- and zero-tides using the chain-and-tape method (McCormick 1994), and woody vegetation, a measure of cover for predators, suggesting increased predation risk (Poe et al. 2009).

The biological community composition of the intertidal zone was sampled at field sites. At each site 10, 0.25 m², quadrats were randomly placed along a 100 m transect in the high, mid, and zero tidal heights at each site. Transect length was occasionally

truncated due to unsuitable habitat (glaciers, large streams or rivers, steep cliffs, or outcroppings that could not be circumvented). For truncated transects, the randomly chosen sampling locations were proportionately modified to reflect true transect length. Tidal height was determined using local corrected tidal predictions and a NOAA citizen science field method (NOAA 2006). Zero-tide height plus local mean higher high water was designated as high-tide, and the midpoint between these two was designated as mid-tide.

Quadrats were assessed for percent cover of sessile invertebrates and algal functional groups (Stekoll et al. 1996). Functional groups were: bladed, filamentous, tubular, saccate, coralline, crustose, and coralline crustose for each green, brown and red algal group. If kelp cover was present, this was assessed and then removed before other percent cover data were recorded. Finally, all mobile invertebrates >10 mm were identified and counted, and sessile invertebrate cover was re-assessed without algal cover.

Analysis

The complete set of unique breeding ($n = 148$) and available locations ($n = 148$) from PWS and KEFJ was used to evaluate models from remotely-sensed data available in both locations. These data included aspect, slope, distance to freshwater, modified effective fetch, sea-surface temperature, and chlorophyll a concentrations. A subset of sites in KEFJ (breeding [$n = 65$] and available [$n = 65$]) was used in conjunction with ShoreZone data (distances to blue mussel, kelp and eelgrass beds), currently available for this location only. Field sites ($n = 60$) were a subset of all sites that were randomly chosen.

Verification ($n = 14$) and transferability ($n = 20$) were assessed using new sites in KEFJ and southeast Alaska, respectively.

All variables were analyzed and transformed for normality as needed. Confidence intervals (95%) were calculated for habitat variables by site type (known breeding or available breeding), and these intervals were evaluated for biological significance. Data were stored in a spreadsheet format and imported into ArcGIS Version 9.3.1 (ESRI, Redlands, California), with model evaluation performed in R Version 2.9.1 (R Foundation for Statistical Computing, Vienna, Austria). A generalized linear model (binomial) was used for all data sets, with sites weighted according to their likelihood of selection.

A priori models were evaluated and ranked by Akaike's Information Criterion corrected for small sample size (AICc), and model weights of evidence were calculated as a measure of relative support for models (Burnham and Anderson 2002). The area under the curve (AUC) from the receiver operating characteristic (ROC) curves was calculated to identify the performance of each model. Models with AUC values >0.50 were considered as performing better than random. The best performing models based on AICc values, model weights of evidence and AUC values were tested against the new sites in KEFJ for verification and in SEAK for transferability.

Biotic community composition analysis was performed for KEFJ and PWS separately and for the two areas pooled. As invertebrate species were rare, count data were square-root transformed to downweight the most abundant species. Bray-Curtis similarity matrices were generated for percent coverage (algal and sessile invertebrates)

and count data (mobile invertebrates) separately and multi-dimensional scaling plots were then performed in Primer-E Version 6.1.10 (Primer-E Ltd, Ivybridge, UK) between known and available breeding sites.

RESULTS

Remotely-sensed Data

The best-fitting remotely-sensed data (RSD) model for all sites was the global model, including all habitat variables, related to both forage (aspect, slope, freshwater, modified effective fetch, sea-surface temperature and chlorophyll a concentration) and predation avoidance (isolation) (Table 1). The RSD forage model, with all variables except isolation, was also well-supported and both models performed similarly well in identifying known breeding territories (Table 1). For ShoreZone-specific models (in KEFJ only), the predation avoidance model with the habitat variable isolation was the best-fitting model, and the simplified forage model was also supported, although neither identified known breeding territories as well as the RSD models for all sites (Table 1). The RSD global model and the RSD forage model were used during model evaluation of verification data in KEFJ, and the RSD forage model alone was used during model evaluation of transferability data in SEAK, where all sites were isolated from the mainland.

Table 1. Model evaluations for remotely-sensed and field habitat variables. Models were for black oystercatcher breeding territories in Kenai Fjords National Park (KEFJ) and Prince William Sound (PWS) sampled in 2007, and verification of models for KEFJ and transferability of models for southeast Alaska (SEAK) sampled in 2008.

Model ¹	Habitat variables ²	AIC _c	ΔAIC _c	w _i ³	AUC ⁴	SD
Remotely-sensed data (RSD), KEFJ and PWS (<i>n</i> = 296)						
RSD global	ASP SLP FW MEF ISL SST CHL	31.19	0.00	0.61	0.77	0.05
RSD forage	ASP SLP FW MEF SST CHL	32.08	0.89	0.39	0.74	0.05
RSD predation avoidance	ISL	40.03	8.84	0.00	0.61	0.04
RSD simplified forage	SLP MEF	42.70	11.51	0.00	0.66	0.03
RSD ShoreZone (SZ), KEFJ (<i>n</i> = 130)						
RSD predation avoidance (SZ)	ISL	9.06	0.00	0.89	0.62	0.04
RSD simplified forage (SZ)	SLP BLMU MEF	13.30	4.24	0.11	0.68	0.04
RSD forage (SZ)	ASP SLP FW BLMU EEL KELP MEF SST CHL	26.06	16.98	0.00	0.57	0.05
RSD global (SZ)	ASP SLP FW BLMU EEL KELP MEF ISL SST	31.59	22.53	0.00	0.78	0.05
	CHL					
Field data, KEFJ and PWS (<i>n</i> = 60)						
Field predation avoidance	ISL VEG	17.71	0.00	0.88	0.75	0.07
Field global	FW ISL VEG TW MR	23.17	4.64	0.09	0.72	0.07
Field forage	FW TW MR	23.35	6.46	0.03	0.66	0.08

Table 1. Continued.

Model ¹	Habitat variables ²	AIC _c	ΔAIC _c	w _i ³	AUC ⁴	SD
Verification data, KEFJ (<i>n</i> = 14)						
Field predation avoidance	ISL VEG	24.17	0.00	1.00	0.83	0.12
Field global	FW ISL VEG TW MR	37.42	13.25	0.00	0.75	0.17
RSD forage	ASP SLP FW MEF SST CHL	44.91	20.74	0.00	0.88	0.11
RSD global	ASP SLP FW MEF ISL SST CHL	56.80	32.63	0.00	0.85	0.12
Transferability data, SEAK (<i>n</i> = 20)						
Field global	VEG TW MR	19.60	0.00	0.75	0.96	0.04
Field predation avoidance	VEG	21.85	2.25	0.24	0.83	0.11
RSD forage	ASP SLP FW MEF SST CHL	37.20	17.60	0.01	0.79	0.12

¹Models ranked by ΔAkaike's Information Criteria adjusted for small sample size (ΔAIC_c).

²ASP aspect cosine transformed, SLP slope (degrees), FW distance (m) to freshwater, BLMU distance (m) to blue mussel bed, EEL distance (m) to eelgrass, KELP distance (m) to canopy kelp, MEF modified effective fetch, ISL isolation from the mainland, SST average summer sea-surface temperature (degrees), CHL average chlorophyll a concentration (mg/m⁻³), VEG distance (m) to vegetation, TW tidal width (m), MR mid-tide rugosity.

³ w_i model weight of evidence.

⁴ AUC Area under the curve for a receiver operating characteristic (ROC) graph

Based on confidence intervals around parameter estimates, biologically relevant differences between known breeding and available breeding sites were apparent for two remotely-sensed data habitat variables (Table 2). Known breeding sites were more than twice as likely to be isolated from the mainland as available breeding sites. Additionally, modified effective fetch was found to have a much narrower range of values for known breeding sites than for available breeding sites. Although distance to blue mussel appears to be different for known breeding (926-1050 m) and available sites (407-865 m), these values imply black oystercatchers are choosing sites further from a food source, which is unlikely and which may correspond to an unsampled important habitat variable. The remainder of remotely-sensed habitat variables of aspect, slope, modified effective fetch, sea-surface temperature, chlorophyll a concentration, distance to kelp bed and distance to eelgrass bed did not show important differences between known breeding sites and available breeding sites. The results of z-tests (significance level <0.05 , Table 3) for the best-performing models indicate distance to freshwater, sea-surface temperature and slope as potentially important habitat variables affecting the performance of these models. Distance to freshwater estimates overlap between site types (Table 2) and are at a distance unlikely to be biologically relevant for black oystercatchers (1568-2106 m for known breeding sites; 1220-1669 m for available breeding sites). Slope estimates also overlap slightly between known breeding sites ($6.4-11.0^\circ$) and available breeding sites ($10.1-13.1^\circ$); sea-surface temperatures were an average of 0.75° different between site types (Table 2).

Table 2. 95% Confidence intervals, means and standard deviations for remotely-sensed and field habitat variables.

Habitat variable	Breeding site				Available sites			
	Lower CI	Mean	Upper CI	SD	Lower CI	Mean	Upper CI	SD
Aspect, RSD (cosine transformed)								
KEFJ, PWS	-0.10	0.02	0.14	0.74	-0.13	0.02	0.09	0.68
KEFJ	-0.07	0.09	0.25	0.66	-0.11	0.06	0.22	0.70
PWS	-0.20	-0.03	0.14	0.79	-0.22	-0.09	0.06	0.07
Slope (degree)								
KEFJ, PWS	6.4	8.1	11.0	10.0	10.1	11.6	13.1	9.6
KEFJ	8.2	11.0	13.7	11.4	12.0	14.6	17.1	10.6
PWS	4.0	5.8	7.5	6.8	7.6	9.3	11.0	7.9
Distance to freshwater, RSD (m)								
KEFJ, PWS	1568	1837	2106	1670	1220	1444	1669	1394
KEFJ	1739	2163	2586	1743	139	1775	2161	1589
PWS	1243	1582	1921	1575	934	1185	1436	1436
Distance to blue mussel (m)								
KEFJ	926	988	1050	926	407	636	865	943
Distance to eelgrass (m)								
KEFJ	3275	4051	4828	3357	4040	4887	5734	3484

Table 2. Continued.

Habitat variable	Breeding site				Available sites			
	Lower CI	Mean	Upper CI	SD	Lower CI	Mean	Upper CI	SD
Distance to canopy kelp (m)								
KEFJ	7842	9267	10693	2864	6639	8160	9680	3955
Modified effective fetch								
KEFJ, PWS	0.0	6.6	13.2	41.0	-5.1	70.0	143.1	459.7
KEFJ	2.4	3.0	3.6	2.5	-51.4	89.5	230.3	579.3
PWS	-2.4	9.4	21.2	54.7	-20.4	53.0	126.4	341.2
Isolation								
KEFJ, PWS	0.28	0.36	0.44	0.48	0.09	0.15	0.21	0.36
KEFJ	0.22	0.34	0.45	0.48	0.03	0.10	0.18	0.31
PWS	0.27	0.37	0.47	0.49	0.10	0.18	0.26	0.39
Summer sea-surface temperature (degree)								
KEFJ, PWS	5.10	5.28	5.45	1.08	5.87	6.03	6.16	0.93
KEFJ	5.17	5.36	5.55	0.80	5.48	5.72	5.95	0.97
PWS	4.94	5.21	5.49	1.25	6.07	6.25	6.42	0.82

Table 2. Continued.

Habitat variable	Breeding site				Available sites			
	Lower CI	Mean	Upper CI	SD	Lower CI	Mean	Upper CI	SD
Chlorophyll a (mg/m ⁻³)								
KEFJ, PWS	0.05	0.06	0.08	0.09	0.07	0.09	0.11	0.12
KEFJ	0.07	0.10	0.13	0.11	0.09	0.12	0.15	0.11
PWS	0.02	0.03	0.04	0.05	0.05	0.07	0.10	0.12
Aspect field (cosine transformed)								
KEFJ, PWS	-0.21	0.06	0.33	0.74	-0.20	0.05	0.29	0.64
KEFJ	-0.48	-0.05	0.39	0.73	-0.41	-0.02	0.36	0.65
PWS	-0.24	0.13	0.50	0.77	-0.23	0.09	0.41	0.68
Distance to freshwater field (m)								
KEFJ, PWS	171.5	244.7	317.8	211.1	117.1	185.9	254.8	189.2
KEFJ	232.6	345.6	458.7	191.4	46.6	157.7	268.9	188.1
PWS	120.3	220.3	320.3	204.1	113.9	203.2	268.1	193.2
Distance to vegetation (m)								
KEFJ, PWS	34.9	79.4	123.9	128.4	4.3	11.6	18.9	20.1
KEFJ	9.3	50.5	91.6	69.7	10.0	14.5	24.6	17.0
PWS	49.9	110.2	170.5	123.1	-0.3	9.9	20.0	22.0

Table 2. Continued.

Habitat variable	Breeding site				Available sites			
	Lower CI	Mean	Upper CI	SD	Lower CI	Mean	Upper CI	SD
Tidal width (m)								
KEFJ, PWS	48.2	68.5	88.7	58.4	21.7	47.8	63.9	44.3
KEFJ	25.1	55.7	86.3	51.8	34.6	62.1	89.6	46.5
PWS	44.3	69.6	94.9	51.7	19.7	39.0	58.4	41.9
Mid-tide rugosity								
KEFJ, PWS	1.05	1.07	1.09	0.06	1.09	1.10	1.13	0.07
KEFJ	1.03	1.05	1.08	0.04	1.04	1.07	1.11	0.05
PWS	1.04	1.08	1.11	0.06	1.10	1.13	1.16	0.06

Table 3. Results of z-tests for parameters from best-performing models. Habitat variables with z-statistic values of ≤ 0.05 are indicated in bold.

Model	Parameters ¹	Test statistic (z)	Pr(> z)
RSD global	ASP	-0.34	0.73
	SLP	-1.42	0.16
	FW	1.84	0.07
	MEF	-0.22	0.83
	ISL	1.52	0.13
	SST	-3.01	0.002
	CHL	0.67	0.50
RSD forage	ASP	0.02	0.98
	SLP	-2.04	0.04
	FW	2.27	0.02
	MEF	-0.62	0.54
	SST	-3.10	0.002
	CHL	0.81	0.42
Field global	FW	0.20	0.84
	ISL	-1.67	0.09
	VEG	-2.75	0.06
	TW	-1.09	0.27
	MR	-0.94	0.35
Field predator avoidance	ISL	-1.37	0.17
	VEG	-3.21	0.001

¹ASP aspect cosine transformed, SLP slope (degrees), FW distance (m) to freshwater, MEF modified effective fetch, ISL isolation from the mainland, SST average sea-surface temperature (degrees), CHL average chlorophyll a concentration (mg/m^{-3}), VEG distance (m) to vegetation, TW tidal width (m), MR mid-tide rugosity.

Field Data

During field model evaluation, the predation avoidance model, which included distance to vegetation and isolation, and the global model with all variables (distance to freshwater, isolation, distance to vegetation, tidal width and mid-tide rugosity) were the most supported (Table 1). Distance to vegetation was 6.8x greater at known breeding sites than available breeding sites (Table 2), therefore for model evaluation for verification and transferability data sets, the field predation avoidance model was used rather than the RSD predation avoidance model, which did not include the habitat variable of distance to vegetation.

MDS plots did not reveal any distinction between known breeding sites and available breeding sites based on intertidal community composition at any tidal height, or for any group of organisms (Figure 2). The most abundant components of the intertidal for both KEFJ and PWS were brown bladed algae, green filamentous algae, mussels, littorinids, and limpets (see Appendix B). With locations analyzed together, an average of $66 \pm 29\%$ /0.25 m² was bare rock, $8 \pm 13\%$ /0.25 m² was brown bladed algae, $5 \pm 13\%$ /0.25 m² was green filamentous algae, and $4 \pm 8\%$ /0.25 m² was *Mytilus trossulus*. Mobile invertebrates were primarily littorinids (0.7 ± 2.7 ind/0.25 m²) and limpets (0.3 ± 0.7 ind/0.25 m² *Tectura persona*, 0.2 ± 0.5 /0.25 m² *T. scutum*, and 0.2 ± 0.4 ind/0.25 m² *Lottia pelta*). In KEFJ, an average of $77 \pm 24\%$ /0.25 m² was bare rock. Algae were predominately brown bladed ($5 \pm 10\%$ /0.25 m²) and green filamentous ($4 \pm 8\%$ /0.25 m²). *Mytilus trossulus* averaged $4 \pm 9\%$ /0.25 m². Mobile invertebrates were primarily littorinids (0.2 ± 0.7 ind/0.25 m²) and limpets (*T. persona* 0.1 ± 0.3 ind/0.25 m²,

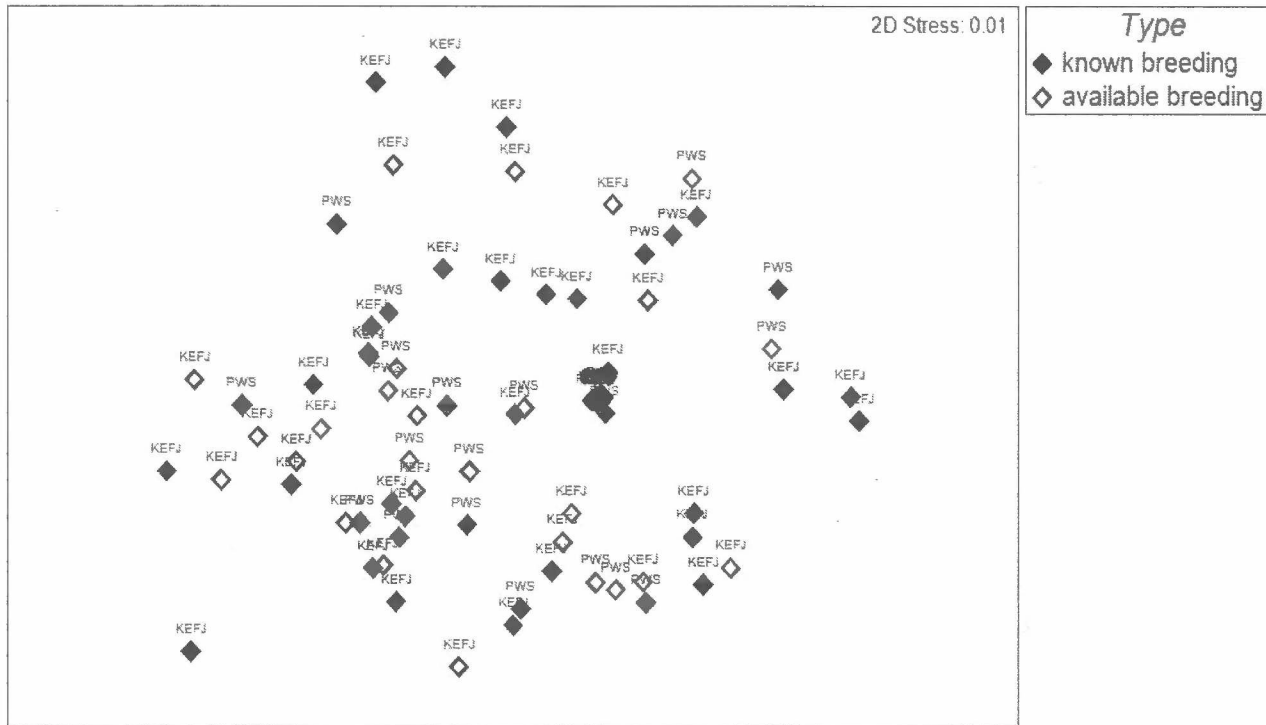


Figure 2. MDS plot of mobile intertidal invertebrate composition at field sites. MDS is from a Bray-Curtis resemblance matrix and has a 2D stress value of 0.01. Field sites were known black oystercatcher breeding sites ($n = 30$) and available breeding sites ($n = 30$) in Kenai Fjords National Park (KEFJ) and Prince William Sound (PWS) in 2007.

T. scutum, 0.1 ± 0.4 ind/0.25 m² and *L. pelta* 0.1 ± 0.2 ind/0.25 m²). In PWS, bare rock covered $56 \pm 29\%$ /0.25 m² of available space. Brown bladed algae ($11 \pm 14\%$ /0.25 m²) and green filamentous algae ($7 \pm 15\%$ /0.25 m²) were the most common cover. *Mytilus trossulus* averaged $4 \pm 8\%$ /0.25 m². Mobile invertebrate communities in PWS were dominated by littorinids (1.0 ± 3.5 ind/0.25 m²) and limpets (*T. persona* 0.4 ± 1.0 ind/0.25 m², *T. scutum* 0.2 ± 0.5 ind/0.25 m², and *L. pelta* 0.3 ± 0.6 ind/0.25 m²).

Model Verification and Transferability

The best-performing model with new site data from KEFJ contained predation avoidance habitat variables, isolation and distance to vegetation. The RSD global model correctly classified the most breeding sites, however, model performance is likely from overfitting due to the extremely high ratio of habitat variables to sites. During evaluation of these models in southeast Alaska, field collected habitat variables explained breeding site selection better than RSD variables. All sites were separated from the mainland due to sampling logistics and spatial limits in survey data, resulting in an inability to identify the importance of this habitat variable for this region. Isolation of all sites also resulted in a uniform distance to freshwater measurement for these sites and limited the field global model to three habitat variables (tidal width, mid-tide rugosity and distance to vegetation), and the predation avoidance model to a single variable of distance to vegetation. However, as all known nests are located at sites isolated from the mainland, this habitat variable should clearly be retained in models for this area. A posteriori models for new data in KEFJ and SEAK were a nested model set of sea-surface temperature, slope and distance to vegetation and distance to vegetation. For sites in

KEFJ, the single-variable of distance to vegetation performed as well as the more complex models; in SEAK the variable of slope improved model classification of sites (Table 4).

Table 4. A posteriori model evaluations for remotely-sensed and field habitat variables. Models were for black oystercatcher breeding territories in Kenai Fjords National Park (KEFJ) and Prince William Sound (PWS) sampled in 2007, and verification of models for KEFJ and transferability of models for southeast Alaska (SEAK) sampled in 2008.

Habitat variables ¹	Data set	AIC _c	Δ AIC _c ²	w_i ³	AUC ⁴	SD
Verification sites, KEFJ ($n = 14$)						
	SST SLP DV	29.17	5.00	0.02	0.73	0.17
	SLP DV	25.23	1.06	0.21	0.71	0.17
	DV	22.10	-2.07	0.63	0.71	0.17
Transferability sites, SEAK ($n = 20$)						
	SST SLP DV	16.42	-3.18	0.42	0.98	0.02
	SLP DV	16.32	-3.28	0.44	0.96	0.04
	DV	21.85	2.25	0.02	0.83	0.11

¹SLP slope (degrees), SST average summer sea-surface temperature (degrees), VEG distance (m) to vegetation,

² Δ AIC_c value for model in relation to a priori models with the same data set.

³ w_i model weight of evidence, when analyzed with a priori models.

⁴ AUC Area under the curve for a receiver operating characteristic (ROC) graph

DISCUSSION

Habitat features related to predation avoidance (isolation and distance to vegetation) were found in the best-supported models during each stage of model evaluation, verification, and transferability analysis. In Kenai Fjords National Park, 65% of nest failures were due to predation, with higher survival rates recorded at isolated sites (Morse et al. 2006). Often birds reduce predation risk by nesting away from avian predators (Suhonen et al. 1994, Johannsen 2001), concealing nests (Martin and Roper 1988), or using locations with high visibility (Johannsen 2001). Currently, sites located farther from woody vegetation can only be measured in the field, however the use of high-resolution imagery could enhance sample size to help clarify the role of vegetation as cover for nest predators in future models.

Although predictive models that included both forage availability and predation avoidance were the most powerful for identifying and classifying sites, further analyses did not identify characteristics of biological communities that differed among sites. This lack of support for forage-related habitat variables could be due to differences in intertidal communities that are more complex than were identified. For example, size-class of prey items, which were not sampled, may be important due to the differing amounts of energy they supply per effort. However, the relationship between size and value is not straightforward, as larger, more energy rich, prey items are more likely to result in bill injury and are avoided by the Eurasian oystercatcher (Rutten et al. 2006).

Forage resources may also be variable at a finer scale than the breeding territory. The microdistribution of limpets and other grazers may play a role in determining forage

availability, with many limpets on vertical surfaces beyond the reach of oystercatchers (Lindberg et al. 1998). Local foraging activity can impact prey availability, as some limpets increase their tenacity to the substrate when nearby predation events occur (Coleman et al. 2004). Alternatively, the lack of difference in intertidal communities may be due to relatively similar near-shore conditions among the study areas. Horizontal gradients related to water flow have been shown to affect the structuring of the low and mid-tide zones in the North Atlantic (Davidson 2005), although this may not be the case in more exposed environments. Finally, as this study focused on breeding territories only, the use of remote foraging sites and of forage resource selection may be underestimated. Identifying use of these remote foraging areas would allow a better understanding of preferred forage for this species.

The only forage-related parameter that was found to improve a posteriori model performance was slope, which may also affect predation risk. Low-sloping beaches contain larger intertidal areas for forage, but also allow chicks to accompany foraging adults (Hazlitt et al. 2002). However, eggs may be vulnerable to waves and extreme high tide events at these sites, resulting in nest flooding and egg loss (Spiegel 2008). Low-sloping beaches are also more commonly used by kayakers and campers, which may prevent access to preferred resources by these birds (Andres and Falxa 1995), although current visitor levels in Kenai Fjords National Park and at Harriman Fjord, PWS have not been shown to affect black oystercatcher productivity (Morse et al. 2006, Spiegel 2008). In fact, human presence may reduce carnivore presence (Boyle and Samson 1985, Spiegel 2008), and therefore decrease predation risk.

The spacing of breeding sites within a habitat may also reduce predation (Picman 1988), and is often signaled by territoriality (Maher and Lott 2000). Territoriality effectively removes high quality habitat from conspecifics (e.g. Bruinzeel et al. 2006). This ability to evaluate and compete for breeding territories increases with experience, resulting in younger pairs breeding in lower quality locations more frequently than older pairs (Velando and Freire 2003). As chick survival is relatively low and adult survival is high (Andres and Falxa 1995), it is unlikely that the low proportion of inexperienced birds in the population have affected the results of this study. Site fidelity also limits territorial choice, as individuals do not immediately alter their site selection with changes in local or regional habitat quality (Johnson 2007). Site fidelity is likely influenced by the costs associated with the adoption of a new territory, as time is invested in gaining knowledge of local resources (Bruinzeel 2007). This cost may explain why black oystercatchers in this region are highly site-faithful and, in Prince William Sound, return to the same nest bowl for an average of three years (Andres and Falxa 1995).

As the models presented in this study were developed at the breeding territory level, they must be interpreted at that spatial scale (Guisan and Zimmerman 2000). For species with relatively discrete populations, such as black oystercatchers, local factors may affect habitat choices, incorporating differing habitat quality and non-habitat related pressures not present elsewhere. Such selection also can occur at multiple spatial scales for different populations (Lantz et al. 2006). In this study, the pressure of predation was consistently identified as a factor in breeding territory selection. On a larger scale, adequate intertidal forage is a requirement that limits black oystercatcher distribution

along the coast of North America (Andres and Falxa 1995).

The two factors of forage availability and predation avoidance represent different life history strategies of maximizing adult body condition versus prioritizing chick survival. Black oystercatchers can be reproductively viable for ten years (Andres and Falxa 1995), which may offset low-survival rates for eggs and young in a stable population (Ricklefs 2000). Long-lived species can trade-off short-term reproductive success for survival and later reproduction through desertion of young during times of low forage. Desertion of young is most often associated with precocial chicks (Martin 1987) and although black oystercatcher chicks are semi-precocial, provisioning continues past fledging (Groves 1982), which requires long-term intensive parental care. As many eggs and young are predated upon, investment in a two or three-egg brood is a bet-hedge that sometimes results in the production of too many chicks. Black oystercatchers practice brood reduction through abandonment of later-hatching eggs, perhaps in response to territorial forage availability (Hazlitt et al. 2002). This strategy requires increased initial investment during egg production, when black oystercatchers are able to freely forage on and off their territory (Purdy and Miller 1988).

Prioritization of adult body condition was not found in the best supported habitat models, perhaps due to the extremely low breeding success often experienced in this species. This study has shown that predation impacts, although typically less predictable than forage resources, were the driving factor for black oystercatcher breeding territory use in south-central Alaska.

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APPENDIX A. PRODUCTIVITY MODELS IN KENAI FJORDS NATIONAL PARK.

A subset of known breeding sites with previous productivity information and remotely-sensed and field habitat variable data ($n = 15$) in Kenai Fjords National Park (KEFJ) was used to model successful sites. Data were stored in Excel format and imported into ArcGIS, with model evaluation performed in R. A generalized linear model (binomial) was used and the response variable was nest success (defined as the survival of at least one chick to fledging from known productivity data from 2001-2004, Morse et al. 2006). A priori models were evaluated and ranked by Akaike's Information Criterion (AICc), corrected for small sample size, and model weights of evidence were calculated as a further measure of relative support for models (Burnham and Anderson 2002). Receiver operating characteristic (ROC) curves were used to calculate the area under the curve (AUC), a measure of the performance of each model for correctly identifying breeding sites. Models with AUC values >0.50 were considered as performing better than random.

The three best-performing models as identified from initial model development (RSD global model with ShoreZone data, Field global model and Field predation avoidance model) were evaluated for this data set. The Field predation avoidance model was the most supported of the three models, with the Field global model performing similarly well. Although the RSD global model correctly classified all successful sites (an AUC value of 1.0), the ratio of habitat variables to sites is extremely high and this likely represents overfitting (Table A-1).

Table A-1. Model evaluations for remotely-sensed and field habitat variables at black oystercatcher breeding sites in Kenai Fjords National Park (KEFJ) with known productivity information.

Model ¹	Habitat variables ²	AIC _c	ΔAIC _c	w _i ³	AUC ⁴	SD
Productivity data, KEFJ (<i>n</i> = 15)						
Field predation	ISL, VEG	19.11	0.00	0.76	0.83	0.12
avoidance						
Field global	FW, ISL, VEG,	25.76	6.65	0.23	0.86	0.12
RSD Global	TW, MR ASP, SLP, FW, BLMU, EEL, KELP, MEF, ISL, SST, CHL	110.00	90.89	0.00	1.00	0.00

¹Models in ranked order by ΔAkaike's Information Criteria adjusted for small sample size (ΔAIC_c).

²ASP aspect cosine transformed, SLP slope (degrees), FW distance (m) to freshwater, BLMU distance (m) to blue mussel bed, EEL distance (m) to eelgrass, KELP distance (m) to canopy kelp, MEF modified effective fetch, ISL isolation from the mainland, SST average summer sea-surface temperature (degrees), CHL average chlorophyll a concentration (mg/m⁻³), VEG distance (m) to vegetation, TW tidal width (m), MR mid-tide rugosity.

³ w_i model weight of evidence.

⁴ AUC Area under the curve for a receiver operating characteristic (ROC) graph

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APPENDIX B: INTERTIDAL COMPOSITION AT STUDY SITES IN KENAI FJORDS NATIONAL PARK AND PRINCE WILLIAM SOUND IN 2007.

Table B-1. Most abundant components of the intertidal communities at field sites in Kenai Fjords National Park (KEFJ) ($n = 26$), Prince William Sound (PWS) ($n = 34$) and both locations ($n = 60$).

Location	Bare		Brown bladed algae		Green filamentous algae		<i>Mytilus trossolus</i>		<i>Tectura persona</i>		<i>Tectura scutum</i>		<i>Lottia pelta</i>		Littorinids	
	%	SD	%	SD	%	SD	%	SD	Count	SD	Count	SD	Count	SD	Count	SD
KEFJ																
Breeding	77	26	6	12	3	6	5	12	0.1	0.3	0.1	0.3	0.1	0.2	0.2	0.6
Available breeding	77	20	3	6	4	10	3	5	0.1	0.2	0.2	0.6	0.1	0.2	0.2	0.7
All	77	24	5	10	4	8	4	9	0.1	0.3	0.1	0.4	0.1	0.2	0.2	0.7
PWS																
Breeding	55	31	8	12	7	15	8	12	0.2	0.3	0.1	0.3	0.1	0.3	0.8	1.7
Available breeding	57	28	13	17	7	15	5	9	0.7	1.2	0.3	0.7	0.4	0.7	0.2	1.0
All	56	29	11	14	7	15	6	11	0.4	1.0	0.2	0.5	0.3	0.6	1.0	3.5
KEFJ and PWS																
Breeding	66	31	7	12	5	12	6	12	0.1	0.3	0.1	0.2	0.1	0.3	0.5	1.4
Available breeding	65	27	9	14	6	13	4	7	0.4	1.0	0.2	0.6	0.3	0.6	0.9	3.6
All	66	29	8	13	5	13	6	10	0.3	0.7	0.2	0.5	0.2	0.4	0.7	2.7