



Physical and biological habitat preferences of black oystercatcher breeding territories in Kenai Fjords National Park

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ON THE COVER

Black oystercatcher in Kenai Fjords National Park, 2009.
Photograph by: Deborah Kurtz, National Park Service.

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Abstract

Black oystercatchers are shorebirds that defend a composite breeding territory in the intertidal zone for foraging and the immediate upland for nesting. Habitat use in birds is often related to both forage resources and predation avoidance. Predation on eggs and chicks is a major source of mortality for many bird species, including black oystercatcher. As these are long-lived birds with many lifetime reproduction opportunities, high adult survival, and therefore forage resources, are expected to be more important factors in habitat use than breeding success, which is based on more unpredictable factors such as predation and flooding events. To identify the major factors influencing black oystercatcher breeding territory use, remotely-sensed and field-collected data were used to develop logistic regression models in Kenai Fjords National Park and to identify intertidal community composition. All known breeding sites were paired with available breeding sites based on substrate and exposure classifications to avoid selection of unsuitable available sites. Greater distance to vegetation and isolation from the mainland, both related to predator avoidance, were the most supported variables in habitat models. Intertidal community composition, which reflects forage availability, varied little between breeding and available breeding sites. These results suggest black oystercatchers are choosing breeding territories to lessen predation risk over foraging opportunities.

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Introduction

Habitat use studies are applied to identify requirements for positive fitness (the ability to successfully reproduce) 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). Individuals of the focal species 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). The two main factors that influence habitat selection in 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 impact 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 both violations of fitness optimization, in which an individual does not act to maximize reproductive viability, and trade-offs with other factors affecting fitness. Perfect knowledge is an assumption that, 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 knowledge of their surroundings due to their mobility (Kristan 2007). Other factors that may affect the ability of birds to use the best foraging sites include incubation demands, which limit shorebirds' 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 parental condition and meeting the needs of growing chicks (Martin 1987).

Additionally, predation risk may affect the use of optimal foraging sites. Predation impacts the process of natural selection 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 to fitness 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 reduces attention to the nest site, but also reduces parental body condition due to loss of foraging time (Smith et al. 1997).

Both forage availability and predation risk may affect the breeding site selection of black oystercatchers, (*Haematopus bachmani*), large shorebirds that inhabit the rocky coast of the eastern North Pacific. Over 60% of the world's population of these birds breeds in Alaska, where they are listed as a species of high concern due to small population size and potential threats during the breeding season (USSCP 2004, Alaska Shorebird Group 2008), a Species at Risk (Stenhouse and Senner 2005) and a Management Indicator Species in the Chugach National Forest (USDA Forest Service 2002).

Forage resources may be expected to be important to black oystercatchers, as they are also considered an indicator of intertidal zone health in the North Pacific (Tessler et al. 2007), and an apex predator, affecting intertidal composition. These birds feed primarily on limpets, chitons, and mussels (Hartwick 1976, Andres and Falxa 1995, Hazlitt et al. 2002) and, in Prince William

Sound, in south-central Alaska, on clams and barnacles (Andres 1998). Foraging on limpets has been found to affect algal cover through altering the microdistribution of limpets in Oregon (Frank 1982), Washington (Wootton 1995) and California (Lindberg et al. 1987). On Aleutian Islands where introduced rats are present, the ensuing lack of black oystercatchers due to increased predation risk has reduced algal communities with the subsequent increase of intertidal grazers (Kurle et al. 2008).

Intertidal communities form clear vertical zonation patterns from the extreme low tide mark to the splash zone (e. g. Dayton 1971). These patterns are influenced by both biological factors and environmental factors. Biological factors include negative interactions, such as predation (Stanley 2008) and competition for space (Connell 1961), and positive interactions, such as facilitation (Menge 1995). Positive interactions can affect community distribution as was found in a rocky intertidal community in New England (Bertness and Leonard 1997). Neighboring sessile organisms reduced environmental stress and increased organisms' ability to persist in the upper intertidal zone, altering the local zonation pattern. Environmental factors affecting intertidal communities include large-scale as well as local features. Climate and ocean circulation (e.g. Stephenson and Stephenson 1949) affect distribution limits and dispersion of the planktonic larvae that settle in the intertidal. Local-scale variation in intertidal species composition is influenced by the microclimate of a site (e.g. Somero 2002) and disturbance regimes such as hard freezes, which differentially affect species (Carroll and Highsmith 1996). Some environmental factors, such as substrate heterogeneity, alter communities at multiple scales. Substrate heterogeneity has been found to affect species richness at large-scales and the biomass of sessile organisms at local-scales (Archambault and Bourget 1996). Together these biological and environmental factors influence the composition and abundance of intertidal communities and therefore regional and local-scale foraging suitability for black oystercatchers.

Black oystercatchers, when breeding, 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 foraging and nesting resources are moderately spatially clumped and highly predictable (Clark and Shutler 1999, Maher and Lott 2000). Additionally, territoriality can also act as a settlement cue for conspecifics, signaling when resources are fully used (Maher and Lott 2000).

Although black oystercatchers defend a composite territory including forage resources, these birds may use forage sites up to 1.5 km from maintained territories (Andres and Falxa 1995). 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). In the black oystercatcher, increased chick predation has been reported during parental trips to remote foraging locations (Andres and Falxa 1995). Chick predation is the most important source of mortality in this species (Andres and Falxa 1995). To mitigate predation losses, black oystercatchers employ biparental care and have cryptic coloration of eggs (Webster 1941).

To maximize lifetime reproductive success in long-lived species such as the black oystercatcher, habitat use would be expected to reflect the importance of maintaining parental body condition rather than avoiding predation on young, which 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 of these primary factors, forage availability or predation avoidance, determine 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 based on a suite of habitat variables relating to these factors, and biological communities were measured and compared for forage related differences.

Methods

Site Selection

Kenai Fjords National Park (KEFJ) is located on the south-eastern coast of the Kenai Peninsula. The park's generally steep coastline is more than 400 miles, and is punctuated with gravel or boulder beaches as well as longer gravel moraines exposed after recent glacial retreats (Tande and Michaelson 2001). Three bays, Aialik Bay, Harris Bay and the southern end of Resurrection Bay were included in this study, as these areas have been the site of historic and comprehensive black oystercatcher nest surveys. These bays are relatively exposed to the Gulf of Alaska; however, many of the numerous coves are sheltered.

Sixty-five known breeding sites were selected, as were 65 available breeding sites in KEFJ. Available sites are sites that were not known to be breeding sites. These sites were used for a priori model evaluation of black oystercatcher breeding site selection (Figure 1). Black oystercatcher breeding locations from yearly boat-based surveys were identified by the National Park Service. Available breeding sites were randomly selected from coastline matching known breeding site substrate and exposure classes, as defined by the ShoreZone classification shoreline GIS layer (Coastal and Ocean Resources, Inc. 2009). Sites were paired on these habitat variables to ensure available sites were located in potential habitat. Substrate is known to affect black oystercatcher nest bowl location and exposure affects wave action and loss of nests to flooding. All sites were defined as 100-m alongshore lengths, centered on the known nest bowl or available breeding point. A subset of sites was selected for field sampling. Field data collection occurred from July to September 2007, with additional field data collected in June 2008.

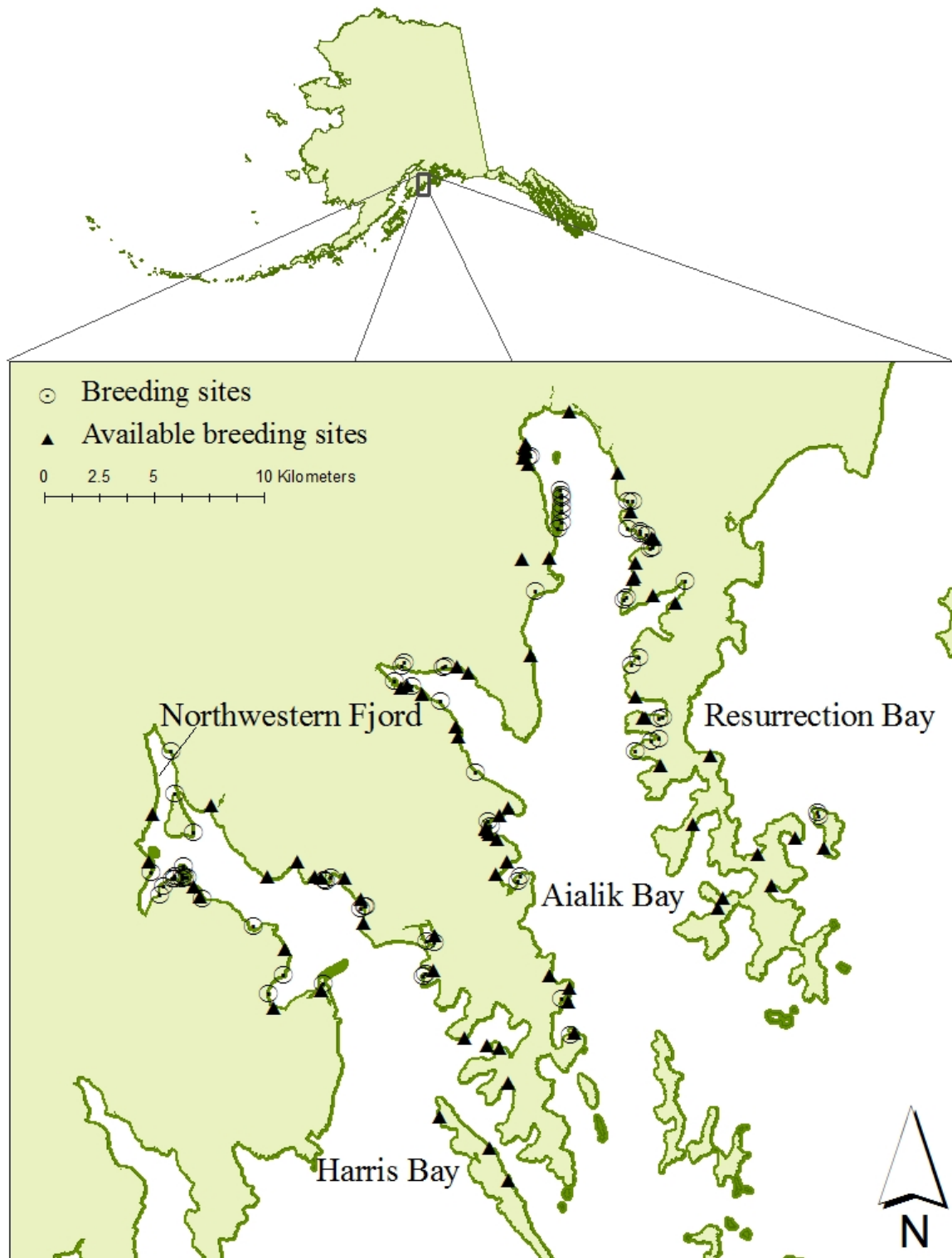


Figure 1. Map of study sites in Kenai Fjords National Park. Known breeding sites and available breeding sites were located in southern Resurrection Bay, Aialik Bay and Harris Bay, including Northwestern Fjord. Available breeding sites were selected to have the same substrate and exposure classes as known breeding sites.

Remotely-sensed Data

Remotely-sensed habitat data were used to model known black oystercatcher breeding sites compared to available breeding sites. Remotely-sensed data included habitat variables related to forage availability and predation risk. Forage availability parameters 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 parameter, 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), persistence of snow in the spring, and algal and vegetation growth. These in turn affect the suitability of a site for intertidal organisms. Aspect was obtained by identifying the shore normal of each site from 1:63360 scale NPS coastline GIS data (National Park Service 2008). Modified effective fetch, a quantitative measure of exposure (Howes et al. 1994), was measured from the NPS coastline mapping data. Exposure is known to affect intertidal biological community composition. Slope is related to the area available for forage, and was calculated from a digital elevation model of the state of Alaska (USGS 2008a) at a resolution of 60 m x 60 m. Slope is related to the area of intertidal forage availability as well as to the ability of young black oystercatchers to accompany adults during foraging trips. Another parameter measured was distance to freshwater, which has the potential to affect the black oystercatcher as these birds occasionally drink freshwater. In addition, 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 (USGS 2008b) 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 and therefore forage available to black oystercatchers. 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 (Geographic Information Network of Alaska 2008). 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. These distances, as well as that to blue mussel (*Mytilus edulis*) beds, a common forage species, were available through the ShoreZone database (Coastal and Ocean Resources, Inc. 2009) for KEFJ 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 paired available breeding sites, were randomly chosen using Hawth's tools (<http://spatial ecology.com>) in ArcView for field data collection. Substrate composition was verified in situ. Oystercatchers were not found breeding at any available breeding sites. Field data included parameters related to forage availability and predation risk. Forage availability parameters included distance to freshwater, tidal width, and rugosity. Predation avoidance parameters 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.

In addition to field measures of the remotely-sensed data habitat variables of aspect and distance to freshwater described above, several field-only habitat variables were measured. Tidal width was taken as the distance from the supralittoral to the zero-tidal height at the center of the site. Rugosity is 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). This method obtains a ratio of a chain lying flush with the substrate to an adjacent, taut, length of tape. Finally, woody vegetation allows cover for predators, increasing predation risk as suggested by Poe et al. (2009).

Additionally, the biological community composition at field sites was sampled at ten randomly placed 0.25 m² quadrats 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, these were 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.



Figure 2. Black oystercatcher breeding site in Aialik Bay, with transect tape laid out.

Analysis

The complete set of unique known breeding ($n = 65$) and available breeding sites ($n = 65$) was used to evaluate models from remotely-sensed data available. These data included aspect, slope, distance to freshwater, modified effective fetch, sea-surface temperature, chlorophyll *a* concentrations, and distances to blue mussel, kelp and eelgrass beds. Aspect was converted to radians and cosine transformed, and each parameter was analyzed and transformed for normality as needed. Confidence intervals (95%) were calculated for every parameter by site type (known breeding or available breeding), and these intervals were evaluated for biological significance.

Data were stored in Excel format and imported into ArcGIS, with model evaluation performed in R. A binomial logistic regression model 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 (AICc), corrected for small sample size, and model weights were calculated as a further 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 for correctly identifying breeding sites. Models with AUC values >0.50 were considered as performing better than random.

Field sites ($n = 60$) were a subset of all sites that were randomly chosen for field study. New sites in KEFJ ($n = 14$) were used to identify the performance of all of the best-performing models in both the remotely-sensed data portion of the study and the field study, and were evaluated as above. A subset of known breeding sites with previous productivity information and current habitat variable data ($n = 15$) was used to model successful sites. The response variable for each of the productivity data models 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). Model and parameter evaluation were performed for field site verification and productivity models as stated above.

During biotic community composition analysis, as most invertebrate species were found only in a few quadrats in the study area, 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 breeding and random available breeding sites.

Results

Model evaluation

Remotely-sensed data model evaluation

The most supported remotely-sensed data (RSD) model on the basis of the Akaike's Information Criterion (corrected) (AICc) and associated model weights was the predator-avoidance model, including the habitat variable of isolation. The global model, including variables relating to both forage availability and predator avoidance correctly classified the highest amount of breeding sites (Table 1), although this is likely due to overfitting.

When confidence intervals were calculated and evaluated for biological relevance, differences between known breeding and available breeding sites were apparent for two remotely-sensed data parameters (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 (926m-1050m) and available sites (407m-865m), these values imply black oystercatchers are choosing sites further from a food source, which is likely not the case.

Field data model evaluation

During field model evaluation, the most supported models consistently included distance to vegetation and isolation (Table 1).

The field habitat variable of distance to vegetation, which exhibited a much greater (and typically higher) range of values for known breeding sites, is also potentially important for identifying black oystercatcher breeding sites (Table 2). Confidence intervals for the distance to freshwater (field and remotely-sensed data measures) overlap only slightly, most likely due to a correlation with the higher proportion of known breeding sites located on islands, and therefore further from a freshwater source.

Verification data model evaluation

As there were several habitat variables that appeared to be potentially influencing black oystercatcher breeding site selection that were not included in the predator avoidance model, the predator avoidance and both global models were included in analysis for verification and productivity data.

The best-performing model with data from sites previously left-out of analysis contained predator-avoidance parameters, and performed well compared to all models when identifying site types (Table 1).

Productivity data model evaluation

The predator avoidance model performed the best of the three models when using nest success as a response variable. The RSD global model correctly classified all sites (an area under the curve of 1.0), however the number of parameters to sites is extremely high, and this is likely an unrealistic performance for this model (Table 1).

Table 1. Model performance for binomial logistic regression models for all data sets, including results from Akaike's Information Criterion (corrected), weight of evidence, and area under the curve estimates.

Model	Parameters ¹	q^2	n^3	AIC _c	Δ AIC _c	w_i^4	AUC ⁵	SD
Remotely-sensed data								
Predator avoidance	ISL	2	130	10.52	0.00	0.86	0.62	0.04
Simplified forage	SLP, BLMU, MEF	4	130	14.14	3.62	0.14	0.72	0.05
Forage	SLP, FW, BLMU, EEL, KELP, MEF, SST, CHL	9	130	26.33	15.81	0.00	0.76	0.04
Global	ASP, SLP, FW, BLMU, EEL, KELP, MEF, ISL, SST, CHL	11	130	31.30	20.78	0.00	0.82	0.04
Field data								
Predator avoidance	ISL, VEG	3	28	8.96	0.00	0.85	0.73	0.10
Global	FW, ISL, VEG, TW, MR	6	28	12.52	3.56	0.14	0.66	0.12
Forage	FW, TW, MR	5	28	21.81	12.85	0.01	0.68	0.10
Verification data								
Field predator avoidance	ISL, VEG	3	14	24.17	0.00	1.00	0.83	0.12
Field global	FW, ISL, VEG, TW, MR	6	14	37.42	13.25	0.00	0.75	0.17
RSD global	ASP, SLP, FW, BLMU, EEL, KELP, MEF, ISL, SST, CHL	11	14	154.00	129.83	0.00	0.96	0.05
Productivity data								
Predator avoidance	ISL, VEG	3	15	19.11	0.00	0.76	0.83	0.12
Field global	FW, ISL, VEG, TW, MR	6	15	25.76	6.65	0.23	0.86	0.12
RSD Global	ASP, SLP, FW, BLMU, EEL, KELP, MEF, ISL, SST, CHL	11	15	110.00	90.89	0.00	1.00	0.00

¹Models in ranked order by change in Akaike's Information Criteria adjusted for small sample size (Δ AIC_c). ASP aspect (radians) 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.

² q number of model parameters

³ n number of sites in model set

⁴ w_i model weight of evidence

⁵ AUC Area under the curve for a receiver operating characteristic (ROC) graph

Table 2. 95% Confidence intervals, means and standard deviations for remotely-sensed and field collected data parameters.

Habitat variable	Breeding site				Available sites			
	<i>Lower CI</i>	<i>Mean</i>	<i>Upper CI</i>	<i>SD</i>	<i>Lower CI</i>	<i>Mean</i>	<i>Upper CI</i>	<i>SD</i>
Aspect (cosine transformed)	-0.07	0.09	0.25	0.66	-0.11	0.06	0.22	0.70
Slope (degrees)	8.2	11.0	13.7	11.4	12.0	14.6	17.1	10.6
Distance to freshwater (m)	1739	2163	2586	1743	139	1775	2161	1589
Distance to blue mussel bed (m)	926	988	1050	926	407	636	865	943
Distance to eelgrass (m)	3275	4051	4828	3357	4040	4887	5734	3484
Distance to canopy kelp (m)	7842	9267	10693	2864	6639	8160	9680	6255
Modified effective fetch	2.4	3.0	3.6	2.5	-51.4	89.5	230.3	579.3
Isolation	0.22	0.34	0.45	0.48	0.03	0.10	0.18	0.31
SST (degrees)	5.17	5.36	5.55	0.80	5.48	5.72	5.95	0.97
Chlorophyll a (mg/m ⁻³)	0.07	0.10	0.13	0.11	0.09	0.12	0.15	0.11
Aspect (field, cosine transformed)	-0.48	-0.05	0.39	0.73	-0.41	-0.02	0.36	0.65
Distance to freshwater (field, m)	232.6	345.6	458.7	191.4	46.6	157.7	268.9	188.1
Distance to vegetation (m)	9.3	50.5	91.6	69.7	10.0	14.5	24.6	17.0
Tidal-width (m)	25.1	55.7	86.3	51.8	34.6	62.1	89.6	46.5
Mid-tide rugosity	1.03	1.05	1.08	0.04	1.04	1.07	1.11	0.05

Biological community analysis

Multi-dimensional scaling plots were evaluated and 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 groups of organisms. The most abundant components of the intertidal were brown bladed algae, green filamentous algae, mussels, littorinids and limpets (Table 3).

Table 3. Most abundant components of the intertidal zone at high, mid and zero-tidal heights pooled, for known breeding sites and available breeding sites separately and averaged together. Data are average percent cover or count per 0.25m².

Intertidal cover		Known breeding sites	Available breeding sites	All sites
Bare substrate	Cover (%)	77	77	77
	SD (%)	26	20	24
Brown bladed algae	Cover (%)	6	3	5
	SD (%)	12	6	10
Green filamentous algae	Cover (%)	3	4	4
	SD (%)	6	10	8
<i>Mytilus trossulus</i>	Cover (%)	4	3	4
	SD (%)	5	5	9
<i>Tectura persona</i>	Count	0.1	0.1	0.1
	SD	0.3	0.2	0.3
<i>Tectura scutum</i>	Count	0.1	0.2	0.1
	SD	0.3	0.6	0.4
<i>Lottia pelta</i>	Count	0.1	0.1	0.1
	SD	0.2	0.2	0.2
Littorinids	Count	0.2	0.2	0.2
	SD	0.6	0.7	0.7

Discussion

This study found that predictive models that included variables related to predator avoidance were the most powerful. Habitat variables related to predator avoidance (isolation and distance to vegetation) were found in all best-supported models during each stage of model evaluation, verification and productivity 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 choose to nest away from avian predators (Suhonen et al. 1994, Johannsen 2001), to conceal nests (Martin and Roper 1988) or to use locations providing high visibility (Johannsen 2001) to reduce predation risk. Although distance to vegetation was identified through field measure, high resolution satellite imagery could be used to identify less vegetated shorelines.

As black oystercatchers may be expected to maximize their fitness, this study expected to find forage availability to be an important factor in identifying breeding sites. However multivariate analyses did not identify characteristics of biological communities that differed between sites, and most forage related parameters were not found to differ at biologically relevant levels. This may be because intertidal communities and forage resources exhibit differences that are more complex than were identified in this study. Size-class of prey items, which were not sampled for, may be important because of differing amounts of energy they supply per effort. However this relationship can also be complex: larger, energy-rich but “risky” prey items, which were more likely to result in bill injury, were avoided by the Eurasian oystercatcher (Rutten et al. 2006). Microdistribution of limpets and other grazers may play a role in determining forage availability to black oystercatchers. Many limpets on vertical surfaces are beyond the reach of oystercatchers (Lindberg et al. 1998) and some limpets increase their tenacity to the substrate when nearby predation events occur (Coleman et al. 2004). A lack of variation in intertidal communities may also be related to geographic characteristics of this area. Although vertical zonation patterns are the most important factor determining intertidal variation, horizontal gradients related to water flow 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, selection for intertidal community composition may be underestimated if oystercatchers often use remote foraging locations. Identification of use and territoriality at these remote foraging areas would allow us to better understand region specific forage habitat requirements for this species.

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 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 2002). This strategy requires increased initial investment during egg

production, when black oystercatchers are more able to freely forage on and off their territory (Purdy and Miller 1998).

Territoriality results in the spacing of nests (Maher and Lott 2000), which may reduce predation (Picman 1988), but also effectively removes high-quality habitat from conspecifics (e.g. Bruinzeel et al. 2006). The ability to evaluate and compete for known breeding sites increases with experience, resulting in younger individuals breeding in lower quality locations more frequently than older individuals (Velando and Freire 2003). As chick survival is relatively low and adult survival is high in this species (Andres and Falxa 1995), it is unlikely that the low proportion of inexperienced birds in the population have had an effect on the results of this study. Territorial choice is also limited by site fidelity, as individuals do not immediately alter their site selection with changes in local or regional habitat quality (Johnson 2007). Adoption of a new territory is not without costs, as time is invested in gaining knowledge of local resources (Bruinzeel 2007). Black oystercatchers are highly site-faithful and, in Prince William Sound, returned to the same nest bowl for an average of three years (Andres and Falxa 1995). However the high level of territoriality exhibited in south-central Alaska in the absence of intertidal forage differences may be due to a conservation of behaviors common to oystercatchers around the world (Hockey 1996).

Slope, a habitat variable in this study, may affect both forage availability and predation and result in unidentified trade-offs for these birds. Low-sloping beaches contain larger intertidal areas and allow chicks to accompany foraging adults while foraging (Hazlitt et al. 2002). However, eggs are also more vulnerable to waves and extreme high tide events at these sites, resulting in nest flooding and egg loss (Tessler et al. 2007). Low-sloping beaches are more commonly used by kayakers and campers, which may prevent utilization of preferred resources by these birds (Andres and Falxa 1995). Current visitor levels in south-central Alaska at 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 the likelihood of carnivore presence (Boyle and Samson 1985, Spiegel 2008), and therefore decrease predation risk.

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, factors affecting habitat choices may be localized, incorporating differing habitat quality and non-habitat related pressures not present elsewhere. Such selection can occur at multiple spatial scales for different populations (Lantz et al. 2006). On a large scale, adequate intertidal forage is a requirement that limits black oystercatcher distribution along the coast of North America (Andres and Falxa 1995). At the territory scale, the pressure of predation was consistently identified as a factor in habitat selection.

This study relied on a previous multi-year study for breeding site data and was therefore limited to the northern three bays of Kenai Fjords National Park. Black oystercatcher surveys in the southern portion of the park at the beginning of the breeding season when detections are highest would allow for validation of remotely-sensed data models there. Additionally, high-resolution GIS vegetation layers would allow for the inclusion of the field parameter of distance to vegetation into Park-wide remotely-sensed data models. Detailed observations of remote

foraging location use by breeding pairs within the park would be helpful for potential future research identifying intertidal community requirements of foraging areas.

This study has shown that predation impacts were the driving factor for black oystercatcher breeding territory use in Kenai Fjords National Park, with use concentrated at sites where woody vegetation is not adjacent to the shore and at sites isolated from the mainland. Therefore, human-related disturbance to these areas should be discouraged, and future human-use development should attempt to utilize wooded coastline. Current backcountry visitor use is encouraged through the placement of bear-proof food lockers, located primarily at relatively unvegetated beaches. Although black oystercatcher breeding territories are often found near these beaches, Morse et al. (2006) did not find a recreational disturbance effect and Spiegel (2008) suggested that in south-central Alaska low levels of human use on beaches may act to reduce nocturnal predation on these birds. Unless sites are found to be attracting predators to the area, moving current backcountry camping locations is not recommended at this time.

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