ARTICLE

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Drones reveal spatial patterning of sympatric Alaskan pinniped species and drivers of their local distributions

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Abstract: The Arctic and its adjacent ecosystems are undergoing rapid ecological reorganization in response to the effects of global climate change, and sentinel species provide critical updates as these changes unfold. This study leverages emerging remote sensing techniques to reveal fine-scale drivers of distribution and terrestrial habitat use of two sympatric sentinel species of the central Bering Sea, the Pacific harbor seal (*Phoca vitulina richardii* (Gray, 1864)) and the northern fur seal (*Callorhinus ursinus* (Linnaeus, 1758)), at non-breeding haul-outs in the Pribilof Islands. We surveyed these species using unoccupied aircraft systems with thermal and visible-light photography, and we applied distributional modeling techniques to quantify the relative influence of habitat characteristics and social dynamics on the local distributions of these species. Drone imagery yielded locations and population counts of each species, and spatial data products allowed quantitative characterization of occupied sites, revealing that conspecific attraction is a driver of local site selection for both species, and Pacific harbor seals and northern fur seals are differentially limited by terrain characteristics. These findings represent new applications of species distribution modeling at local scales, made possible by ultra-high resolution drone surveillance and photogrammetric techniques, which add new spatial context to past observations and future scenarios in this changing ecosystem.

Key words: drones, habitat selection, remote sensing, sentinel species, spatial ecology, spatial modeling.

Résumé : L'Arctique et ses écosystèmes adjacents subissent une réorganisation écologique rapide en réponse aux effets du changement climatique mondial, et les espèces sentinelles fournissent des mises à jour essentielles à mesure que ce changement se déroule. Cette étude met à profit les nouvelles techniques de télédétection pour révéler les facteurs de répartition à petite échelle et l'utilisation de l'habitat terrestre de deux espèces sentinelles sympatriques du centre de la mer de Béring, le phoque commun du Pacifique (*Phoca vitulina richardii* (Gray, 1864)) et l'otarie à fourrure du Nord (*Callorhinus ursinus* (Linnaeus, 1758)), lors de d'échoueries non reproductrices dans les îles Pribilof. Les auteurs ont étudié ces

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espèces au moyen de systèmes d'aéronef sans pilote à l'aide de photographies thermiques et en lumière visible, et ils ont appliqué des techniques de modélisation de la répartition pour quantifier l'influence relative des caractéristiques de l'habitat et de la dynamique sociale sur les répartitions locales de ces espèces. L'imagerie par drone a permis de déterminer les emplacements et les chiffres de population de chaque espèce, et les produits de données spatiales ont permis la caractérisation quantitative des sites occupés, révélant que l'attraction conspécifique est un facteur de sélection locale des sites pour les deux espèces, et les phoques communs du Pacifique et les otaries à fourrure du Nord sont différentiellement limités par les caractéristiques du terrain. Ces résultats représentent de nouvelles applications de la modélisation de la répartition des espèces à l'échelle locale, rendues possibles par la surveillance par drones munis d'équipement à ultra haute résolution et les techniques photogrammétriques, qui ajoutent un nouveau contexte spatial aux observations passées et aux scénarios futurs dans cet écosystème en évolution. [Traduit par la Rédaction]

Mots-clés : drones, sélection de l'habitat, télédétection, espèces sentinelles, écologie spatiale, modélisation spatiale.

Introduction

Global climate changes are driving major ecological shifts worldwide (Parmesan and Yohe 2003), and the Arctic is experiencing transformations with unprecedented environmental and biophysical disruptions (Box et al. 2019). Arctic marine ecological communities are restructuring around a poleward shift of species ranges (Kortsch et al. 2015), and the Arctic-adjacent Bering–Chukchi Sea complex is increasingly stressed by anomalously warm water events (Carvalho et al. 2021). These marine heatwaves can disrupt entire food webs from the bottom up, cascading into spatial redistributions, unusual mortality events, and body condition losses in top predator sentinel species, such as seabirds and pinnipeds (Jones et al. 2019; Boveng et al. 2020; Kuletz et al. 2020; Romano et al. 2020). Simultaneously, climate change exposes Arctic fauna to novel threats such as invasive species (Chan et al. 2019), disease vectors (Parkinson et al. 2014) and anthropogenic contaminants (Macdonald et al. 2005), threatening Arctic food webs and the human cultures and economies that depend on them. Monitoring of sentinel species, such as marine mammals, at ecologically important or vulnerable sites can reveal the occurrence and severity of these ecological changes when they occur (Bossart 2010; Fossi and Panti 2017). Monitoring programs require spatial and temporal coverage sufficient to detect meaningful changes, alongside robust understandings of specific biology and natural history to accurately interpret those changes.

Situated in the central Bering Sea, the Pribilof Islands are a key site for monitoring the sea's ecological health and changes. The five volcanic islands reside near the "Bering Sea green belt", a highly productive region located over the continental shelf break (Springer et al. 1996), and the archipelago's geographic isolation enhances its ecological significance among highly productive marine waters (Sinclair et al. 2008). For this reason, it hosts large seabird colonies and breeding populations of three species of pinnipeds: Pacific harbor seals (*Phoca vitulina richardii* (Gray, 1864)), the majority of the global population of northern fur seals (*Callorhinus ursinus* (Linnaeus, 1758)), and a small population of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) belonging to the endangered western distinct population segment (NMFS 2008). The archipelago also hosts two Alaska Native Unanga communities on its largest islands, Saint Paul and Saint George, for whom these seabird and pinniped species hold great importance to their culture, history, and traditional needs (Torrey 1980; Veltre and Veltre 1981). Select species of the islands, particularly northern fur seals but including harbor seals and Steller sea lions, receive regular research and

monitoring from tribal, federal, and academic groups, including an Indigenous Sentinels Network operated by the tribal governments on each inhabited island.

Pinnipeds of the Pribilof Islands are studied as sentinel species of the Bering Sea ecosystem, reflecting regional shifts in prey abundance and abiotic stressors. Monitoring and protection are also prescribed by the United States Marine Mammal Protection Act (MMPA 1972) and the Fur Seal Act (1966). However, the remote location of the Pribilof Islands poses logistical challenges to regular population monitoring, particularly of Otter Island and Walrus Island, which are less accessible due to their distance from local communities and lack of infrastructure. For example, the harbor seal stock of the Pribilof Islands has been subject to especially infrequent monitoring since this population chiefly uses Otter Island for terrestrial habitat. Sparse surveys of Otter Island documented a decline of 83% between 1974 (1,250 seals) and 1995 (244 seals), and a further decline by 2010 (212 seals; Withrow and Jemison 2016), but the infrequency of these surveys yielded insufficient data to estimate a current population trend until the survey described in this study (Richmond et al. 2019; Muto et al. 2020).

Pinnipeds use haul-outs for a variety of critical terrestrial behaviors that include breeding, molting, resting, and socialization (Montgomery et al. 2007), and Otter Island is used for such purposes by Pribilof harbor seals: historical accounts describe the island as a breeding site (Kenyon 1962) and mother–pup pairs have recently been documented in drone surveys conducted during the breeding season in 2019 (Divine et al. 2019). Historically, Otter Island was also a large fur seal haul-out for as many as 3000–4000 non-breeding males (Elliott 1882), but during the commercial sealing era, laborers periodically cleared these haul-outs with the intent to relocate males to adjacent islands for sealing, leading to abandonment of the island until 1917 when a lone adult male was sighted (Hanna 2008). An absence of studies or records thereafter conceals any trends on the island until 1974 when 10 individuals were sighted and, co-occurring with the region's decline in harbor seals, by 1995 1,774 fur seals were present on Otter Island (Withrow and Jemison 2016). Concomitantly, during 1972–2014 northern fur seals experienced a long-term decline of ~66% throughout the Pribilof Islands (Gelatt et al. 2015), with pup production further decreasing approximately 3.7% during 2016–2018 (Towell et al. 2019). Similarly, Steller sea lions in the Pribilof Islands represent only a token of their historical population, estimated to number more than 15,000 in 1786 (Kenyon 1962); the 2015 survey efforts by contrast counted just 337 non-pup individuals and 48 pups throughout the Pribilof Islands, including 13 non-pups on Otter Island (Fritz et al. 2015).

Otter Island exemplifies key challenges of species monitoring, being remote, frequently subject to hostile weather, and host to species that are easily flushed. Such circumstances severely limit conventional ground and aerial survey techniques, but remote sensing technologies can mitigate these challenges, increasing access and unlocking new scales of coverage and spatial context for animal research (de Leeuw et al. 2010; McDermid et al. 2010). Inexpensive and portable unoccupied aircraft systems (UASs or drones) particularly lower the barriers to aerial surveys of remote and inaccessible locations with minimal disturbance (e.g., Arona et al. 2018). Simultaneously they provide high-resolution data products that reveal ever finer dynamics of animal movements, distributions, and population changes, informing past observations and future predictions of key sites and species (Chabot and Bird 2015).

This study leverages spatial data products from a UAS survey of Otter Island (Fig. 1) to count and map the three at-risk pinniped species that cohabitate the island as a seasonal haul-out site. Using UAS surveillance and photogrammetric techniques, we locate pinnipeds in the three-dimensional context of their haul-out sites, we characterize terrestrial habitat associations for each pinniped species, and we model how terrain and social factors

Fig. 1. Location of the Pribilof Islands (right) and Otter Island (red inset, left), featuring the UAS flight path (yellow) over a targeted region of interest (purple) from a UAS survey over sympatric haul-outs of northern fur seals, harbor seals, and Steller sea lions on the island's north coast. Map created using ArcGIS Pro 2.6.1; world-map credit: National Geographic and Esri; satellite imagery credit: GeoEye, Maxar.
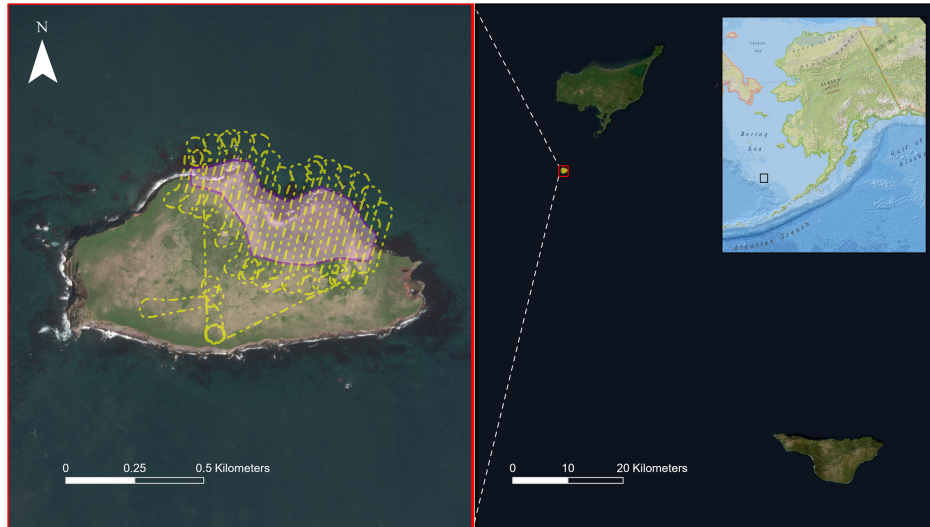
might influence fine-scale site selection and distribution of the most abundant species, harbor seals and northern fur seals. The observed relationships among these sympatric species in a shared landscape reveal similarities and differences in non-breeding habitat use, and suggest potential drivers for haul-out site selection in this remote but ecologically important habitat.

Material and methods

We carried out surveys of Otter Island ([Fig. 1](#)) on 3 September 2018 using two fixed-wing UASs equipped with visible-light (RGB) and thermal infrared (TIR) camera systems (equipment details in **Appendix A**). UAS imagery was collected at a low enough ground-sample distance (GSD) in each spectral range that individual seals could be discriminated against background substrates, classified to species by shape and color, located precisely within the landscape, and counted. Counts and derived estimates from these data are now included in National Oceanic and Atmospheric Administration (NOAA) records ([Boveng et al. 2019](#); [Richmond et al. 2019](#); [Muto et al. 2020](#)).

Study sites

UAS surveys were flown over the entirety of Otter Island and regions of interest (ROIs) on the north and south coasts where pinnipeds were identified ([Fig. 2](#); survey details in **Appendix A**). All flights were conducted during 1400–1630 AKDT, corresponding to a cresting mixed semidiurnal high tide of 0.45–0.56 m above mean lower-low water (0.54–0.43 m below mean higher-high water), or 0.67–0.78 m above the North American Vertical Datum of 1988 (NAVD88) as recorded at Village Cove, Saint Paul Island. The seasonal timing of the survey was estimated as peak molting season for harbor seals and just before the molting season for northern fur seals and Steller sea lions.

Fig. 2. Orthomosaic products of Otter Island. UASs were used to survey (*a*) the whole island in RGB imagery, and ROIs were identified along the north and south coasts (red polygons). UASs were then used to survey these regions in synoptic (*b*) RGB imagery and (*c*) TIR imagery, which were used in conjunction to identify and count pinnipeds. Orthomosiacs created using Pix4Dmapper 4.3; map created using ArcGIS Pro 2.6.1.
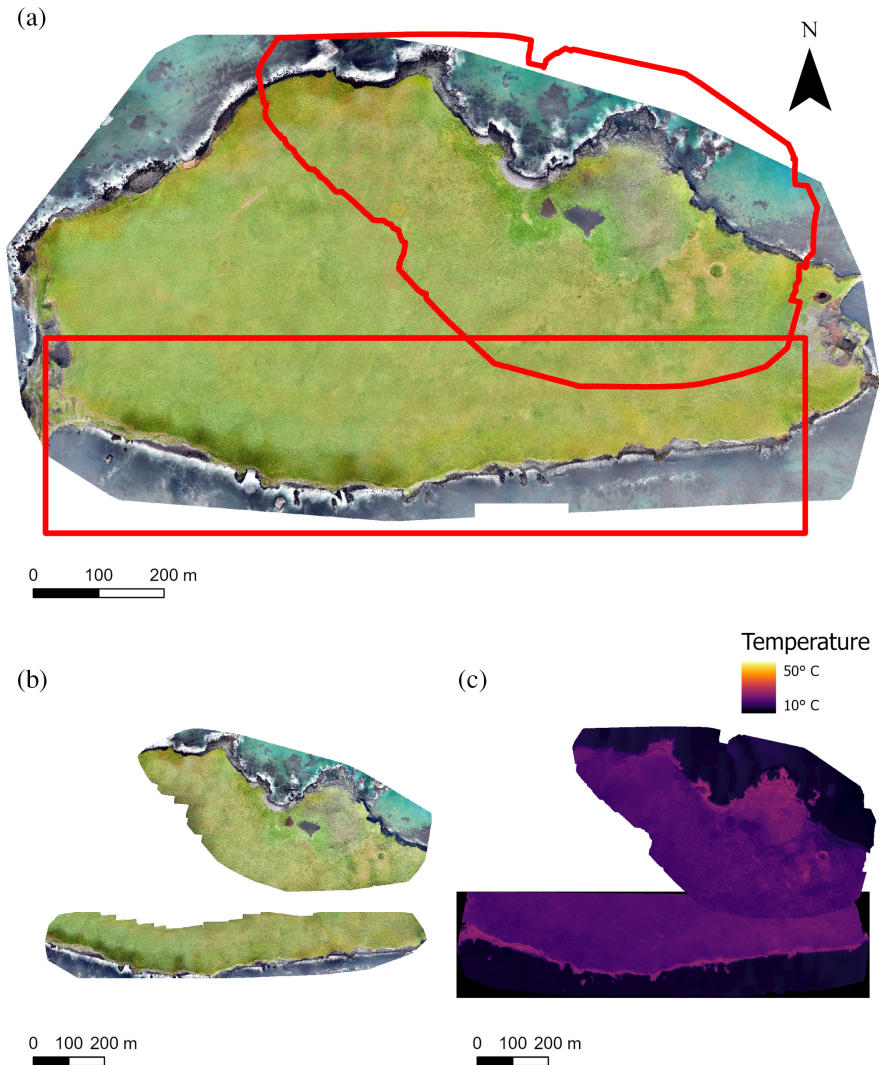
Ethics

Research was conducted under NMFS Permit number 19436 and Alaska Maritime National Wildlife Refuge Research and Monitoring Special Use Permit number 74500-18-021.

Photogrammetric data preparation

Image sets from UAS surveys were processed using Pix4D software to create RGB and TIR orthomosaic products (Figs. 2b and 2c) and a digital surface model (DSM) of the entire island. Orthomosaics were manually examined and edited to remove artifacts, and then were coregistered using ArcGIS Pro 2.6.1 to align the two mosaics as closely as possible (details on UAS imagery processing, editing, and alignment in **Appendix B**).

Fig. 3. Examples of each species—harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*), and Steller sea lions (*Eumetopias jubatus*)—identified in our north coast ROI, with identical coverage from RGB imagery (top) and TIR imagery (bottom). TIR imagery was used chiefly to locate and confirm animal presence, and RGB imagery was used to additionally discriminate individuals among clusters and identify species. Layout created using ArcGIS Pro 2.6.1.
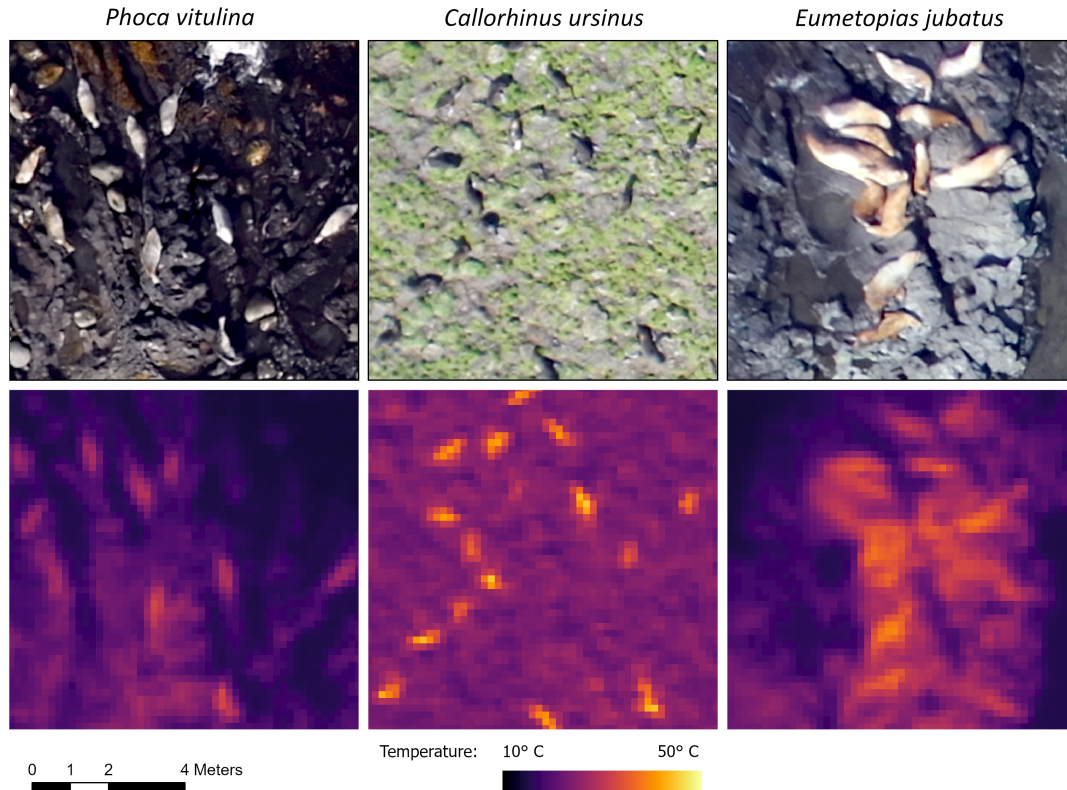

Preliminary data evaluation

Using the edited, coregistered, and overlaid RGB and TIR mosaics, an expert analyst identified all pinnipeds at each site, identifying animals based on shape and color in each RGB orthomosaic and by heat signature in the corresponding TIR orthomosaic, and classifying species based on shape, size, color, and posture (Fig. 3). Counting was conducted in ArcGIS by placing a point feature at the approximate center of the body of each discernible animal and alternating the display between orthomosaic layers (RGB and TIR) to corroborate or reject the detection; uncertain detections were discarded.

Spatial data generation

From the DSM of the island and the point set of pinniped locations, we generated a suite of raster data products to describe the habitat characteristics of Otter Island as topographic predictors (Fig. 4): 'Aspect', 'Elevation' (relative to NAVD88), 'Slope', 'Distance from shore' (three-dimensional surface), 'Rugosity' (arc–chord ratio rugosity index; Du Preez 2015), and 'Sky view factor' (an index of topographic openness); and as two dynamic biological predictors: '*C. ursinus* proximity' and '*P. vitulina* proximity' (distance between a given cell and the closest individual of each species, respectively). We considered these variables to be biologically relevant to all three pinniped species, though to different degrees: we expected that elevation, slope, distance from shore, rugosity might affect the energetic cost of locomotion

Fig. 4. Habitat products of Otter Island derived from a photogrammetric DSM, describing topography and species distribution on the island. DSM created using Pix4Dmapper 4.3; map created using ArcGIS Pro 2.6.1.
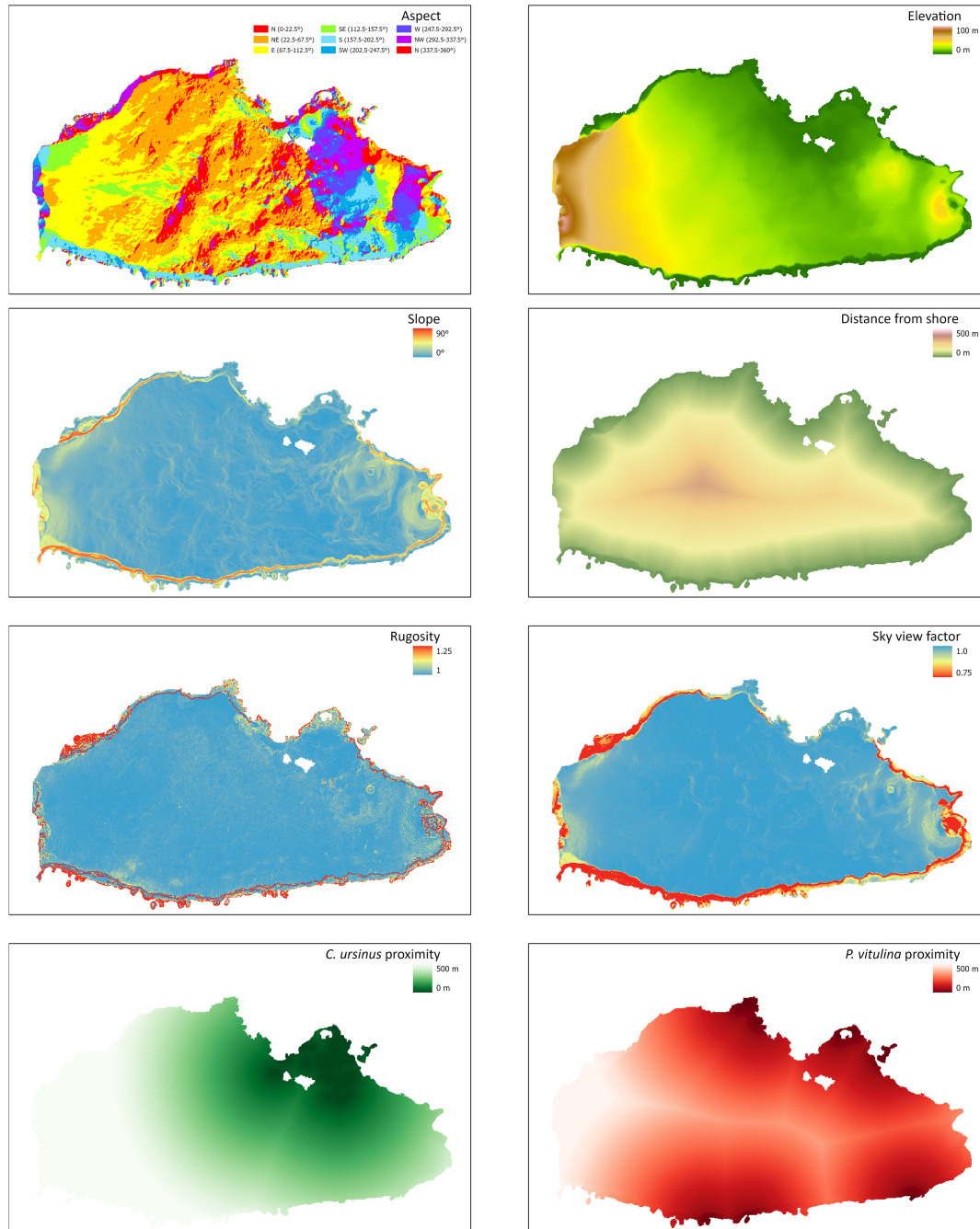
or create functional barriers to habitat access; we expected that different aspects, distances from shore, rugosity values, and sky view factor might influence thermoregulation by modulating exposure to wind, sea-spray, and insolation; and we expected that *C. ursinus*

proximity and *P. vitulina* proximity might enable potential social dynamics of conspecific and interspecific interactions.

Topographic products were generated at a 2 m resolution, this being considered a scale germane to the body size and terrestrial locomotive ability of all three species. All regions seaward of the surf-line, and inland water features were omitted. All variables were derived from the DSM using ArcGIS Pro 2.6.1 (details in **Appendix C**), with the exception of 'Sky view factor' which was derived using System for Automated Geoscientific Analyses (SAGA) 7 (Conrad et al. 2015). Species proximity data were generated as either raster products, using the distance accumulation tool in ArcGIS, for background pseudoabsence data, or as point values using the "nndist" function in the "spatstat" R package (Baddeley and Turner 2005) for identified presence locations.

We excluded 'Sky view factor' from spatial analysis because it correlated significantly with 'Slope' across the entirety of Otter Island (Table S1[1]), so we preferentially used 'Slope' as the more parsimonious predictor. '*E. jubatus* proximity' was not considered for spatial analyses because the species had a limited presence in the landscape (12 individuals in a single thigmotactic cluster), but all three species were used to calculate descriptive statistics of their local haul-out sites. Descriptive statistics were calculated for the locations of each species and described as mean ± standard deviation or, for 'Aspect', as μ, κ parameters from a maximum likelihood estimation of a von Mises distribution calculated using the "circular" R package (Agostinelli and Lund 2017), where κ is a measure of concentration and $\kappa = 0$ indicates a uniform (not concentrated) distribution of values around μ.

Spatial modeling

We tested the potential influence of terrestrial habitat qualities on seal presence by modeling the probability of pinniped occurrence in response to the derived spatial variables, and we conducted these statistical analyses using R 4.0.2 (R Core Team 2020). To fit these models we created a presence–absence dataset for each of our two focal species. For presence locations (response variable = 1) we used the points located by visual inspection for *C. ursinus* ($n = 511$) and *P. vitulina* ($n = 132$), respectively, and for pseudoabsence locations (response variable = 0) we used a commensurate quantity of background points randomly generated across background data. We applied spatial constraints to background data for each species, with the concern that pseudoabsences sampled from too large of a background area can yield highly accurate but uninformative models, as in the common modeling example "no polar bears live in the tropics" (VanDerWal 2009; Barve et al. 2011). As an estimate of relevant background habitat, we generated pseudoabsence points only within 2× the maximum observed distance from shore for each species (*C. ursinus*, 242.2 m; *P. vitulina*, 28.2 m). We also ensured that pseudo-absence points were not generated in cells that contained presence points for the species being considered. For all points we extracted raster values for each predictor variable or, in the case of conspecific distance at presence points, we used the "nndist" function to quantify and assign for each seal location the planar distance to its nearest neighboring conspecific.

We first explored data using generalized additive models (GAMs) because they can model response variables with non-Gaussian error distribution models, and they incorporate smoothing functions to allow the modeling of non-linear relationships that commonly occur in ecological systems, such as our dataset's cyclic 'Aspect' variable. We generated GAMs using the "mgcv" R package (Wood 2017) with a binomial error distribution and a logit link function. GAMs used the following structure:

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[1]Supplementary data are available with the article at https://doi.org/10.1139/dsa-2021-0050.

$$\text{logit}(p_i) = c + f_1(x_1) + f_2(x_2) + \ldots$$

where p is a probability parameter denoting a binary outcome of species occurrence (1) or pseudoabsence (0) with a binomial distribution given c, an estimated constant, and x_i, habitat predictor variables modified by estimated smoothing functions, f_i. All predictors were smoothed using thin plate regression splines, except 'Aspect' which was smoothed using cyclic cubic regression splines, and we used the maximum likelihood (ML) method for smoothness selection.

We generated species-specific local distribution models using partitioned *C. ursinus* and *P. vitulina* data subsets from our animal counts. We first attempted to generate models using only terrain characteristics as predictors, and then included dynamic biological predictors derived from a posteriori identified animal locations. Model residuals were tested for spatial autocorrelation using Moran's I with the "spdep" R package (Bivand and Wong 2018) and by examining semivariograms generated and modeled using the "gstat" R package (Pebesma 2004). Models that met the assumption of spatially independent residuals were subsequently backward selected according to the ad hoc criteria outlined by Wood and Augustin (2002), stepwise eliminating the term with the highest estimated *p*-value that matched all three criteria. We compared models by their ML scores instead of their generalized cross validation scores, as appropriate for our fitting method. Significance of each term in a fitted model was evaluated as its estimated *p*-value with $\alpha = 0.5$. Model selection was concluded when no remaining terms fit elimination criteria. If all terms in a selected model were estimated to be significant linear relationships (estimated degrees of freedom = 1) we then fit a generalized linear model (GLM) including only those predictors in our final model with the following structure:

$$\text{logit}(p) = c + b_1 x_1 + b_2 x_2 + \ldots$$

where p is again a probability parameter denoting a binary outcome of species occurrence (1) or pseudoabsence (0) with a binomial error distribution, given c, an estimated constant, and x_i, habitat predictor variables as selected from candidate GAMs, now modified by estimated linear coefficients, b_i. For each model and variable we calculated marginal effects of the means using the "ggpredict" function in the "ggeffects" R package (Lüdecke 2018), and we plotted these using ggplot2 (Wickham 2016).

Results

Descriptive statistics

Visual inspection of RGB and TIR imagery identified 511 northern fur seals, 132 harbor seals, and 12 Steller sea lions across the north coast haul-out areas of Otter Island and 20 additional harbor seals on the south coast (Fig. 5). Northern fur seals sprawled inland across a single haul-out field, harbor seals were generally clustered in scattered haul-out sites near the surf zone, and Steller sea lions clustered in a single thigmotactic group near the surf zone. Extracted values from derived spatial products (Fig. 4) quantitatively described habitat associations for each species (Table 1).

Candidate models

GAMs that modeled 'Probability of *P. vitulina* occurrence' and 'Probability of *C. ursinus* occurrence' in response to only terrain characteristics ('Aspect', 'Distance from shore', 'Elevation', 'Rugosity', 'Slope') yielded candidate models that were unsuitable owing to significant autocorrelation among residuals. This was confirmed in variograms of these candidate models (Figs. S1 and S2[1]), which revealed strong positive relationships between semivariance and distance between points. GAMs including both terrain characteristics

Fig. 5. Locations of hauled out pinnipeds on the north and south coast of Otter Island, detected visually using synoptic RGB and TIR imagery. Orthomosiac created using Pix4Dmapper 4.3; map created using ArcGIS Pro 2.6.1.
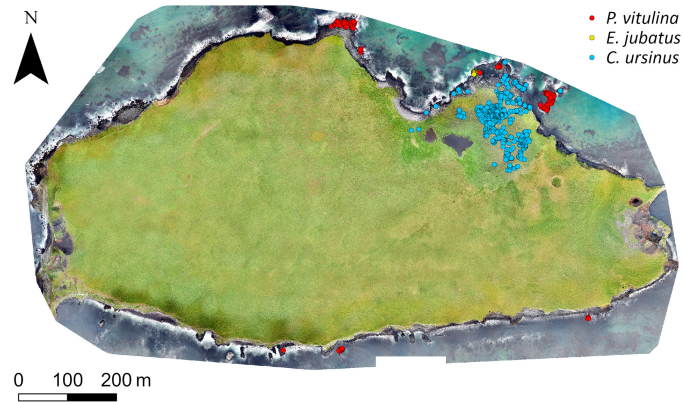

Table 1. Descriptive statistics (μ, κ for aspect, or mean ± standard deviation for all other variables) of each species identified and located in haul-out areas on Otter Island: northern fur seal (*C. ursinus*, $n = 511$), harbor seal (*P. vitulina*, $n = 132$), and Steller sea lion (*E. jubatus*, $n = 12$).

Variable	*C. ursinus*	*P. vitulina*	*E. jubatus*
Aspect	304.8°, 1.2	31.4°, 0.5	277.5°, 0.6
Distance to shore	53.2 ± 26.1 m	3.7 ± 2.8 m	3.4 ± 1.0 m
Elevation	5.4 ± 2.4 m	1.4 ± 0.5 m	2.5 ± 0.1 m
Slope	5.3 ± 4.1°	6.4 ± 4.6°	5.5 ± 2.6°
Rugosity	1.02 ± 0.04	1.08 ± 0.07 m	1.05 ± 0.09 m
C. ursinus proximity	2.0 ± 2.8 m	172.3 ± 159.0 m	43.0 ± 2.2 m
P. vitulina proximity	84.3 ± 25.9 m	2.7 ± 10.3 m	12.2 ± 0.9 m
Sky view factor*	0.99 ± 0.01	0.96 ± 0.06	0.99 ± 0.00
E. jubatus proximity*	113.9 ± 37.9 m	273.1 ± 163.6 m	1.0 ± 0.3 m

*Variables were not included in modeling: Sky view factor was excluded due to collinearity with slope, and *E. jubatus* proximity was excluded due to the species' limited presence in the landscape.

and dynamic species distributions ('*P. vitulina* proximity', '*C. ursinus* proximity') yielded suitable candidate models for 'Probability of *C. ursinus* occurrence' (92% deviance explained, ML score = 56.739) and for 'Probability of *P. vitulina* occurrence' (76.1% deviance explained, ML score = 43.661) without significant spatial autocorrelation among residuals ($p = 0.79$ and $p = 0.80$, respectively).

Selected models

Backwards stepwise selection reduced each candidate model to only significant effects, all of which were estimated to be linear relationships; from these we fitted GLMs that included only the selected variables. The final selected model describing 'Probability of *C. ursinus* occurrence' included '*C. ursinus* proximity', 'Rugosity', and 'Elevation' as significant linear predictors (Table 2), with '*C. ursinus* proximity' conferring the largest marginal effect, followed by minor effects of 'Rugosity' and 'Elevation' (Fig. 6). The final selected model describing 'Probability of *P. vitulina* occurrence' included '*P. vitulina* proximity' and 'Slope' as significant linear predictors, with '*P. vitulina* proximity' also conferring the largest marginal effect, followed by a smaller marginal effect of 'Slope' (Table 3, Fig. 7).

Table 2. Coefficients for the selected GLM of the probability of *C. ursinus* occurrence in response to terrain and conspecific distribution.

Variable	Estimated coefficient	SE	*z*-value	*p*-value
Intercept	16.29	5.38	3.03	2.46×10^{-3}
C. ursinus proximity	−0.28	0.04	−6.73	1.65×10^{-11}
Rugosity	−9.82	4.90	−2.00	4.52×10^{-2}
Elevation	−0.28	0.09	−3.04	2.34×10^{-2}

Discussion

Distributional characteristics of haul-out sites

Distribution modeling techniques at an ultra-fine scale revealed differential drivers of habitat selection and haul-out structure for non-breeding harbor seals and northern fur seals at Otter Island. Conspecific proximity positively predicted occurrence of each species more than any terrain characteristic, and both species also showed terrain affinities, with harbor seal haul-out sites associated with low terrain slope, and northern fur seal haul-out sites associated with low elevations and smooth terrain complexity. Between the species, terrain had a marginal effect on harbor seal occurrence that was orders of magnitude larger than marginal effects of elevation and rugosity observed for northern fur seal occurrence (Figs. 6 and 7).

The primacy of conspecific attraction in our models agrees with the documented importance of conspecific proximity and interactions among each species at haul-out sites. Male northern fur seals engage in a variety of social behaviors in non-breeding haul-outs that appear critical to their behavioral ontogeny (Gentry 1997). Harbor seals, by contrast, show very passive conspecific attraction, persistently grouping in an apparent antipredator strategy (Kreiber and Barrette 1984; da Silva and Terhune 1988; Godsell 1988) whose benefits accrue with group size up to about 10 individuals (Terhune 1985), though some sites continue recruiting until viable terrain is apparently saturated (Krieber and Barrette 1984).

Contrary to our fitted model (Fig. 7a, Table 3), harbor seals do not preferentially select sites at minimum distance to neighbors, but frequently show aggression to conspecifics that approach within a body-length (Sullivan 1982; Kreiber and Barrette 1984). The absence of this minimum spacing likely reflects limiting aspects of our modeling: the spatial scale of our input data, which did not resolve distances smaller than 2 m; the afield distribution of pseudoabsence points; and the penalization of 'wiggliness' used during GAM exploration, which selected toward a linear relationship between variables. A more targeted, spatially precise analysis of social structuring in haul-outs may reveal how antagonistic conspecific interactions produce patterns of individual spacing amid site selection, which are visible in imagery (Figs. 3 and 5) but not our selected models (Fig. 7).

Physical characteristics of haul-out sites

Past literature includes many qualitative descriptions of pinniped haul-out sites and their characteristics, here complemented by quantitative measurements and modeling from photogrammetric data products. Harbor seal haul-outs generally occur on near-shore substrates, including sandbanks, mudflats, gravel, glacial ice when available and rocky reefs, platforms and outcroppings (Stewart 1984; Yochem et al. 1987; Thompson 1989; Thompson et al. 1989; Reder et al. 2003; Eguchi and Harvey 2005), with a possible preference for rock substrates (Montgomery et al. 2007). Shoreline substrates on Otter Island generally consisted of rock platforms/outcroppings and cobblestone beaches, though sandy beaches

Fig. 6. Marginal effects of the mean for (*a*) *C. ursinus* proximity, (*b*) rugosity, and (*c*) elevation with 95% confidence intervals (shaded) in the selected GLM of *C. ursinus* occurrence.
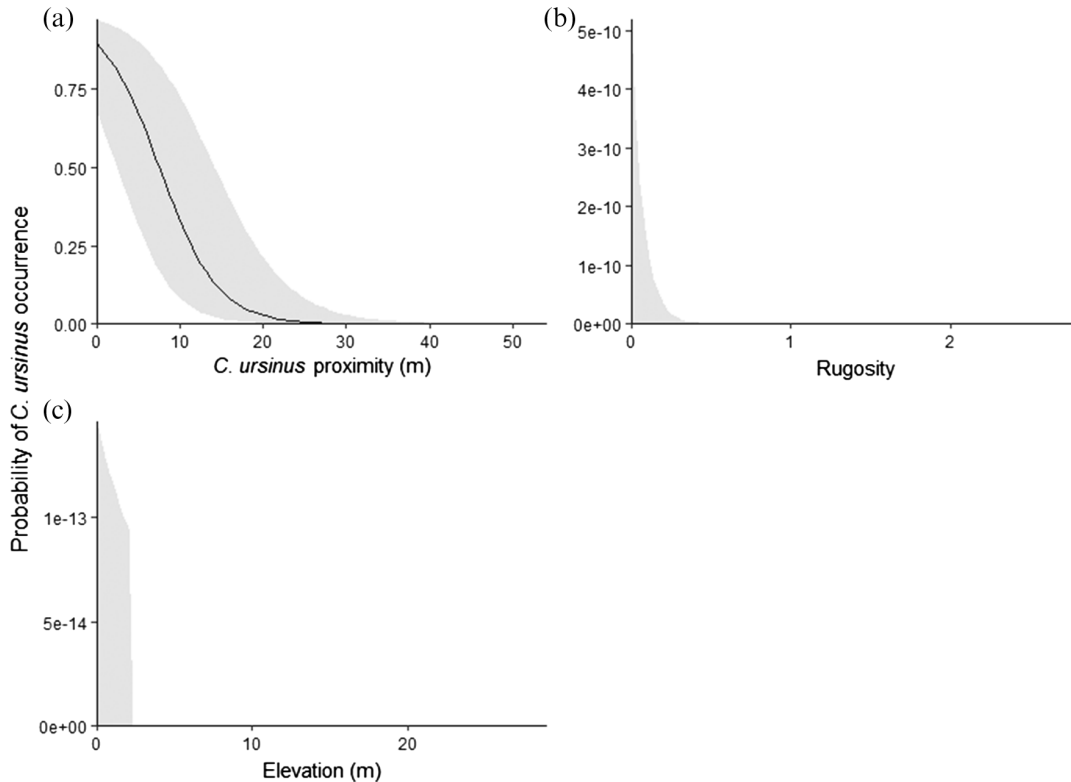

Table 3. Coefficients for the selected GLM of the probability of *P. vitulina* occurrence in response to terrain and conspecific distribution.

Variable	Estimated coefficient	SE	*z*-value	*p*-value
Intercept	3.46	0.49	7.03	2.14×10^{-12}
P. vitulina proximity	−0.13	0.04	−2.13	3.29×10^{-2}
Slope	−0.08	0.02	−5.54	3.11×10^{-8}

are found elsewhere in the Pribilof Islands. Elliott (1882) describes harbor seal haul-outs in the Pribilof Islands as "detached water-worn rocks" and "the margin of the surf-wash".

Our findings that harbor seals selected sites with low slope (6.4 ± 4.6°; Table 1) and that probability of occurrence decreases at higher slopes (Table 3) matched qualitative descriptions of harbor seals in Humboldt County, California, which preferentially selected sloping profiles that facilitate landing (Sullivan 1980). The same account describes harbor seals avoiding waves and sea spray, which was not apparent in any aspect preference in our survey ($\kappa = 0.5$), but notably the same low wind conditions that enable UAS deployment might entail low waves and sea spray.

Curiously, 'distance from shore' did not significantly predict harbor seal occurrence at Otter Island, despite the very limited and inefficient terrestrial mobility of this species (Garrett and Fish 2015) and their described preference for water-adjacent haul-out sites

Fig. 7. Marginal effects of the mean for (*a*) *P. vitulina* proximity and (*b*) slope with 95% confidence intervals (shaded) in the selected GLM of *P. vitulina* occurrence.
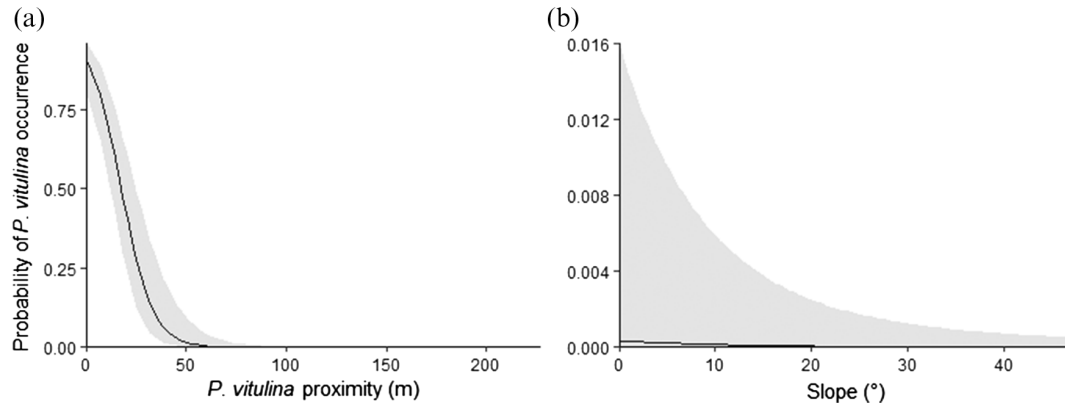
(Elliott 1882, Sullivan 1980; Terhune and Brillant 1996). But rather than a general rule of the species, this might reflect spatial context of Otter Island, where most coastline consists of steep bluffs that abut the surf zone, proximal to the water but inaccessible to harbor seals owing to steep slopes and high elevation gain. Given that *P. vitulina* pseudoabsences were generated within 28 m of the surf zone, many absences occurred on steep inclines with variable distance from shore, and inland flats were not abundant among background data; slope may therefore represent the most parsimonious if not mechanistically complete explanation of harbor seal site selection. Spatial analysis of alternative haul-out locations, such as beaches, mudflats, and other consistently low-lying coastal topographies, might better distinguish preferences and restrictions associated with phocid locomotion in the absence of slope limitations.

Notably, because terrestrial haul-out sites of harbor seals are often within or adjacent to intertidal zones, inundation of potential resting sites during high tides and storms can yield decreased harbor seal attendance. Tides were relatively high at the survey time of this study, which likely resulted in lower counts and restricted viable habitat for harbor seals. For all pinnipeds and especially phocid species, it is also likely that terrestrial site selection is influenced significantly by the adjacent marine–terrestrial interface, possibly even more so than by *in situ* topographic characteristics. Though not explored in this analysis, UAS techniques under ideal survey conditions can describe near-shore bathymetry, and special treatment of intertidal zones may be appropriate for phocid site-selection models.

Fewer accounts describe haul-out locations of northern fur seals and Steller sea lions. Rookery and haul-out sites of Steller sea lions are described as generally rocky shorelines and wave-cut platforms (Loughlin 2009), which fits the occurrence of the single cluster of Steller sea lions detected in this survey at a low-slope, low-elevation, near-shore rock outcropping (Fig. 5, Table 1). Otariids as a clade favor rock, sand or shingle beaches in exposed shorelines for breeding (Gentry 1997), which might also generally characterize non-breeding haul-out sites. Indeed, non-breeding haul-outs of northern fur seals have occasionally recruited into breeding sites (Lloyd et al. 1981; Lee et al. 2018), and conversely rookeries can degrade into non-breeding haul-outs (Gentry 1997). A recolonized rookery of northern fur seals in the South Farallon Islands, California, is described as granite, cobble, talus, and gravelly sand substrates amid a landscape of spires, slopes, and flats (Lee et al. 2018). Considering the complex social and reproductive dynamics that occur in rookeries, it would be expected that rookeries recruit to more stringent environmental criteria than

non-breeding haul-outs, so the latter may be less restricted. Elliott (1882) describes non-breeding male fur seals in the Pribilof Islands as roaming widely, as far as a mile inland, and in some sites ascending steep slopes to high elevations.

In this case of Otter Island, northern fur seal locations reveal general ranges of habitat selection extending farther inland and to higher elevations than harbor seals or Steller sea lions (Table 1), even though modeling indicated a slight preference for lower elevations (Fig. 6*c*). This might also reflect the distribution of *C. ursinus* pseudoabsences, which ranged up to 242 m inland to hilly sites where elevation, more than any other variable, may have discouraged access. Amid the topography of Otter Island, northern fur seals largely selected low-lying flats, contributing to our model's predictions toward low elevations with low rugosity (Figs. 6*b* and 6*c*).

Still, these terrain preferences are relatively trivial, for example, when compared to the marginal effect of slope on probability of *P. vitulina* occurrence (Fig. 7*b*), suggesting that terrain hardly limits northern fur seals by comparison. This finding corroborates the relative agility of fur seals, which are able to locomote quadrupedally over land—in stark contrast to harbor seals whose terrestrial locomotive movements are limited to body flexion (Garrett and Fish 2015). Given that our ROI consisted largely of terrain accessible to fur seal locomotion by one route or another, it is possible that analysis covering a greater diversity of northern fur seal haul-outs and adjacent boundaries might better capture the range and limits of northern fur seal occupancy amid the prevailing influence of conspecific attraction.

Additional possible predictors

Selected models for both harbor seals and northern fur seals did not retain any terms to account for interspecific exclusion; this was surprising given the apparent segregation that occurred between harbor seal haul-out regions and the northern fur seal haul-out region along the north coast (Fig. 5), and past reports of harbor seals avoiding sites frequently disturbed by sympatric otariids (Sullivan 1980). In the setting of Otter Island, however, many northern fur seals occupied an inland field that was generally inaccessible to harbor seal locomotion. Additionally, our model did not differentiate persistent and ephemeral animal presence, and some northern fur seals were recorded in close proximity to hauled out harbor seals, even though they appeared to be active in the surf zone and not necessarily a persistent presence. Sampling from a greater diversity of haul-out sites and sustained observations over time might therefore reveal interspecific influences not evident in this instantial UAS survey.

Other temporally dynamic factors could also influence haul-out composition in ways not represented in a single record of imagery. Both harbor seals and northern fur seals show high site fidelity—though non-breeding male fur seals do move between preferred haul-out sites—and conspecific recruitment can occur throughout their multi-day haul-out durations (Yochem et al. 1987; Gentry 1997). It is therefore likely that prior site occupation is a predictor of future site occupation across scales of days and potentially years. For this reason, both conspecific and interspecific dynamics might better be modeled through time-lagged components from surveys across multiple visits rather than a single survey's summary. Sustained observations across time could also capture the local importance of dynamic environmental and circumstantial variables such as weather, diel cycle, and seasonality, all of which are known to influence northern fur seal attendance (Gentry 1997), and tides, which affect harbor seal site attendance (Stewart 1984; Watts 1996; Simpkins et al. 2003). Consequently, the models of this analysis are most specifically applicable to the conditions under which our survey took place and may not necessarily generalize to different circumstances that might motivate differential uses of the landscape for purposes such as

behavioral thermoregulation. Additionally, distributional modeling is a scale-sensitive technique, and it is possible that variables smoothed or resampled to coarser resolutions would highlight different relationships at landscape scales. This reason therefore qualifies our findings to the spatial scale of our analysis—approximately that of individual adult pinnipeds.

Disturbance represents a major site-specific driver that, presently absent on Otter Island, could critically influence haul-outs threatened by humans and other predators. Anthropogenic disturbance can cause harbor seals to avoid locations (Sullivan 1980; Allen et al. 1984; Montgomery et al. 2007) or shift their diel activity (London et al. 2012)—or, alternatively, cause no discernible effects at all (Renouf et al. 1981). Occasional anthropogenic disturbance is thought to minimally affect northern fur seal site selection, since many sealing grounds remained occupied through two centuries of regular disturbance and mortality (Gentry 1997), but chronic removal did appear to induce abandonment of Otter Island by northern fur seals in the 19th and early 20th centuries (Hanna 2008). Periodic or infrequent anthropogenic disturbance, therefore, represents an unlikely driver of northern fur seal haul-out selection or avoidance, but site abandonment remains possible in response to higher frequencies and intensities of disturbance. Additionally, reduced densities in a declining population could reveal sensitivities once masked by high-density effects, like the conspecific attractions that we observed.

Limitations and future applications

For both species, selected models did not retain some terms that are generally known to be biologically important for the species; for example, the importance of elevation and distance from shore were not evident in our selected model of harbor seal locations, despite the species' limited mobility and flight-ready disposition. Such findings illustrate limitations of our modeling approach, where finite presence data and choice of pseudoabsence data can constrain the possible outcomes of model selection. Although we checked all variables for collinearity, cooccurrence of habitat variables at localized regions or scales could obscure nuanced effects, especially in a linear model structure. Wider sampling of haul-out sites across a variety of locations would better capture the plasticity and limitations of pinniped terrestrial habitat use for model training; diverse selections of background or pseudoabsence locations might discriminate further conditions of unsuitable habitat; and, conversely, more constrained pseudoabsences could describe topographic preferences within the aggregating influences of conspecific attraction. The models described in this paper, while informative, are one of many analytical interpretations possible for such fine-scale spatial data.

Beyond the scope of this dataset, repeat surveys spanning a variety of diel and seasonal conditions would provide more complete and robust characterizations of pinniped habitat preferences and limitations at Otter Island and similar sites. Surveys of additional non-breeding haul-out sites would be necessary to further describe pinniped–habitat relationships at the scale of species traits. Critically, the patterns described by this analysis unfold only within the greater context of distribution and abundance at a population scale, where haul-out and rookery sites are chiefly selected according to basal organismal needs that are generally determined by their marine context, such as forage availability, thermal tolerance, and predator avoidance (Gentry 1997; Montgomery et al. 2007; Liwanag 2010). But nested within these patterns, local dynamics determine how coarse changes manifest through patterns of individual behaviors within a landscape. As large-scale population trends unfold through survival, mortality, immigration and emigration, fine-scale spatial analyses can inform how individual habitat selections scale into herd dynamics and population trends across regional habitat gradients.

Conclusion

Ever finer scales of remote sensing data are creating new opportunities to characterize species abundances and distributions at the level of individual organisms and their behaviors. In the example of this study, models of distributed pinnipeds across haul-out habitats on Otter Island revealed key specific insights that harbor seal and northern fur seal distributions are each shaped primarily by conspecific attractions and secondarily by terrain associations, with greater terrain limitations for harbor seals than fur seals. Our findings corroborate many qualitative descriptions of these sentinel species, but critically establish quantitative characterizations and statistical insights that can inform observed distributions and habitat selection of these dynamic populations. Amid drastic biogeographic shifts in the Bering Sea ecosystem and others worldwide, such insights from emerging remote sensing techniques will establish further context for observed changes, informing species monitoring and management strategies, and bridging new scales of spatial ecology.

Competing interests

The authors declare there are no competing interests.

Contributors

ELR, LMD, EEM, JML, and DWJ conceptualized and administered the study design. ACS, EN and DWJ planned the field operations and methodology, and ACS, ELR, LMD, EEM, EN, and JML conducted the investigation. GDL and DWJ designed the formal analysis, which GDL conducted. GDL curated, visualized, and interpreted the data, under supervision of DWJ. GDL wrote the manuscript's original draft, which all authors reviewed, commented on, and approved the final version.

Data availability

Drone imagery, flight logs, and spatial data products used in this analysis—orthomosaics, digital surface models, derived habitat variables, and seal locations—are available at the Duke Research Data Repository: https://doi.org/10.7924/r4833xs44.

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Appendix A: UAS imagery and collection

UAS flights were conducted using senseFly (Cheseaux-sur-Lausanne, Switzerland) eBee Plus fixed-wing small UAS with a S.O.D.A. sensor (5472 pixels × 3648 pixels, shutter speed 1/1000, aperture f/2.8, ISO 100–800) measuring reflectance in digital red, green, and blue bands (RGB) or a ThermoMap sensor (640 pixels × 512 pixels, spectral bandwidth 7.5–13.5 nm, thermal resolution 0.1–0.2 °C) measuring a thermal infrared band (TIR). Sensors were always located at ~5° off-nadir, relative to the aircraft. Owing to limitations of thermal photography, TIR was collected at a much lower GSD than RGB. Surveys entailed either a single eBee collecting only RGB data or two eBees flown in a synoptic flight pattern at deconflicted altitudes, such that TIR and RGB sensors captured the same regions nearly synchronously. Flights were planned to achieve targets of >90% longitudinal overlap and 65%–80% latitudinal overlap between adjacent images, depending on sensor and flight objective.

Field sites were accessed by Zodiac without disturbing pinniped haul-outs, and drones were launched by hand from grassy terrestrial launch-and-recovery zones away from the haul-outs. Surveys were planned and executed using eMotion flight control software on a laptop ground control station. Flight plans consisted of parallel, overlapping transects along each region's shortest axis—to minimize possible animal movement between adjacent photographs—repeating for the extent of the survey's target area. All synoptic transects were spaced 27 m apart, yielding estimated overlaps of >95% longitudinal, 70% lateral between TIR images and 90% longitudinal, 80% lateral between RGB images; TIR was collected at 14 cm target GSD from 75 m altitude, estimated above reference elevation data, and RGB was collected at 2.35 cm target GSD from 100 m altitude. The complete survey of Otter Island yielded estimated overlaps of 90% longitudinal, 65% lateral between its RGB images; RGB was collected at 2.75 cm target GSD from 117 m altitude. Images, UAS position, and system data were collected and stored in removable memory aboard the aircraft during each flight; position and system data were also telemetered to the ground control station over VHF where they were actively monitored and logged. Surveys were carried out on 3 September under amenable flight conditions that entailed winds <32 km/h, clear visibility >4.8 km and no precipitation. Mapping flights took place during 1405–1441 and 1451–1508 AKDT, south coast ROI survey flights took place during 1524–1543 AKDT, and

north coast ROI survey flights took place during 1601–1619 AKDT. Tide data were obtained from the tide gauge at Village Cove on St. Paul Island, NOAA Station ID 9464212.

Appendix B: Orthomosaic and DSM processing, editing, and alignment

Orthomosaics and DSMs were generated in Pix4Dmapper 4.3, using a standard "3D Maps" workflow with the "alternative" image calibration option and "geometrically verified matching" strategy for matching image pairs. All DSMs were generated using smoothing and noise filtering, and from those models the orthomosaics were derived. Images from all surveys on Otter Island were pooled to create the RGB orthomosaic and DSM of the entire island.

During orthomosaic creation, inconsistencies between adjacent images such as moving animals can produce a 'ghost effect' where moving features appear blurry or transparent; however, this can be eliminated by manual editing in the Pix4D software to define specific images to use in target regions of the orthomosaic. Therefore, for each synoptic survey dataset, we manually edited both RGB and thermal orthomosaics to ensure that, wherever animals occurred, they were described by only a single image at a time; and to further reduce inconsistencies in animal positions between our synoptic orthomosaics, we verified timestamps between collocated RGB and thermal images as we edited each orthomosaic, ensuring that each animal's position was described by thermal and RGB images that were taken within seconds of one-another, as close as possible without compromising image quality. For this process, animals were identified based on shape and color in the RGB orthomosaic, heat in the thermal orthomosaic, or a combination thereof as both orthomosaics were being reviewed and edited in tandem.

Once orthomosaics had been generated and cleaned of 'ghost effects,' we coregistered each thermal spatial index orthomosaic to its synoptic RGB orthomosaic using ArcGIS Pro 2.6.1 using manual control points that could be identified in both spatial data products (as many as could be identified to achieve a satisfactory warp), and warped using a first- or second-order polynomial transformation (the lowest order necessary to achieve a satisfactory warp); satisfactory warp was determined by visual inspection of conspicuous terrestrial habitat features when the two products were overlaid, and corresponded to post-warp RMSE values of ≤ 0.20 in each case. This coregistration yielded paired color and thermal spatial products that were aligned as closely as possible according to terrain features to describe animal locations in the same spatial and temporal frames. When necessary during the counting process, original, not-mosaicked photographs were reviewed to confirm animals that may have been obscured by motion or omitted at the margins of the mosaicking process.

Digital surface models were examined for obvious systematic errors in ArcGis Pro by placing line features along the top of the surf-zone at gradually inclined beaches around the island and extracting elevation values. In the DSM from the north coast survey there was a clear bias of higher elevation values correlating with eastward locations along the surf line, indicating a systematic error in the DSM product—possibly the 'bowling/doming effect' that commonly occurs during elevation model construction from mapping by parallel UAS transects (James and Robson 2014). The full-island DSM product showed low and spatially heterogeneous variability in surf-zone elevation estimates (2.95 ± 0.59 m, mean ± standard deviation), suggesting the absence of this systematic error. Inland regions were not evaluated for DSM accuracy because there were no ground control points or other known elevation data beyond the surf-zone. We standardized our DSM's elevation estimates to NAVD88 by subtracting 2.19 m from each cell, this being the difference between

our mean surf-zone elevation estimate (2.95 m) and the mean tidal height above NAVD88 on Saint Paul during our mapping survey (0.76 m).

Appendix C: GIS processing of terrain products

The 2 m downsampled DSM was treated as the variable 'Elevation', disregarding the vertical contribution of vegetation at inland sites (≤0.5 m) for this and all derived variables. 'Distance from shore' was generated as surface distance between each cell and a coastline feature at the tidal height at time of survey, accounting for elevation using the "distance accumulation" tool in ArcGIS. The variables 'Slope', and 'Aspect' were generated using their respective tools in ArcGIS, and 'Rugosity' was calculated as the arc–chord ratio—an index of topographic complexity that is decoupled from slope (Du Preez 2015)—by taking the ratio of each 2 m cell's summed surface area (calculated at the DSM's original GSD) to the cell's planar area at 2 m.