Habitat Suitability Modeling for
Western Snowy Plover
in Central California

Beau MacDonald • Travis Longcore • Shawna Dark
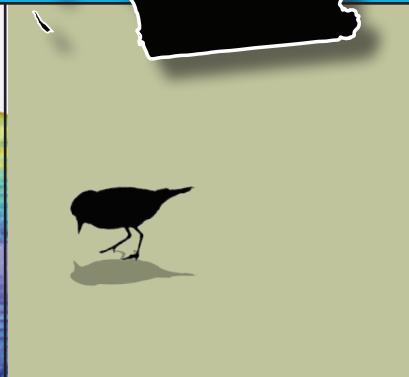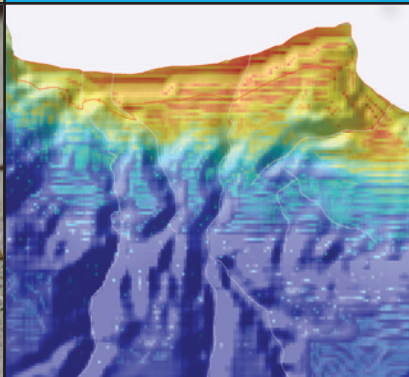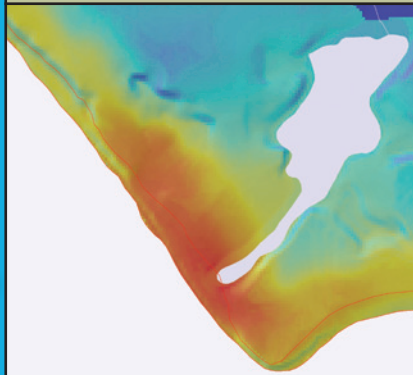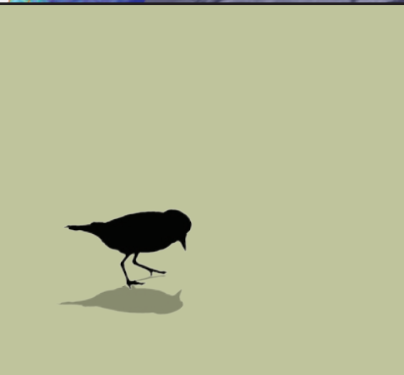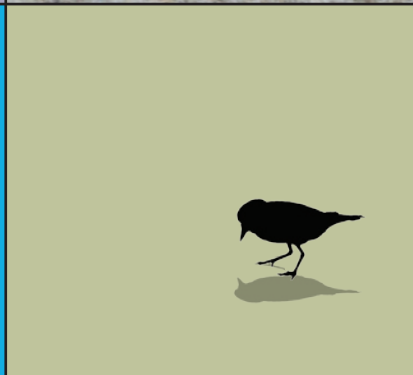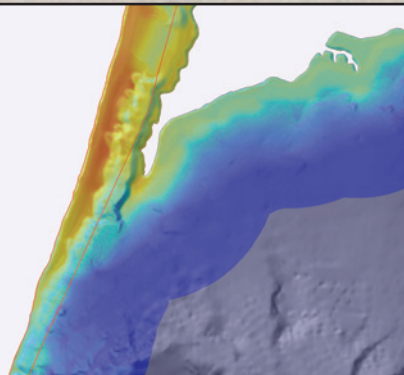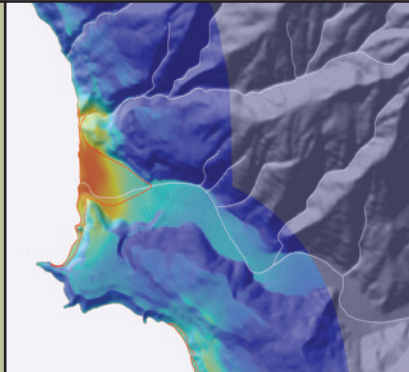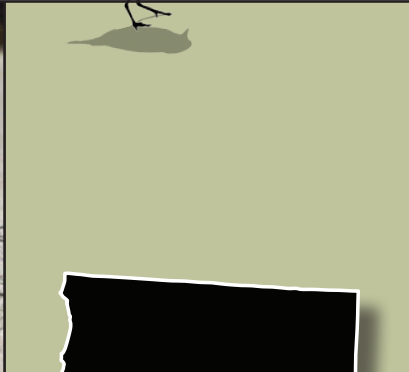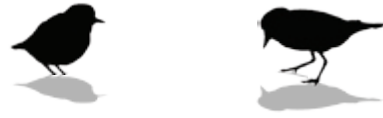
Habitat Suitability Modeling for
Western Snowy Plover
in Central California

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ACKNOWLEDGMENTS

Cover photos: Larry Wan

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EXECUTIVE SUMMARY

The Pacific coast population of Western Snowy Plovers *(Charadrius alexandrinus nivosus)* is a federally listed threatened species, having experienced significant and pervasive population declines within its range in California, Oregon, and Washington.

Recovery of the species depends on the effective use of management resources because human-associated disturbance is a key factor in reducing or eliminating nesting habitat. Within the large extensive tracts of potential habitat, managers must decide where to pursue conservation actions and weigh the benefits of those actions against the costs of implementation. Geographic Information Systems (GIS)-based predictive habitat modeling is an approach that can identify and rank nesting habitats for Western Snowy Plover. We implemented a series of habitat models for the central coast of California (Recovery Unit 5 in the U.S. Fish and Wildlife Service Recovery Plan for the species).

Recovery Unit 5 (RU5) encompasses roughly 700 km of coastline in San Luis Obispo, Santa Barbara, and Ventura counties. It has remarkable geographic diversity, with predominantly west-facing beaches in San Luis Obispo County and south-facing beaches in much of Santa Barbara and Ventura Counties. The recovery unit also includes the northern California Channel Islands of San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, and San Nicolas. An average of 1,000 Western Snowy Plovers nest in RU5, which is approximately half of the population of the Pacific Coast. A broad array of management actions is taken for Western Snowy Plover in RU5, ranging from nothing to intensive management.

We took two approaches to develop habitat suitability models for Western Snowy Plover. The first is a deductive method, where environmental variables to predict habitat were selected based on the existing scientific literature and its description of the habitat preferences of the species. Such preferred habitat includes sand spits, dune-backed beaches, estuary and lagoon salt pans, beaches at creek and river mouths, bluff-backed beaches, dry salt ponds, and sand and gravel bars in rivers.

We consulted the literature to identify variables that could best describe optimal habitats, with our final models including elevation; slope gradient; distance from the coast; distance from streams and estuaries; distance from major rivers; landward boundary (e.g. dune, bluff); beach substrate (e.g. sand, gravel); beach width plus adjacent sand dunes/river sand bars; wave height; wind speed; and air/sea temperature. We intentionally excluded vegetation, presence of beach wrack, and other factors that could be influenced by management. Data were obtained or calculated from existing sources or developed for this purpose from remotely sensed information (e.g., description of landward boundary, beach width, and beach substrate from aerial photography). The continuous variables were standardized using fuzzy-logic linear or nonlinear functions with inflection points based on recorded species' preferences before being used in the deductive models. Habitat suitability models were calculated from the continuous and categorical variables using Idrisi multi-criteria evaluation procedures.

Inductive models are built from species occurrence data and the modeling procedure selects

RU5 CA-88
Coal Oil Point Reserve
Santa Barbara County

Deductive Model
Pacific Coast WSP
Habitat Suitability

Predicted Habitat
Suitability Value

High : 0.962

Low : 0.000

WSP nests recorded
- 2004
- 2003
- 2002

WSP survey sites
CA-88: 882

UCSB
Coal Oil
Point

UC
Natural
Reserve
System

1:10,000

RU5 CA-80
Morro Strand/
Atascadero Beach
San Luis Obispo County

Deductive Model
Pacific Coast WSP
Habitat Suitability

Predicted Habitat
Suitability Value

High : 0.947

Low : 0.000

WSP nests recorded
- 2006
- 2005
- 2003

WSP survey sites
CA-80: 801, 802

Morro Strand
State Beach

California
State Parks

Morro Rock
City Beach

City of Morro Bay

1:22,500

those environmental variables and their values that best predict existing occurrences to extrapolate to potential habitat. We used nest site data obtained from beach managers to run the Maxent model with the same environmental variables as our deductive models, while keeping some nest site data aside to check the accuracy of the predictions.

Our deductive habitat models were also tested using nest site data and performed well. Beaches identified in the Recovery Plan as recovery sites encompassed high habitat suitability values as would be expected. For most beaches, our habitat suitability values for nest sites were statistically greater than at non-nest sites within recovery beaches. In instances where this was not true, a lack of management at high suitability value areas was the obvious and overwhelming explanation. For example, at Coal Oil Point in Santa Barbara County, which is intensively managed for Western Snowy Plovers, nest sites are concentrated in areas with high suitability values *(Figure ES-1)*. By contrast, nest sites on the Morro Bay Strand in San Luis Obispo County are also found at some locations with high habitat suitability values, but are conspicuously absent from others *(Figure ES-2)*. This reflects the different patterns of ownership and associated level of management.

FIGURE ES-1 (TOP LEFT). Western Snowy Plover nest sites recorded at Coal Oil Point, Santa Barbara County. Nests are located at sites with higher habitat suitability values than sites without nests, even though lower value sites are also managed for plovers.

FIGURE ES-2 (LEFT). Western Snowy Plover nest sites recorded along Morro Strand. With uneven management effort, nest sites are located in high suitability sites within managed areas, but also within lower habitat suitability sites that are intensively managed. Sites without management, despite having high suitability values defined by physical variables in the model, are not used for nesting.

Our inductive models were not as useful. They returned high suitability values for areas with nest site data, but did not return generalized rules that were able to extrapolate such high values to areas with known high habitat value but no nest point data.

We conclude a deductive approach provides a number of advantages for conservation planning in a heavily human-dominated landscape, even though it does depend on the existence of a well-developed natural history for the species in question. With this information, however, it can extrapolate the ideal conditions to locations where the species is no longer present and indeed is useful for identifying locations that would be excellent habitat if appropriate management were undertaken. Such sites are simply not ranked highly by inductive models when the training data are geographically clustered and the actual potential range is large.

Our model results should be useful for identifying, accurately delimiting, and assessing critical habitat for the species within RU5. Our deductive model gives gradations of habitat suitability within (and outside) existing recovery sites that might be used both to concentrate efforts within those sites and to reconfigure them during future recovery planning efforts.

By comparing the models that we developed with existing survey data we provide convincing evidence that many sites are indeed nesting habitat for western snowy plover, but it is only ongoing beach disturbance that consistently and chronically interferes with nesting. The model results, validated by the nest site and historic data, provide the basis for strong argument that "take," as defined under the Endangered Species Act, is regularly occurring at high habitat suitability value sites that have wintering populations of Western Snowy Plovers but are not managed for the species.

PHOTO BY CALLIE BOWDISH

Western Snowy Plovers *(Charadrius alexandrinus nivosus)* have declined significantly as a breeding species on the Pacific coast since the 1970s (Page et al. 1991). Although they exhibit high site tenacity, human disturbance and predators (both native and exotic) have contributed to a reduced breeding range (Page et al. 1995; Lafferty 2001), leading to the listing of the Pacific coast population segment (Pacific Coast Western Snowy Plover) as Threatened under the Endangered Species Act in 1993. Since that time, numerous grass-roots and agency efforts have been undertaken to protect snowy plover breeding habitat through management actions, including symbolic fencing, docents, predator control, and other efforts to reduce disturbance and predation (e.g., Page et al. 1995; Lafferty 2001).

The recovery plan for Western Snowy Plover, issued as a draft in 2001 and finalized in 2007, provides many recommendations for the conservation of the species (USFWS, U.S. Fish and Wildlife Service 2001, 2007a). In particular, the recovery plan lists many actions to be taken to enhance breeding sites, including five techniques to reduce predation, six ways to reduce impacts of pedestrians, and five other methods to reduce various types of

disturbance. Although it is not likely that any one action will be most effective at all sites, research could provide guidance about which management actions are associated with increases in population size or distribution. In 1995, management actions were considered too recent to have shown effects on populations (Page et al. 1995). Sufficient time has now passed to document the benefits of reducing human disturbance (Lafferty 2001; Ruhlen et al. 2003; Lafferty et al. 2006), banning dogs (Lafferty et al. 2006), predator exclusion (Koenen et al. 1996; Lauten et al. 2004; Neuman et al. 2004; Hardy and Colwell 2008), and other techniques at individual sites.

The recovery plan also prescribes ongoing monitoring of the species, and recommends improvement of methods to monitor plover population size. The development of improved techniques to map plover breeding habitat and determination of its essential biophysical features are also listed as recovery tasks. Determination of these biophysical features is also necessary to assess the effects of any management scheme — the right management in the wrong location will yield far fewer benefits than in the right location.

The purpose of this study is to provide a tool that will help managers and other researchers better manage the Western Snowy Plover in Recovery Unit 5, located in central California. Our primary goal was to develop a habitat suitability model for the Western Snowy Plover that would allow for an examination of the species' current and potential distribution given appropriate management actions. The specific objectives of this study were:

- To create and validate a habitat suitability model based on the physical characteristics of the landscape that documents the potential and historical habitat for the Western Snowy Plover.

- To create and validate a habitat suitability model based on the known presence of the Western Snowy Plover.

- To compare the above two models in an attempt to identify why the Western Snowy Plover is not found at locations where the physical environment is suitable.

- To identify potential management actions that may improve the overall distribution and population size of the Western Snowy Plover.

In this report, we discuss the two types of habitat suitability models developed for the Western Snowy Plover in Recovery Unit 5. The results of this study are likely to provide insight into refined population monitoring and management techniques. With the adoption of such techniques, future monitoring efforts will allow analyses and conclusions not possible with the current monitoring schemes. The results of this investigation will also inform the ongoing public debate about the efficacy of the recreational restrictions that have been imposed at public beaches for the protection of Western Snowy Plovers.

This report is divided into several sections. The introduction provides an overview of habitat suitability modeling and a general literature review of Western Snowy Plover habitat, breeding, and conservation. An understanding of how these models function and the differences between inductive and deductive models is essential for a robust interpretation of the model outcomes. In addition, both models rely on pre-existing information about snowy plovers. As such, a review of the ecology and conservation issues of this species will provide a background within which to evaluate the modeling process and provide proper inferences of the model results to the species.

A detailed outline of the methodology used to model suitable habitat for the Western Snowy Plover is presented next. This section discusses uncertainties and limitations inherent to models; the acquisition and quality assurance process for the species-occurrence data; and methods used to select and prepare sets of environmental variables required for both types of habitat suitability models. Specific deductive and inductive approaches are explained, followed by a review of the statistical methods used to evaluate and compare models.

Results are given first for deductive models, and then inductive models. Models are evaluated and compared based on their ability to achieve the stated objectives of this study. Predicted habitat suitability values are shown as tabular data and graphically as charts and maps. Maps include the full Recovery Unit 5 coastline and individual sites identified as known, potential, or historical habitat; beach names at sites and subsites are derived from established conventions. To facilitate the interpretation and discussion of the results, they are arranged geographically, north to south, and implications associated with outcome of the habitat suitability models at any particular location are placed with the maps. We present our conclusions in a final section.

1.1 HABITAT SUITABILITY MODELING

Species distribution modeling, also referred to as ecological or environmental niche-based modeling, and as habitat suitability modeling, has become fundamental to theoretical and applied biogeographical research (Araújo and Guisan 2006). These models are utilized in allied disciplines such as ecology, conservation biology, evolutionary biology, paleoecology, and wildlife and ecosystem management (Guisan and Thuiller 2005; Wiens and Graham 2005; Elith and Leathwick 2009). In conservation biogeography, as in other research, models are created to investigate and synthesize data, and to analyze and predict complex relationships (Whittaker et al. 2005). Models are inherently abstract and uncertainty is a given condition (Fielding and Bell 1997; Araújo et al. 2005; Barry and Elith 2006; Pearson et al. 2006). Within the contributing disciplines and throughout the modeling literature, inconsistent uses of not-necessarily-conventional terms are encountered and expected (Corsi et al. 2002; Araújo and Guisan 2006; Kearney 2006; Soberón 2007). For example, depending on context, there are multiple interrelated and specific meanings for "scale," "species," "environment," "niche," and "habitat."

Quantifying habitat quality is important for conservation and management of wildlife populations and natural resources. Since the early 1980s, habitat suitability models have been used to evaluate wildlife habitat and the effects of management activities and land-use change (Schamberger et al. 1982; Verner et al. 1986). Functions describing resource selection statistically connected biological survey data to environmental variables, with resulting estimates of patterns of biodiversity at species, community, and ecosystem levels (Boyce et al. 2002; Ferrier et al. 2002). Models (e.g., Morrison et al. 1987; Buckland and Elston 1993; Akçakaya et al. 1995; Milsom et al. 2000; Lindenmayer et al. 2001) informed wildlife managers and conservation planners. Species distribution models as tools evolved and received greater recognition (Shaf-

fer 1997; Guisan and Zimmerman 2000; Scott et al. 2002). New modeling techniques were developed and evaluated (Austin 2002; Busby 2002; O'Connor 2002), refined (Engler 2004; Graham et al. 2004), and reevaluated (Rushton et al. 2004; Guisan et al. 2006; Hirzel et al. 2006; Austin 2007). Development and testing of more powerful, accurate, and versatile models (Elith and Graham et al. 2006; Phillips et al. 2009), along with innovative interdisciplinary applications, has intensified to respond to conservation challenges.

The basic concept underlying these models is the ecological niche (Grinnell 1917): each species is found within specific ranges of environmental variables, enabling individuals to survive and reproduce. Values of niche variables (e.g., herbaceous canopy cover, climate, elevation, etc.) are related to the habitat quality for a given species on a suitability scale from 0 = "not habitat" to 1 = "habitat of maximum suitability." Habitat Suitability Index (HSI) scores (also referred to as habitat suitability values, or HSV), also on a 0–1 scale, are usually calculated using a mathematical formula representing hypothesized relationships among the individual variables. Wildlife–habitat relationships may be supported by empirical data, expert opinion, or both (Van Horne 2002; Johnson and Gillingham 2004).

Advances in our understanding of these relationships, especially at landscape or regional scales, have been concurrent with geographic information system developments. Now that geographic information system (GIS) software and high-speed computer hardware are widely available, the use of habitat suitability models among biologists is increasing. In addition to providing a powerful analytical tool, GIS technology allows land and wildlife managers to utilize novel sources of land cover, vegetation, and other habitat data, namely remote imagery from aerial photographs and satellite sensors and GIS databases of elevation, surface water, climate data, and ecological land types.

To build a habitat suitability model either the deductive or the inductive approach may be adopted *(Figure 1)*. In the deductive approach, habitat–species relationships are drawn from expert knowledge. In the inductive approach, instead, relationships are generalized from a sample of observations where species' presence or abundance is matched with specific or estimated values of the environmental variables at corresponding locations (Boone and Krohn 1999; Corsi et al. 2000). The correct approach strictly depends on the availability of data on the species' occurrence (Stockwell and Peters 1999; Brotons et al. 2004). Data availability is a major constraint in building large-scale models of species distribution (Osborne et al. 2001). Inductive modeling is a "data-hungry" approach that requires a large amount of optimally-assessed information to be able to predict species occurrence (Hirzel and Guisan 2002).

According to ecological niche theory (Hutchinson 1957), each species depends on the existence of a specific set of environmental conditions for its long-term survival. This concept refers to not only the abiotic physical environment but also to biotic factors of the respective ecosystem determining resource abundance as well as trophic chain interactions. As a consequence of such biotic interactions (competition, predation), but also because of geographic barriers to dispersal and colonization, as well as anthropogenic pressures, species in reality never fully occupy their fundamental niche, i.e. the ecological-geographical space that meets their requirements (Anderson et al. 2003; Soberón and Peterson 2005). Instead, a species almost always occupies a subset of its fundamental niche only, called the realized niche (Brown and Lomolino 1998).

The main implication for species distribution modeling is that occurrence records by definition can only be sampled from the realized niche. Therefore, predicted results for the inductive modeling approach tend to underestimate the "potential" distribution (Phillips et al. 2006). Two key factors determine the degree to which observed localities can be used to estimate the niche or distribution (Pearson et al. 2006; Pearson 2007). First, is the species present in all suitable areas, and absent where conditions are not suitable? This is sometimes referred to as being at equilibrium, and both the dispersal ability of the species and competitive exclusion can affect

FIGURE 1. Flow chart documenting the general modeling process for both inductive and deductive habitat suitability models.
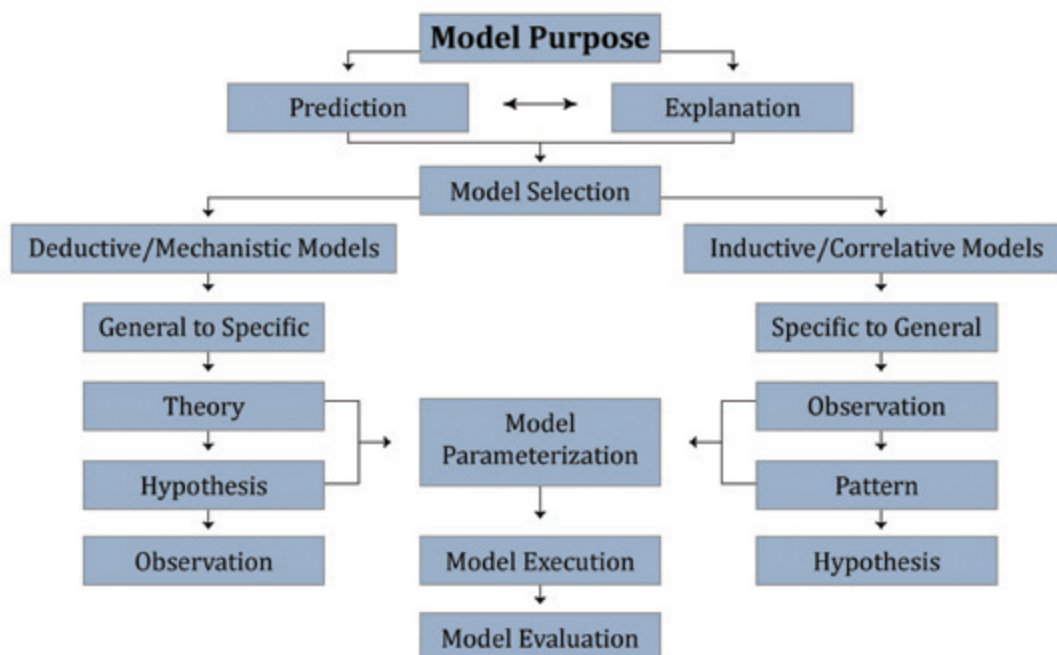
this. Next, do recorded species' presences provide an adequate sample of the environmental space it occupies? If the occurrence records used to build a correlative species' distribution model do not provide useful data as to the species' environmental requirements, "garbage in, garbage out" applies: the model cannot provide useful output. If both conditions are true, the model will make an excellent prediction; if both are false, model results must be (at best) cautiously interpreted. We need both types of information to model the intersection of environmental space with geographical space.

On the contrary, when the information available comes from a miscellany of sources (e.g., small samples, non-regular and non-spatially-stratified sample designs, samples collected according to an irregular time scale), the deductive approach is the only reliable choice. This approach is particularly useful to model rare species, species with low detectability, or common species scarcely studied, so it is particularly suitable for biodiversity assessment (Ottaviani et al. 2004; Pearce and Boyce 2006). Instead of using known observation of the species, deductive models rely on its defined biological and ecological requirements to generate predictions regarding its suitable habitat. Requirements are derived from the literature and/or expert opinions which are translated into values and rules that describe the relationships between the species and a number of environmental variables (e.g., land use, surface water, vegetation, elevation, etc.). These relationships are then applied to GIS data layers resulting in an overall estimate of habitat suitability within a defined geographic area of interest.

Deductive models are cost-effective and extremely useful when location data are not sufficient in quality (e.g., due to age, non-random sampling, or accuracy) or quantity (Corsi et al. 2000; Guisan and Zimmerman 2000; Stockwell and Peterson 2002a, 2002b). Although expert-based models often are the best and sometimes the only information available to develop, assess, and meet conservation and management objectives, they

too can result in an over or underestimation of a species' actual distribution. If the defined model values and rules do not accurately reflect the auto-ecology of the species, model results may poorly represent reality (Guisan et al. 2007), as will models with variables that do not actually influence the distribution of the species but are included because we do not have knowledge suggesting likewise. Models with these constraints must be validated intensely.

If ecological or environmental variables are badly chosen, or if critical data are omitted, any model can be adversely affected; a proxy variable may be needed for unavailable data. Selection of a spatial scale to match the intended analysis with data available, species' ecology, and environmental processes is crucial (Huston 2002; Hartley and Kunin 2003). Data must be a reasonable interpretation of true conditions. When landscape mosaics or environmental gradients are constrained to homogeneous patches, habitat structure is poorly represented (Kristan 2003) and predictive ability of a model will be compromised, whatever the goal. Spatial autocorrelation of ecological variables (Legendre 1993) can affect either model type, not only those that incorporate occurrence data (Segurado et al. 2006; Dormann et al. 2007). Autologistic methods that incorporate a spatial component or methods that otherwise explicitly address bias or autocorrelation may also produce models whose accuracy is less affected by particular ecological traits (Segurado and Araújo 2004).

McPherson and Jetz (2007) found three (of 13) ecological traits had the most influence on avian species' distribution models, as assessed with both logistic and autologistic models. Accuracy was significantly lower for species with a wide range; for migrants rather than non-migrants; and for those with an affinity for wetlands. All three characteristics apply to Western Snowy Plover. However, their models were done at a coarse-resolution continental scale; they noted that methodological factors did not capture anthropogenically-modified habitat or wetlands well; and their analysis indicated the influence of

these variables would not prevent the creation of reasonably accurate models. Our models used higher-resolution data that more accurately represented environmental conditions available. Guisan et al. (2007) tested whether species' traits affected the performance of species' distribution models and found that models varied more by species than among techniques: species with narrow and specialized niches tended to be better modeled. Tsoar et al. (2007) reported similar results for birds. Trials of particular techniques for modeling species' distribution and assessments of the variability of their predictions have been extensive (e.g., Elith and Graham et al. 2006; Pearson et al. 2006; Elith and Graham 2009).

For this study, we chose to use both the deductive and inductive modeling approaches. While data from nest and window surveys (a snapshot of abundance taken during a particular survey "window") are available for the Pacific Coast population of Western Snowy Plover, the data are not collected in a consistent and random framework that is best suitable for a quantitatively rigorous modeling approach such as the inductive modeling process. By using both modeling approaches, we were able to examine the differences between the two models, validate the models, and examine the most appropriate modeling approach for our objectives. Both approaches will be described in more detail in the methods section.

1.2 WESTERN SNOWY PLOVER

Snowy plovers *(Charadrius alexandrinus)* are very small shorebirds with a cosmopolitan distribution; their total range of 1,000,000–10,000,000 km² is comparable with other migratory waterbirds (BI, BirdLife International 2008). Over each of the past five decades, the species has experienced population declines of 10%–30%. Abundance is approximated because few well-monitored populations exist outside North America and Europe. Estimates were 586,000 birds in the late 1990s (Morrison et al. 2001) and

280,000–460,000 birds in 2002 (BI 2008). A 2006 estimate of 240,000–378,000 birds (WI, Wetlands International 2006) incorporated populations with anomalous increases plus new data from additional locations, thus true declines may be more substantial. However, snowy plovers are not believed to have experienced the rapid, severe losses (a greater than 30% decline in ten years or three generations) required to meet the IUCN/World Conservation Union Red List criterion to be listed as Near Threatened on an international scale (IUCN 2009) and so are evaluated for conservation prioritization as a species of Least Concern.

At other taxonomic levels or spatial scales, this assessment is problematic. Strategies for conservation are influenced by the distinctions drawn between species, subspecies, and populations (Haig et al. 2006). Uncertainties have consequences. Twelve geographic races or subspecies of snowy plover were described in the 1960s (Jacobs 1986). Now, five are identified. Of these, three may be elevated to full species, which has implications for their conservation: Kentish plover *(C. a. alexandrinus)*, which no longer breeds in Britain but occurs throughout the Palearctic, Afrotropical and Indomalayan biogeographic realms; Peruvian plover *(C. a. occidentalis)* of western South America; and North American Western Snowy Plover *(C. a. nivosus)* (Sibley and Monroe 1990).

Based on combined data from genotypic and phenotypic analyses which indicated that reproductive isolation has led to strong divergence between Eurasian and American populations, Küpper et al. (2009) proposed a taxonomic revision to recognize two separate species, Snowy plover *(C. nivosus)*, and Kentish plover *(C. alexandrinus)*. Two North American subspecies have been described (AOU, American Ornithologist's Union 1957): Cuban Snowy Plover *(C. a. teniurostris)*, with light-colored plumage, present on Puerto Rico, other Caribbean Islands, and the Yucatán Peninsula (Haig et al. 2006); and Western Snowy Plover *(C. a. nivosus)*, with pale brown

dorsal feathers and a disjunct breeding range extending across continental North America (Page et al. 1995).

Pacific Coast Western Snowy Plovers are those individuals that nest on the mainland coast, peninsulas, offshore islands, bays, estuaries, or rivers of the U.S. and Baja California within 50 miles (80 km) of the Pacific Coast. Pacific Coast Western Snowy Plovers have decreased by at least 10% per decade since the 1970s (Page et al. 1995; USFWS 2006, 2007a). This population was listed under the United States Endangered Species Act (ESA) as a threatened species (USFWS 1993).

Breeding sites for Pacific Coast Western Snowy Plovers are located from Damon Point, Washington to Bahía Magdalena, Baja California, and are most abundant from San Francisco Bay southward (Page and Stenzel 1981; Palacios, Alfaro, and Page 1994; USFWS 2006). Principal nesting habitats are barren to sparsely vegetated dune-backed beaches (Wilson-Jacobs and Meslow 1984), sand spits, estuary and lagoon salt pans, and creek and river mouth beaches (Page and Stenzel 1981). Birds nest less frequently on bluff-backed beaches, dry salt ponds (Page and Stenzel 1981), and sand or gravel river bars (Tuttle et al. 1997).

The continental interior population breeds at alkaline desert lakes and salt flats, the Gulf of California, and San Joaquin Valley marshlands, with scattered habitat through western states. East of the Rocky Mountains, sites exist from Canada through north-central Texas and central Mexico (Page et al. 1991; Howell and Webb 1994; Hickey et al. 2003). The Gulf Coast range extends along the Texas barrier islands to western Louisiana (AOU 1998) and into Florida (Haig et al. 2006).

Historically, breeding and wintering Pacific Coast Western Snowy Plover were common in central to southern California *(Figure 2)*. Called *Aegialitis nivosa* in the 19th to early 20th centuries, birds were residents on mainland (Willett 1912) and island sandy beaches (Howell 1917), and prevalent from Monterey Bay to Mexico (Grinnell 1915). Museum egg set collections date to 1875. Records for Los Angeles County date to 1883; in 1903, between Santa Monica and Ballona Creek, a distance of about 3 km, the beach reportedly had 50 nesting snowy plover pairs. No urban-adjacent nests were reported there after 1908 (Page and Stenzel 1981).

Changes in habitat availability began to alter established patterns. By the 1940s, plovers on

all southerly beaches were less plentiful and less widely distributed (Grinnell and Miller 1944). The last nest record for Los Angeles County was in 1949; regional records indicate breeding occurred at only one Orange County beach. Pacific Coast Western Snowy Plovers were missing from sections of San Diego County. No birds were located at multiple historic sites in Ventura, Santa Barbara, San Luis Obispo, and Monterey Counties (Page and Stenzel 1981).

Comprehensive surveys in 1979–1981 (Page and Peaslee 1977; Henderson and Page 1979; Spear 1979; Stenzel and Peaslee 1979; Page and Stenzel 1981) and 1988–1989 (Herman, Bulger, and Buchanan 1988; Page and Bruce 1989) assessed the status of Pacific Coast Western Snowy Plover at all known historic and existing coastal and inland breeding sites within California, Oregon, Washington, Nevada, and Utah. It was determined that populations in the region west of the Rocky Mountains had declined by about 20% between the late 1970s and 1980s. Pacific Coast Western Snowy Plovers declined sharply but rates of change at individual sites varied markedly. Decline was attributed chiefly to habitat damage and destruction due to urban development and increased human recreational use (Page et al. 1991; Page et al. 1995).

Western Snowy Plover was designated a high-risk species by the U.S. Audubon Society in 1976 (Panjabi et al. 2005). Birds were absent from 33 of 53 California coastal breeding sites by the late 1970s, and human modifications to 28 sites were believed to preclude further use (Page and Stenzel 1981). By the early 1990s, California had lost 44 of 53 known sites (Stenzel et al. 1994); 19 of 26 historic Oregon sites were unoccupied; and plovers were gone from 3 of 5 Washington sites (Page et al. 1995). Snowy plovers were listed as Threatened in Oregon (1975), as Endangered in Washington (1981), and as a California species of special concern (1978) (USFWS, 1993). Differences in protection-levels between states continue to affect management strategies even with federal listing.

Pacific Coast Western Snowy Plovers were restricted to fragments of their former range and historic habitat. Data from 1979–1981, 1989, and 1991 surveys (Page and Stenzel 1981; Page et al. 1991) and from after ESA-listing (1995, 2000, 2002–2009) (USFWS 2007a, 2009b) indicate the early-mid 1990s U.S. population low was less than 1000 breeding adults. Annual breeding-season window surveys occur within a narrow time frame at designated U.S. Pacific Coast sites, and follow a specific protocol, producing population indices useful for detecting long-term regional trends; surveys also occur during winter (Elliott-Smith and Haig 2006a, 2006b). Spatially and temporally replicated observations are natural experiments that can identify trends but data must be cautiously interpreted (Atkinson et al. 2006; USFWS 2006).

Page et al. (1986) compared extensive survey data with museum specimens from 1861–1978, data from an earlier study of egg set collections, and recorded sightings dating to 1875, and found snowy plovers in California still wintered at or within a few km of all known areas of historical use. This implied birds were never entirely eradicated from winter habitat, and that any decline would be evident in reduced numbers at certain beaches (Page and Stenzel 1981). This also emphasized the importance of winter habitat.

Thousands of interior-breeding birds from west of the Rocky Mountains migrate to the Pacific Coast, including the California Channel Islands, San Francisco Bay, and central to southern California beaches. The San Joaquin Valley attracts lesser numbers. Many winter in Mexico where surveys are minimal (Page, Stern, and Paton 1995; Page et al. 1997). Interior birds disperse in spring to the Great Salt Lake, Salton Sea, Mono Lake, and other inland breeding grounds (Page et al. 1991; Stenzel et al. 1994).

In contrast to the interior-nesting birds that migrate to and from Pacific beaches, Pacific Coast Western Snowy Plover individuals almost never travel to the interior (Stenzel et al. 1994). The

coastal birds may be non-migratory year-round residents of one beach, or migrate to beaches not chosen for nesting or to estuarine salt or mud flats (Page et al. 1986; Warriner et al. 1986). Wintering flocks may travel between coastal sites. At any given beach, day to day distribution and abundance are extremely variable. Populations naturally fluctuate over the years with changes in habitat conditions and weather (Stenzel et al. 1994).

1.2.1 Pacific Coast Western Snowy Plover Natural History and Breeding Biology

Shy and cryptically camouflaged, sparrow-sized (15–17 cm; 34–58 g) Western Snowy Plovers have pale sand-brown upper parts, buff-white bellies, a white collar, black bill, and gray to black legs. Breeding adults have dark lateral shoulder patches, eye-stripes, and forehead bars that are brown in females and black in males *(Figure 3)*; sexes are distinguishable by plumage early in the breeding season (Page et al. 1995; USFWS 2001).

Banded, resighted birds have provided extensive data about demographics, distribution, and behavior (Stenzel et al. 2007), which are critical for conservation efforts (USFWS 2006). Snowy plovers, especially males, are known for breeding site fidelity. Wintering site fidelity has also been documented. Extensive banding (n=4170) at interior and coastal sites in 1984–1993 was followed by detection efforts in 1985–1995. Results from geographically representative data samples showed 98.6% of banded nesting birds resighted (n=907) were in their natal or nesting site breeding ranges, consistent with independent data from 1977–1983 and 1969–2002 (USFWS 2006). In central California, 84% of males and 59% of females were breeding-site faithful. Consecutive-year resighting rates elsewhere were 64.1–77.8% for males and 40.9–65.8% for females (Stenzel et al. 1994). Stenzel et al. (2007) quantified natal dispersal rates and distances as part of a population-viability study that provided the first estimate of true survival for a juvenile shorebird. Males were more likely to disperse for winter;

FIGURE 3. Pacific Coast Western Snowy Plover female, Santa Barbara County, CA. Photo courtesy of Larry Wan.

females dispersed for breeding; and dispersal distances were usually within 10 km of natal site (>64%) and rarely >50 km (16%).

Males create shallow scrapes in the sand or gravel substrate as prospective nest sites before mate selection concludes. Breeding adults pair off and may make multiple nesting attempts if eggs are not viable, are predated, or are destroyed by wind, flooding, or high tides before hatching (Page et al. 1995). A typical nest contains three dark-speckled buff-colored eggs *(Figure 4)*, which hatch about 27 days after sustained incubation following clutch completion; single-egg nests may be abandoned.

Plovers do not nest colonially (Page et al. 1995) but nest density varies by site and by year (cf. Page and Stenzel 1981; Page et al. 1996; Powell 2002). Colwell et al. (2006) found social attraction influenced nest-site selection for local yearlings and immigrant plovers at northern sites. Temporary monogamous pair-bonds are formed to share incubation duties; adults are serially

FIGURE 4. Western Snowy Plover nest at Coal Oil Point Reserve. Photo courtesy of Callie Bowdish.

FIGURE 5. High-quality habitat with abundant wrack. Photo from Coal Oil Point Docent Manual.

polygamous. Females usually desert their brood within a few days after hatching to renest with another mate, often on the same beach, sometimes many km away (Warriner et al. 1986). At sites with long nesting seasons, males raise two broods and females may triple clutch. On the central to southern California coast, nesting pairs may form in February, and the breeding season extends from March through September (Stenzel et al. 1994). At the far northern end of the range, birds may move south soon after breeding (Widrig 1980).

Males care for their chicks until they fledge, protecting them against predation by using distrac-tion techniques or alarm calls. Broods may travel several km from the nest before fledging. Parents lead young to feeding sites but do not feed them; the precocious chicks walk to obtain food within hours. Except for tiny chicks (Colwell et al. 2005), disturbed plovers run. Both eggs and chicks are subject to predation and to weather-related mortality (Page and Stenzel 1981; Stenzel et al. 2007).

Predators and other hazards vary by year at individual beaches (cf. George 2003, 2006, 2009; CDPR, California Department of Parks and Rec-reation 2005, 2009; Orr 2005, 2006; Sandoval 2005a, 2009; Smith 2005; U.S. Navy 2002, 2006a; Applegate and Schultz 2009), and range-wide (cf. Robinson et al. 2007; Hardy and Colwell 2008; Harvey 2008; Knapp and Peterson 2008; Lauten et al. 2008; Page et al. 2008; Pearson et al. 2008). Among others, avian predators include corvids, gulls, raptors, and owls; mammals include coy-ote, fox, skunk, raccoon, opossum, weasel, do-mestic and feral cats, and dogs (USFWS 2007a).

Marine and terrestrial invertebrates found on wave-deposited kelp and debris called wrack are the major food source for the Pacific Coast Western Snowy Plovers; the wrack line coincides with the high tide line. Prey include arthropods, chiefly amphipods, isopods, and other crus-taceans; polychaetes; beetles, flies, and other insects. Sandy beach macrofauna are essential for shorebirds, seabirds, marine mammals, and fish (Tucker and Powell 1999; Dugan et al. 2000; Dugan et al. 2003). Sites that provide high-quality breeding and wintering snowy plover habitat usually have abundant wrack deposition *(Figure 5)* throughout the year (Lafferty 2001; Sandoval 2005a).

Plover foraging behavior is distinct: they pause and look; then run; then stop and seize their prey (Page et al. 1995). Pacific Coast Western Snowy Plovers do not probe the sand deeply like wading birds with longer beaks. They pick macrofauna off wrack deposited within the intertidal zone and on dry sand above the high tide line; obtain

food from the sand surface; and glean insects from on and beneath low dune vegetation. Plovers forage on beaches, tide flats, and dredge spoils; at edges of lagoons, marshes, and salt ponds; and on dry salt pans and sand and gravel river bars (Page et al. 1995).

Geographic behavioral adaptations, unique breeding habitat preferences, low dispersal rates, nest site fidelity, and the virtual reproductive isolation of coastal and interior populations, in the context of their declining populations, have major ecological and conservation implications. The Pacific Coast Western Snowy Plovers had initially qualified for federal listing as a distinct population segment (DPS) because taxa at other than species-level may be considered under ESA if certain conservation criteria are met (USFWS 2006).

Some between-population differences in species migration patterns have been found to be genetic, not environmental (Berthold 1991; Berthold et al. 1992). There was no evidence for genetic differentiation between coastal and interior populations of Western Snowy Plovers (Gorman 2000; Funk, Mullins, and Haig 2007), but gene flow is limited. Given their population declines, populations could be demographically independent, which indicates behavioral adaptation and some level of reproductive separation (Funk, Mullins, and Haig 2007). Both genetic and demographic criteria may define populations (Wright 1978). Crandall et al. (2000) have argued that reliance solely upon molecular techniques and genetic data analyses as criteria to determine population units for conservation to the exclusion of ecologically relevant adaptive diversity will enhance neither evolutionary potential nor species survival.

In a comprehensive finding, the Threatened status of the Pacific Coast Western Snowy Plover was upheld in response to petitions that challenged the validity of the ESA listing; litigants were California municipalities on the central coast with numerous plovers and their habitat

to protect. Data from banded and resighted birds provided the most compelling evidence that Pacific Coast Western Snowy Plovers were a behaviorally distinct population, reproductively isolated, even from other subspecies members that winter on the coast (USFWS 2006). USFWS (2006) reaffirmed that the Pacific Coast Western Snowy Plover was both discrete and significant under its DPS policy, and found that delisting and loss of federal protection for the population and its habitat would potentially lead to its extirpation. Loss of within-species variation of the Pacific Coast Western Snowy Plover would significantly reduce biodiversity: 20% of *C. a. nivosus* would be lost. Furthermore, the equally site-faithful interior-breeding birds would not likely recolonize the Pacific coast, thus very substantial range contraction would result, with a 3200 km coastal gap.

1.2.2 Habitat and Species Conservation

The primary threat range-wide to Pacific Coast Western Snowy Plovers is decreased habitat availability. Specific causes and effects vary geographically, but include fragmentation, degradation, and loss of habitat due to expansion of urban development and increased recreational beach use. Intensified predation upon plovers has been traced to varied anthropogenic influences that disturb natural environments and facilitate predators (USFWS 2007a). Disturbances include encroachment from human-introduced non-native invasive plants. For example, beach grasses planted to stabilize dunes, *Ammophila* spp., have extensively altered the natural open structure of coastal dune habitat throughout the central and northern part of the snowy plover's U.S. range. Giant reed, *Arundo* spp., is a problem in the southern part of the range; plants wash down riparian corridors in major storms and then take root on nesting beaches. Pampas grass, *Cortaderia* spp. is another problem. Grasses have narrowed beaches, reduced unvegetated dune habitat, and provide cover or perches for predators.

Globally, habitat fragmentation and landscape modification are the primary cause of species extinction (Fischer and Lindenmayer 2007). There are, however, less-drastic scenarios that may occur in response to habitat loss. A taxon may extend its range into marginal habitat or exist at higher densities in extant habitat. Restoration may allow for range expansion, or habitat enhancement may improve lesser-quality habitat to allow populations to thrive at greater density. Both restoration and enhancement may have unknown benefits and costs.

The Charadriidae (Plovers) are an entirely wetland-obligate family, and the majority of species have declining populations. Wetland habitats worldwide have deteriorated and disappeared (WI 2006). Status and trends reports for conterminous U.S. wetlands based on analyses of remotely sensed imagery have estimated change over decades, with no functionality or habitat quality assessments made. Complex transitional environments were aggregated (after Cowardin et al. 1979) to produce the reports: e.g., all sandy, mud, or rocky coastal beaches, sand spits, tidal flats, shoals, and sand bars were grouped as marine intertidal non-vegetated wetlands. All estuaries on the Pacific Coast (e.g., Coos Bay, OR; San Francisco Bay, CA; Morro Bay, CA; Mugu Lagoon, CA) were excluded from long-term studies because they are discontinuous patches (Dahl 2006). Results were grim: in California, by the mid-1980's, 91% of original wetlands had been eradicated (Dahl and Johnson 1991). Complementary research found that 80% of coastal marshes in California and 75% of southern coastal wetlands were lost (CDPR 1988). Every remnant estuarine ecosystem had experienced major alterations from a range of human activities (Onuf 1987).

Recent Pacific Coast wetlands inventories have used innovative techniques to identify and comprehensively map existing wetlands. These often incorporate a strong historical ecology component (e.g., Grossinger 2001; Stein et al. 2007) to create detailed reference ecosystems,

based on varied collateral data, that can inform subsequent habitat restoration. Many remaining wetlands retain extraordinary diversity, and detailed schemes have been designed to capture this within a standardized classification system (Ferren et al. 1995). Southern and central California coastal ecosystems, including wetlands communities, are influenced by the Mediterranean climate and distinctive topography (Ferren et al. 1996; Zedler and West 2008). Remnant wetlands no longer function naturally (Zedler 1996), but regional conservation strategies (Zedler 1996; Sutula et al. 2002; Hickey et al. 2003), analyses of wetlands connectivity (Haig et al. 1998), and investigations of target species (Page et al. 1999; Taft and Haig 2006) have guided some wetlands restorations towards functional and ecologically sound conclusions (e.g., Lafferty 2000; Armitage et al. 2007; Zedler and West 2008). Some directly affect Western Snowy Plover recovery (e.g., Wehtje and Fahy 2000; Fancher et al. 2005; Lafferty et al. 2006).

Successful conservation of coastal habitat has evolved toward systems-based approaches that incorporate landscape-scale conservation of large-scale natural processes (Baillie et al. 2000) and that also anticipate future conditions. Environmental change, human-driven or otherwise, is a given condition. Assessing the effects of various types of human disturbance at this same scale is also critical (Burton 2007). The exact consequences of climate change for coastal shorebirds are challenging to predict (Sutherland 2006), as are appropriate responses (Zedler 2004; Sutherland 2004). Flooded landscapes could increase wetland habitat, but sea-level rise may have disastrous consequences, including extensive losses of low-lying coastal salt marsh habitat (Hughes 2004), and negative impacts on estuarine morphology and function, including decreased availability of prey for water birds (Austin and Rehfisch 2003).

Threats to sandy beaches seem imminent: sea-level rise as a response to global climate change will affect beach dynamics, diminish their width,

and threaten ecosystem functionality (Schlacher et al. 2007). Processes that would be a natural response to a rising sea, cliff erosion and shoreline retreat, may not be able to keep pace creating new beaches. Armored shores and other infrastructure built to constrain rising sea-levels may destroy many remaining sandy beaches. Pacific Coast Western Snowy Plovers and many other shorebirds rely on sandy beaches, and any historic habitat on sand and gravel bars within major river floodplains that could function as potential replacement habitat has in most instances already been eradicated by urban development.

Sandy beaches are frequently underappreciated for their biodiversity and for the ecological services they provide (Schlacher et al. 2007). Specifically protected and managed beaches and coastal dune systems provide breeding habitat for Pacific Coast Western Snowy Plover (USFWS 2007a, 2009b). Sandy beaches in California collectively provide wintering habitat for thousands of interior-breeding and coastal Western Snowy Plovers (USFWS 2007b, 2009a). Historically, they provided excellent breeding habitat as well (Stenzel et al. 1994). Some are designated critical habitat (USFWS 2005) because they are essential to support the wintering population. Loss of extant high-quality wintering habitat would intensify population decline (Norris 2005). Maintenance of both coastal and estuarine habitat for migrant wintering shorebird populations is crucial. Overwinter survival is conditional upon the quality and habitat composition of wintering sites (LeDee, Cuthbert, and Bolstad 2008).

Beaches are dynamic environments valued for their economic and social significance but they endure escalating human pressures (Schlacher et al. 2007). In some urban-adjacent Pacific coast areas, damage to habitat has accrued for a century. Remote locations are increasingly accessed. The U.S. Pacific coastline is environmentally protected to a greater or lesser degree depending on jurisdiction. Sites in Baja California, Mexico are likely to have experienced similar pressures with less stringent protection.

According to USFWS (2006), intensive intervention in the U.S. helped Pacific Coast Western Snowy Plover stabilize at an estimated 4800 birds. U.S. birds are regularly surveyed (USFWS 2009a, 2009b), and range-wide estimates are calculated by applying a small correction factor to the number of birds counted on annual U.S. surveys. Doubling the result roughly captures the other half of the Pacific Coast Western Snowy Plover range in Mexico. Habitat there occurs mostly on sandy beaches, and there may have been unanticipated declines. Population estimates for Mexico have been based on 1992 data. North American data from the International Snowy Plover Survey, when available, should provide a more accurate picture (USFWS 2007c).

A draft Recovery Plan (USFWS 2001) was formulated to guide conservation efforts. The recovery objective is to remove the Pacific Coast Western Snowy Plover from the List of Endangered and Threatened Wildlife and Plants by achieving specific goals. Recovery is defined as reversing the decline of a species, eliminating threats, and ensuring the species' long-term survival. Demographic recovery criteria were based on a population viability analysis (PVA) (Nur et al. 1999) that considered alternative scenarios and indicated that a well-distributed 3000-adult breeding population could be established in 25 years with appropriate management. The updated final Recovery Plan (USFWS 2007a) adjusted this projection to 40 years. Maintenance at specified levels for an additional ten years; productivity increases for breeding adult birds; and ensuring long-term protection of breeding and wintering plovers and their habitat are required recovery components (USFWS 2007a). Under ESA, habitat protection is critical (Noss, O'Connell, and Murphy 1997).

The study area for this project is Recovery Unit 5 (RU5) *(Figure 7)* under the Western Snowy Plover Population Draft Recovery Plan (USFWS 2001), along the central to southern California coast. Data from RU5, its 32 designated recovery sites, and from additional breeding-season and winter window survey sites were essential to this

FIGURE 6. Recovery Units 1–6

Western Snowy Plover Pacific Coast Population Species Recovery Units (RUs)

The PVA divided the Pacific Coast Western Snowy Plover metapopulation into six subpopulations that exchange individuals regularly but are geographically separated by unsuitable habitat. Subpopulation locales became designated as U.S. Recovery Units (RUs) *(Figure 6)*, one in Washington and Oregon, and five in California. Present and historic breeding sites within each unit were identified and specific population goals were indicated for each site (USFWS 2001, 2007a). Population data are collected following range-wide protocols during one-day breeding-season and winter window surveys. Nest monitoring and auxiliary data are gathered at current breeding sites. Site monitoring is conducted with varying frequency and intensity. The monitoring schemes, management, and ownership differ between and within the designated sites, and the six RUs act autonomously under the Recovery Plan.

research. RU5 is critically important for species recovery and long-term conservation. About half of the U.S. Pacific Coast Western Snowy Plover breed here during early spring through late summer. The wintering population in RU5 represents about half the birds present on the U.S. Pacific Coast, and includes year-round residents plus inland-breeding birds from west of the Rocky Mountains (USFWS 2001, 2007a, 2009a, 2009b). RU5 includes three California counties on the U.S. mainland and northern California Channel Islands. Four analysis areas created for modeling correspond to geographic and jurisdictional entities: mainland San Luis Obispo (SLO), Santa Barbara (SB), and Ventura (VEN) Counties, and the California Channel Islands (NCH) of San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, and San Nicolas.

1.2.3 Habitat for Pacific Coast Western Snowy Plover in RU5

Beaches in central to southern California at the center of the Pacific Coast Western Snowy Plover range have historically been prime habitat. The RU5 mainland coast is roughly 400 km long; the island coast about 300 km long. Diverse landscapes include high cliffs, rocky shores, coastal bluffs, sand spits, extensive dune systems, estuaries, and wetlands. Sandy beaches occur as tiny pockets at the mouths of high-gradient creeks, along narrow bluff-backed terraces adjacent to steep foreshores, covering sand spits and ocean overwash areas, within dune complexes, and as wide, flat expanses. Narrow rocky beaches are more common to the north; wider, sandy beaches predominate in the south; and dunes form wherever conditions are suitable (USACOE, United States Army Corps of Engineers 1971; Griggs et al. 2005).

San Luis Obispo County has 53 km of sandy beach along 150 km of coast; Santa Barbara County has a 177 km shoreline with 140 km of sandy beach; and Ventura County has sandy beaches along almost all the 66 km coast (USACOE 1971; California Coastal Commission

FIGURE 7. Study area for Western Snowy Plover habitat suitability modeling.

2003). The northern California Channel Islands have the only north-facing coastlines and a microhabitat array: sheer rock on Santa Barbara and Anacapa Islands; substantial cliffs along Santa Cruz Island, with pocket beaches and a few long beaches on the south coast; and rocks, terraces and sandy beaches on San Miguel, Santa Rosa, and San Nicolas Islands.

Based on the recorded preferences of Pacific Coast Western Snowy Plover throughout its range, its optimal breeding habitat is found along sandy beaches and salt pans, close to a wetland, with a landward boundary of an estuary, sand spit, dunes, or low bluffs. Actual locations of suitable quality habitat are determined by environmental processes and patterns operating at multiple scales. Weather and topography have a synergistic relationship. Geology and climate are the broad framework: coastal landforms include terraces created by tectonism and climate fluctuation, erosion-resistant headlands, mountain ranges aligned to direct stream flows, and structural depressions for wetlands. Currents and wave parameters affect beach morphology. Point Conception is the coastal California biogeographic and climatic divide. Northern beaches are subjected to more extreme conditions, including persistent wind, high surf, intense storms, and omnipresent fog. Winter storms strongly affect the pocket beaches at creek mouths along rocky shores or north of headlands.

Beach sand is mainly derived from coastal watershed mountains. Weathering fragments rocks, and sediment eventually reaches the coast via runoff; particle size, stream velocity and magnitude affect its transport. The Santa Maria, Santa Ynez, Ventura, and Santa Clara Rivers drain large watersheds, and supply enormous volumes of sand to the central and southern California mainland coast, even with upstream diversion. Beach-deposited sand and gravel move along the coast, entrained by wave action. The littoral drift moves sand south-southeast to east following the shore. Most waves and wind are from the northwest.

Resistant coastal outcrops trap or deflect sand; low-relief areas accumulate it. Dunes occur in low-lying inland areas near beaches with persistent unidirectional wind and ample dry sand. Dunes can be low ridges or massive features, but they are an evanescent landform: they migrate, blowout, consolidate, erode, and become vegetated, all of which affect habitat quality in different ways. Strong winds and blowing sand are attributes of the west-facing beaches; winds diminish somewhat midway through the breeding season (Wehtje and Fahy 2000; CDPR 2005; Applegate and Schultz 2009). Beaches are highly dynamic. Individual beach profiles change dramatically with seasonal erosion and deposition. Wider beaches may follow high-rainfall winters because the volume of river-transported sediment is greater (Ritter et al. 2002; Griggs et al. 2005). Extreme precipitation events during El Niño years may instead cause extensive coastal erosion and reduce habitat availability (Applegate and Schultz 1999, 2000; Hubbard and Dugan 2003).

Beach morphology influences critical biotic factors. Kelp forest communities fringe the Pacific, and although species richness and abundance fluctuate in response to weather patterns and other variables, wrack deposition reliably replenishes food and debris on beaches (Donnellan 2004). Beach faces or wave slopes are measured along a reflective (steep) to ultra dissipative (flat) gradient. Intermediate to flat sandy beaches receive and retain more kelp and debris, thus have higher macrofaunal concentrations (Defeo and McLachlan 2005). Snowy plover abundance was positively correlated with species richness, abundance, and biomass of wrack-associated macrofauna (Dugan et al. 2003).

Central to southern California beaches are naturally littered with marine debris, wood fragments, and rocks. In addition to the value of wrack as a food source, items like kelp, driftwood, shells, or rocks have potential advantages and are associated with plover nests (Page and Stenzel 1981). Some nests are lined with debris

bits or constructed near objects. Within the central California dune complex, early-season nest locations were strongly correlated with the presence of debris (Wehtje and Fahy 2000). Object presence, especially kelp, and a suite of sand dune features have been positively correlated with site choice, nest density, and nest success (Page et al. 1985; Page et al. 1995; Ellison 2001). Adjacent objects at an inland site were negatively correlated with nest success, but researchers noted that in the barren landscape, objects may have acted as a visual cue to attract predators (Page et al. 1983). In contrast, abundant coastal debris might camouflage birds and hide movements to nests (Page et al. 1985). Objects may serve as landmarks or disrupt predators (Maclean and Moran 1965). Vegetation or debris may create windbreaks (Tomkins 1944) or shield birds (Bergstrom 1982), but other near-nest objects were too small to protect inland plovers from predation or weather (Purdue 1976). Near the Santa Maria estuary, plovers favored nest locations on a slight slope with good visibility to enable them to scan for predators, rather than sites protected from winds and blowing sand, or those with a particular substrate (Wehtje and Fahy 2000). In a warmer climate, locations with an unobstructed view were selected over cooler, sheltered sites (Amat and Masero 2004).

Object color may be important. At salt evaporation ponds in RU3, the southern San Francisco Bay, plovers nested more often in microhabitats with white objects than at random sites (Marriott 2003). These salt ponds are not a natural part of the landscape, but the restoration now in progress to a functional tidal marsh will not benefit plovers as much as other birds because they will lose exclusive habitat (Robinson et al. 2007). Unlike coastal salt pans, salt ponds have a rough caliche-like surface, and plovers nest here where other species show no interest. In RU5, near Point Conception and on the Channel Islands, caliche occurs along marine terraces, where plovers nest when sandy beaches below do not provide habitat (U.S. Navy 2006c).

Pacific Coast Western Snowy Plovers find dredge spoils to be another attractive man-made habitat (Wilson-Jacobs and Dorsey 1985; Page et al. 1995), presumably because of concentrated debris. At Morro Bay, large numbers of plovers breed and winter on the peninsula that separates the Pacific Ocean from the estuary. Morro Rock was historically isolated except at low tide, with shifting channels north and south. Southern access has been maintained by dredging huge volumes of sand from the harbor entrance. No dredge-spoils disposal site has been an unqualified success (Orme 2005), except as plover habitat enhancement. Shell fragments, pebbles, and stones were repeatedly dumped at the Morro Bay sand spit tip (Hutchinson et al. 1987) and along Morro Strand north of Morro Rock (Larson 2002). Long-term dredging will remain the response to sand accumulation within Pacific Coast harbor ship channels (Griggs et al. 2005). There are disadvantages, however, as when established sandy beach plover habitat is instead destroyed to provide access.

Microhabitat features like sand grain size and color were also found to influence local plovers (Ellison 2001), but for a regional analysis were problematic without data from all sites. Models that derive landforms from high-resolution lidar data (e.g., Elliott-Smith et al. 2005), combined with data extracted from remotely sensed images by discerning particular sand signatures might be successful. Apparent snowy plover preferences have been recorded in the context of numerous studies with various objectives. Diverse environmental elements at macro and micro-scales have been correlated with nest site selection, nest and fledging success, and plover abundance, among other factors.

The environmental niche-based habitat suitability models used for this project translated interactions between generalized environmental variables and ecological requirements into geographical space for Pacific Coast Western Snowy Plover. Both the deductive and inductive models' input derived digital data layers with specified environmental parameters. Our initial models were deductive or mechanistic, predicting species distribution based on generalized habitat preferences. Deductive models quantitatively defined relative suitability of particular factors prior to model input. Inductive or correlative models input known nest site locations with more-minimally-processed environmental data to determine specific conditions at those sites. Models were designed to quantitatively identify locations of potential Western Snowy Plover habitat, which was defined as similarity to optimal conditions. Model outputs expressed possibility or likelihood that environmental conditions at a given location were desirable habitat and were potentially a measure of habitat quality.

A prerequisite to modeling was to define essential elements that constitute suitable habitat, as was determining the investigative scale. An appropriate scale for Pacific Coast Western Snowy Plover species' distribution modeling could range from continental to beach-level. The research objective to identify historic and potential habitat within RU5 indicated a regional landscape-scale approach. Literature was reviewed to identify, select and parameterize independent variables, and obtain quantitative and qualitative data comparable site to site, either regionally or range-wide. Site-specific derived variables and non-standardized measurements were innovative but less relevant at this scale. Expert biological and ecological opinion was also sought to ensure essential model elements were interpreted correctly. Emphasis was placed upon central-range sites that resembled the study area, but pertinent information about environmental feature preferences was reviewed for Washington to Baja California sites.

Species living at geographical range limits occupy habitat that is marginal along one or more of the environmental dimensions that define an ecological niche. A taxon in decline predominantly because of habitat loss may occur in comparatively marginal habitat when use of remaining high-quality habitat is precluded. Data from minimal quality habitat as input for species distribution or habitat suitability models is problematic for both inductive and deductive techniques. An inductive approach may under-predict historic or potential distribution if currently occupied habitats that provide presence data are marginal when compared with historic sites. When deductively modeling habitat suitability based on recorded preferences, that portion of the landscape most similar to input as optimal conditions will be selected. Poor quality sites may offer valuable insight on environmental constraints, but extrapolation of parameters to other locales may not give ideal results. Nevertheless, even marginal habitat is disappearing. Identifying lesser-quality or "potentially decent" locations may also be valuable to achieve species recovery.

2.1 LIMITATIONS AND UNCERTAINTY

Addressing the limitations and assumptions associated with specific habitat suitability models is critical to proper interpretation and inference. We directly addressed these limitations, and this section will provide a brief (but not complete) review of the salient issues related to the nature of the data used for this project.

Species-occurrence data are inherently messy. When compared with samples from a well-executed study, ecological data obtained from non-replicated observations may be flawed (Gotelli and Ellison 2004). For this project, data varied widely in accuracy and quality; were collected without a sampling strategy; and consisted of presence-only data where observed occurrences were recorded without sites of species' absences. Some data were acquired over decades at multiple sites by numerous individuals using non-standardized techniques; other data were collected annually according to specific protocol but were more limited in scope, although collected over a larger geographic extent. Likewise, some of the recently collected data had high spatial accuracy and precise geographic coordinates; and some of it did not. Historical data varied in geographic precision, sometimes citing general locations of presence. For example, "Los Angeles County, On the Beach" was recorded for an 1894 snowy plover egg now in the Western Foundation of Vertebrate Zoology collection.

In addition to issues associated with presence data, the environment was inconsistent: reliably precise geographic coordinates placed nest sites from three years prior within an estuary. Other data chosen as model input represented generalized snapshots of ephemeral conditions. In dynamic shorebird habitats, rates of change fluctuate with different temporal and spatial scales. Storms modify beach profiles; severe events affect disparate conditions aside from beach morphology for years afterward. Sand dunes migrate; river mouths shift considerable distances; and habitat boundaries continually change. These

models were landscape-scale representations of historical breeding-season conditions, which neither attempted to incorporate every real-world interaction nor were over-fitted to nest data.

Obviously, physical factors that influence the geographic distribution of a species operate simultaneously along a continuum of scales, ranging from interactions with food and water resources at a fine scale to medium-scale topographic features, to coarse-scale dimensions of climate. It is important to mention issues associated with the use of spatially-referenced data which represent these physical variables within a geographic information system (GIS). High resolution vector and raster data, including hydrography and digital elevation models (DEM), were selected for relative not absolute accuracy. Data chosen were the best available to compare across the region, considering the grain-size of all intended input.

Modifications were made to data layers as model suites evolved. Km-resolution climate data were too large; nest points were the finest-grain data. DEM available at several resolutions were an integral component: 30-m pixels were standard; 10-m were preferable and the ultimate choice. Lidar data to interpolate DEM at 5-m or 1-m resolution existed, but only for part of the coastline; at beach scale they are an excellent option (Elliott-Smith et al. 2005). Dataset size was an issue. Our landscape-scale models examined an entire region with four slightly overlapping analysis areas. To calculate and statistically validate models, enormous numbers of pixels were manipulated. Deductive model input for one area, ten layers of 10-m resolution data, exceeded 4.5 GB for Santa Barbara County alone.

GIS data used for model input were limited to physical environment variables. Vegetation or land cover layers were intentionally excluded because often they incorporate human modification. Proliferation of non-native invasive plant species negatively affects snowy plover habitat, but this was excluded information. Effects of climate change will challenge wetland-obligate

species that prefer sandy beaches; these are not modeled. Anthropogenic influences were removed from vector data before rasterizing hydrology and coastline data.

Deductive model input received additional processing, which generated sets of layers with fuzzy-logic habitat suitability values that replaced original raw-data derived values. New values for environmental variables were based on recorded species preferences from the literature. Fuzzy methods assigned pixels numerical values corresponding to gradual degrees of set membership with user-input functions. The process was inherently slightly subjective but less so than other methods evaluated, including traditional raster schemes which produced ranked habitat suitability classes with discrete thresholds.

Model-building and evaluation procedures were adapted to the unevenness of the data, and several levels of analyses were undertaken. Pixels with multiple nests were not counted multiple times; removal of duplicate values may lessen effects of spatial autocorrelation even though nest abundance may instead indicate particularly desirable habitat rather than sampling bias. Assumptions, limitations, and uncertainties affected the statistical analyses used. Parametric procedures were often not appropriate. Model results gauge similarity to optimal conditions and are explicitly interpreted as a possibility or likelihood; although expressed on a 0.0–1.0 scale, they are not interpreted as statistical probabilities.

2.2 VARIABLE INCLUSION AND DEVELOPMENT

This section is arranged as follows: a review of GIS data used for model development, their sources, and methods to prepare them are discussed first. Acquisition and processing of vector data are discussed, then construction of the raster data, including environmental variable selection, data sources for individual layers, and geoprocessing of continuous and categorical data. Next, fuzzy-logic processing of environmental layers for deductive models and rationales for particular values and functions chosen to create them are described. Model parameters and techniques used to generate final deductive models within Idrisi GIS software (Clark Labs 2006) and methods specific to final inductive models created with Maxent species-distribution modeling software (Phillips et al. 2004, 2009) are explained. Statistical methods used to evaluate and compare models are discussed in the last section.

2.3 SPECIES-OCCURRENCE DATA

Beach and sub-site polygons: Known geographical locations of historic and current Western Snowy Plover breeding and wintering sites were used for validation of deductive and inductive models. California site polygons were digitized from USFWS draft Recovery Plan (2001) maps; 1-m resolution color satellite imagery (USDA NAIP 2005) and digital topographic maps (USGS 1:24,000 DRGs) were used as collateral data and to locate and digitize window-survey and sub-site beaches, along with input from window survey participants, annual reports, and field visits. Polygons were clipped with the finalized coastline and beach length calculated.

Standardization of beach names and site boundaries was critical. Many individual beaches have multiple names; some names changed during the time frame data were collected; and boundaries shifted during this investigation. Sub-sites were created to capture the smallest geographical unit of data collected for the Pacific Coast Western Snowy Plover; 73 are used in this analysis.

We required geographical ordering and the flexibility to aggregate sub-sites. Hierarchical numbering of sub-sites (691–1045) related them to RU5 Recovery Plan site designations (CA69–CA100). Some sites correspond directly (e.g.,

San Carpoforo Creek, CA-69 = 691). Some are divided into several sub-sites because of differences in management of individual beaches, even though they are under the same jurisdiction and may themselves sometimes aggregate data (e.g., CA-84 (841–846) and CA-85 (851–855) at Vandenberg AFB; and CA-99 (991–995) at NBVC Mugu Lagoon). Others, like the Pismo/Oceano/Guadalupe Dunes complex, CA-83 (831–8312), were subdivided to capture additional management and monitoring variability due to ownership and jurisdictional differences.

Nest points: Presence-only data available for Western Snowy Plover nests at some monitoring sites provided deductive model validation and inductive model input. Data were assembled for substantial portions of the mainland geographical range within RU5. Nine CA-sites had data from all or most of the area within the designated site (n = data years input): CA-78, Estero Bluffs/Villa Creek (2); CA-80, Morro Strand (3); CA-81, Morro Bay Sandspit (6); CA-83, Pismo/Oceano/Guadalupe Dunes (0–11); CA-84 and CA-85, Vandenberg AFB (11); CA-88, Coal Oil Point Reserve (3); CA-96 through CA-98, Ventura County (6); and CA-99, NBVC Mugu Lagoon (9). Several thousand nest locations were compiled. By area, SLO had 1,847; SB, 3,304; and VEN, 1,030. Earliest data were from 1987; some sites include 2009 data.

We acquired nest point data from multiple sources in diverse formats. Site managers from two sites provided years of spatial data as GIS files; owners and monitors from three other sites provided tables of coordinates that augmented data derived from other sources. About half of the point data were derived from annual reports of site monitors or others that included hard-copy or digital maps of nests, which were first georeferenced, then points were digitized, validated, aggregated, and re-projected. Data are maintained in an ArcGIS geodatabase by site by year and aggregated by site and by region. Modified sets of nests by county (SLO, SB, VEN) were used for inductive model input; for all models, the same duplicate points within 10-m pixels were removed for the modeling process.

Other Vector Data: Pre-existing digital GIS data were also used. National Hydrography Dataset (NHD) (USGS 2006b) high-resolution data for central and southern California were selected as the source for coastlines, flowlines (streams, rivers), and other wetlands (estuaries, lakes). Use of NHD data allowed for alignment of all hydrologic data and a mean high higher water coastline that corresponded with the wrack deposition line. The coast was edited to remove offshore rocks, and manmade features (piers, jetties) were removed to approximate historical conditions without excluding habitat (e.g., Santa Barbara Harbor Sandspit; north Morro Bay Sandspit). The coastline was used to create clipping/extraction masks for rasters and county-line clipped buffers to extract comparative statistics.

2.4 ENVIRONMENTAL VARIABLES

Raster data: Raster layers were processed separately with identical parameters for the four analysis areas: mainland San Luis Obispo (SLO), Santa Barbara (SB), and Ventura (VEN) Counties; and the six northern California Channel Islands (NCH). Grid cells were ten square meters. Initial geographic extents for the three mainland raster sets encompassed the entire hydrologic network contributing to coastal drainage and the jurisdictional boundary for that County. The NCH raster was the smallest extent that would capture all six islands although it was unlikely Anacapa and Santa Barbara Islands would meet many criteria for potential habitat.

Early models investigated a 20-km coastal strip for habitat suitability. Deductive models were designed to predict potential and historic habitat, including creek and river sand bars. The literature stated Pacific Coast Western Snowy Plovers nested that far inland on northern California stream bars (Tuttle et al. 1997; Colwell et al. 2005). Reports and site monitors (Sandoval 2005b; Applegate and Schultz 2007) had indicated nest sites comparatively far (~1.5 km) inland in the Pismo/Oceano/Guadalupe Dunes near the

Santa Maria River. Potentially, historic sites could exist near the Santa Ynez or Ventura Rivers or along the Santa Clara River floodplain.

Initial inductive models did not adequately differentiate high from low-quality habitat within the 20-km coastal strips: the entire coast was selected. As models evolved, the coastal region was narrowed and rasters were clipped to 4-km and then to 1-km widths. Deductive models made reasonable predictions with any size coastal strip, but all models ran faster with smaller rasters. Our final models used a 1-km coastal region that captured all CA-site and window-survey site polygons used for evaluation and excluded only one nest point. After initial processing, environmental layers with exact dimension (pixel numbers) and extent (bounding geographical coordinates) were extracted with masks of 1-km landward and 150-m seaward buffers merged and clipped to the area boundaries.

Variable selection: The literature search for Western Snowy Plover habitat preferences throughout their range revealed factors or constraints that potentially determined or influenced habitat quality. Physical parameters that should be included were identified. Variables could be either quantitative (continuous measurements) or qualitative (categorical data). Primary variables were: elevation; slope; proximity to the coast; proximity to an estuary or stream; stream/river characteristics and magnitude; landward boundary (e.g., sand spit, dune, or bluff-backed); macro-scale beach substrate (e.g., rocks, gravel, or sand); beach width above the high tide zone; air and sea temperature; wind patterns; and wave height.

Other variables were considered or included in trials: various other climate variables; aspect; seasonal beach profiles; beach foreslope/littoral zone width; submarine features; wave/circulation patterns; drift/current anomalies; dune characteristics; estuarine characteristics; micro-scale substrate (e.g., grain size and color); kelp presence/absence; wrack characteristics (e.g., zone width,

% cover, spp. composition); terrestrial vegetation (e.g., presence/absence, spp. composition, % cover); and presence/absence of adjacent Western Snowy Plover population/s and their location/density/abundance.

Our research required an ongoing refinement of data layers to support analysis of physical conditions. Earliest deductive models used ranked-value classes for continuous data and input five variables: elevation, slope, aspect, distance to coastline, and distance to streams and waterbodies. Aspect was removed; landward boundary and beach substrate were added. The classified values for non-categorical data were superceded by fuzzy-logic processing (explained in section 2.5) for deductive model input. Inductive models required derived data layers that maintained their "raw" or original values.

2.4.1 Continuous data variables

Digital elevation models: DEMs (*Table 1*) were the primary reference layer to which all raster layers were matched for dimensions and extent and from which blank rasters and congruent polygons were created. Elevation was considered a primary constraint on habitat location. National Elevation Dataset (NED) (USGS 2006a) DEM for analysis areas were downloaded, reassembled, reprojected, and clipped to match the selected hydrologic and jurisdictional boundaries. Mainland resolution was 10-m (1/3 arc-second decimal degrees); CA Channel Islands coverage at 30-m resolution was resampled to 10-m. NED merged best available (highest-resolution, best quality) data into seamless raster coverage; the pilot-study models had mosaicked 65 USGS 10-m and 30-m quads for the study area.

Slope gradient: Steep slopes are a constraint; slope gradient identified unsuitable cliffs and rocky headlands, bluff-backed very narrow beaches and overly steep dunes. Almost-flat areas combined with other features indicate desirable sites: floodplains, terraces, pocket beaches, and expanses of flat sand. Slope was derived from

DEM and calculated as percent grade rather than degrees because studies in which it was quantified expressed it that way. Calculated values may be misleading for steep slopes: 45° = 100%.

Distance rasters: Distances from the coast and from streams and waterbodies were included because those locations provide essential ecological services. Together, they also roughly determine locations of sandy beach and coastal dune habitat. Other GIS models for birds in coastal regions have included these variables (Gibson et al. 2004; Long et al. 2008). Shorebird HSI models, like those for clapper rail and least tern, that primarily used generalized land-cover metrics to generate habitat variables, had measures of wetland proximity (Lewis and Garrison 1983; Carreker 1985). Our layers were based on edited vector data clipped to analysis areas, then rasterized and mosaicked with a blank raster. Zero values were reclassified as nodata and straight-line Euclidean distance was calculated.

Major rivers extend a great influence over the geographic location of high-quality habitat. Present-day and historic wetland complexes are located where floodplains meet the ocean. Major rivers convey large volumes of sand to feed beaches and dunes. We thought stream magnitude was a useful variable, and raster trials on small (7.5' quad) DEM to calculate Shreve (additive) magnitude with the ArcGIS (ESRI 2005) hydrologic suite were promising. Flow direction and accumulation were determined; the stream network was roughly identified; and individual branches were ordered by magnitude. In general, these stream magnitude calculations with landscape scale DEM at 10-m resolution were unsuccessful. In RU5, many areas are true sinks (e.g., major river floodplains), and not incorrect elevations. We tried alternative calculations by drainage basin. Distances from major (Santa Maria, Santa Clara) and large rivers (Santa Ynez and Ventura Rivers; Calleguas Creek) were a compromise, processed like other distance rasters, designed to give features extra weight.

Climate data: Climate affects Pacific Coast Western Snowy Plover habitat quality. According to the literature (e.g., Page 1988; Persons and Applegate 1997; Applegate et al. 2000; Wehtje and Fahy 2000; Larson 2001; Orr 2005), strong winds and blowing sand frequently eradicate nests. Nest losses due to flooding from high tides are more common early in the season when beaches are narrow and winter storms have not subsided. Extreme weather conditions are more prevalent north of Point Conception. All west-facing beaches report nest losses from high surf and blowing sand, but they also occur along the southwestern Santa Barbara coast and on the Channel Islands. Mainland RU5 beaches farther east or south in Santa Barbara and Ventura Counties experience severe weather, intense winds and high tides but in general are more sheltered.

Climate data are often used in continental-scale environmental-niche models (Busby 2002; Pearson and Dawson 2003; Luoto et al. 2005; Elith et al. 2006). Our inductive model trials used annual air temperature and precipitation means, and means of driest-quarter temperatures and coldest-quarter precipitation; all contributed to the models. Raw and derived variables at 1-km resolution (Hijmans et al. 2005) were mosaicked, downsampled, and filtered. Unfortunately, these data created for continental investigations were missing large sections of coastline. Downsampling to a much finer grain added uncertainty rather than differentiated locations. In addition, coastal and marine variables like wind and wave conditions were potentially better predictors for Western Snowy Plover than precipitation and temperature.

We assembled a historical dataset from NOAA Western Regional Climate Center terrestrial data and National Buoy Data Center marine data for 42 weather stations located roughly from San Francisco to San Diego, CA *(Table 1)*. Annual mean values for wind speed, wave height, air and sea temperature, and precipitation were calculated. Data were analyzed to determine correlations regionally and by analysis area. Some

VARIABLE (continuous)	UNIT	SOURCE	CITATION
distance from coast	meters	vector data	Page and Stenzel 1981; Wilson-Jacobs and Meslow 1984; Palacios et al. 1994; Powell 2002; Hubbard and Dugan 2003; CDPR 2005; Sandoval 2005a, b; M. Colwell, pers. comm.; H. Gellerman, pers. comm.; G. Greenwald, pers. comm.; J. Iwanicha, pers. comm.; C. Sandoval, pers. comm.
elevation above sea level	meters	DEM	Persons 1995; CDPR 2005; Sandoval 2005a,b; U.S. Navy 2006c
slope gradient	%	DEM derived	Palacios et al. 1994; Powell 1996; Wehtje and Fahy 2000; Hubbard and Dugan 2003; Elliott-Smith et al. 2005; M. Colwell, pers. comm. ; C. Sandoval, pers. comm.
distance from stream/waterbody	meters	vector data	Page and Stenzel 1981; Page et al. 1995; Wehtje and Fahy 2000; Colwell 2005, 2006; Fancher et al. 2005; Orr 2005
distance from major river	meters	vector data	Page and Stenzel 1981; Page 1988; Perry 1994; Wehtje and Fahy 2000; S. Harvill, pers. comm.
air/sea temperature	°C	point interpolation	C. Sandoval, pers. comm.
wind speed	kmph	point interpolation	Persons and Applegate 1996; Applegate and Schultz 1999, 2003; Wehtje and Fahy 2000; Larson 2001; U.S. Air Force 2003; CDPR 2005; Orr 2005; C. Sandoval, pers. comm.
wave height	meters	point interpolation	Persons 1995; Applegate and Schultz 1999; U.S. Air Force 2003; CDPR 2005; Orr 2005; C. Sandoval, pers. comm.

TABLE 1. Continuous environmental variables used for habitat suitability models.

associations were intuitive: wind speed, wave height, and precipitation were positively correlated with latitude; and temperature was negatively correlated. Results by analysis area were quite different: wind speed, wave height, and temperatures were not correlated at this scale and were identified as individual predictor variables. Data points for mean air and sea temperature, mean wind speed, and mean wave height were exported and regional grids at 100-m resolution were interpolated by inverse distance weighting, with outlier points added for smoothness. Raster grids were mosaicked, clipped, downsampled to 10-m resolution, and smoothed by filtering.

2.4.2 Categorical data variables

Qualitative and quantitative data derived from remotely sensed imagery are now a common input for statistical and GIS-based avian habitat suitability models at multiple scales (Hatten and Paradzick 2003; Gottschalk et al. 2005). Coastal features in RU5 were qualitatively classified from two complementary sets of very-high-resolution color aerial imagery. The California Coastal Records Project (CCRP) (Adelman and Adelman 2002–2010) is a compilation of photographs of the mainland coast taken from a helicopter paralleling the shoreline. Their recent images overlap

FIGURE 8. Beach characteristics at Oso Flaco Creek, central CA dune complex, CA-83. Above image is an oblique CCRP photo (© 2002-2010 Kenneth and Gabrielle Adelman, California Coastal Records Project, *www.californiacoastline.org*). Top-right corner image is a screen shot from NAIP imagery.

slightly for continuity, and indicate geographic coordinates of the camera. Six or seven time-series comparisons were available. Color satellite images at 1-m resolution were available from the National Agriculture Imagery Program (NAIP) (United States Department of Agriculture 2005) as composite mosaics.

Two environmental variables could only be categorical data: landward boundary and beach substrate. Based on literature (e.g., Page and Stenzel 1981; Wilson-Jacobs and Meslow 1984) and expert biological opinion, we ranked land-ward boundary types by suitability: barrier beach, sandspit, or estuary (very high); dune-backed

Beach width fluctuated seasonally and annually (Griggs et al. 2005; Revell and Griggs 2006) and inclusion was problematic. Width above the wrack zone was first GIS-estimated: the vector coast was the mean higher high water line and DEM defined elevation change. Next, remote sensing software classified land cover type from the 1-m NAIP imagery to identify beach substrate and to potentially devise width calculations. Neither quantitative method was adopted. Beach width became qualitative, acceptable given the dynamic environment, and we assigned suitability values: <50 m (medium); 50-100 m (high); >100 m (very high).

Classification methods were subjective but consistently applied (by one person). Except for the Channel Islands, which only used NAIP data, both sets of images were compared for the full study area. Landward boundary and beach substrate were classified primarily with oblique CCRP images; beach width was classified mainly with NAIP imagery *(Figure 8)*.

Landward boundary and substrate at the center of CCRP images were coded and recorded with geographic coordinates. As image classification progressed southward, interpretive methods were maintained but more efficient methods were devised to align CCRP images with features, enter GIS data, and interpolate rasters. The vector coast was aligned with reprojected NAIP imagery and USGS topographic maps, which became collateral data to align CCRP and NAIP images and to estimate beach width. Points were generated 100 m apart, and 10,000 selected by a 150-m coastal buffer as sample data points. Assigned values derived from images were recorded for features at those points. Qualitative features were assigned numerical habitat suitability values as described in *Table 2*. Points were buffered at 250 m for landward boundary; 100 m for beach substrate, beach width, and another layer merged with width that captured dune and river sand outside the 150-m coastal strip. Buffers were rasterized, mosaicked, and then filtered to smooth values.

(high); bluff-backed or scrub (medium); and cliff-backed (low). Beach substrates were similarly ranked: sand (very high); sand/gravel (high); sand/rocks (medium); rocks/gravel (low); rocks (not suitable). Landward boundary types were probably stable over historical time, unless modifications were made. Beach substrates were altered by severe storms but generally maintained type.

VARIABLE (categorical)	CLASSIFICATION	SUITABILITY	HSV*	CITATION
1) dunes/beach width	< 50 meters	medium	0.5	Page and Stenzel 1981; Hutchinson et al. 1987; Stern et al. 1991; Perry 1994; Powell and Collier 1994; Applegate and Schultz 1999; Orr 2005; R. Glick, pers. comm. C. Sandoval, pers. comm.
	50-100 meters	high	0.75	
	>100 meters	very high	1	
2) landward boundary	cliff-backed	low	0.25	Page and Stenzel 1981; Wehtje and Fahy 2000; Persons and Ellison 2001; M. Colwell, pers. comm.; M. Ruane, pers. comm.; C. Sandoval, pers. comm.
	low bluffs/scrub	medium	0.5	
	dune	high	0.75	
	estuary, sandspit	very high	1	
3) beach substrate	rocks	none	0	Willett 1912; Howell 1917; Page and Stenzel 1981; Wilson-Jacobs and Dorsey 1985; Stern et al. 1991; Palacios et al. 1994; Powell and Collier 1994; Tuttle et al. 1997; Persons and Ellison 2001; Marriott 2003; C. Sandoval, pers. comm.
	rocks/gravel	low	0.25	
	rocks/sand	medium	0.5	
	gravel/sand	high	0.75	
	sand	very high	1	
*New HSV assigned to sample points generated 100m apart; points buffered, rasterized, filtered				

TABLE 2. Categorical environmental variables used for models and their associated classification and suitability.

2.5 FUZZY PROCESSING OF ENVIRONMENTAL VARIABLES FOR DEDUCTIVE MODELS

The continuous-value environmental variables (elevation, slope, distance, climate) were processed further before they were included in our deductive models. Fuzzy processing was based on the logic of fuzzy set theory (Zadeh 1965). In classical set theory, an element either does or does not belong to the set. Set membership is assessed in 0/1 binary terms (0 = does not belong; 1 = does belong). This is also referred to as a crisp set. Fuzzy sets are sets or classes without sharp boundaries, whose objects have degrees of membership along a continuum of values in the real number interval [0, 1], indicating a continuous increase from non-membership to complete membership. Gradual membership of set elements is a transition described by a fuzzy membership grade function, where values range from 0.0–1.0 (Zadeh 1965; Hill and Binford 2002; Eastman 2006). This is also called the "possibility."

Our deductive environmental niche-based models describe the potential suitability of a given geographical location in RU5 to serve as habitat for Pacific Coast Western Snowy Plovers on a 0–1 scale. Model outputs were interpreted as the possibility, not the statistical probability, that the location represented by that 10-m pixel was similar to optimal conditions. When gradients rather than absolute thresholds define a species' response to environmental variables, fuzzy categories rather than discrete boundaries more logically represent ecological niche concepts. This approach integrates non-stochastic uncertainty, thus Western Snowy Plover habitat choices are intentional, not a random event (Hill and Binford 2002; Araújo and Guisan 2006). Fuzzy components were part of USFWS HSI models for multiple species (Schamberger et al. 1982; Hill and Binford 2002; Busby 2002). Fuzzy climate-envelope models were used to predict distributions of invasive alien plants and indigenous insects (Robertson et al. 2004).

Based on information about Pacific Coast Western Snowy Plover habitat preferences from the literature, along with expert opinion about their ecological requirements, the relative suitability of particular environmental variables as habitat were quantitatively defined and converted into "factors" prior to deductive model input. Original environmental variables expressed values as ini-

tially derived, and were not scaled with respect to the model, while a factor was standardized or numerically scaled to a specific range within 0–1 by using a fuzzy-logic procedure that directly related original values to relative suitability (Eastman 2006). This approach to modeling directly addresses the concern that many theoretical models of species' distribution do not consider the ecology of the species being modeled when environmental and biotic factors are incorporated (Austin 2002, 2007; Guisan et al. 2006).

Western Snowy Plovers in RU5 are at the center of their geographical range at a confluence of optimal values along multiple environmental gradients. Values were set specifically for RU5, with the intent to provide general predictions for a heterogeneous landscape-scale region. A species' response to these gradients is a modeled as a series of response curves whose patterns are related to its fundamental niche. Three general types of ecological gradients (Austin and Smith 1989; Guisan and Zimmermann 2000) contributed to models: resource gradients that addressed energy actually consumed (e.g., distance from food source or distance from water); direct gradients, environmental parameters not consumed but physiologically important (e.g., wind speed, wave height); and indirect gradients that directly affected habitat without physiological relevance (e.g., elevation, beach width).

2.5.1 Fuzzy environmental variables

Processing was done within Idrisi GIS software (Clark Labs 2006). Fuzzy-set membership functions in the FUZZY module produce sigmoidal, J-shaped, linear, or user-defined curves. Definition of the relationships between original variables and new factors, and selection of parameters for individual variables was based on information obtained from the literature. Exactly which function was used depended on the availability of information to infer fuzzy membership, and on the relationship between the criterion and the decision set (Eastman 2006). Function inflection points *(Table 3)* defined fuzzy-set curves, and

ENVIRONMENTAL VARIABLES (Unit of Measurement)	FUZZY SET FUNCTION (Curve Shape)	INFLECTION POINTS (Original Value)	NEW HSV
1) distance from coast *(meters)*	user-input	0	0.75
		50	1
	linear increase	100	1
	then decrease	500	0.5
2) elevation *(meters)*	user-input	-30	0
		-0.0000001	1
	linear increase	0	0
	then decrease	0.0000001	1
		30	0
3) slope gradient *(percent)*	user-input	0	0.75
		2	1
	linear increase	6	1
	then decrease	10	0.75
		15	0.5
		25	0
4a) distance from water *(meters)*	sigmoidal	0	1
	monotonic decrease	500	0
4b) distance from major river *(meters)*	J-shaped	0	1
	monotonic decrease	1000	1
	to asymptote	1500	0.5
4a) + 4b) distance from (water + major river) *(HSV adjustment)*	user-input	2	1
		1	0.95
		0.75	0.75
		0.0001	0
5) air/sea temperature *(mean, degrees C°)*	linear	12	0.75
	monotonic increase	16	1
6) wind speed *(mean, km per hour)*	J-shaped	0	1
	monotonic decrease	10	1
	to asymptote	25	0.75
7) wave height *(mean, meters)*	J-shaped	0	1
	monotonic decrease	0.75	1
	to asymptote	2.5	0.75

TABLE 3. Final fuzzy layer parameters used for deductive (Idrisi) model.
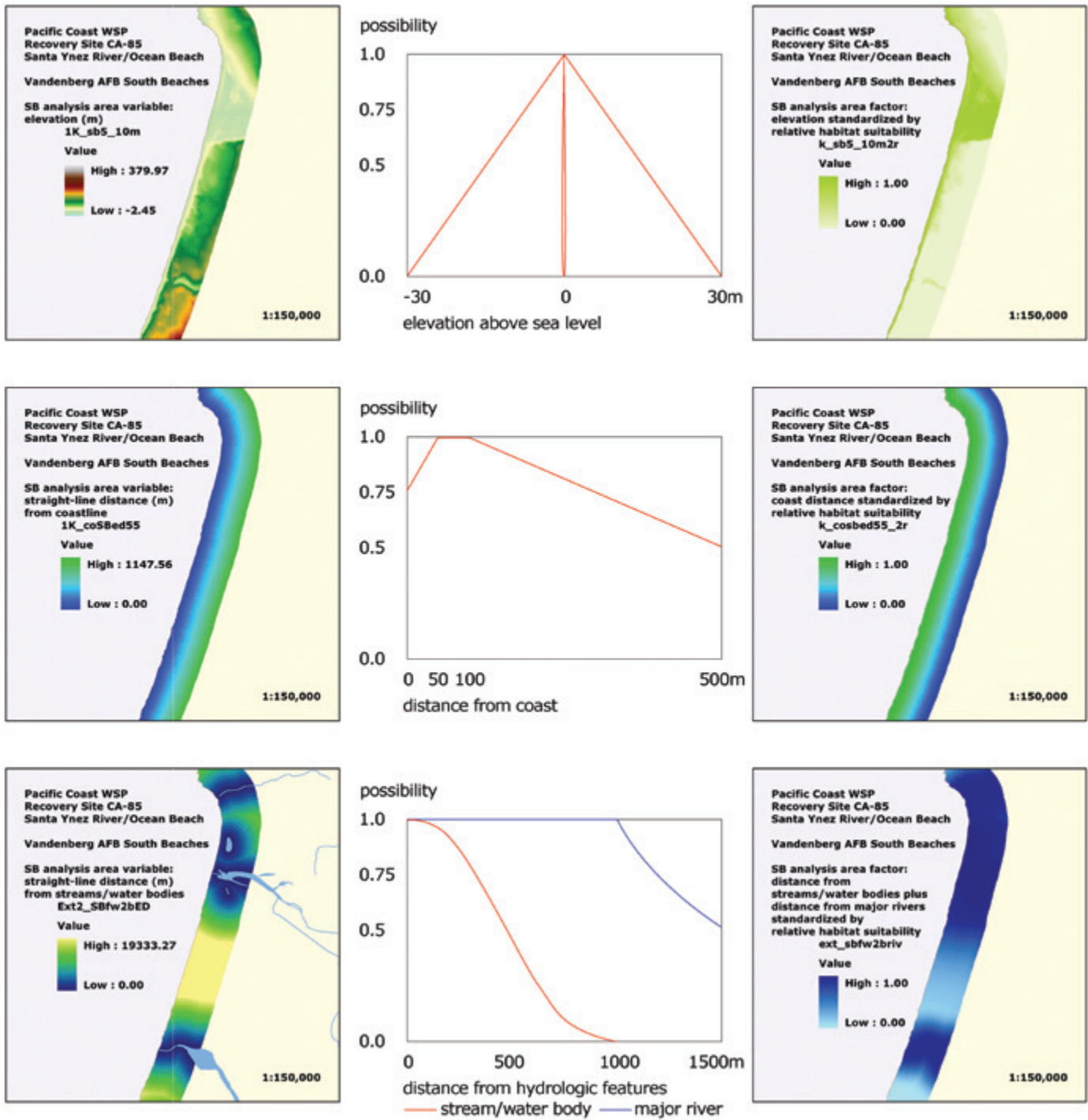
FIGURE 9. Figures on the left represent variables with values in meters: elevation above sea level, distance from coast, distance from hydrologic features. Center graph represents fuzzy-set membership function (curve) applied to each layer. Figures on the right represent new factors with HSV scaled 0–1.

corresponded to environmental variable values chosen for their inherent ecological meaning. Higher values (within the 0–1 range) represented higher suitability, with an optimal HSV of 1.0.

Figure 9 illustrates the process used to create the factors or fuzzy layers. Figures on the left represent three original variables: elevation above sea level, distance from the coast, and distance from streams/water bodies. The graphs represent fuzzy-set curves applied to variables: original values are on the x-axis, and new values are on the y-axis. Figures on the right represent new factors with their HSV scaled between 0–1. For example, in the "distance from coast" panel (9b) it was assumed (based on the literature) that suitability within the intertidal zone increased with distance from a value of 0.75 at the mean high higher water coastline and peaked between 50–100 meters. This maximum suitability range received a 1.0 value. Suitability then decreased linearly to 0.5 at 500 m inland from the coast and to 0.0 at the study area boundary. "Elevation above sea level" (9a) was also linear. The 0.0 value at 0 m was ocean level; some terrestrial habitat is below sea level. "Distance from hydrologic features" (9c) combined two decreasing functions, sigmoidal (streams/water bodies) and J-shaped (major rivers).

2.6 DEDUCTIVE MODELING APPROACH

We used Idrisi GIS software (Clark Labs 2006) to create our deductive models. For each analysis area (SLO, SB, VEN, NCH), ten environmental variables standardized along 0.0–1.0 gradients were combined using multi-criteria evaluation (MCE). Three were categorical variables, *Table 2*; and seven were continuous data, first derived from raw values and then processed as factors with fuzzy values, *Table 3*. A single habitat suitability value was calculated for each geographical location represented by a raster pixel. MCE procedures were designed for use without model training data (e.g., known nest sites) in situations where research studies exist to guide model development (Eastman 2006).

Raster-based GIS may employ several MCE decision-making strategies. Boolean overlays are extreme forms that reduce variables to binary statements (0/1 = unsuitable/suitable). The logical operators AND (intersection) or OR (union) combine layers. Logical AND is very cautious: a pixel must meet every criterion, or it is excluded from consideration. Logical OR produces the opposite result: the pixel will be included if only one layer has an acceptable value. The approaches differ in type and degree of risk that the decision will be "wrong." Binary layers or discrete thresholds may also be constraints to exclude areas from consideration. Locations farther than 1 km inland were masked to achieve a similar result.

Factor-weighted linear combinations are standard GIS MCE techniques to combine rasters. Analogous to coefficients in an equation, relative weights are assigned to individual factors prior to aggregation, typically with pair-wise comparisons between variables. While some criteria were potentially more influential in determining habitat suitability for Western Snowy Plovers, evidence in the literature did not support a scheme to rank specific factors by degree of importance. Application would have introduced additional subjectivity and uncertainty. Standardized factors were instead weighted identically (ten layers, each with weight 0.1).

An additional set of weights was applied on a pixel-by-pixel basis to factor HSV scores as determined by rank order (1–10, low to high value) across factors at each location (raster pixel). Order weights controlled layer aggregation and allowed model results to fall along a continuum between logical AND and logical OR. With environmental variables represented as fuzzy sets, AND/OR logic was implemented as the extreme minimum or maximum value at a given location. The traditional fuzzy-set operation, logical AND, was evaluated as the minimum value for a pixel across all factors. A high aggregate score was possible only when all factors had high scores. This minimized the area selected as suitable and the risk-level of the prediction. Logical OR
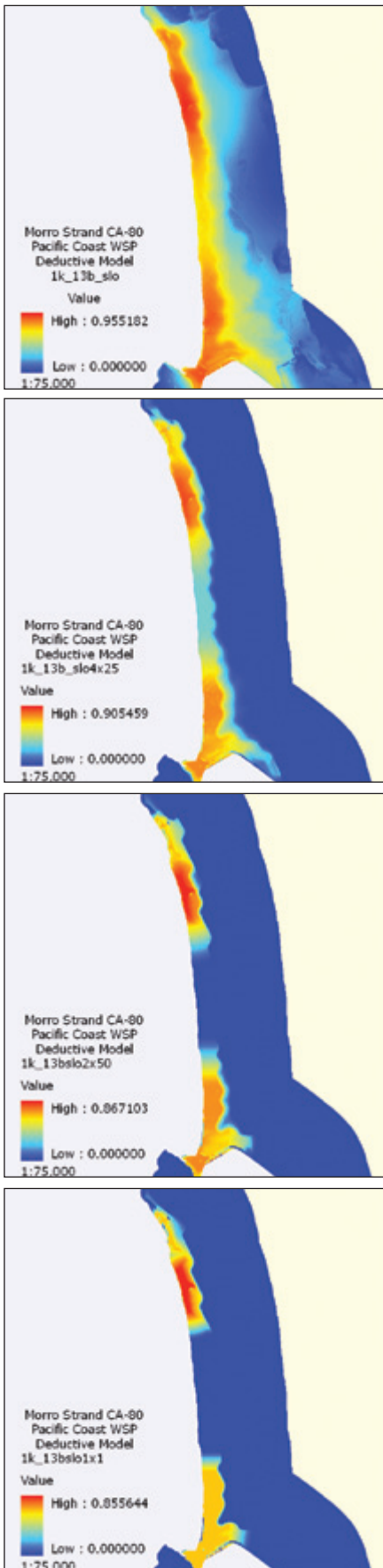
FIGURE 10. Diagram showing deductive model progression with minimization.

returned the value of the single most suitable factor to determine the aggregate score, thus maximized the area chosen as suitable. The degree to which order weights were evenly distributed (or not) controlled the overall tradeoff between factors. Risk level was affected by the relative position and skew of order weights.

Models were linear combinations of information from environmental variables derived by multiplying the standardized value (HSV scaled between 0–1) of each 10-m raster cell within a layer by its factor weight, then applying an order weight to each pixel, and then aggregating layers. Our primary deductive models were linear combinations with equal factor weights and equal order weights, where all factors could tradeoff and compensate for one another. This produced solutions or predictions with an average level of risk, defined as midway between AND and OR extremes (Hill and Binford 2002; Eastman 2006).

Alternative deductive models were developed by varying the number and value of order weights applied pixel-by-pixel to the same equally-weighted factors, which provided other possible solutions. These ranged from the middle-ground prediction used in our primary models to true fuzzy-set minimization. For example, *Figure 10* shows four alternatives in close-ups at recovery site CA-80, Morro Strand State Beach. In the first figure on the left, all factors are weighted equally. The series progresses by amount of minimization applied by order-weighting the factor values at each pixel prior to aggregation. The amount of suitable area and overall HSV decreased with each option, while "hot spots" predicted to have the "best" habitat become more apparent. We do not present site-by-site results for all minimization models, but we compare those from the least restrictive option we tried (corresponding to the second figure in the series) with our primary model.

2.7 INDUCTIVE MODELING APPROACH

We used Maxent species distribution modeling software (Phillips, Dudík, and Schapire 2004; 2009) for the inductive modeling process. All inductive models require presence data (e.g., known species' occurrences). While presence/absence data are necessary for traditional statistical methods, many new techniques (Guisan and Zimmermann 2000; Elith and Graham et al. 2006) have been developed to accommodate

presence-only data. Climate envelopes (Busby 2002; Pearson and Dawson 2003) use presences only; genetic algorithms (GARP, Stockwell and Peters 1999; Peterson 2001) and ecological niche factor analysis (ENFA, Hirzel et al 2002; Engler et al. 2004) generate "pseudo-absences" (Graham et al. 2004; Rushton 2004); other types model species' presence against "background" data (Brotons et al. 2004). Several logistic regression based methods correct for the possibility of true presences in the background, including generalized additive models, boosted regression trees, and multivariate regression splines; other techniques with high predictive ability are machine-learning methods like random forests, artificial neural networks and maximum entropy approximation models (Elith and Graham 2009; Phillips et al. 2009).

Maximum entropy methods are parametric, maximum likelihood techniques derived for statistical mechanics, with other applications in astronomy and investment optimization (Phillips et al. 2004). The process derives the model that best fits the data and is similar conceptually and mathematically to the Akaike Information Criterion (AIC) for model selection (Burnham and Anderson 2003). It has been described as modeling the probability of covariate predictor variables conditional on species' presence (Elith and Graham 2009).

Maxent is a machine-learning method that estimates species' distributions using sample data to train models. Very generally, the algorithm converges during training iterations (~1000 in our models) to the optimal "distribution of maximum entropy" (the most spread out or closest to uniform), subject to the constraint that derived values of environmental variables under this distribution are expected to closely approximate their average value over the sample sites (Jaynes 1957; Phillips et al. 2006). "Regularization" parameters lessen model complexity and avoid over-fitting the models to the data (Phillips and Dudík 2008).

Like the deductive models, the inductive models expressed habitat suitability of a pixel that represented a geographic location as a function of environmental conditions at that site. Environmental variables (eight continuous data, Table 1; three categorical data, Table 2) differed from the deductive model input in that continuous data variables (DEM-derived, distance, and climate) were non-standardized real-number values as originally derived from measurements, not the standardized fuzzy-set factors.

These models input nest site (x,y) coordinates with the variables to predict a geographical distribution to correspond to an ecological niche. While the ideal situation would be to have one dataset with which to calibrate models, and a different independently-sampled dataset to evaluate the models, it is common to split presence-only data into sets of training points and test points. Nest data were randomly partitioned after duplicate points within pixels were removed. Specified percentages of training and test points were generated for model replicates by subsampling without replacement. Final models used 50% for training and set aside 50% for testing. "Sample predictions" made by the software assessed environmental variable values at training points first, then acquired values for randomly generated "background" points within the coastal strip. Background points, although called "pseudo-absences," were not implied species' absences, but instead indicated the set of environmental conditions available in the modeled region.

Based on the values predicted at sample and background points, software-fitted functions derived "features" from the environmental variables to extend the predictions. Functions could alternatively be specified or constrained based on prior knowledge. Continuous data functions produced five feature types: linear, quadratic, and product features to constrain means, variances, and covariances of variables to match the empirical values; thresholds analogous to Boolean constraints; and "hinge" or piecewise features to model complex relationships (Phillips and Dudík

2008). As an option, categorical data quantifying degrees of a property (e.g,, rocky to sandy beach substrate) could be modeled as if continuous (Phillips et al. 2006), but better results were achieved with categorical data treated as such.

Model outputs were a single value for each geographical location represented by a raster pixel. Actual output was an exponential function that assigned probability to a site during model training, and was presented in three formats. Raw values, scale-dependent upon background points, summed to one over the entire predicted area and were extremely small. Cumulative values were defined in terms of omission rates. A logistic format output scaled comparably to our deductive models became available in later Maxent versions.

Logistic output (0.0–1.0) is an estimate of probability of presence, conditional on the environmental conditions. Higher numbers meant a higher predicted probability of species' occurrence: 1.0 is most suitable. A value greater than 0.5 meant the species was predicted to be present with higher probability than at sites with typical conditions; a value of 0.5 had average log probability and could be interpreted as being suitable as a typical occurrence point, but not necessarily with perfect conditions (Phillips and Dudík 2008). Alternatively, logistic output may be interpreted as the relative suitability of a location.

We created models first for mainland areas (SLO, SB, VEN) with Western Snowy Plover nest-presence data. For the northern Channel Islands (NCH), with no nest data, two methods were tested. First, NCH and adjacent Ventura (VEN) rasters were merged and VEN points input. Second, Maxent models could be generated then projected onto alternate environmental variables, with predictions constrained to within the range of the data used to train the models. Projections have other applications (e.g., climate change scenarios) but here they shifted predictions to a new geographic region. Models derived from Santa Barbara (SB), with the widest array of mainland conditions and the most point-data, were projected to NCH layers with even more environmental variability; these were the two largest regions modeled.

2.8 STATISTICAL METHODS FOR MODEL EVALUATION AND COMPARISON

Given the profusion of environmental niche modeling techniques, it is not surprising that various methods produce quite different results (Elith and Graham 2009), or perform better or worse with particular datasets (Elith and Graham et al. 2006; Pearson et al. 2006; Guisan et al. 2007; Peterson et al. 2007; Wisz et al 2008), or that numerous techniques exist to evaluate these models (e.g., Boyce 2002; Fielding 2002; Anderson et al. 2003; Burnham and Anderson 2003; Segurado and Araújo 2004; Allouche et al. 2006; Araújo and Guisan 2006; Barry and Elith 2006; Hirzel et al. 2006; Raes and ter Steege 2007).

For applied research, model evaluation metrics should depend on study goals and the usability of the model rather than statistics alone (Guisan and Zimmermann 2000). These deductive and inductive models were designed to predict historic and potential breeding-season habitat for Pacific Coast Western Snowy Plovers within USFWS Recovery Unit 5. Statistical evaluations of models address whether these specific objectives were achieved.

2.8.1 Evaluation and comparison with beach window-survey site polygons

Relative habitat suitability had the value range of 0.0–1.0 and was expressed as either a possibility (deductive models) or a likelihood or probability (inductive models). The initial and primary criterion for evaluation was to capture all known breeding and wintering sites with a predicted mean habitat suitability value (HSV) of 0.7 or above. This threshold remained through development of multiple suites of both deductive and inductive models. Criteria for model evaluation were the location of window-survey sites rather

than the species' abundance associated with these sites. Window-survey data were intended to provide trends for range-wide comparison to ascertain progress of snowy plover recovery rather than to be used for site-by-site comparison.

Digitized polygons of the 73 window-survey sites along with inland coastal buffer zones of 150-m for each analysis area were used to clip and extract summary statistics from HSV rasters produced by the models. We used these to evaluate models and to compare the deductive and inductive models. Summary statistics of HSV by pixel by site were used in multiple comparisons. These data were used to assess whether predicted HSV at window-survey sites exceeded the 0.7 threshold established prior to modeling; to rank predicted site suitability by model output; to compare predictions at window-survey sites with values for the entire coastline; to compare results of several versions of inductive models with and without considering the predictor variables; and to compare the predictions of deductive and inductive models at sites where Pacific Coast Western Snowy Plovers were known to be present.

2.8.2 Evaluation with known nest locations: deductive models

Nest points used to generate the inductive models and evaluate the deductive models were spatially identical sets: the same nests flagged as duplicates within the 10-m pixels were excluded. We expected that nest locations would have higher predicted mean HSV than non-nest locations. To test this, the predicted HSV from the deductive model raster cells were extracted to nest points, and tables of points for each polygon (survey site) were exported. Rasterized points were used to create no-data raster masks to extract values of non-nest pixels. HSV for nest and no-nest pixels were aggregated by site. Site combinations were made to include areas without nest data contiguous to sites with data. Histograms were compared visually before nest and non-nest pixel means were tested with an ANOVA.

Some ecological data may not meet assumptions required for powerful statistical analyses. When applied to non-identically distributed non-normal data with non-homogeneous variances, parametric analyses like ANOVA, based on known probability distributions, are problematic. A non-parametric Monte Carlo randomization technique was used in addition to the ANOVA. This method explicitly relaxed the assumption of normality. Randomizations are distributed normally prior to application of a test statistic. Data are randomized and resampled with parameters simulated directly to estimate their distribution. Significance tests are not based on comparisons with F-ratios as in ANOVA. Unlike ANOVA, Monte Carlo tests do not always produce identical results. Nevertheless, they fall within a small range and values compare very favorably with ANOVA test statistics (Gotelli and Ellison 2004).

Randomization was programmed in R (R Foundation 2008). For each test at a given site, the pixels were randomly reassigned to nest (1) or no-nest (0) groups, with the same number of nest/no-nest pixels as in original data. The absolute difference between the observed predicted HSV means (obs m) of nest and no-nest samples $|obs\ m(1) - obs\ m(0)|$ was compared with the absolute difference between simulated HSV means (sim m) calculated 10,000 times $|sim\ m(1) - sim\ m(0)|$. At least five replicate simulation runs were made for each site and site combination. The null hypothesis (H0) under consideration was that the pattern in the data was no different than expected from random sampling, meaning an observed HSV mean different from the simulated HSV mean would not be expected. We chose a one-tailed test because we expected nest locations would have predicted mean HSV greater than non-nest locations. Test statistics calculated were p H0 = n simulations where H0 = true; H0: $|obs\ m(1) - obs\ m(0)| <= |sim\ m(1) - sim\ m(0)|$. The results were directly comparable with ANOVA tests H0: $p > F$; HA: $p \le F$.

Figure 11 is an extreme example of the outcome we expected, from Coal Oil Point Reserve, CA-88.

Model Habitat Suitability Values where WSP nests recorded
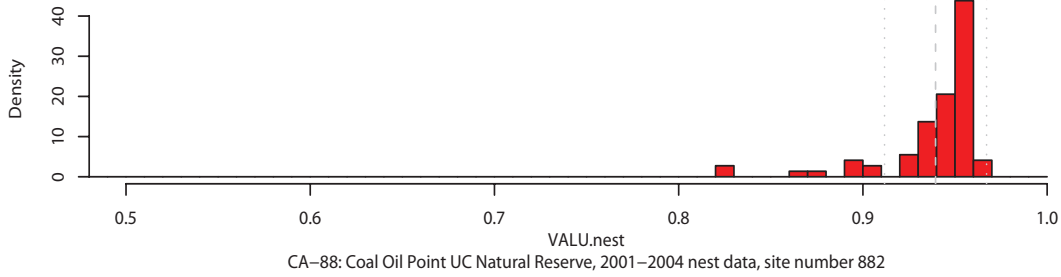
VALU.nest

CA–88: Coal Oil Point UC Natural Reserve, 2001–2004 nest data, site number 882

Model HSV where no WSP nests recorded

VALU.none

Coal Oil Point Reserve, HS Model 1K_13BSB, site number 882

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 73) and non–nest (n = 1569) pixels, Model 1K_13BSB, site number 882
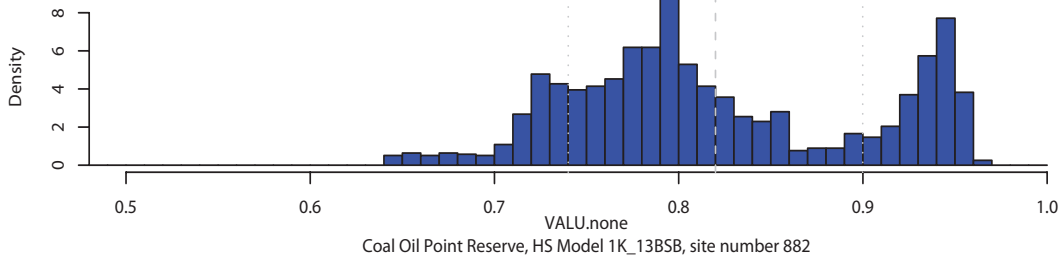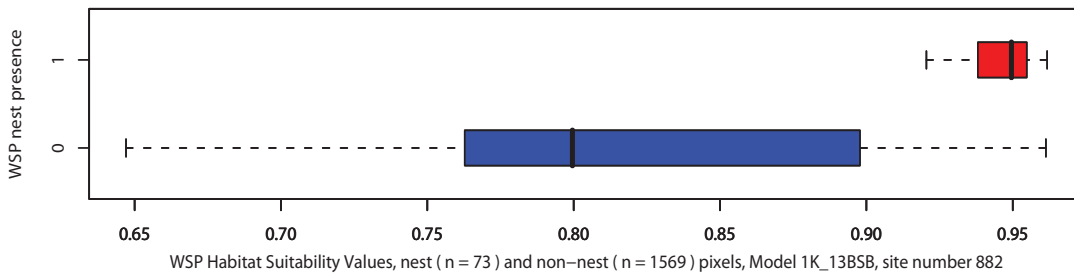
FIGURE 11. Deductive model evaluation with nest locations, a) histograms and box plots show mean HSV at pixels with nests = red, no-nests = blue; b) randomization graph shows observed predicted HSV with simulations = green. Results from Coal Oil Point Reserve, CA-88: higher HSV at pixels with nests, as expected.

Randomization analysis of grouped HSV means

Simulated and observed absolute differences between HSV means, Model 13B
WSP nest (n = 73) and non–nest (n = 1569) pixel groups, site number 882

40

Model Habitat Suitability Values where WSP nests recorded

CA−85: Santa Ynez River Mouth, Vandenberg AFB, S South Beaches, 1994−97, 1999−2000, 2002−06 nest data, site number 853.5

Model HSV where no WSP nests recorded

Santa Ynez River Mouth, Vandenberg AFB, southern South Beaches, HS Model 1K_13B2SB, site number 853.5

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 799) and non−nest (n = 3412) pixels, Model 1K_13B2SB, site number 853.5

FIGURE 12. Deductive model evaluation with nest locations, a) histograms and box plots show mean HSV at pixels with nests = red, no-nests = blue; b) randomization graph shows observed predicted HSV with simulations = green. Results from VAFB, CA-85, southern subset of beaches: only location without higher HSV at nest sites.

Randomization analysis of grouped HSV means

Simulated and observed absolute differences between HSV means, Model 13B2
WSP nest (n = 799) and non−nest (n = 3412) pixel groups, site number 853.5
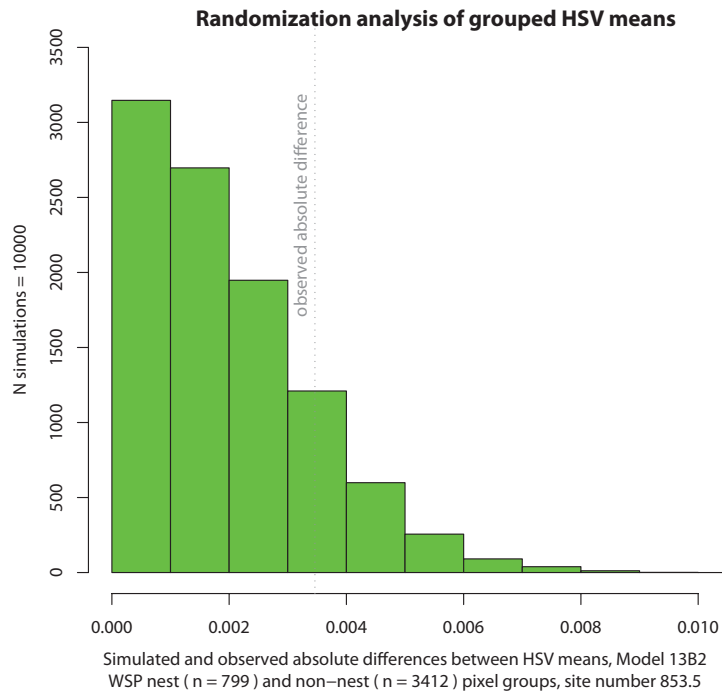
Histograms and box plots *(11a)* illustrate the predicted mean HSV at pixels where nests were recorded (red), and values at no-nest pixels (blue). The randomization graph *(11b)* for one simulation replicate indicates the disparity between the absolute differences between the mean for observed values (grey dashed line, at right) and those for 10,000 simulated differences (green bars). *Figure 12* shows one opposite outcome, from southern Vandenberg Air Force Base, CA-85. Mean HSV are similar for nest sites and no-nest sites *(12a)* but neither the randomization nor ANOVA results were significant at α = 0.05 *(12b)*.

2.8.3 Evaluation of alternative inductive models

Our intent was to develop inductive models with the same environmental data input as deductive models to enable the two types of predictions to be more directly comparable. Inductive model trials were extensive; data combinations were replicated multiple times. Numerous software-generated metrics were produced as integral components of model output, including training and test gain, entropy, and AUC (area under the ROC or receiver operating-characteristic curve). These helped to make comparisons between alternative inductive models and to evaluate the contributions of individual environmental variables.

Regularized training and test gain assessed the likelihood (ln gain ≈ likelihood) of training and test point values (according to the model) as compared with random background points. The gain was related to deviance, a measure of goodness of fit used in generalized additive and generalized linear models (Phillips et al. 2006; Phillips and Dudík 2008). Gain, like entropy, was interpreted as a relative versus absolute measure.

AUC statistics are used extensively to assess a model's ability to distinguish test sites from random sites (Fielding 2002). Test gain values were a better metric to differentiate models here because AUC were consistently high (always > 0.975; usually > 0.99; 1.0 is "perfect"). The region from which background points were selected was narrowed from a 20-km to a 4-km to a 1-km strip because initial models predicted the entire coast as highly suitable (as compared with background points). High AUC values persisted. Given the configuration and scale of the modeled region, further refinement might exacerbate the under-prediction we anticipated might occur in unsampled areas and could exclude potential habitat over and above historic locations farther inland on sand bars. Final models used 50% of the point data for training and 50% for testing models. Later evaluations held aside 90% and 95% of the data for testing; AUC values were maintained with the modified partitions.

As in the deductive models, the objective was a regional, landscape-scale habitat suitability prediction for RU5. Some trials used different predictor variables for each analysis area, based on contributions of individual layers and jackknife results from earlier trials. For example, with eight environmental features, all models used elevation, distance from the coast, wave height, beach substrate and landward boundary, but additional climate data, beach width, distances from streams/waterbodies and from major rivers varied by area. In other trials, the SB area was split at Point Conception into two sets of raster layers, one for the northern west-facing beaches and another for the southern south-facing beaches.

Percentage contributions were calculated for individual variables and interpreted like coefficients. Jackknife or "leave one out" statistics recalculated training and test gain and AUC "with only" and "without" each variable, which gave another comparison of variable performance and interaction. Variables with highest "with only" values provided the most useful information by themselves; those with lowest "without" values had the most data not contained elsewhere. Values were relative, not absolute *(Table 4)* (Phillips et al. 2006).

	SAN LUIS OBISPO	SANTA BARBARA	VENTURA
MAXENT CALCULATIONS			
Regularized training gain	2.138	1.720	2.738
ln gain ≈ likelihood	8.485	5.586	15.468
Test gain	3.556	3.429	3.788
ln gain ≈ likelihood	35.024	30.861	44.170
Test AUC	0.992	0.992	0.991
Entropy	6.416	6.788	6.293
ENVIRONMENTAL VARIABLES % CONTRIBUTED TO MODEL*			
dunes/beach width	4.04	1.41	34.89
landward boundary	7.02	1.80	11.64
beach substrate	23.40	20.54	4.48
distance/coast	10.01	4.63	12.96
elevation	27.33	25.57	5.90
slope gradient	0.55	1.53	0.45
distance stream/water	3.69	0.34	8.66
distance major river	3.60	4.51	4.95
mean air/sea temperature	2.83	1.47	4.13
mean wind speed	0.41	4.84	5.31
mean wave height	17.12	33.35	6.61

VARIABLE JACKKNIFE RESULTS: TEST GAIN**	with only	without	with only	without	with only	without
dunes/beach width	1.65	3.55	1.37	3.38	1.78	3.75
landward boundary	1.65	3.54	1.40	3.40	1.93	3.78
beach substrate	1.67	3.54	1.95	3.40	1.30	3.74
distance/coast	0.88	3.41	1.22	3.33	1.26	3.66
elevation	1.51	3.44	1.29	3.39	1.95	3.75
slope gradient	0.44	3.53	0.21	3.41	0.73	3.75
distance stream/water	0.71	3.53	0.31	3.42	0.82	3.76
distance major river	1.66	3.44	0.68	3.36	1.71	3.73
mean air/sea temperature	1.32	3.52	1.46	3.42	2.02	3.79
mean wind speed	1.32	3.55	1.28	3.39	2.29	3.80
mean wave height	1.28	3.55	1.49	3.41	1.40	3.78

* Percentages sum to 100% and do not include variable interactions. **Jackknife results show test gain recomputed "with only" one variable included and "without" that variable; highest "with only" values provide the most useful information alone; lowest "without" have the most data not found elsewhere.

TABLE 4. Summary of parameters and jackknife tests used to evaluate variables for inductive (Maxent) model development. Values are final composite model means.

2.8.4 Inductive model variability and inductive composite models

Response curves generated by the software for any one environmental-data "feature" in a given area did not vary much between model replicates, probably because our models used many data points for each area (after duplicates were removed, SLO n=1699; SB n=3027; VEN n=710) and the algorithm rarely converged earlier than 1000 iterations. Some software-generated curves produced for "features" by the inductive model functions were visually similar to curves created by specifying inflection points for the deductive

FIGURE 13. Comparison of environmental-data response curves: a) "features" produced by inductive models; b) "factors" created as input for deductive models.
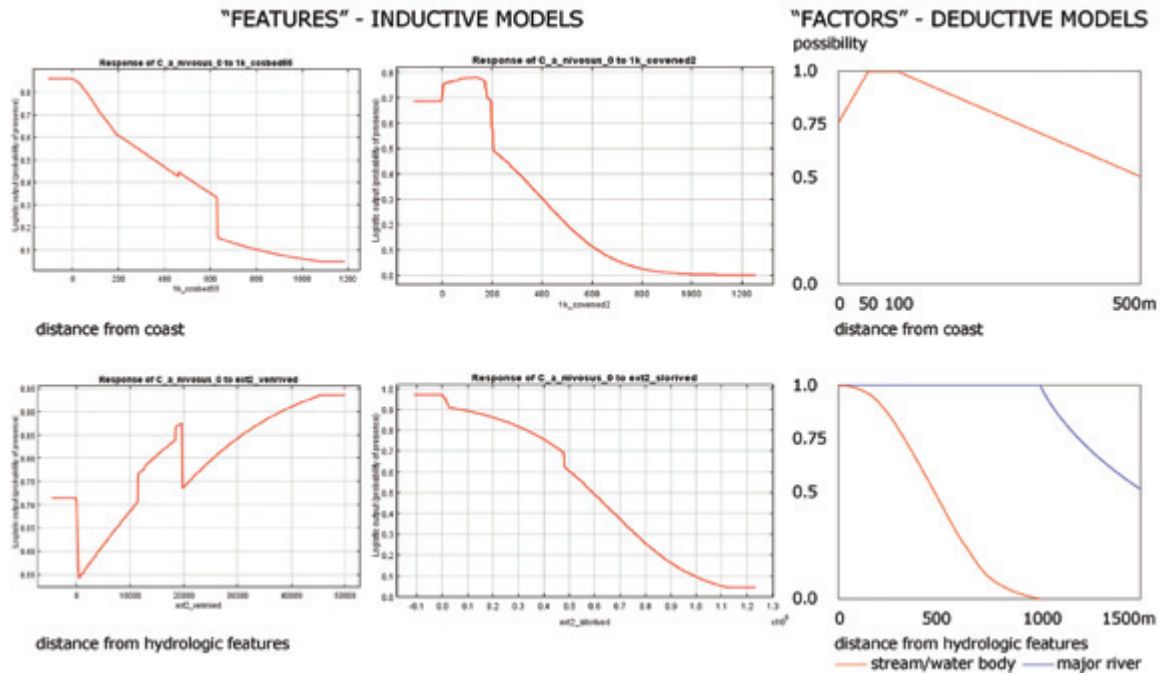
model fuzzy-set "factors"; others, however, were very different *(Figure 13)*. Unlike the deductive model layers, not all the values on which they were based represented optimal conditions.

Our comparisons between model replicates indicated very high variability for predictions at the pixel level. This could affect model quality when replicates were aggregated into composites for each analysis area, and we chose to make composite predictions rather than select an individual "best" model. The variability of the predicted HSV at locations with recorded nest sites was used to estimate the uncertainty of the inductive models. For 50 "final" replicate models for each mainland analysis area (SLO, SB, VEN), random subsets of 50% training and 50% test points were selected by bootstrapping, or subsampling with replacement. The "sample predictions" at test and training points were extracted and pixel-level summary statistics generated for individual models.

ANOVA was used to select a set of models from the 50 to include in composite models, and 15

were chosen for each analysis area. The relatively large number of nest points per area and the inclusion of many models in the ANOVA created statistical tests with thousands of degrees of freedom. We determined that our 15-model composites of inductive model replicates — to be used for comparison with the deductive models — were an acceptable aggregation because although the predictions were highly variable at the level of individual pixels, overall the selected models did not differ significantly ($\alpha = 0.01$) from one another.

We used two summary grids (for each area) to create models. Our primary results used to compare with deductive models were the grid for each area with the pixel value indicating the maximum HSV achieved at that location (from among all 15 models). Our alternative model output was the average (mean) HSV achieved at any one pixel. Model parameters were tuned in response to performance issues and software upgrades. More efficient memory usage (in Maxent 3.3; Phillips, Dudík, and Schapire 2009) let models run more rapidly and let the summary statistics grids (five

rasters built simultaneously) for replicate runs be generated within the software. Prior to this, the program crashed when it accessed completed replicates to compile summary grids, and individual files for each run were instead exported to perform the calculations. Projection of model predictions onto other environmental layers (e.g., applying SB model predictions to the NCH layers which did not have nest-point data), another memory-intensive task, was also supported by this upgrade.

2.8.5 Alternative interpretation for inductive models

"Threshold values" were calculated by Maxent to help evaluate models and results (e.g., thresholds for minimum training point presence, or maximum test point sensitivity and specificity). When applied as intended to results, Boolean presence/absence grids depicted habitat predicted as either suitable or unsuitable. A "low" threshold value (equal to ~10% of the predicted area using cumulative output) was suggested by developers (Phillips et al. 2004), but any value could become the dividing line. Threshold selection is a subjective process (Hill and Binford 2002), and representations of model outcome are very sensitive to threshold application (Whittaker et al. 2005). Potentially, a threshold may compound uncertainty by forming an arbitrary boundary which may have no meaning to the species.

We devised an alternative method to use several thresholds as map-classification breaks. To develop a regional scheme, logistic thresholds generated for individual models used in composites were compared. Thresholds chosen to create breaks were statistically and ecologically relevant values whose means did not differ significantly ($\alpha = 0.01$) across the three mainland areas. A 0.7 HSV was the logical upper class-break because it was also our threshold for suitability and performance evaluation. Locations remote from nest-point data were also mapped using a variant with values shifted much lower.

Given that HSV predictions were unaffected, the supplemental comparisons did not change our model performance evaluation criterion to capture all known Western Snowy Plover sites with a predicted mean HSV over 0.7. By using this classification method *(Table 5)*, however, similarities became apparent between inductive and deductive model results which were less (or not at all) evident when results were directly compared on a 0.0–1.0 continuous scale. This approach recognized that inductive models might differentiate suitable habitat effectively if interpreted in another way, and provided additional validation for deductive results.

LOGISTIC THRESHOLD CALCULATED BY MAXENT	SLO	SB	VEN	HSV CLASS BREAK
10 percentile training data presence	0.664	0.716	0.713	0.7
Equal training sensitivity and specificity	0.448	0.575	0.423	0.5
Equate entropy of thresholded and non-thresholded distributions	0.129	0.116	0.137	0.125
Minimum training point presence	0.053	0.050	0.070	0.05
Prevalence (average of logistic output over background sites)	0.022	0.026	0.021	0.02
Balance training omission, predicted area and threshold value	0.018	0.022	0.017	0.02
Fixed cumulative value 1.0 logistic threshold	0.013	0.009	0.012	0.01
Equate entropy of thresholded and non-thresholded distributions plus training omission	0.002	0.002	0.005	0.005

TABLE 5. Logistic threshold map-classification breaks (expressed as HSV) for alternative inductive maps. SLO, SB and VEN values are means of thresholds calculated for models used in composites.

Our models were designed to predict historic and potential breeding-season habitat for Pacific Coast Western Snowy Plover within USFWS Recovery Unit 5. We developed deductive and inductive models with the same environmental variables to be able to directly compare the two types of predictions. Model outputs with a value range of 0.0–1.0 were expressed as either a possibility (deductive models) or a likelihood or probability (inductive models) that the location represented by that 10-m pixel was similar to optimal conditions.

The primary criterion for model evaluation was the ability to identify all known Western Snowy Plover breeding and wintering sites within RU5 with a predicted mean habitat suitability value (HSV) of 0.7 or above. Results are given first for deductive models, and then for inductive models. Models are then compared.

Predicted HSV are shown graphically as charts and maps and as tabular data. Maps include the full RU5 coastline and larger-scale maps of the individual beaches identified as known, potential, or historical habitat. Results are arranged geographically, north to south. To facilitate their interpretation, discussion of beach-level results and the implications associated with the outcome of the habitat suitability models at particular locations are placed with the maps. Additional quantitative assessments follow, with statistical evaluations of the models presented as tables, charts and graphs.

3.1 RESULTS OF DEDUCTIVE MODELS

Based on environmental variables only, the deductive models quantitatively identified locations of potential Western Snowy Plover habitat. Potential habitat was defined as similarity to optimal conditions. The conditions modeled approximate idealized historical mid-summer breeding-season conditions. Models were validated first by ensuring that all areas classified as potential high quality habitat matched historic

REGIONAL SUMMARY OF DEDUCTIVE MODEL PREDICTED HSV					
area	**Survey site beaches**			**150-m coastal strip**		
	mean	**stdev**	**max**	**mean**	**stdev**	**max**
SLO	0.826	0.048	0.947	0.712	0.112	0.955
SB	0.793	0.056	0.964	0.722	0.104	0.964
VEN	0.899	0.014	0.980	0.839	0.101	0.980
NCH	0.767	0.044	0.935	0.653	0.090	0.935

TABLE 6. Regional summary, habitat suitability values predicted for known RU5 Western Snowy Plover sites as compared with 150-m coastal strip.

and current use locations at window-survey and monitoring sites, and then were evaluated by direct comparison with nest point data.

It bears noting that nesting data from the California Channel Islands have been more difficult to obtain than for mainland beaches. We do not have nest point data available with which to make direct comparisons and evaluations as we did for the mainland. Our results for island sites are presented for each island as a whole rather than as an analysis of the individual beaches. Island sites remain, however, a critical recovery component subject to changing habitat conditions.

3.1.1   Habitat suitability maps of analysis areas

Our deductive models successfully identified areas that are currently occupied by Western Snowy Plovers, or are identified as recovery beaches in the Recovery Plan.

We set values for input environmental variables specifically to provide general predictions for a heterogeneous landscape-scale region. To examine this large area at a comparatively fine scale and make valid assessments at the level of individual beaches, we divided RU5 into four areas. This maintained the integrity of the coastal watersheds, corresponded to the three county jurisdictions on the mainland (SLO, SB, VEN), and grouped the northern California Channel Islands (NCH) together as one similar but very diverse region.

We aggregated survey sites by analysis area to compare their predicted HSV with that of a 150-m "beach-width" strip along the entire coastline. Regional summary statistics were an indicator of how well the model predicted overall habitat quality, and individual variability. *Table 6* lists the mean HSV, standard deviation, and maximum HSV for the beaches and the coastal strip by area. Of the four areas, Ventura (VEN) has the highest maximum (0.980), the highest mean overall (0.839), and the highest mean at survey sites (0.899), with less variability (0.014) than the other areas (0.044–0.056). Mean predicted HSV at all survey beaches was always higher (0.767–0.899) than HSV for any coastline strip (0.653–0.839). For Santa Barbara (SB), the HSV for beach sites (max = 0.964; mean = 0.793) represents stretches of south-facing beaches with high HSV, along with less-optimal habitat. San Luis Obispo (SLO) (max at sites = 0.947; max overall = 0.955; mean = 0.826) also has beaches with moderate HSV, but high values at most other sites, even along the northern rocky coast. The islands (NCH) (max = 0.935) have little high-HSV habitat. The NCH mean HSV for beach sites (0.767) is comparable with SB, but the overall mean HSV is much lower (0.653). NCH site variability (0.044) is a measurement between islands because of site aggregation by island; however, the within-island variability is likely to be higher.

Regional maps give another overview of deductive model results. In northernmost RU5, small high-HSV pocket beaches occur sporadically at creek mouths along a rocky coastline with high cliffs. The model predicts multiple high-HSV
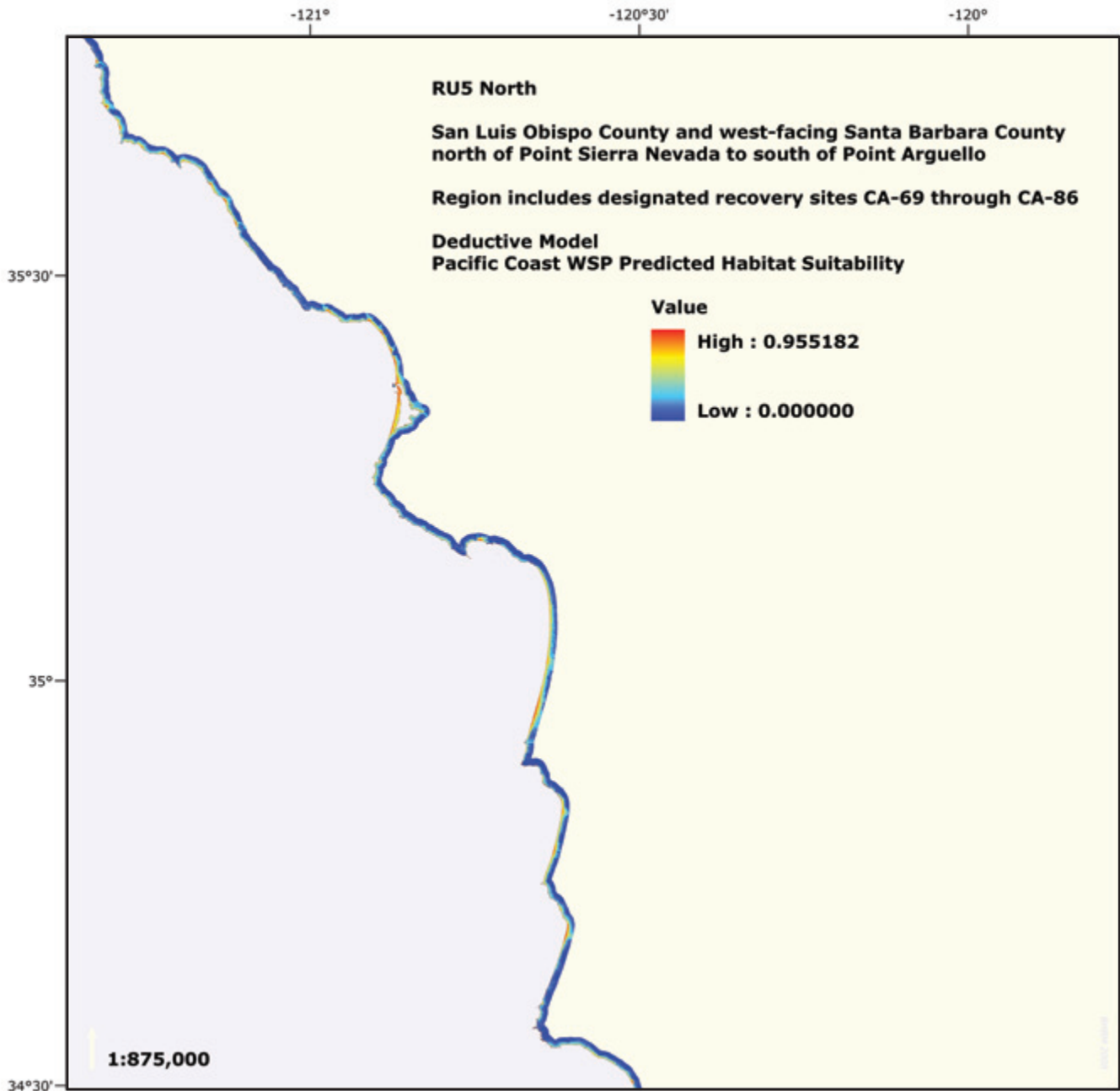
FIGURE 14. Deductive model predicted habitat suitability for northern RU5, San Luis Obispo County and Santa Barbara County west-facing beaches.

sites along Morro Bay. South of San Luis Obispo, the west-facing central California dune complex overall has moderate values, but higher-HSV sites in the north near Pismo Beach and near the Santa Maria River. West-facing beaches farther south have highly variable conditions, with suitable, but not optimal habitat, and highest HSV predicted near the Santa Ynez River. Near Point Conception, beaches are narrow, rocky, and subjected to climatic extremes. Predicted habitat suitability

values for RU5 beaches north of Point Conception are shown in *Figure 14*.

A rocky coastline with some pocket beaches at ephemeral creeks continues for some distance east along the south-facing coast. Stretches of wider, more sheltered sandy beaches occur along the Santa Barbara Channel at perennial creek mouths and sloughs, beginning near Santa Barbara. Past the Rincon Point headlands, beaches
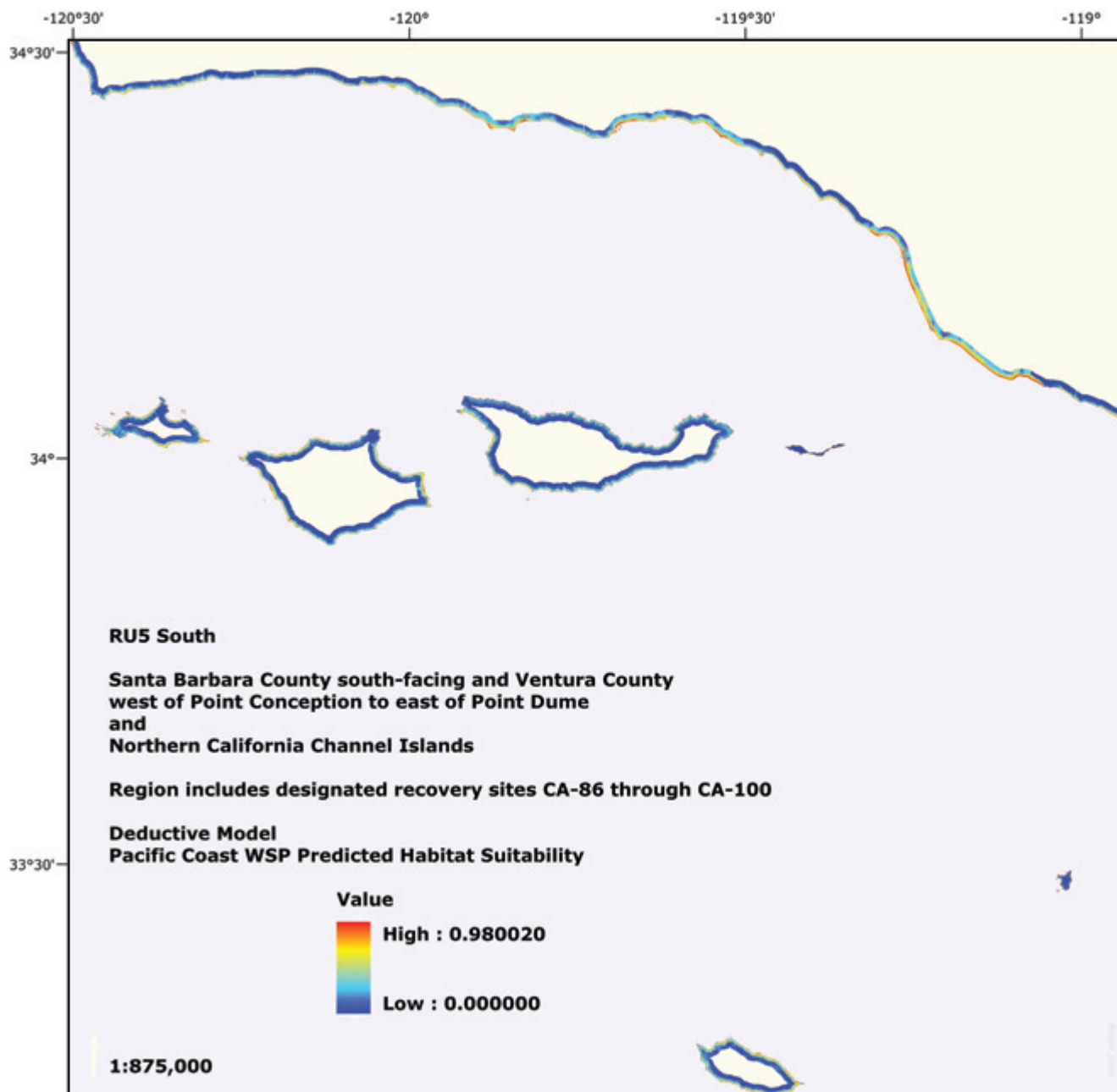
FIGURE 15. Deductive model predicted habitat suitability for southern RU5, Santa Barbara County south-facing beaches, Ventura County beaches, and the northern California Channel Islands.

face south-west. Ventura beaches at the edge of the Oxnard Plain have optimal conditions: they are dune-backed, wide, flat, and sandy. Southernmost mainland beaches of RU5 are at Mugu Lagoon. The northern Channel Islands have limited very good habitat, and substantial rocky coastlines. Predicted habitat suitability for deductive models is shown for the RU5 beaches south of Point Conception in *Figure 15*.

3.1.2 Deductive predictions compared with known survey sites

Deductive models were intended to predict historic and potential habitat for Pacific Coast Western Snowy Plovers. That is, they excluded the effects of current management. They provide estimates of habitat suitability ranging from 0.0–1.0. Our criterion for model evaluation was that all known historic and current sites would

have a mean HSV greater than 0.7. In the resulting models, mean HSV exceeded 0.7 at 71 of 73 sites evaluated, and the two remaining sites had mean HSV values between 0.69 and 0.70.

These sites are identified by established beach names used by window-survey monitors and by numbers (691–1000) we defined for this research. We differentiated beaches based on identified differences in their jurisdiction and management (see Methods). Designated Pacific Coast Western Snowy Plover recovery sites listed in the Recovery Plan (USFWS 2001; 2007a) are identified by CA-site numbers (CA-69–CA-100).

Figure 16 illustrates how sites relate to sub-sites (outlined). At San Carpoforo Creek *(16a)*, recovery site CA-69 directly corresponds to beach 691. At Morro Strand (formerly Atascadero Beach) *(16b)*, CA-80, two sub-sites correspond to Morro Strand State Beach (801) and Morro Rock City Beach (802); the southern portion of Toro Creek, CA-79 (791), is visible at the north. Finally, Santa Barbara Harbor/Point Castillo, CA-90 *(Figure 16c)*, has three sub-sites: West Beach (901), Santa Barbara Harbor (902), and East Beach (903).

We compare the mean and maximum habitat suitability values predicted by our deductive models for individual beach sites within the four analysis areas in the charts below: San Luis Obispo County *(Figure 17)*; Santa Barbara County *(Figure 18)*; and Ventura County and the northern Channel Islands, grouped by island *(Figure 19)*.

Table 7 lists the mean HSV, standard deviation, and maximum HSV predicted for survey sites by our deductive model. Sites are listed north to south. The table indicates (*) the recorded presence of Western Snowy Plovers at specific locations during recent surveys. We interpret these only as geographical locations of beaches Western Snowy Plovers are known to use. Window survey data are snapshots intended to reveal broad population trends, not to measure recovery at individual beaches. Data are from range-
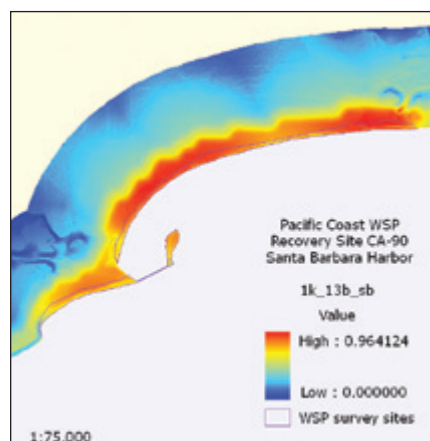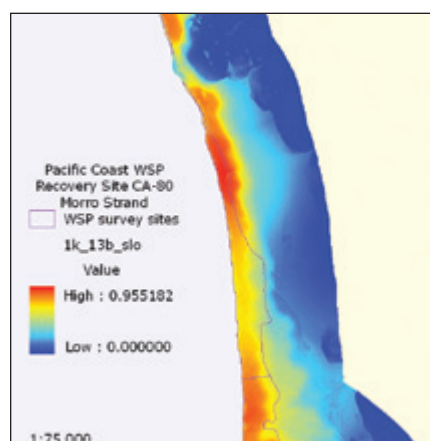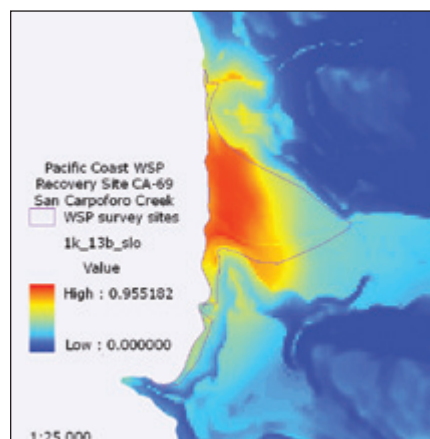
FIGURE 16. Deductive model HSV for designated recovery beaches: a) CA-69, San Carpoforo Creek, b) CA-80, Morro Strand, c) CA-90, Santa Barbara Harbor. Window survey site beaches are outlined.

FIGURE 17. San Luis Obispo County mean and maximum HSV predictions for deductive models. RU5 sites CA-69–CA-83; window-survey beaches 691–837.
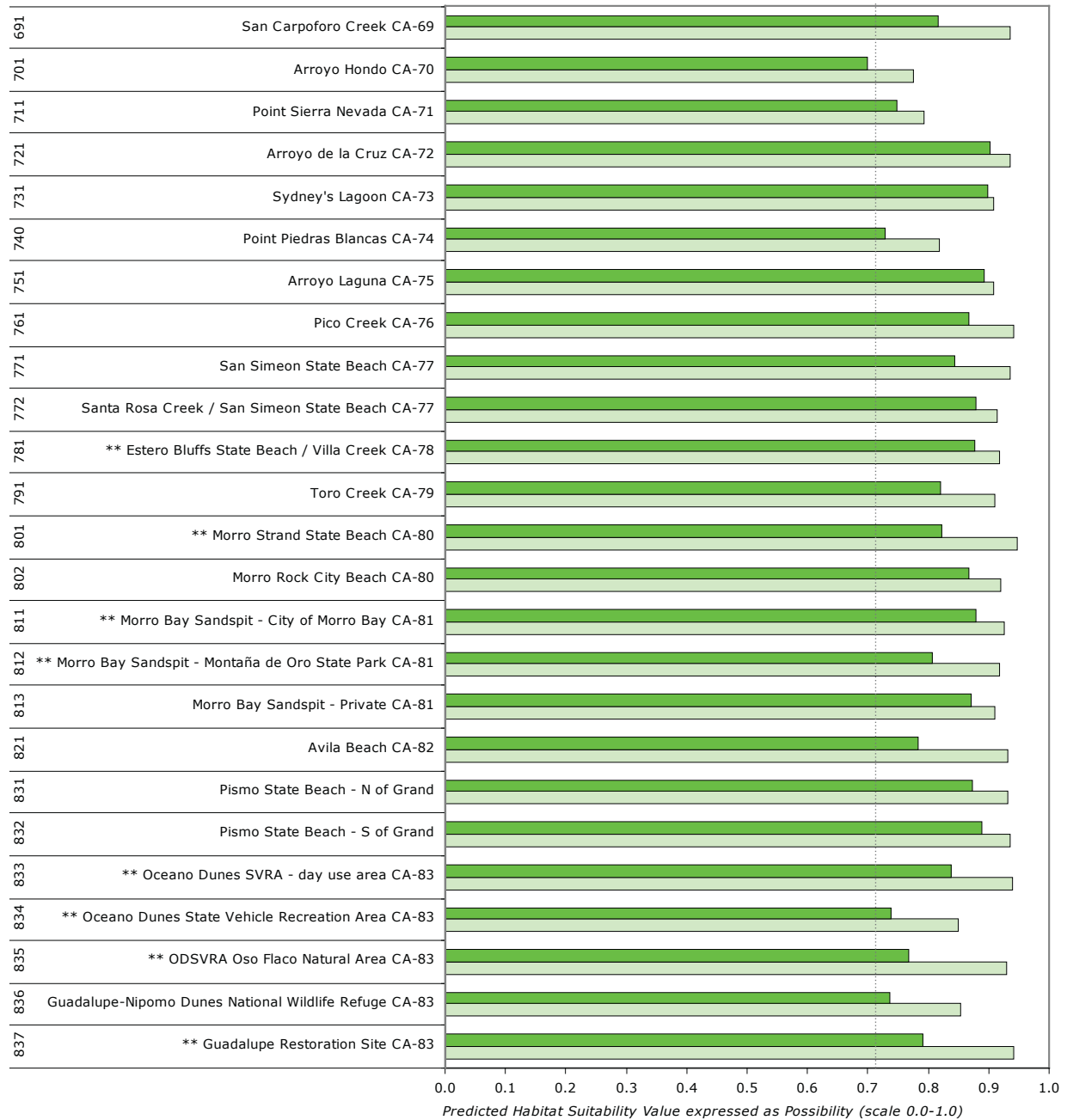
Predicted Habitat Suitability Value expressed as Possibility (scale 0.0-1.0)

■ Mean Habitat Suitability Value predicted within survey site, deductive models.
□ Maximum HSV predicted within survey site, deductive models.
⋯⋯ Mean HSV, San Luis Obispo County 150m coastal zone
** starred sites have nest data available

838	** Rancho Guadalupe Dunes Preserve CA-83	
839	Mussel Rock beach CA-83	
8310	Paradise beach	
8311	Point Sal State Beach	
8312	Brown's beach [local name]	
841	** Vandenberg AFB North - Minuteman open access	
842	** Vandenberg AFB North - Minuteman Beach CA-84	
843	** Vandenberg AFB North - Shuman Beach CA-84	
844	** Vandenberg AFB North - San Antonio Beach CA-84	
845	** Vandenberg AFB North - Purisima North CA-84	
846	** Vandenberg AFB North - Purisima Colony CA-84	
851	** Vandenberg AFB South - Wall Beach CA-85	
852	** Vandenberg AFB South - Surf Beach North (N end) CA-85	
853	** Vandenberg AFB South - Surf Station Beach CA-85	
854	** Vandenberg AFB South - Surf Beach North (S end) CA-85	
855	** Vandenberg AFB South - Surf Beach South CA-85	
861	Jalama County Beach CA-86	
871	Hollister Ranch CA-87	
872	Gaviota State Beach	
873	Refugio Beach State Park	
874	El Capitan Beach State Park	
875	Haskell's Beach	
881	Ellwood Beach	
882	** Coal Oil Point UC Natural Reserve CA-88	
883	Isla Vista Beach	
884	Campus Beach	
891	Goleta Beach CA-89	
901	Santa Barbara West Beach CA-90	
902	Santa Barbara Harbor CA-90	
903	Santa Barbara East Beach CA-90	
911	Carpinteria Spit Beach - Santa Claus Lane	
912	Carpinteria City Beach CA-91	
913	Carpinteria State Beach CA-91	

Predicted Habitat Suitability Value expressed as Possibility (scale 0.0-1.0)

■ Mean Habitat Suitability Value predicted within survey site, deductive models.
□ Maximum HSV predicted within survey site, deductive models.
⋯⋯ Mean HSV, Santa Barbara County 150m coastal zone
** starred sites have nest data available

FIGURE 19. Ventura County and Northern California Channel Islands mean and maximum HSV predictions for deductive models. RU5 mainland sites CA-95–CA-99; window-survey beaches 951–995; RU5 island sites CA-92, CA-93, CA-94 and CA-100; window-survey beaches 920–1000 grouped by island.

- ■ Mean Habitat Suitability Value predicted within survey site, deductive models.
- ■ Maximum HSV predicted within survey site, deductive models.
- ⋯⋯ Mean HSV, Ventura County 150m coastal zone ⋯⋯ N CA Channel Islands 150m coastal zone
- ** starred sites have nest data available
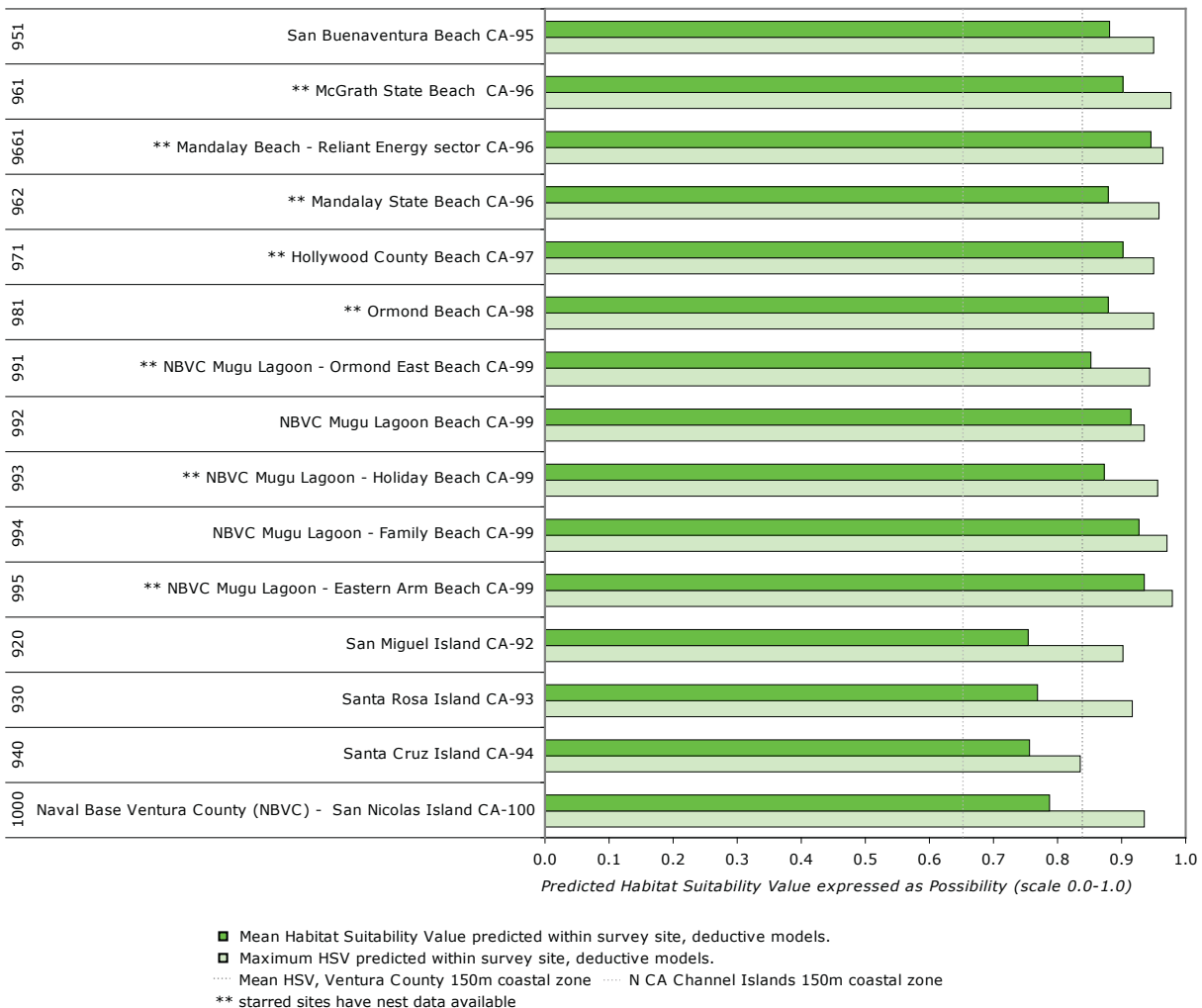
wide breeding-season window surveys (1991, 95, 2000, 2002–2009) (Page et al. 1991; USFWS 2007a, 2009b), and from winter window surveys rangewide (2004–2009, USFWS 2009a) and for RU5 (George 2003, 2006, 2009). Sites where nest-site location data were available are indicated (**). HSV comparisons are made regionally across analysis areas between window-survey sites and the entire coastal strip as a whole (using a 150-m buffer). Northern California Channel Islands site data are aggregated by island when reported by window surveys and are analyzed similarly here.

The beach-level deductive model results provide a basis to evaluate current management schemes and to assess variation in habitat quality within recovery beaches. We next review the model results for each recovery beach, north to south, and compare them to known management and occupancy patterns. To help interpret maps, 1-m resolution color images (USDA NAIP 2005) with sites superimposed are placed next to the beach-level maps of predicted HSV. Quantitative assessments of model performance at nest sites follow maps.

TABLE 7. Habitat suitability values predicted for known RU5 Western Snowy Plover sites. Sites where Western Snowy Plovers recorded on winter or summer window surveys (*); sites with nest point data (**).

RU5 WSP SITES AND WINDOW SURVEY BEACHES		HABITAT SUITABILITY VALUES			
Beach name	**CA-site**	**site**	**mean**	**stdev**	**max**
San Carpoforo Creek	CA-69	*691	0.817	0.094	0.936
Arroyo Hondo	CA-70	701	0.699	0.042	0.776
Point Sierra Nevada	CA-71	*711	0.748	0.038	0.793
Arroyo de la Cruz	CA-72	*721	0.903	0.025	0.936
Sydney's Lagoon	CA-73	*731	0.898	0.009	0.909
Point Piedras Blancas (1–2)	CA-74	*740	0.729	0.030	0.819
Arroyo Laguna	CA-75	*751	0.893	0.008	0.907
Pico Creek	CA-76	761	0.867	0.062	0.941
San Simeon State Beach	CA-77	*771	0.845	0.074	0.936
Santa Rosa Creek / San Simeon SB	CA-77	*772	0.878	0.030	0.913
** Estero Bluffs SB / Villa Creek	CA-78	*781	0.877	0.042	0.918
Toro Creek	CA-79	*791	0.819	0.045	0.910
** Morro Strand State Beach	CA-80	*801	0.823	0.062	0.947
Morro Rock City Beach	CA-80	802	0.867	0.037	0.921
** Morro Bay Sandspit - City of Morro Bay	CA-81	*811	0.879	0.030	0.926
** Morro Bay Sandspit - Montaña de Oro SP	CA-81	*812	0.807	0.074	0.918
Morro Bay Sandspit - private	CA-81	813	0.872	0.035	0.909
Avila Beach	CA-82	821	0.783	0.105	0.931
Pismo State Beach - N of Grand		831	0.872	0.043	0.931
Pismo SB - S of Grand		*832	0.889	0.019	0.935
** Oceano Dunes SVRA - day use area	CA-83	*833	0.839	0.079	0.940
** Oceano Dunes SVRA	CA-83	*834	0.739	0.067	0.849
** ODSVRA Oso Flaco Natural Area	CA-83	*835	0.768	0.081	0.930
Guadalupe-Nipomo Dunes NWR	CA-83	*836	0.737	0.069	0.853
** Guadalupe Restoration Site	CA-83	*837	0.791	0.084	0.942
** Rancho Guadalupe Dunes Preserve	CA-83	*838	0.805	0.095	0.946
Mussel Rock beach	CA-83	*839	0.792	0.071	0.908
Paradise beach		*8310	0.755	0.067	0.848
Point Sal State Beach		*8311	0.692	0.030	0.758
Brown's beach (local name)		8312	0.794	0.028	0.851
** Vandenberg AFB N of Minuteman Beach		*841	0.737	0.050	0.844
** VAFB North - Minuteman Beach	CA-84	*842	0.753	0.084	0.904
** VAFB North - Shuman Beach	CA-84	*843	0.739	0.088	0.932
** VAFB North - San Antonio Beach	CA-84	*844	0.791	0.054	0.929
** VAFB North - Purisima North	CA-84	*845	0.733	0.040	0.825
** VAFB North - Purisima Colony	CA-84	*846	0.729	0.057	0.825
continued on next page					

TABLE 7 (continued). Habitat suitability values predicted for known RU5 Western Snowy Plover sites. Sites where Western Snowy Plovers recorded on winter or summer window surveys (*); sites with nest point data (**).

RU5 WSP SITES AND WINDOW SURVEY BEACHES		HABITAT SUITABILITY VALUES			
Beach name	CA-site	site	mean	stdev	max
** Vandenberg AFB S - Wall Beach CA-85	CA-85	*851	0.881	0.042	0.933
** VAFB South - Surf Beach N (N end)	CA-85	*852	0.875	0.058	0.939
** VAFB South - beach at Surf Station	CA-85	*853	0.832	0.049	0.913
** VAFB South - Surf Beach N (S end)	CA-85	*854	0.746	0.021	0.803
** VAFB South - Surf Beach South	CA-85	*855	0.702	0.043	0.792
Jalama County Beach	CA-86	*861	0.751	0.093	0.920
Hollister Ranch	CA-87	*871	0.746	0.063	0.879
Gaviota State Beach		872	0.758	0.077	0.908
Refugio Beach State Park		873	0.786	0.060	0.903
El Capitan Beach State Park		*874	0.702	0.034	0.818
Haskell's Beach		875	0.815	0.072	0.911
Ellwood Beach		*881	0.762	0.026	0.814
** Coal Oil Point UC Natural Reserve	CA-88	*882	0.825	0.082	0.962
Isla Vista Beach		883	0.721	0.050	0.877
Campus Beach		884	0.881	0.033	0.935
Goleta Beach	CA-89	891	0.846	0.087	0.960
Santa Barbara West Beach	CA-90	*901	0.837	0.063	0.905
Santa Barbara Harbor	CA-90	*902	0.882	0.048	0.952
Santa Barbara East Beach	CA-90	*903	0.916	0.035	0.964
Carpinteria Spit Beach - Santa Claus Lane		911	0.935	0.015	0.958
Carpinteria City Beach	CA-91	*912	0.831	0.054	0.922
Carpinteria State Beach	CA-91	*913	0.816	0.032	0.875
San Buenaventura Beach	CA-95	*951	0.881	0.042	0.949
** Santa Clara River Mouth/McGrath SB	CA-96	*961	0.901	0.070	0.978
** Mandalay Beach (at Reliant Energy)	CA-96	*9661	0.947	0.015	0.965
** Santa Clara River Mouth/Mandalay SB	CA-96	*962	0.880	0.035	0.958
** Hollywood County Beach	CA-97	*971	0.902	0.029	0.949
** Ormond Beach	CA-98	*981	0.879	0.058	0.950
** NBVC Mugu Lagoon - Ormond East	CA-99	*991	0.852	0.068	0.943
NBVC Mugu Lagoon Beach	CA-99	*992	0.914	0.010	0.936
** NBVC Mugu Lagoon - Holiday Beach	CA-99	*993	0.872	0.078	0.957
NBVC Mugu Lagoon - Family Beach	CA-99	*994	0.928	0.018	0.971
** NBVC Mugu Lagoon - Eastern Arm	CA-99	*995	0.936	0.041	0.980
San Miguel Island (1–8)	CA-92	*920	0.753	0.070	0.902
Santa Rosa Island (1–11)	CA-93	*930	0.770	0.062	0.916
Santa Cruz Island (1–2)	CA-94	*940	0.755	0.051	0.835
NBVC San Nicolas Island (1–15)	CA-100	*1000	0.788	0.056	0.935

California State Parks has had primary jurisdiction over the northernmost section of RU5 since 2005. Hearst San Simeon State Park now extends south from the San Luis Obispo county line along a 30-km section of coast and encompasses seven of the nine designated recovery beaches. Jurisdiction over San Carpoforo Creek is shared with the U.S. Forest Service. Active management and monitoring by California State Parks San Luis Obispo Coast District was extended beyond San Simeon State Beach to all northern sites in 2008. San Luis Obispo Coast District management of plover habitat extends south through the Morro Bay Sandspit and includes all or a large portion of eleven designated recovery sites.

Several management practices that affect snowy plovers are common to these state-owned beaches. All employ some form of predator management; very different strategies exist that are adapted to changing predator pressures. Nest exclosures are used when appropriate. Dogs are prohibited on state beaches; day use areas and campgrounds allow leashed dogs. As a rule, at nesting beaches, State Parks places symbolic fencing above the high tide line during the breeding season to delineate plover habitat and direct the public away from nesting plovers. Informative signs accompany fencing. Public outreach and habitat protection and enhancement are components of site management (Orr 2006; CDPR 2009).

Overall, northern San Luis Obispo County has the least amount of high-quality habitat in the Recovery Unit, but has several small beaches that are of very high quality when they are wide enough *(Figure 20)*, although storms and high tides are a
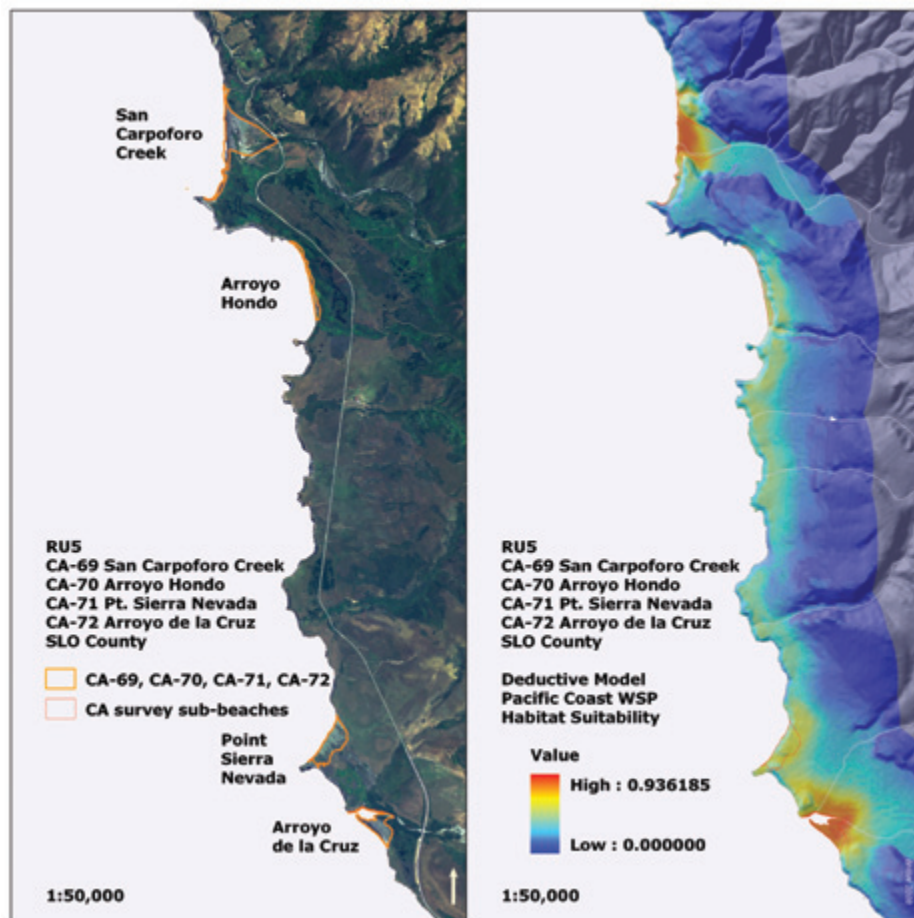
FIGURE 20. Deductive model HSV for San Carpoforo Creek, CA-69; Arroyo Hondo, CA-70; Pt. Sierra Nevada, CA-71; and Arroyo de la Cruz, CA-72.

constraint. San Carpoforo Creek (CA-69) and Arroyo de la Cruz (CA-72) are more-protected sites at the mouths of intermittent creeks. Both are state beaches. At San Carpoforo, a small sandspit forms, and both sites have mostly sandy beaches of sufficient width to be appropriate, high quality nesting habitat, although beaches could only support a few nests. At each site, maximum HSV = 0.936. Arroyo de la Cruz also has very high mean HSV (0.903). In summer window surveys, plovers are typically present at both sites. San Carpoforo Creek is more remote, has had recent nests (e.g., 2006), and employs symbolic fencing (Orr 2006; CDPR 2009). Surveys continue to indicate that San Carpoforo Creek is important wintering habitat (George 2002, 2009; USFWS 2009a). Although Arroyo de la Cruz is isolated from large human

population centers, it is fairly accessible to the public and there are consequently no nesting plovers. Snowy plovers have not been recorded during rangewide winter window surveys but have been observed during RU5 winter surveys. The presence of unleashed dogs chasing them has also been recorded (George 2006). With the increase in monitoring and management, both of these northern sites could be successful.

This stretch of coast is otherwise characterized by high gradient cliffs and rocky headlands. Arroyo Hondo (CA-70) is an extremely narrow beach, with the second-lowest HSV scores for an RU5 designated recovery site (mean = 0.699; max. = 0.776). The beach at Point Sierra Nevada (CA-71) is much less narrow, backed by wind-

FIGURE 21. Deductive model HSV for Sydney's Lagoon, CA-73; Pt. Piedras Blancas, CA-74; and Arroyo Laguna, CA-75.
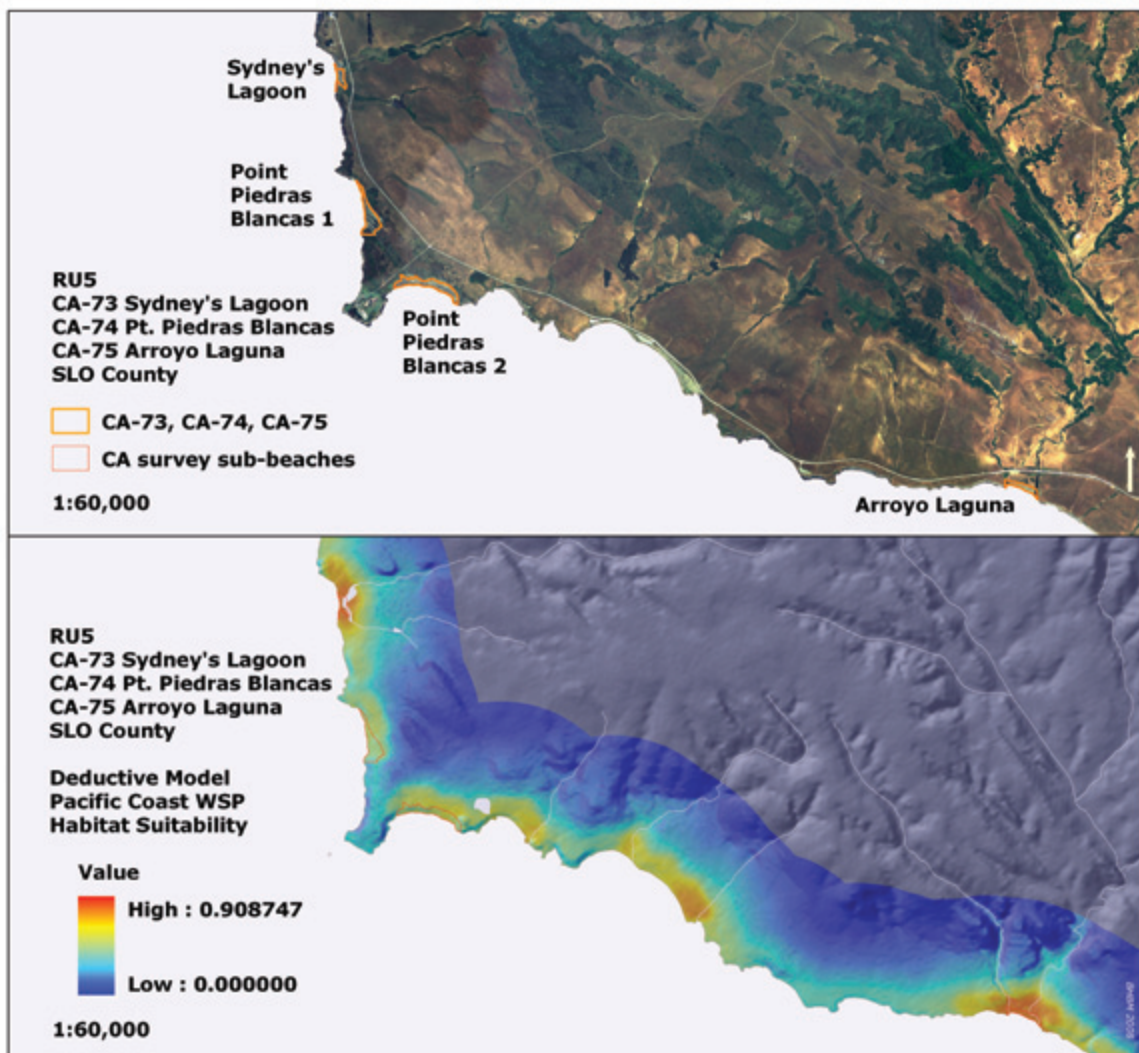
blown dunes, but it is unprotected with a north-west aspect that would tend to amplify harsh weather conditions and perhaps preclude nesting success. It has a comparatively low HSV (max. = 0.793); like Arroyo Hondo, no nesting has been recorded. It is surveyed during rangewide and RU5 winter window surveys and owned by State Parks.

Sydney's Lagoon (CA-73) and Arroyo Laguna (CA-75) *(Figure 21)* have a comparable environment, with predicted habitat suitability of similarly high quality (means = 0.898, 0.893; HSV maxima = 0.909, 0.907). Symbolic fencing has been used at Sydney's Lagoon to protect recent nests (e.g., 2006, 2009), and plovers use most of the sandy beach. Arroyo Laguna has had seasons where

elephant seal has made it difficult for plovers to occupy the beach, but that is not always a problem. Arroyo Laguna is a much larger beach than Sydney's Lagoon, and symbolic fencing is occasionally used to protect nests (e.g., 2006). The site has the potential to support more breeding birds. Sydney's Lagoon, Arroyo Laguna, and sandy but narrow and unprotected Point Piedras Blancas (CA-74) (HSV max. = 0.819) provide very important winter habitat (George 2006, 2009; USFWS 2009a). These three sites should benefit from an increased State Parks presence.

In mid-northern San Luis Obispo County *(Figure 22)* the topography is different because there are no headlands and the beaches are wider and more frequent along the coast. Presumably this

FIGURE 22. Deductive model HSV for Pico Creek, CA-76; and San Simeon Beach, CA-77.
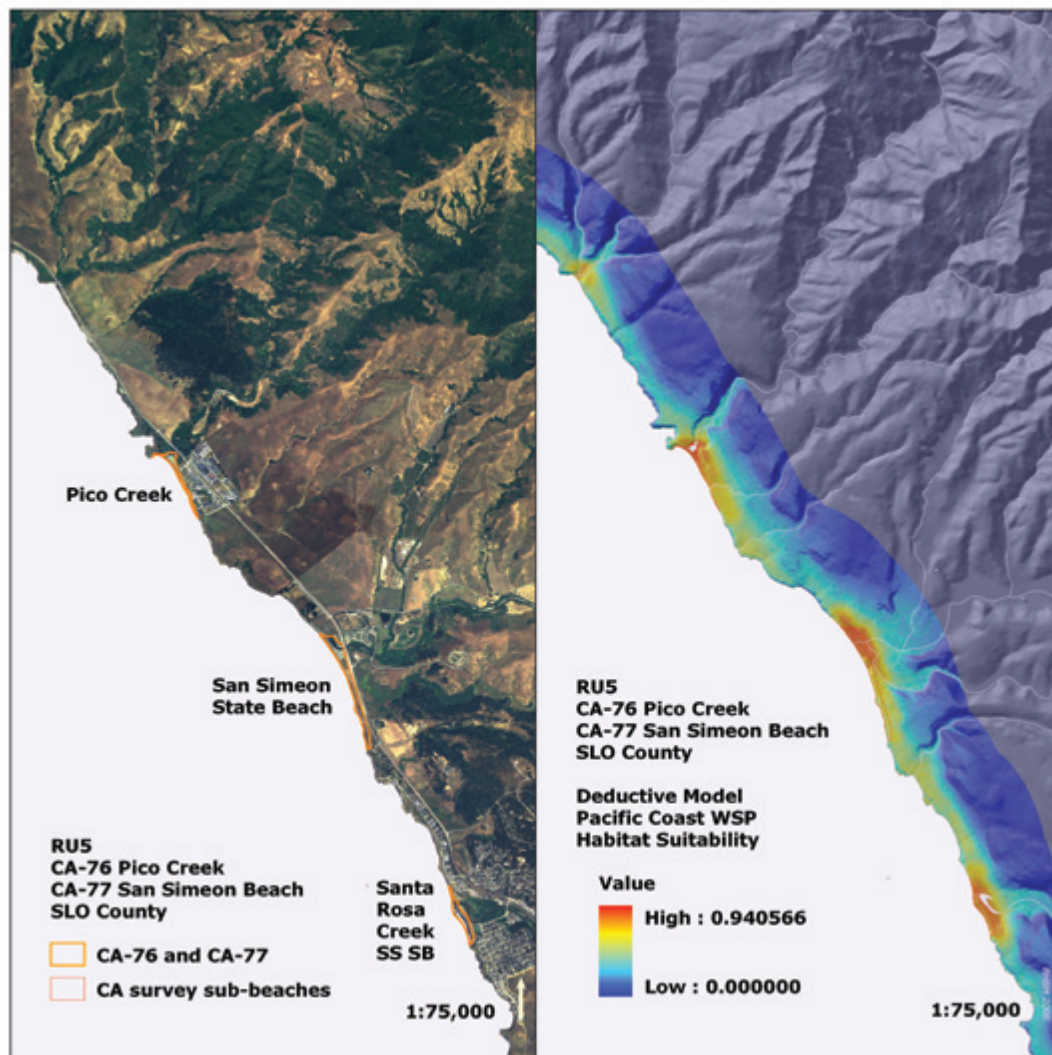
allows for easy movement of birds from beach to beach. Adjacent Highway 1 allows easy human access so public use is high, especially when compared with the beaches to the north. Habitat quality is high and virtually identical at Pico Creek (CA-76) (max. = 0.941; mean = 0.867), San Simeon Creek Beach, and at adjacent Santa Rosa Creek (CA-77, subunits 771 and 772) (maxima = 0.936, 0.913; means = 0.878, 0.845).

Pico Creek has not recently and does not now support wintering (Page et al. 1986; George 2006, 2009) or breeding birds. San Simeon Creek Beach has typically had many wintering birds on surveys (George 2003, 2006; USFWS 2007b), and has supported a few nesting plovers most years during 2001–2009 (CDPR 2009; USFWS 2009b). The major differences between these beaches are that Pico Creek is privately owned, and not managed for plovers, while San Simeon Beach is state-owned, and managed for recovery, with symbolic fencing during the breeding season. At San Simeon and Santa Rosa Creeks, the number of wintering birds declined during the period 2004–2009 (George 2002, 2009; USFWS 2009a), tracking the increase of haul out by marine mammals on the beach. Each of these three beaches has similar habitat values so differences in plover occupancy almost certainly reflect different management schemes and the current presence of elephant seals.

Estero Bluffs/Villa Creek (CA-78) *(Figure 23)* has a high predicted HSV (max. = 0.918; mean 0.877) similar to the San Simeon beaches. Villa Creek regularly records large numbers of wintering and breeding snowy plovers (George 2002, 2009; USFWS 2009a, 2009b) and has had reliable nesting each year since 2001. During the period 2001–2009, the total number of nests averaged about 40 per year and fluctuated from a low of 16 to a high of 64, while the percentage of chicks hatched has varied from 5% to 55% . Very high predator pressure is reported. Many are unidentified; skunk and gull spp. are most common (Larson 2001; Orr 2005; CDPR 2009). The major challenge here would appear to be effective

predator management strategies. Estero Bluffs allows public access while protecting nesting plovers by using symbolic fencing and rerouting trails. Management, intensive monitoring and comparatively favorable environmental factors each contribute to success at Villa Creek. Located on the north side of the Morro Bay Bight, it is more sheltered than any site farther north in San Luis Obispo County, includes small wetlands at the mouth of Villa Creek, and fairly recently became part of the California State Parks system (Orr 2005; CDPR 2009).

Estero Bluffs State Park extends east of Villa Creek. Two pocket beaches near Villa Creek and a small beach north of San Geronimo Creek have recent nests. Neither of these sites has great habitat (max. HSV = 0.702–0.768), but nests have been recorded regularly during 2005-2009, although numbers are declining (Orr 2005, 2006; CDPR 2009).

Our model indicates there are two other nearby sites with higher maximum HSV than at any location within Estero Bluffs State Beach or at Villa Creek proper (CA-78) — or within the next designated recovery site down the coast, at Toro Creek (CA-79). These sites are not identified for plover recovery, given their location in the town of Cayucos. Cayucos State Beach, between Cayucos Creek and Little Cayucos Creek, has a maximum HSV of 0.920. It was listed in 1986 as a strong wintering location (Page and Stenzel). At the south end of Cayucos, Old Creek has higher maximum HSV (0.942). This beach is within the discontinuous narrow northern unit of Morro Strand State Beach. It is not monitored and managed like the southern unit (within CA-80), which has breeding plovers, but it is regularly censused by State Parks and others for plovers (CDPR 2009; George 2009).

At Old Creek, disturbance of wintering birds by unleashed dogs has been documented as a major concern. For example, in 30 minutes, 12 unleashed dogs were observed on the beach (2002); and during another survey where no snowy

plovers were observed, off-leash dogs chased other shorebirds (2006). In early December 2009, 107 snowy plovers and an unrecorded number of people and unleashed dogs shared the narrow beach at high tide; on the following day, there were no birds but ten unleashed dogs (George 2003, 2006, 2009).

The recovery sites of Morro Bay (CA-79 through CA-81) *(Figure 24)* are some of the most complex management and human interface zones for the species in RU5. There is a large human population combined with excellent Western Snowy Plover habitat (if managed properly) that leads to tradeoffs between uses. Some areas have exceptional and large areas of nesting and wintering

habitat but these are heavily used as recreational sites. With the exception of Toro Creek, all sites (but not all sub-sites) are heavily managed for plover recovery but simultaneously are used extensively and intensively by human visitors.

Toro Creek (CA-79) has high HSV scores (max. = 0.910; mean = 0.819) but supports no plovers because the site is not managed for plovers. North of the City of Morro Bay and south of Cayucos, extensive visitor use (with unleashed dogs) precludes consistent plover occupancy (notwithstanding high numbers on a single winter window survey and one lone bird in 2007). Toro Creek formerly supported moderate numbers of wintering birds (Page and Stenzel 1986)

FIGURE 23. Deductive model HSV for Estero Bluffs State Park/Villa Creek, CA-78.
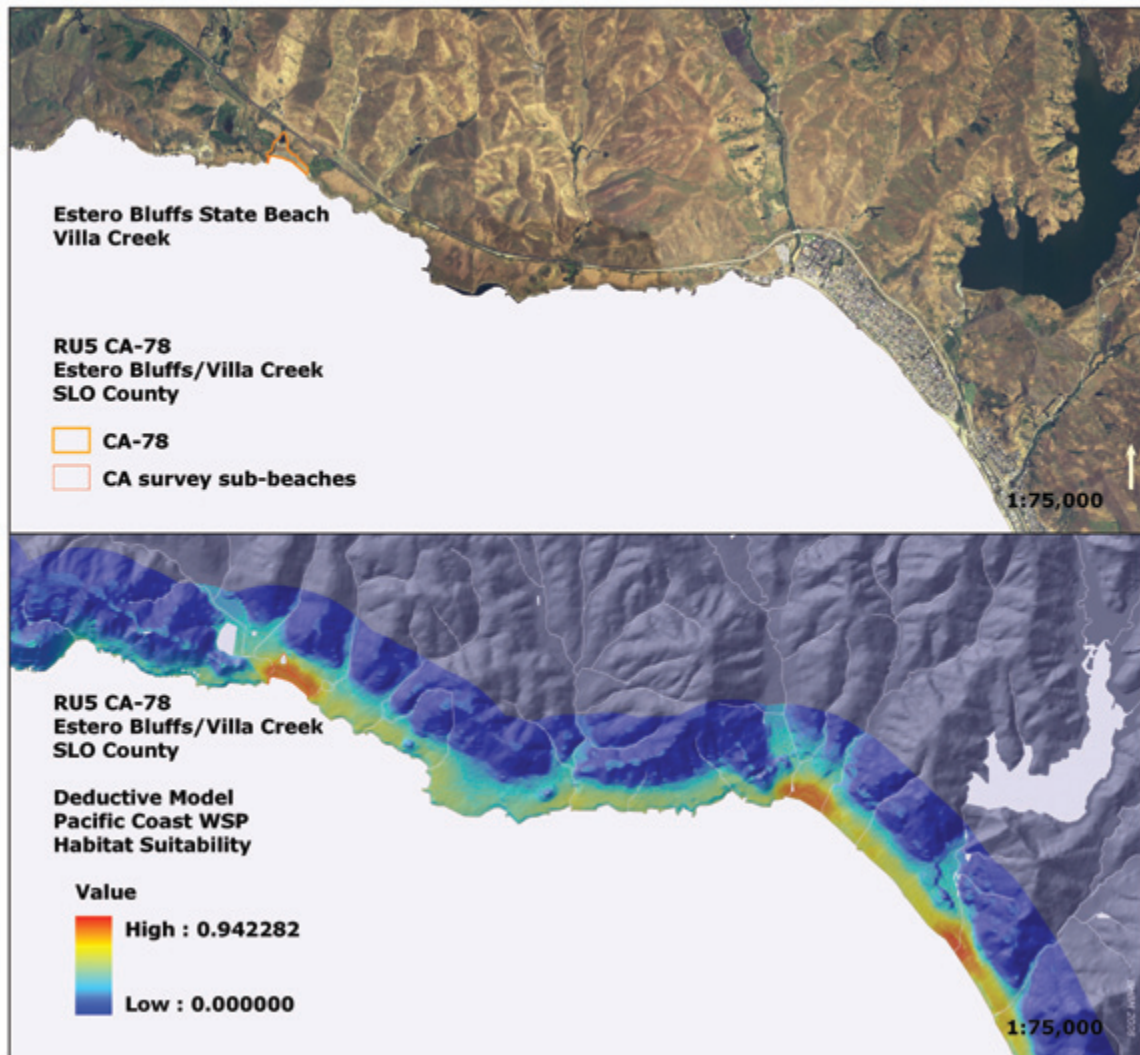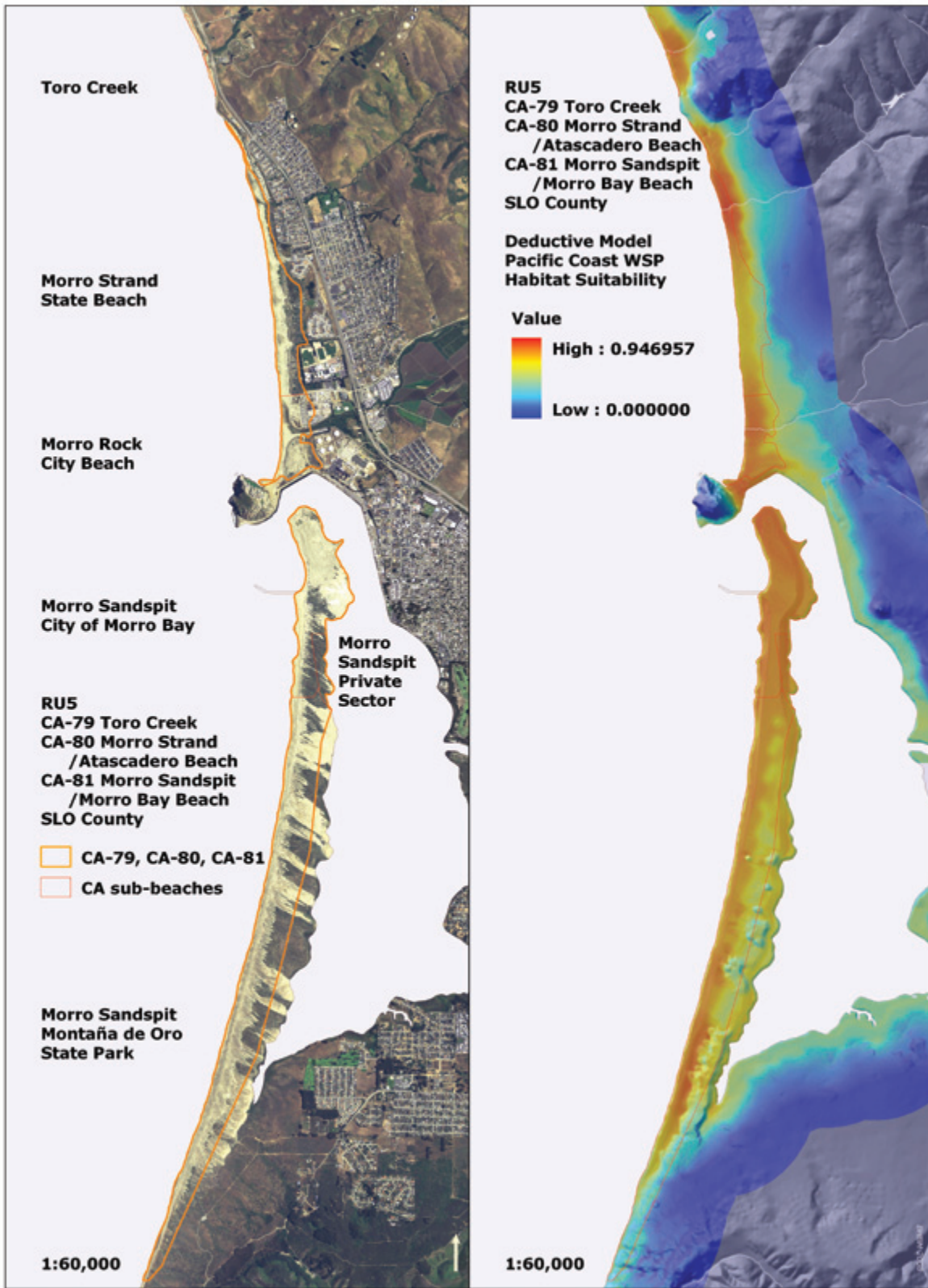
FIGURE 24. Deductive model HSV for Toro Creek, CA-79; Morro Strand, CA-80; and Morro Sandspit, CA-81.

and was described as a very productive nesting beach in 1988 (Page); breeding birds were present more recently. Now there are no nests and virtually no birds observed. Corporate priorities or changes in desired land-use have brought about extensive planning and restoration in the immediate surroundings, site of a Chevron tank farm. The high HSV scores at Toro Creek, however, indicate that plovers would almost certainly nest on this beach if recreational use were managed to allow it.

Our physical habitat model identifies Morro Strand State Beach/Atascadero Beach (CA-80) (801) as the highest quality habitat in San Luis Obispo County (max. = 0.947). It supports plovers on winter and summer window surveys and has nesting in variable numbers over time (USFWS 2009a, 2009b). The beach is wide enough to be able to segregate some high use recreation sites near the water from high-HSV plover nesting sites. A full complement of strategies are needed for this urban-adjacent beach: symbolic fencing; signage; outreach and education; volunteers; and enforcement of dog, kite, and trespassing laws. Major predators are crows; management is adaptive (Larson 2002, 2003; CDPR 2009). As long as State Parks management is continued, this pattern should be able to be maintained.

In contrast, directly to the south is an area of beach owned by the City of Morro Bay (802) that has similarly high HSV scores (max. = 0.921, mean = 0.867), yet no plovers ever nest because of extremely high visitor usage. It is not a state park and is managed completely differently; the City is not protecting habitat values from ongoing degradation through recreational disturbance, even though the site has high habitat value for plovers.

The Morro Bay Sandspit (CA-81) is a dynamic location constantly reshaped by natural and human processes. Sand forms the northern end of a 300–600 m wide sand spit. This grades into a beach, dune, and sand sheet complex that ex-

tends 6.5 km south. On the ocean side, a 10–150 m wide barrier beach lies between the high tide line and foredunes, except at the southern end, where steep sandy bluffs back the beach. Overall, it is excellent plover habitat. Moving east towards the estuary, an elevated section of consolidated, older, heavily vegetated dunes provides little plover habitat (Hutchinson et al. 1987; Orr 2006).

The sandspit is divided between three landowners: City of Morro Bay (811), State Parks (812), and a small private parcel on the estuary side of the spit (813). Similar to Morro Strand, the patterns of occupancy by plovers reflect the different management schemes of the two major entities. The full suite of management strategies used at Morro Strand — and then some — are implemented by SLO Coast District State Parks on the sandspit at Montaña de Oro State Park. The City owns the tip of the sandspit, and has placed dredge spoils there, which would improve the site as nesting habitat for plovers, but because concomitant reductions in human disturbance have not been implemented, these sites are not used for nesting. Nest distribution along the sand spit showed a shift from dredge spoils at the sand spit tip (1987) to the barrier beach (2000) (Persons and Ellison 2001), and the pattern remains: far more plovers are observed on the State Parks sector compared with the City sector on summer and winter surveys and in inventories of nests (George 2003; Orr 2005, 2006; CDPR 2009; USFWS 2009a, 2009b). Habitat suitability values are similarly high in both areas (City of Morro Bay, max. = 0.926, mean = 0.879; Montaña de Oro State Park, max. = 0.918, mean = 0.807), and extend over a large area. Again, our model indicates that the difference in occupancy is attributable only to the difference in management, not to any inherent difference in physical habitat suitability.

Avila Beach (CA-82) *(Figure 25)* similarly has a high maximum HSV score (0.931). The highest predicted HSV for the SLO area, 0.955, is on a river sand bar 100 m northwest of the site
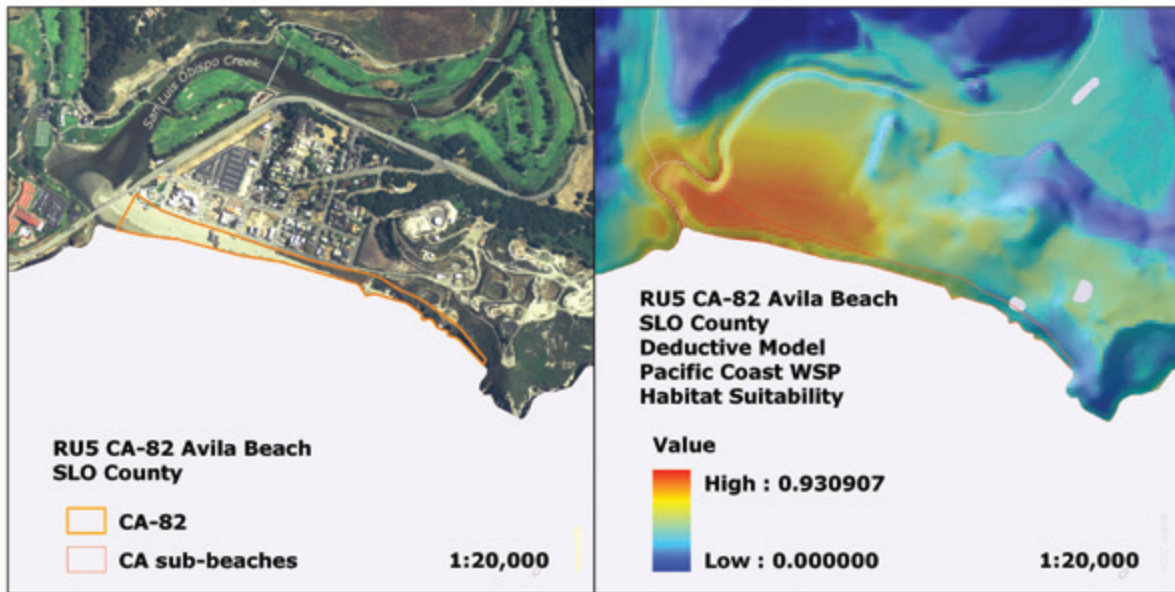
FIGURE 25. Deductive model HSV for Avila Beach, CA-82.

boundary. Environmental factors leading to this determination are the proximity to the beach of San Luis Obispo Creek, the gentle slope of the creek approaching the beach, with gradient-associated sand bar deposition, and the sheltered location and south-facing aspect of the beach, which are all favorable conditions. Avila Beach, however, has high human recreational use, a history of adverse environmental issues, and no management for plovers. Any effort to manage for plovers by removing the ongoing habitat disturbance, however, would probably be met with rapid recolonization by the species and such management is specifically suggested in the Final Recovery Plan (USFWS 2007a).

Pismo State Beach is not included as a recovery site, but it is sometimes used by plovers and the southern portion of the beach is included on winter window surveys. We divide it into northern (831, unsurveyed) and southern (832, surveyed) sites. Recent surveys have been negative (2003–2009) (USFWS 2009a, 2009b), but nesting has occurred in the recent past (Perry 1994; Tipton and Burton 1997; 1998). Pismo State Beach has high recreational use because of its location in the City of Pismo Beach. Pismo Creek enters from the north, and Meadow Creek meanders through

wetlands on the inland side . The habitat suitability values are very high (sites' max. = 0.931, 0.935; mean = 0.872, 0.889), especially at the southern end of the beach, but without control of recreational use, nesting is impossible.

The central California dune complex, recovery site CA-83 *(Figure 26)*, is a patchwork of landowners and management strategies; we divide it into seven sub-sites (833–839) for this analysis. USFWS described the region as "the most unique and fragile ecosystem in the State of California" in 1980, and land-use issues have been a concern for a century (USFWS 2008). Plover data have been collected for some time (Page 1988; Perry 1994). It is also the location of the only off-road dune vehicular recreation area on the California coast, which is deeply entrenched in local culture, and owned and managed by a separate division of California State Parks, the Off-Highway Motor Vehicle Division, Oceano Dunes District. The CA-83 unit also includes a National Wildlife Refuge, two counties, and private lands. Each piece has a slightly different management approach or lack thereof and varied results.

Individual sectors extend from the sandy beach to foredunes to backdunes; nesting occurs in the
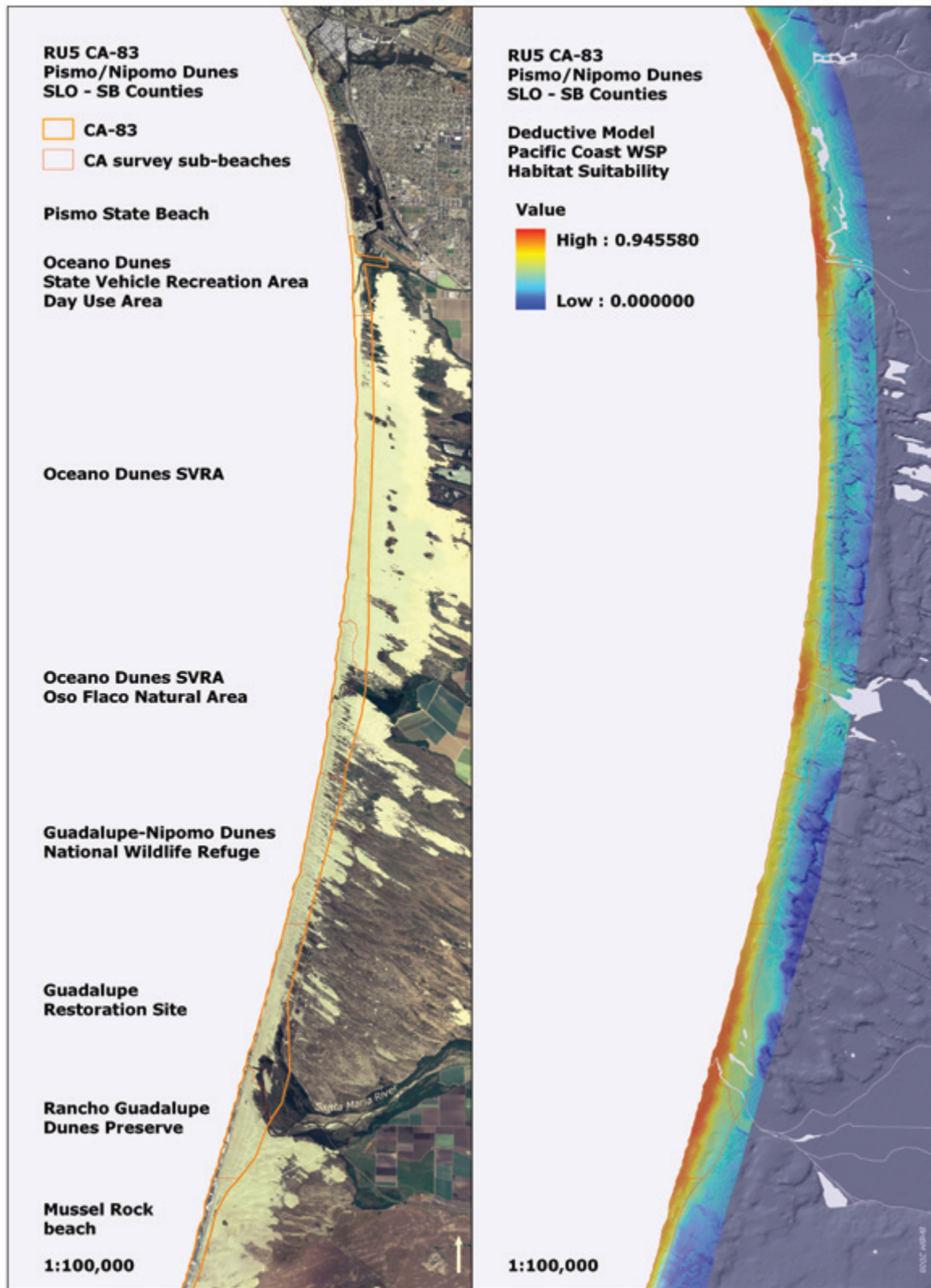
FIGURE 26. Deductive model HSV for the central California dune complex, designated as recovery beach CA-83, Pismo/Nipomo Dunes.

backdunes in natural blowouts. Many environmental factors are similar throughout the region: strong west and north-west winds, blowing sand, high surf. Beach width varies, as does proximity to fresh water. In a dynamic environment, there is variability over time at individual sites. Encroachment from non-native vegetation and its negative effects upon plover habitat is a factor we do not specifically model, but many areas incorporate its eradication into their management programs. Predators are a major concern. There are large areas of would-be exceptional habitat that are not managed for plovers, while some areas with lower HSV scores are actively managed for plovers.

The Oceano Dunes State Vehicle Recreation Area (ODSVRA) Day Use Area (833) encompasses the mouth of Arroyo Grande Creek. Despite very high HSV scores for plovers, it is intensively used for off-road recreation and provides the access way for the dunes to the south. Because it is close to the creek, this sub-unit has the highest maximum (0.940) and mean (0.839) HSV of all of CA-83. It was included in earlier surveys along with Pismo Beach (Perry 1994; CDPR 1999) but had only 14 nest sites from 1998–2001 and no nests thereafter almost certainly because of the high recreational vehicle use.

The remainder of the Oceano Dunes SVRA (834) is actively managed and monitored for plovers. Years of reports are available; and extensive data are collected (we used 11 years of nest data). Birds are banded to enable fledge success rates to be calculated, allowing comparisons of productivity and management strategies between years for different parts of the site (CDPR 2005, 2006) and to compare Oceano Dunes with other sites. According to our model, this is good-quality habitat (max. = 0.849; mean = 0.739), but of substantially lower quality than the Day Use area, but the management, through use of very large seasonal exclosures, frequent patrols, and habitat enhancement allows plovers to occupy this unit over a large area (Tipton and Burton 1997; CDPR 1999, 2005, 2006). Our model suggests, however,

that these management actions would be even more effective if applied in areas of the recovery site (CA-83) with higher habitat suitability values.

Oso Flaco Natural Area (835) is located around Oso Flaco Creek and Oso Flaco Lake behind the dunes, which causes the predicted habitat suitability value for plovers to increase (max. = 0.930) because of the proximity to fresh water. The beach is narrower but scores slightly higher mean HSV (0.768) than the southern portion of the ODSRVA to the north. It is managed as a restored "natural area" by ODSVRA, meaning that there is more restricted access and off-road vehicles are not permitted. Because access is restricted, human usage is lower. As it is throughout ODSVRA and CA-83 as a whole, predator management is an ongoing concern (CDPR 2005, 2006).

The Guadalupe-Nipomo Dunes National Wildlife Refuge (836) includes property formerly owned by Mobil. The NWR was established in 2000 and intensive plover monitoring began in 2002. The Refuge is isolated and protected from off-road use. Public access is by foot from north or south, about a 3 km hike along the beach. Signs indicate habitat is closed during the breeding season. Overall, the site provides plover wintering and breeding habitat, but is of average quality (mean = 0.737; max. = 0.853), according to our model, when compared with adjacent sections of CA-83 with higher quality habitat (around the creeks and rivers). Nevertheless, active management for plovers and regular monitoring have allowed a high level of nest initiation. Nest loss to predation, particularly unknown avian predators, is high, and improved predator management strategies have been strongly recommended (Applegate and Schultz 2009).

The Guadalupe Restoration Site (837) is just north of the Santa Maria River, which is large and has an estuary, making it high quality habitat for plovers (max. = 0.942; mean = 0.791). This site has about 75% of the number of nests as the ODSVRA in a substantially smaller area. Our

model would attribute this to the most desirable habitat on the shifting sand spit west of the Santa Maria River estuary. The combination of physical features and no public access make it an excellent site for plovers. An extensive restoration was required for the southern half of this property (formerly owned by UNOCAL, and now by Chevron), which was completed in 2005. The effects of the restoration process on the plover population are well-documented (Wehtje and Fahy 2000; Wehtje 2005). The site extends inland as well as to the north; management for predators and intensive plover monitoring are in place in the restored habitat, which is in the southwest corner of the property, near the river.

To the south of the Santa Maria River is the Rancho Guadalupe Dunes Preserve (838), which also has high predicted HSV (max. = 0.946; mean = 0.805). These high values are achieved despite it being a very large site that not only extends inland for 1 km (or more) but also stretches south from the river for roughly 2.25 km. It is owned by Santa Barbara County and managed by the Center for Natural Lands Management. It consistently supports nesting plovers with low variation between years. The site has a moderate number of visitors, as compared with more accessible locations in CA-83, on-site management by a ranger, regular monitoring, and a predator management program that most often encounters coyotes and corvids (Sandoval 2005b; Applegate and Schultz 2007).

Finally, Mussel Rock beach (839), a small portion of land not actively managed, rounds out CA-83 at its southern end. Predicted HSV are not much different (mean = 0.792; max. = 0.908) than the other sub-units. Fewer than twenty birds are observed on winter and summer surveys and no nest information is available. We include three other beaches to the south of CA-83 that are occasionally surveyed. Point Sal State Beach (8311) has the lowest predicted HSV (mean, 0.692; max. = 0.758) of any RU5 site we consider; all three beaches are narrow and a challenge for nesting because of the winds and high surf.

Vandenberg Air Force Base (VAFB) includes two distinct areas that are designated as recovery sites. The northern beaches are near San Antonio Creek and at Purisima Point (CA-84) and the southern beaches are near the Santa Ynez River (CA-85). VAFB beaches are between Point Sal and Point Arguello and face west, with extreme weather conditions, including intense storms, high winds, blowing sand, high surf, and subsequent erosion of beaches (Applegate and Shultz 1999, U.S. Air Force 2003).

Although managed by a single owner, the area is very large. VAFB itself has about 55 km of coastline; plovers use about a third of that, with the rest rocky cliffs. We divide *(see Table 7)* the northern beaches (CA-84) into six sub-sites (841–846) that correspond to their VAFB sector designations; we divide the southern beaches (CA-85) into five sub-sites (851–855) that correspond both to their designations by VAFB (Persons 1995, Persons and Applegate 1997) and reflect additional differences at the central southern beach. All of the beaches, because of their size, have relatively low mean HSV, but high maximum HSV. This indicates that the polygons that delineate the recovery beaches extend over large areas of suitable, but variable, habitat quality — which draws the scores down, while within those areas there are truly exceptional habitats for Western Snowy Plover nesting.

Breeding season and winter window surveys always record very high numbers of plovers at both sets of beaches (USFWS 2009a, 2009b). VAFB has a long history of management and monitoring for Western Snowy Plover; there are years of detailed annual reports and associated data (we used 11 years of nest data). Management strategies are proactive, and include banding a sample percentage of plovers to represent their large population to calculate reproductive success, intensive predator control measures, invasive-species eradication, daily monitoring, fencing beaches where required, restricting recreational activities in response to human-caused nest losses, and strong enforcement of the limited ac-
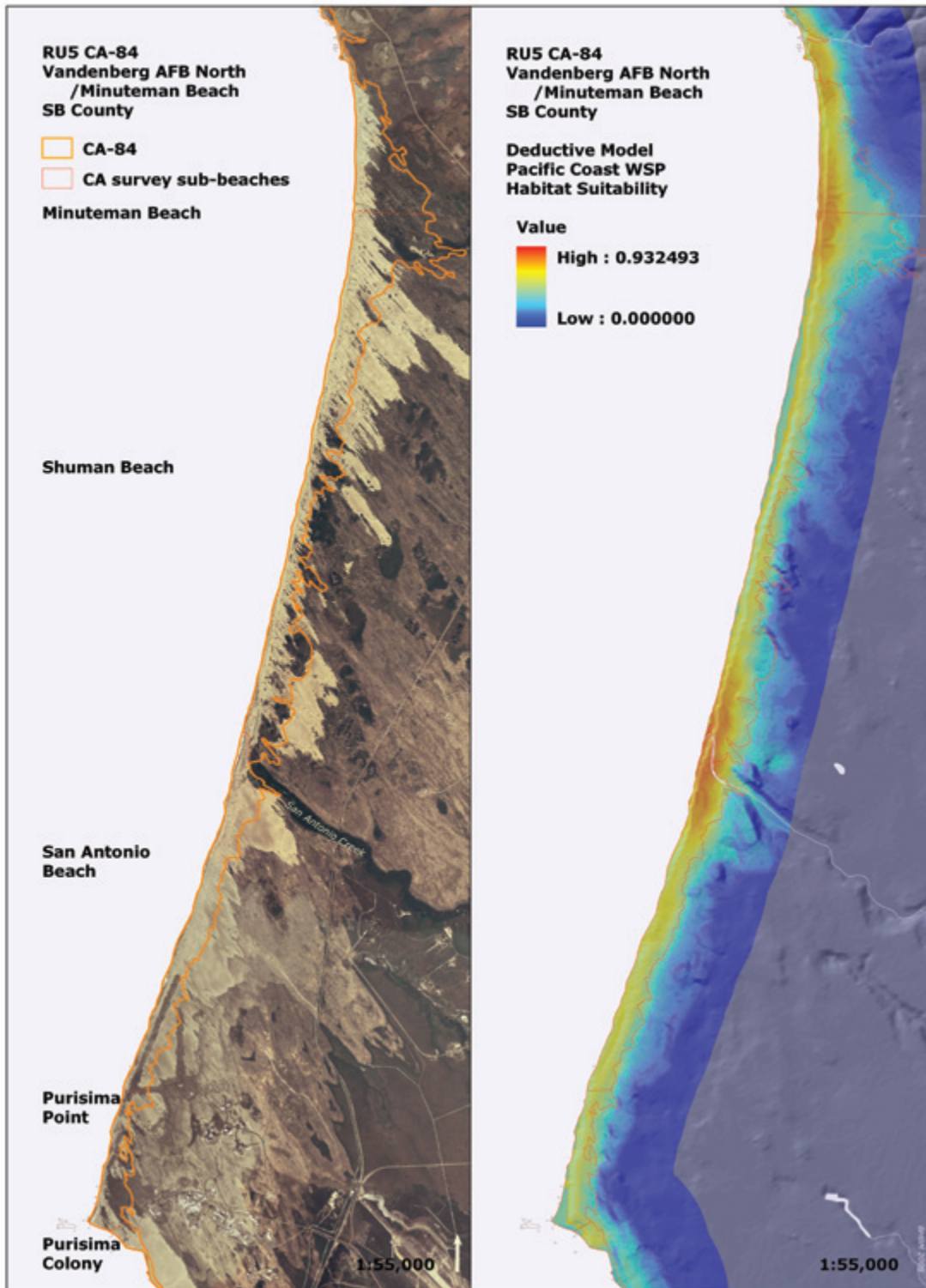
FIGURE 27. Deductive model HSV for Vandenberg Air Force Base, northern beaches, CA-84.

cess expected on a military reservation (Persons and Applegate 1997; U.S. Air Force 2003), all of which helps to explain why the site continues to be occupied at high densities.

The northern beaches *(Figure 27)* include the continuous strip of Minuteman (842), Shuman (843), and San Antonio (844) Beaches, all with very good habitat quality, with maximum HSV
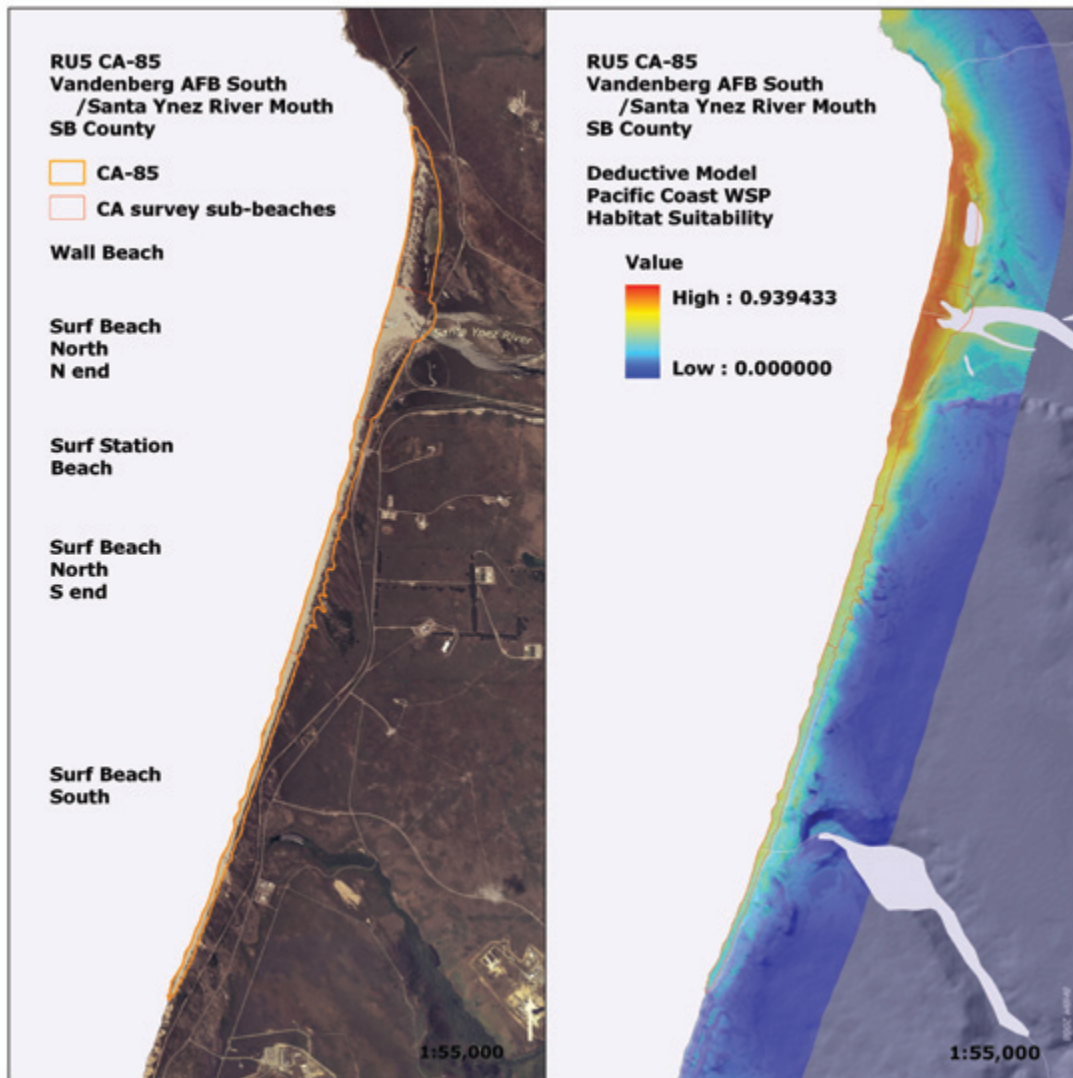
FIGURE 28. Deductive model HSV for Vandenberg Air Force Base, southern beaches, CA-85.

(sites' max. = 0.904 to 0.932) clustered around Shuman and San Antonio Creeks. At the southern end of the northern beaches, Purisima Point (845) and Purisima Colony (846) include inland dunes, and both have moderate HSV (sites' max. = 0.825) and can experience adverse weather conditions that decrease habitat values.

The southern beaches at Vandenberg Air Force Base (VAFB) *(Figure 28)* begin about 6 km south of the Purisima beaches. Wall Beach (851) and Surf Beach North (852; 853) surrounding the mouth of the Santa Ynez River have high HSV (sites' max. = 0.913 to 0.939). HSV are declining, but still suitable (max. = 0.803, 0.792) on Surf

Beach North (854) south of Surf Station, then the beach narrows substantially at Surf Beach South (855). These beaches can also be adversely affected by high winds because of their due-west orientation. The intensive management at VAFB to some degree makes up for the moderate habitat values on Surf Beach; these areas support many nesting birds. Surf Beach is a public access point for the area and also has a railway station that provides convenient access. Of the VAFB beaches, unauthorized uses are greatest here compared with other locations within the property because of the greater accessibility. We examine the VAFB beaches in further detail in our model performance evaluations using nest data.

FIGURE 29. Deductive model HSV for Jalama Beach, CA-86.
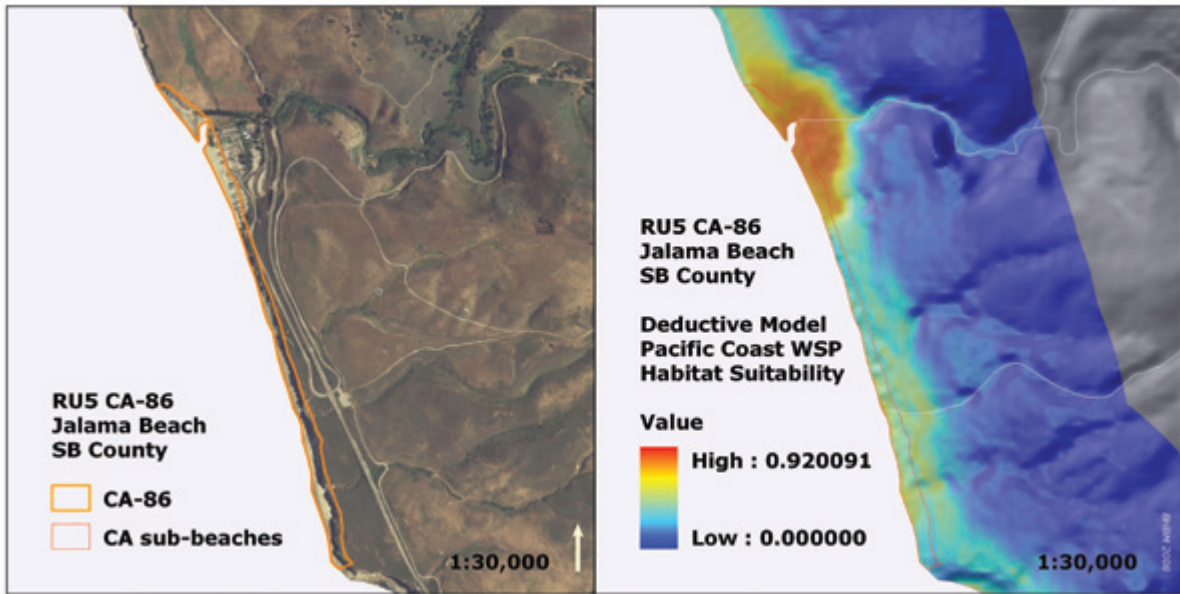
FIGURE 30. Deductive model HSV for Hollister Ranch, CA-87.
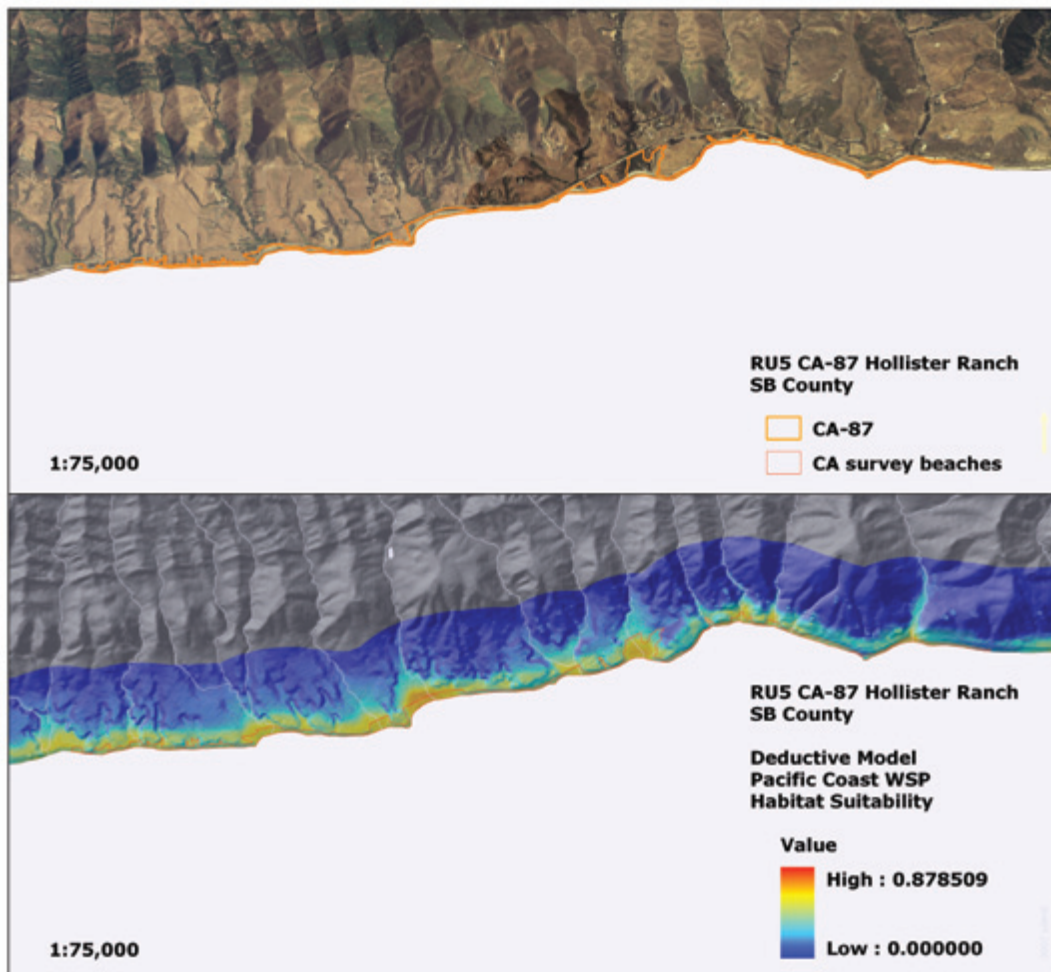
Jalama Beach (CA-86) *(Figure 29)* is a small beach south of VAFB that is protected from the weather somewhat by its location between Point Arguello and Point Conception. It is often windy, but not too windy, and the presence of the low-gradient, warm stream debouching through the dune beach and dune gives it a high HSV (max. = 0.920). The site is, however, a very popular Santa Barbara County Park that permits long-term camping. It is subject to frequent disturbance including high summer recreational use, unleashed dogs, and beach grooming. With appropriate management, our models indicate that this site could easily support breeding Western Snowy Plovers.

The beaches of Hollister Ranch (CA-87) (871) *(Figure 30)* are spread along a narrow strip below coastal bluffs along a largely undeveloped stretch of coast. The western end of the south-facing Santa Barbara coast has higher tides and stronger, more persistent winds. Some of the pocket beaches have high average HSV (max. = 0.879). The beaches are not managed for plovers and thorough surveys have not been undertaken; Hollister Ranch has been included on winter window surveys only twice, but birds were observed both times (USFWS 2009a). A Hollister Ranch Advisory Board report (2006) stressed landscape-scale planning for perpetual management of this working ranch. It promoted outreach to the regional educational and scientific community, and encouraged conservation of natural resources. More specifically, it noted that hundreds of snowy plovers are seen each winter; that a few plovers nest each year on wider, sandy beaches near fresh water; and that the common practice of driving on beaches could present a problem for nesting plovers. Our habitat suitability models could be used to prioritize more complete and regular surveys.

Three small beaches at the mouths of creeks on the south-facing Santa Barbara coast are regularly surveyed for wintering and breeding plovers (George 2003; USFWS 2009a, 2009b). Gaviota State Beach (872), Refugio Beach State

Park (873), and El Capitan Beach State Park (874) are popular beaches managed for recreation, but each has high-enough HSV (sites' max = 0.818 to 0.908) to indicate nesting is potentially possible. Two other small beaches, Haskell's and Ellwood Beach, have similar HSV but are quite narrow.

Coal Oil Point Reserve (CA-88) (882) *(Figure 31)* has been the site of a very successful habitat restoration (Lafferty 2000, 2001) and management program for Western Snowy Plovers (Lafferty 2001; Lafferty et al. 2006), and the deductive model provides insight on the reasons for this. The HSV near Devereux Slough are very high (max. = 0.962; mean = 0.825) along the nearby beach, in the foredunes, and adjacent to the slough, due to a combination of desirable environmental factors, and this is the site that was chosen to restrict human disturbance and for active management (Lafferty 2001).

Nesting plovers are protected by permanent and seasonal symbolic fencing and a vigilant docent program supported by the greater Santa Barbara and UCSB communities. Dogs are not allowed. Predator management techniques are often innovative and vary by year depending on the threat; skunks are a severe problem. As a result of intensive management, the site went from no breeding pairs to dozens of breeding pairs in five years, and fledging rates are very high (Sandoval 2005a, 2009). In addition to nesting sites along the beach, a substantial number (15 of 64) of recent nests were established on the mud flats nearer to the slough (Sandoval 2009), which would indicate the site will support additional birds, and it confirms predictions of the model. Coal Oil Point also provides critical wintering habitat for hundreds of Western Snowy Plovers (USFWS 2009a).

In addition to Coal Oil Point (part of the UC Natural Reserve System), the University of California owns Isla Vista Beach (883), which is narrow with moderate HSV for this stretch of coast (max. = 0.877), and Campus Beach (884), with a higher HSV (max. = 0.935; mean = 0.881) due mainly

FIGURE 31. Deductive model HSV for Coal Oil Point UC Natural Reserve, CA-88.
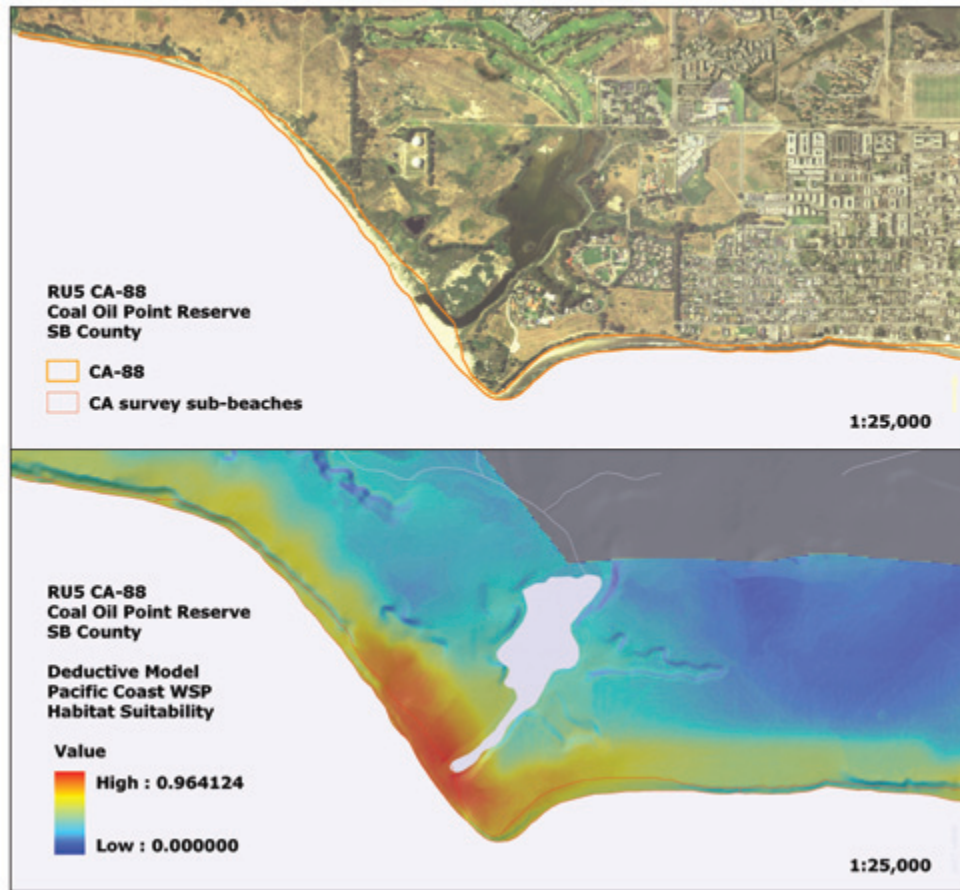
FIGURE 32. Deductive model HSV for Goleta Beach, CA-89.
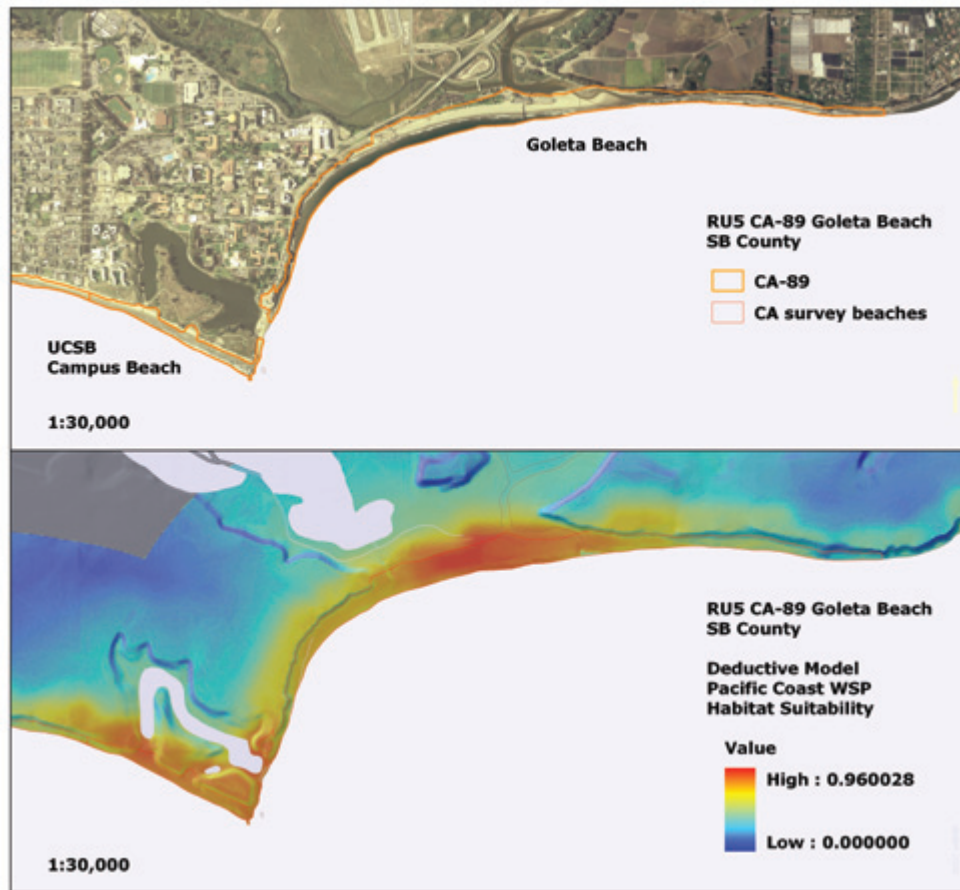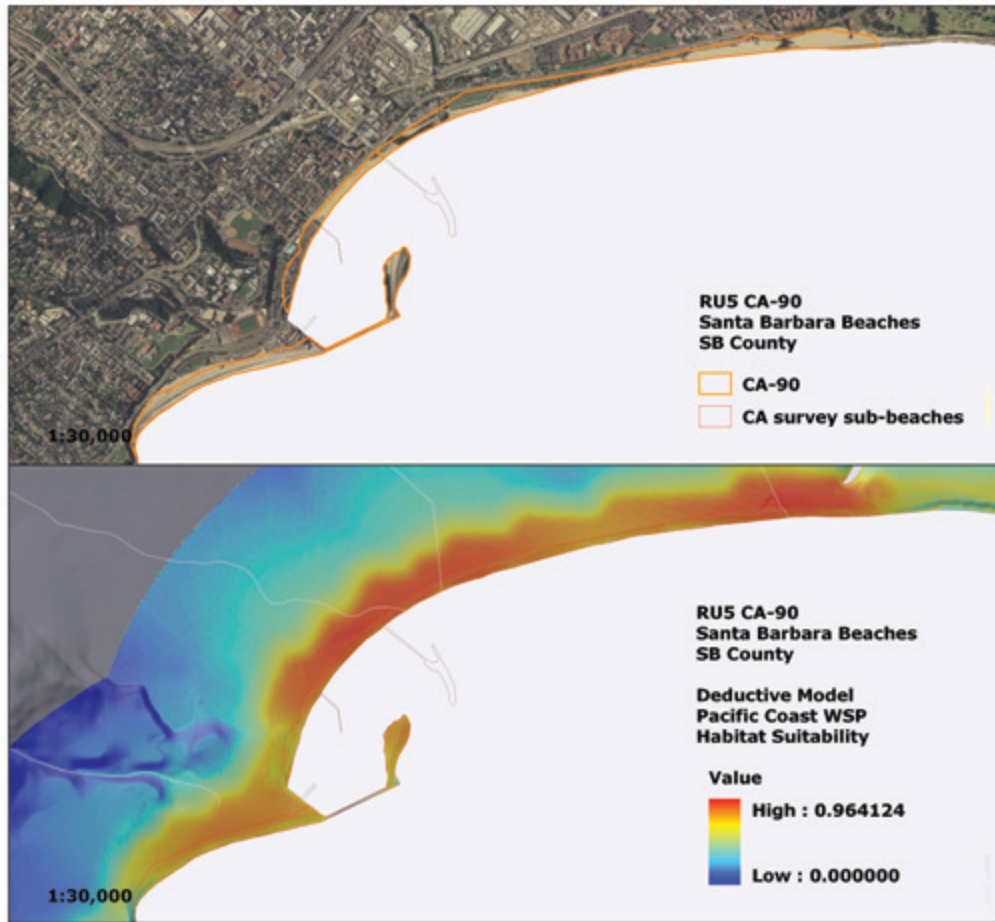
FIGURE 33. Deductive model HSV for Santa Barbara Harbor/Point Castillo, CA-90.

to its location at the UCSB campus lagoon and wider sandy beach. Santa Barbara County-owned Goleta Beach (CA-89) *(Figure 32)* also has concentrations of high HSV (max. = 0.960), due to its fairly wide sandy beach and proximity to Goleta Slough. Its less-urbanized location between UCSB, Santa Barbara Airport, and agricultural land may help maintain habitat quality. Wintering plover numbers at Goleta Beach have been fairly high in the past (Page et al. 1986) but not recently. These beaches are regularly surveyed for winter and breeding birds but they are heavily used for recreation and consequently have limited plover occupancy.

South-facing beaches of Santa Barbara proper (CA-90) *(Figure 33)* similarly have areas identified as very high quality habitat based on the physical parameters (sites' max. = 0.905 to 0.964). The City of Santa Barbara has multiple reasons to

protect its natural resource and uses particularly visible signage to stress the sensitivity of sandy beach habitat, including the importance of wrack as a food source. Harbor Master Plan policies for West Beach (901) and the sandspit (902) specifically protect Western Snowy Plover, and Santa Barbara Audubon has a strong presence. Dogs are prohibited on City beaches. The story of the first snowy plover nest established in Santa Barbara in 72 years — and the three chicks that hatched on the sandspit prior to Fourth of July 2005 fireworks — is part of local lore.

Nevertheless, all beaches are heavily to very heavily used for recreation and are groomed regularly during the summer, although restrictions on its frequency have been imposed. East Beach (903), with the highest HSV (mean = 0.916; max = 0.964) in the County, lies in front of some of the largest hotels in this resort city. Winter use
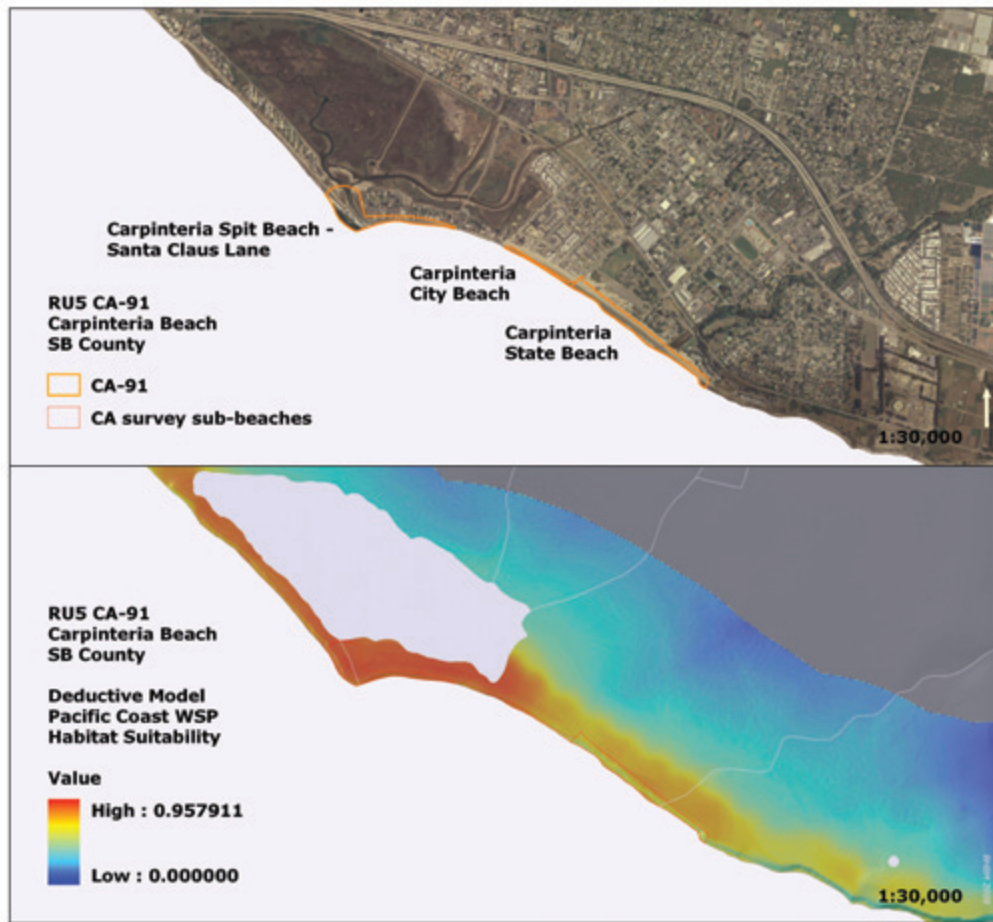
FIGURE 34. Deductive model HSV for Carpinteria Beach, CA-91.

by plovers has been observed when other disturbances are at a minimum, suggesting that the model has correctly identified these beaches as having intrinsic attractiveness to snowy plovers.

The beaches along the Carpinteria Salt Marsh (911) and those within the CA-91 recovery site, Carpinteria City Beach (912) and Carpinteria State Beach (913) *(Figure 34)* have high maximum HSV, which actually extends west beyond the designated recovery beaches to encompass the sand spit between the salt marsh and Pacific Ocean; overall HSV on the sand spit is very high (max. = 0.958; mean = 0.935). The presence of houses in this area of would-be prime habitat removes it from use, however. Carpinteria City Beach (HSV max. = 0.922) and the western edge of Carpinteria State Beach (HSV max. = 0.875) have high-quality habitat but values decline toward the east as the beach narrows. For those two sites, mean

HSV are not as high as either the Santa Barbara beaches to the west or the Ventura County beaches further down the coast. The range of human disturbances on these beaches from various recreational activities stands in the way of significant use by plovers.

The coast of Ventura County is almost entirely sandy beach that would under natural circumstances all be high quality habitat for Western Snowy Plovers. Based strictly on ecological requirements provided by the physical environment, this is where plovers should flourish. Our habitat suitability predictions for every site are high: maxima range from 0.936 – 0.980; mean HSV range from 0.852 – 0.947 (Table 7). Surveys on all beaches have always recorded substantial numbers of birds during winter surveys (Page et al. 1986; George 2006; USFWS 2009a).

The high levels of recreational use, however, diminish the realized value of these beaches to plovers. Persistence and productivity of plovers on these beaches is predominantly the result of variations in recreational use and associated disturbances (i.e., beach grooming, subsidized predator density, etc.). Jurisdictional and land-use conflicts affect management; non-recreational factors directly influence Western Snowy Plover success. The Ventura USFWS office, Ventura Audubon, and a small dedicated volunteer corps have forged relationships with multiple entities to encourage plover conservation.

San Buenaventura Beach (CA-95) *(Figure 35)* is an urban-adjacent beach. There are no recent nests recorded thus no monitoring. The site is censused during breeding window surveys, and results are unpredictable: for the most part, plovers have not been present, nevertheless, 3 were seen in 2007, 22 in 2002, and 4 each in 1995 and 1991. Again, no breeding is recorded here because of recreational use. Plovers use the site during the winter when recreational activity is lower, and roughly 60 birds are typically counted on the winter surveys (George 2006; USFWS 2007a, 2009a).

High quality physical habitat extends outside the designated recovery beach to include the area around the mouth of the Ventura River. Within the CA-95 site, maximum HSV = 0.949, and the beach is narrow. Just 1–1.5 km east, on wide sand bars deposited beside and within the river, maximum HSV = 0.969. Sediment flow varies but the Ventura River channel is constrained by mountains and fairly stable, unlike the natural pattern of Calleguas Creek or the Santa Clara River. These physical characteristics and the HSV pattern based on other environmental variable suggest that with proper management this site around the river mouth could be a successful nesting beach similar to Coal Oil Point.

At the Santa Clara River Mouth (CA-96) *(Figure 36)*, highest-quality snowy plover habitat is found along the Santa Clara River sand bars, within the estuary, and near McGrath Lake, all at McGrath State Beach (961, max. = 0.978; mean = 0.901). The northern end of Mandalay State Beach (962, max. = 0.958) is also predicted as a high-HSV location, although the beach is narrow for its entire length. High habitat values are reflected in the presence of nesting birds each year at both of these sites, but they are most abundant, as expected, in the area near the Santa Clara River. We consider the small high-HSV section of the beach between McGrath and Mandalay owned by Reliant Energy separately (9662, max = 0.965; mean = 0.947). One nest has been found here.

California State Parks supervises both McGrath and Mandalay Beaches, but Ventura County Parks operates Mandalay Beach. Consistent monitoring has been done since 1998. Plovers benefit from local management actions, primarily provided by State Parks, including public education, solid fencing along all major nesting areas, informative signs, and predator control through the use of nest exclosures. Law enforcement actions differ by agency. Dogs are prohibited on state beaches, and this restriction is enforced at McGrath but off-leash dogs are common at Mandalay. With consistent State Parks management, the Santa Clara River Mouth should be able to support additional birds and meet or exceed its recovery goal. Mandalay Beach is more problematic given the width of the beach and the management differences.

Hollywood Beach (CA-97) has high predicted HSV (max. = 0.949) at the wider southern end; the northern section is narrow like adjacent Mandalay. It is owned by Ventura County. The County prohibits dogs on this beach during daylight hours and allows them on a leash the rest of the time; apparently it does little to enforce the law. The proximity of residences to the beach, its heavy use, and opposition to restrictions on activities are other constraints. A few birds do nest farther up the beach, where it is regularly groomed, but the southern end is symbolically-fenced and designated as a nesting area by the County of Ventura Harbor Department (Smith

FIGURE 35. Deductive model HSV for San Buenaventura Beach, CA-95.
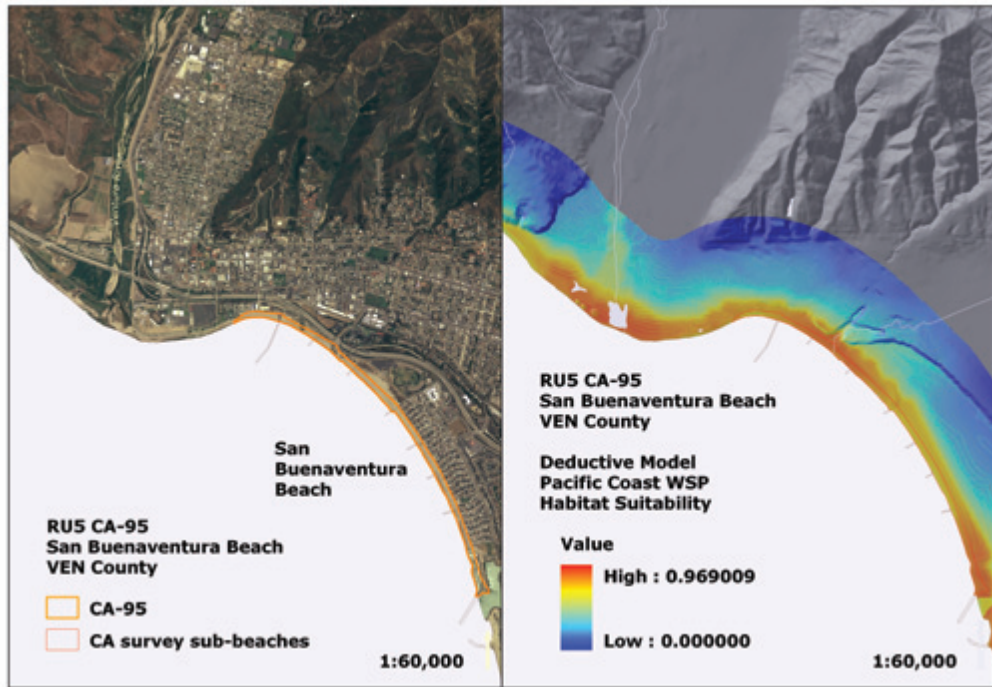
FIGURE 36. Deductive model HSV for Santa Clara River Mouth/Mandalay State Beach, CA-96; and Hollywood Beach CA-97.
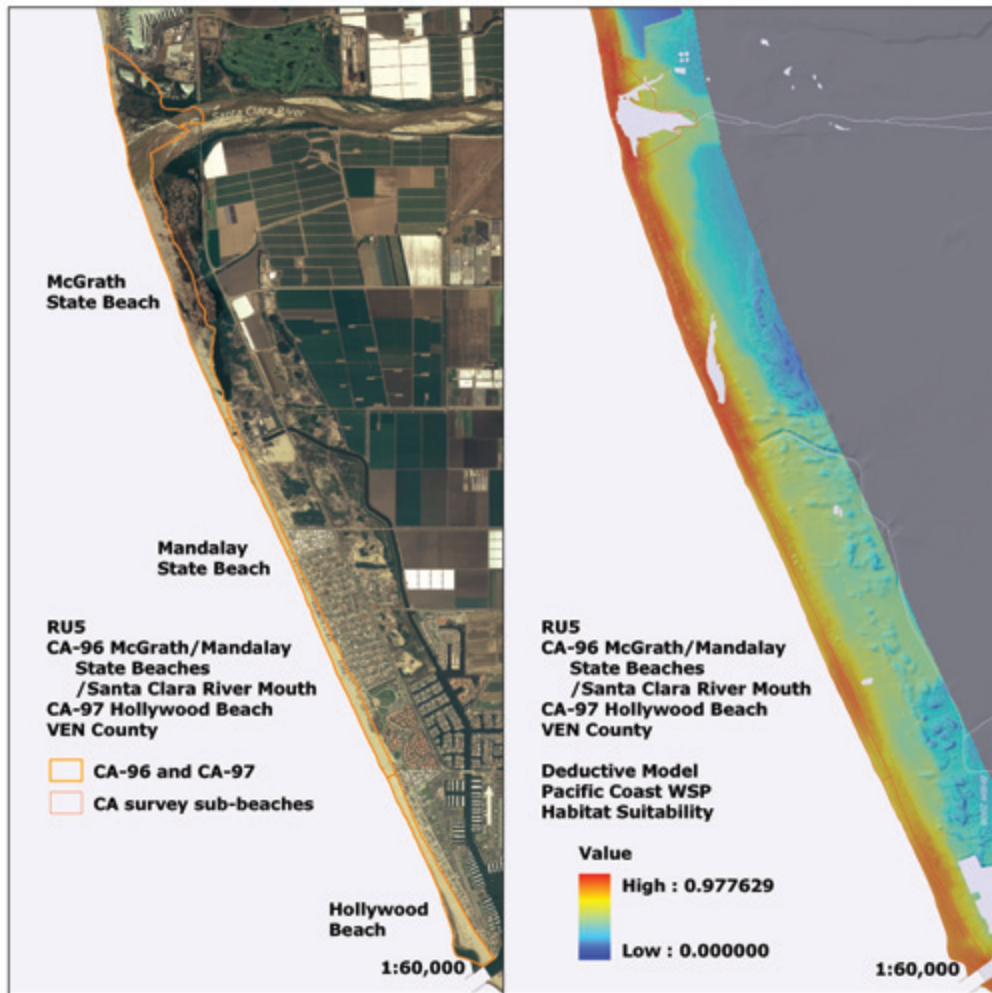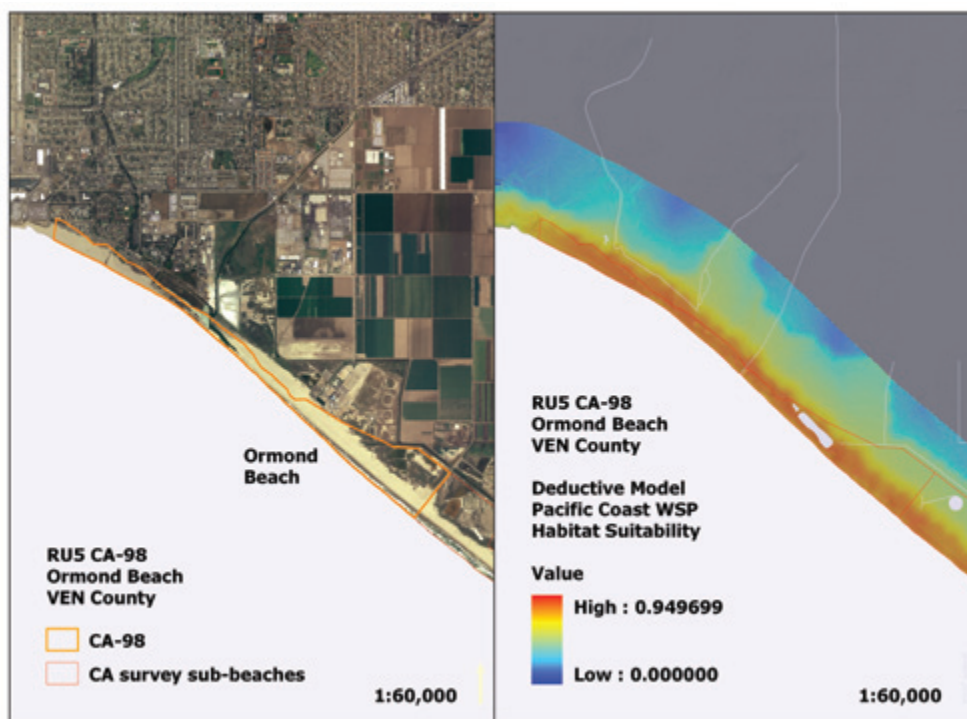
FIGURE 37. Deductive model HSV for Ormond Beach, CA-98.

2005). Somewhat ironically, to improve access to the Channel Islands Harbor, recent habitat alterations included dredging some of the southern sandy beach where plover nests tend to cluster. Nesting plovers are always present; they are not abundant, but numbers of breeding birds have increased in recent years (USFWS 2009b). Local outreach and docent programs to promote plover recovery will be important here.

Ormond Beach (CA-98, site 981) *(Figure 37)* is long, wide, flat, sandy, dune-backed, and adjacent to wetlands, so predicted HSV are high all along this beach: max. = 0.950, mean = 0.879. The eastern end extends back into the dunes. Numbers of window-surveyed breeding birds and of nests fluctuate, but the recent trend appears to be a slow increase. Large numbers of wintering birds are surveyed every year (USFWS 2009a, 2009b). Comprehensive snowy plover monitoring has been done at Ormond Beach since 2003.

Nest exclosures are used as predator protection, and solid fencing is placed around most of the nesting area to decrease human disturbance. Recreational activities at Ormond Beach include kite flying, paragliding (now banned), regular use by unleashed dogs, and other significant disturbances (Smith 2005). With the help of USFWS and others, public outreach and education programs and efforts to recruit volunteers or docents have been established in Ventura County. These are critical. There have been a range of owners and management schemes. Conservation plans have been made, approved, changed, abandoned, and then resurrected. Ideally, the California Coastal Conservancy will help the City of Oxnard implement efforts here that local activists and the Nature Conservancy have supported.

Consider, again, that we specifically excluded human-influenced factors. Nevertheless, based on apparent plover preferences, we calculated HSV separately for the section with a power plant at nearby Mandalay Beach. We did not similarly partition Ormond Beach, but a similar pattern (no nests) occurs here. This power plant is adjacent to the Halaco smelter (E.P.A. Superfund) site, and drains flow from upland pesticide-intensive agricultural fields, sod farms, and industrial buildings. Cleanup at the superfund site has begun (February 2010), and a well-executed ecological
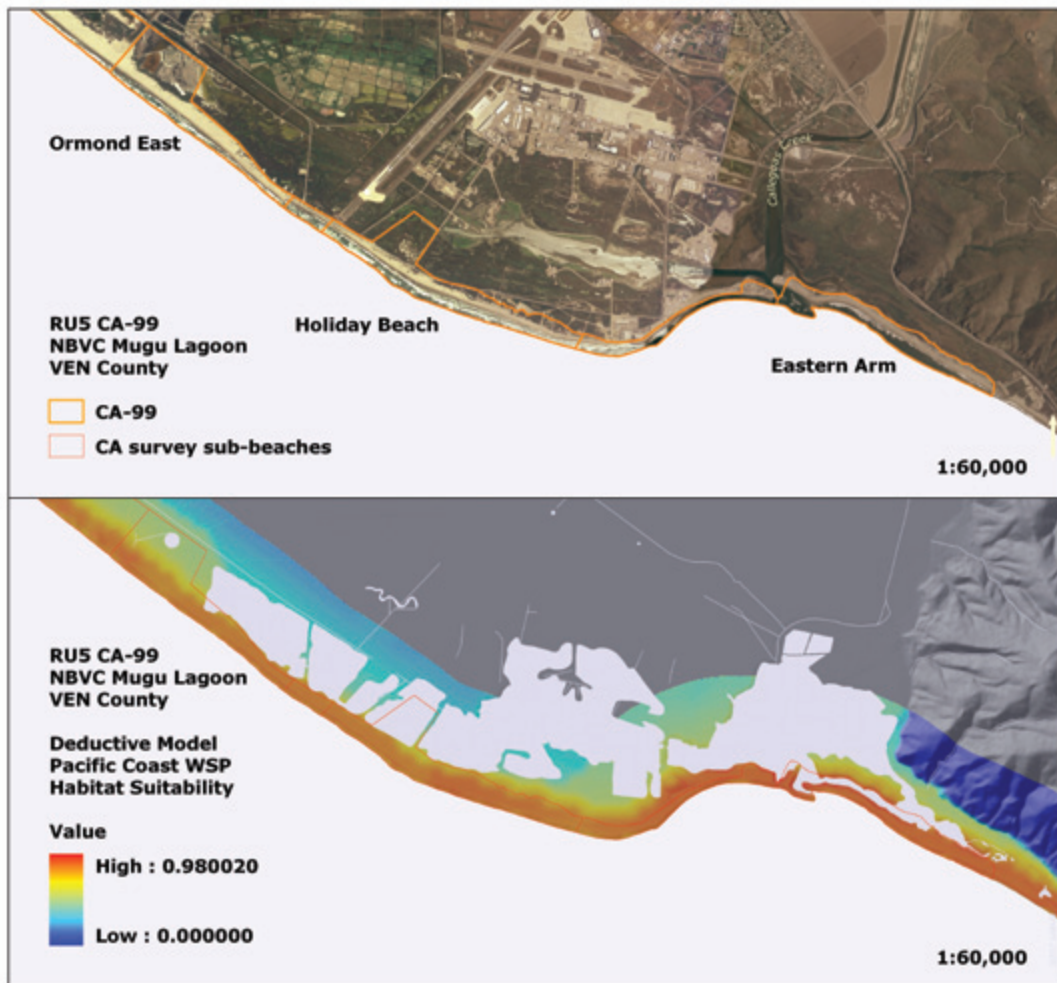
FIGURE 38. Deductive model HSV for NBVC Mugu Lagoon, CA-99.

restoration at Ormond Beach would be a regional success story. Long-term effects would extend far beyond ensuring that snowy plover habitat with intrinsically high suitability would support the increased productivity needed for Ventura County to reach species' recovery goals. Dunes and wetlands were once linked along this coastal plain, and a local restoration model to emulate might be Mugu Lagoon.

Mugu Lagoon *(Figure 38)* is protected and managed by U.S. Naval Base Ventura County. It is contiguous to Ormond Beach, separated by a fence that runs into the sea to prevent public access. Access is similarly restricted on all sides. Western Snowy Plovers nest on three Mugu Lagoon beaches: Ormond East (991), Holiday Beach (993), and Eastern Arm (995). The site

has a long-established, well-funded, intensively-managed program of habitat management and restoration, endangered species monitoring, and effective predator management techniques (U.S. Navy 2002, 2006a), which go along with the highest recorded HSV (max. = 0.980 at Eastern Arm) in the entire RU5 study area. The high HSV is caused in part by the proximity of inland wetlands to coastal beaches that provides a range of foraging habitats for birds; Mugu Lagoon is the significant estuary in this region. Salt pans, low dunes, wide beaches, and the mouth of Calleguas Creek also contribute to the model calculating high HSV (sites' maxima = 0.936–0.980; sites' means = 0.852–0.936).

High numbers of both wintering and breeding birds have been and continue to be recorded

regularly (Page and Stenzel 1981; Page et al. 1986; USFWS 2009a, 2009b). This site is critically important for RU5 as a whole, and is an essential component in the rangewide scheme for species' recovery. It is has relationships with Channel Islands populations, and is the southernmost RU5 site on the mainland; there are very large gaps between RU5 and Bolsa Chica and Camp Pendleton, the two large concentrations of plovers to the south.

Mugu Lagoon biologists have stressed the value of banding plovers at this location, in part to study population dynamics in the southern part of the range; for example, it is believed that the majority of breeding Mugu birds migrate south, and are replaced in the winter by birds from the north, but this cannot be confirmed (U.S. Navy 2005). Banding data are crucial research components (USFWS 2006; Stenzel et al. 2007). Banding would enable the plovers' reproductive success and other metrics to be calculated to better evaluate site productivity, and would then allow multiple comparisons to be made between geographically dispersed RU5 locations that band birds (Vandenberg AFB and Oceano Dunes SVRA band now; Guadalupe-Nipomo Dunes NWR formerly banded plovers).

We made a site-productivity comparison between contiguous Ormond Beach (981) and Ormond Beach East (991) based on number of nests. We had data for Ormond Beach for 2003–2009 and Ormond Beach East for 1998–2006; we compared 2003–2006 nest data. Sites were monitored at the same frequency by biologists with site-specific local expertise, and shared similar detectability and high predicted habitat quality: HSV (981), max. = 0.950, mean = 0.879, stdev = 0.058; HSV (991), max = 0.943, mean = 0.852, stdev = 0.068. Ormond Beach is larger (area = 0.973 km2) than Ormond Beach East (area = 0.661 km2). During 2003–2006, 86 nests were recorded at Ormond Beach (981), and 268 nests were recorded at Ormond Beach East (991). Management strategies almost certainly affected productivity.

Mugu Lagoon adjoins Point Mugu State Park. This is the western end of Santa Monica Mountains National Recreation Area, the patchwork of protected lands that extends well into Los Angeles County. There are no additional RU5 mainland beaches window-surveyed for breeding or wintering plovers. Mugu Beach is the last wide Ventura beach. It begins at the NBVC fence and narrows very quickly to Point Mugu Rock; physical conditions and HSV are like those up the coast (max. = 0.962). Past the rocky headlands, dune or bluff-backed beaches are sandy but very narrow at high tide.

All State Parks beaches here are managed intensively for heavy recreational use; extensive beach-adjacent and on-the-beach campgrounds encompass creek mouths at La Jolla and Big Sycamore Canyons where high HSV are predicted (max. = 0.894; 0.889). Down the coast, outside parklands, high-use beaches are much less regulated. South of County Line beach, near Little Sycamore Canyon, swaths of high-HSV beach (max. = 0.909) front a large residential complex and occur on high-use Staircase beach, at the extreme northwestern end of Leo Carrillo State Park. This is the actual county line and RU5/RU6 boundary.

According to the Recovery Plan, the RU5 breeding population has fluctuated over three decades, but there is no evidence of overall decline. At the same time, major changes have occurred on the California Channel Islands: the decline and loss of the San Miguel Island (CA-92) *(Figure 39)* population and its decline on Santa Rosa Island (CA-93) *(Figure 40)*. At the closest mainland sites, Vandenberg AFB and Coal Oil Point, populations have increased (USFWS 2007a). Island birds are nonetheless expected to be 20% of the RU5 population, unchanged from the Draft Plan (USFWS 2001). Many island sites are remote and difficult to access, are monitored irregularly, and therefore have little data available for analysis. This is especially true for San Miguel and Santa Rosa Islands.

FIGURE 39. Deductive model HSV for San Miguel Island, CA-92.

RU5 CA-92
San Miguel Island
Units 1- 8

CA-92

CA survey sub-beaches

1:90,000

RU5 CA-92
San Miguel Island

Deductive Model
Pacific Coast WSP
Habitat Suitability

Value

High : 0.902381

Low : 0.000000

1:90,000
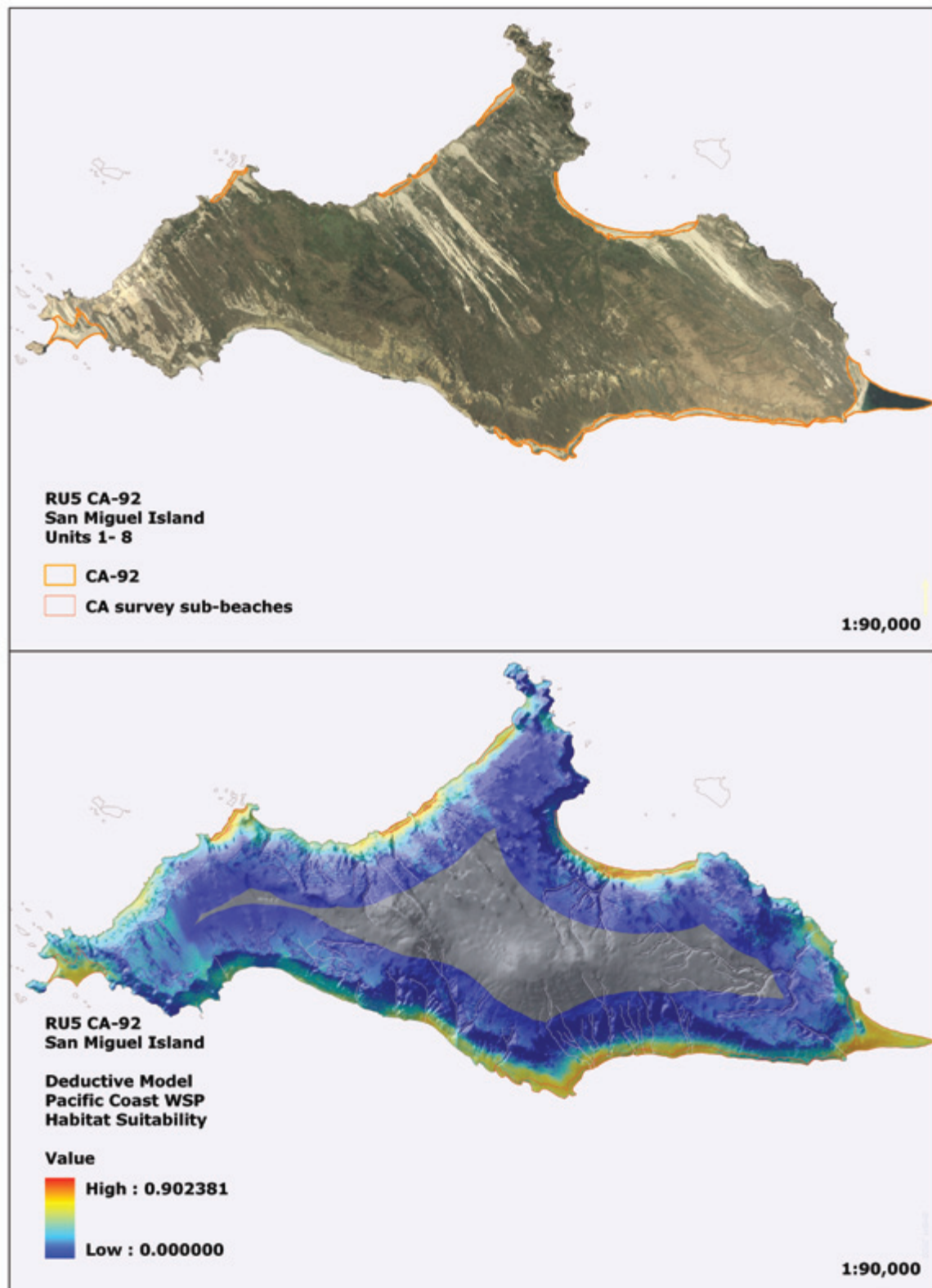
FIGURE 40. Deductive model HSV for Santa Rosa Island, CA-93.

RU5 CA-93
Santa Rosa Island
Units 1-11

☐ CA-93
☐ CA survey sub-beaches

1:160,000

RU5 CA-93
Santa Rosa Island

Deductive Model
Pacific Coast WSP
Habitat Suitability

Value
High : 0.916307

Low : 0.000000

1:160,000

FIGURE 41. Deductive model HSV for Santa Cruz Island, CA-94.
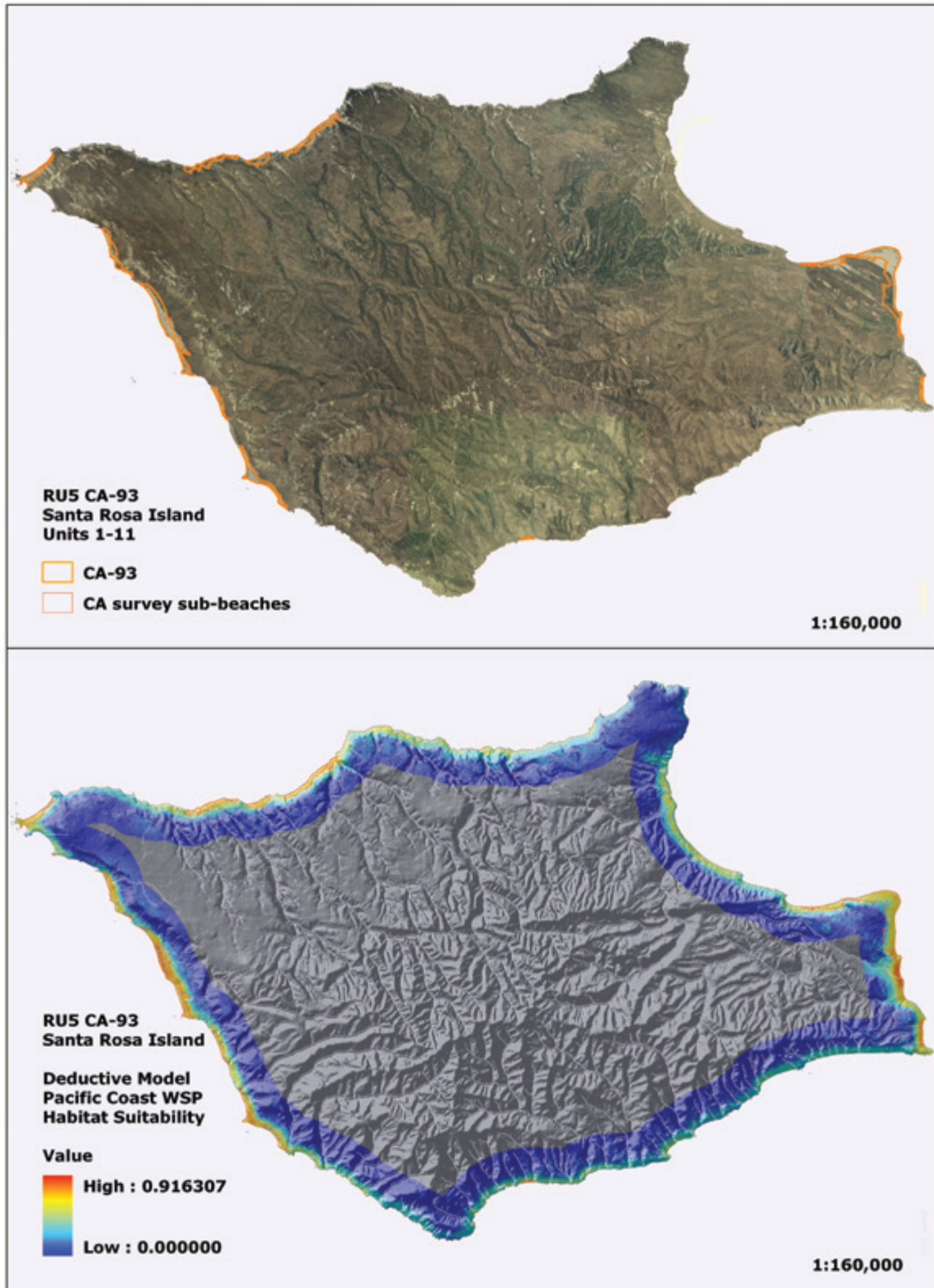
FIGURE 41. Deductive model HSV for Santa Cruz Island, CA-94.

The habitat on the northern California Channel Islands has many considerations that differ from the mainland sites and some that are the same. Santa Cruz Island (CA-94) *(Figure 41)* is the largest, with higher elevations, and a range of climate patterns. Microclimate and weather conditions (especially winds) on all the islands vary based on the orientation of beaches, which have far greater variability in aspect than mainland sites. Wind data show that strong winds can come from any direction at any time of year, and indicate how erratic island weather can be. North and west-facing beaches experience more extremes, but very desirable locations face northwest to north-east in coves protected by rocky headlands. Sandspits build up at the eastern ends of some islands, and cliff-backed east-facing beaches are often sheltered from storms. As on the mainland, south-facing sandy beaches are favorable sites.

Management differs by jurisdiction, and jurisdictions can vary, even within islands. Santa Rosa and San Miguel are part of Channel Islands National Park, owned by the National Park Service (NPS). The eastern end of Santa Cruz is owned by NPS; the western end is owned by the Nature Conservancy (TNC). The University of California (UC) central valley field station coordinates surveys at two recovery beaches, near Fraser Point on Forney Cove, and on the south coast between Morse Point and Punta Arena. Lowest HSV for any island's sites are on Santa Cruz (max. = 0.835), which has had no nests recently, and few wintering individuals. Our model identifies Christy Beach, where central valley canyons meet the western shore, as of much higher suitability (max. = 0.894). TNC and the UC could explore this possibility since the central valley zone where TNC allows no public access extends to the coast.

San Miguel has good HSV (max. = 0.902, mean = 0.753). Highest HSV are along dunes at northwest facing Simonton Cove and north-facing Cuyler Harbor, which is the landing site for the island and thus more disturbed. Santa Rosa beaches

with high HSV are within 5–10 km of Sandy Point on north-west and south-west coasts. The east-facing beaches on the truncated eastern tip of the island have the highest predicted HSV (max. = 0.916, mean = 0.770), starting at the Skunk Point sandspit, then south to East Point, with the central area that captures the drainage from the eastern part of the island the highest. Plovers wintered on San Miguel in 2008 after being absent (USFWS 2009a), while Santa Rosa has very high numbers of wintering birds with close to 200 birds each of the past several years.

High-HSV sites predicted by our deductive model align with USFWS recovery sites on San Miguel, Santa Rosa, and Santa Cruz Islands. There is no Western Snowy Plover habitat on Santa Barbara and Anacapa Islands. We made our primary comparisons for each island with aggregated beaches, and mean values were over our 0.7 criterion. Although the model identifies high quality habitat at many locations throughout the Channel Islands, predictions may lead to unreasonable assumptions for several reasons. For example, on San Miguel and Santa Rosa Islands, the primary plover predator is the recently reintroduced native bald eagle (D. Richards, pers. comm.); Santa Cruz Island also has bald eagles. San Miguel and San Nicolas Islands have large populations of elephant seals, fur seals, and California sea lions. At many locations, marine mammal haul-out and breeding sites have displaced potential snowy plover habitat, setting up situations where one sensitive species was essentially destroying the habitat of another through disturbance. On San Nicolas, feral cats were a problem for many years (a situation that is now rectified) (Spear 1979; USFWS 2007a; Harvey et al. 2008).

San Nicolas Island (CA-100) *(Figure 42)* has the highest predicted HSV in the northern California Channel Islands (max. = 0.935). The USFWS-designated recovery sites for San Nicolas Island (Units 1–15) are discrete beaches. San Nicolas Island is part of U.S. Naval Base Ventura County and is the only island with a Western Snowy Plover monitoring program. U.S. Navy monitoring

FIGURE 42. Deductive model HSV for San Nicolas Island, CA-100.
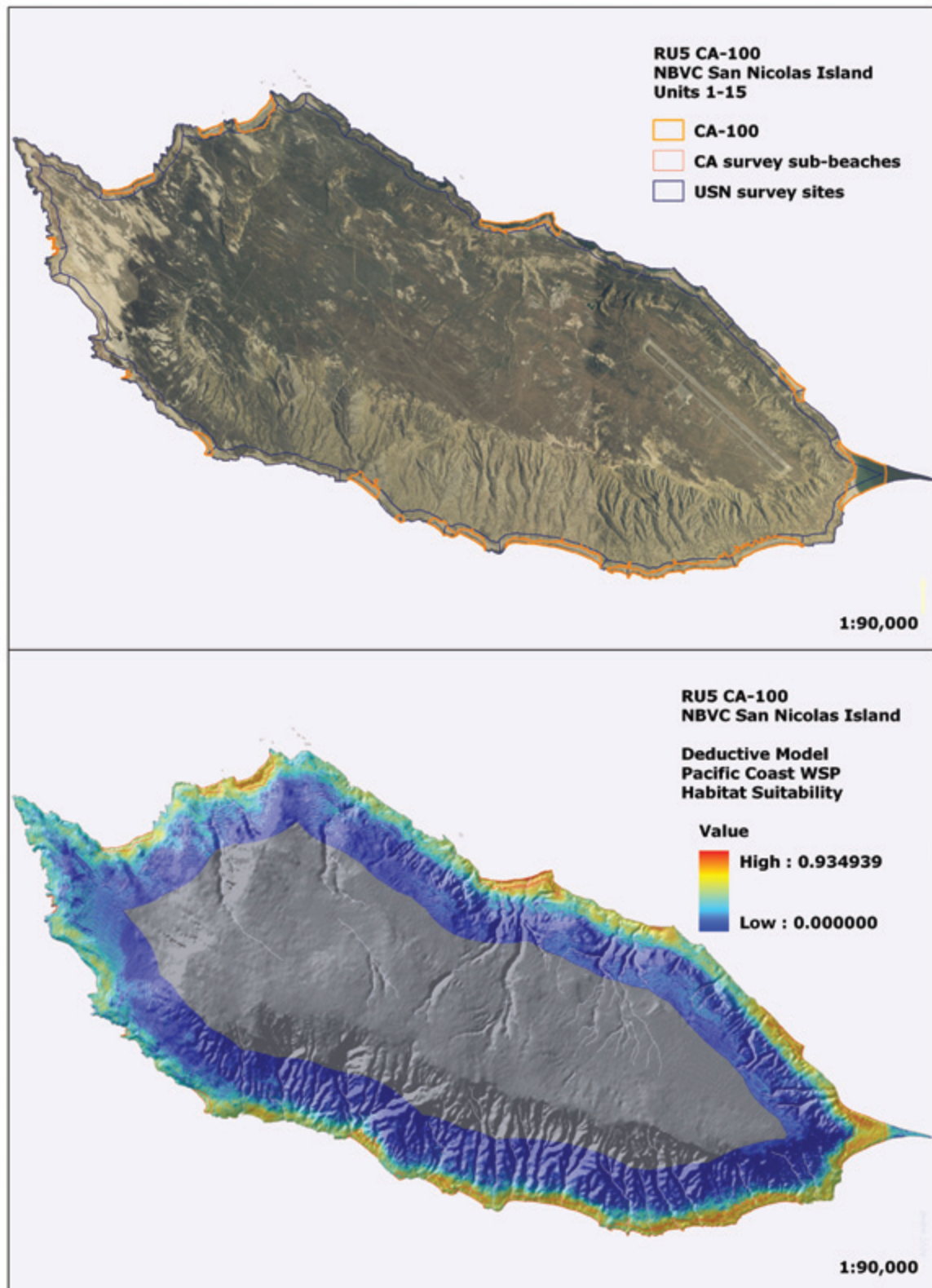
divides the island perimeter into 30 continuous sectors named for beaches. San Nicolas beach-level data from breeding-season and winter window surveys conducted during 1993–2006 (U.S. Navy 2006b, 2006c) were made available for additional analysis. In addition to window surveys, selected breeding sites were surveyed from a distance twice a week (H. Gellerman, C. Sandoval, pers. comm.), and new surveys began in 2009 (M. Ruane pers. comm.). This information will help fill the island data gap.

We briefly discuss San Nicolas Island beaches we identified as high-HSV sites and compare them with data we have. Our model identified current, recent, and historic sites regardless of how they were divided. Clockwise from western-most Vizcaino Point (HSV max. = 0.75), and facing north-west, important plover beaches are the Red Eye beaches (max. = 0.813); and northern Tender Beach (max. = 0.914); then facing north-east, west to east, the central coast cluster: NAVFAC Beach, Tranquility Beach, Anchor Point, and Cissy Cove (sites' max. = 0.907, 0.935, 0.925, 0.916); and the eastern Coast Guard beaches and Sand Spit east to west along south-west to south-facing beaches along the many southern sites, including Daytona Beach, Dutch Harbor, Area 264/263, and Elephant Seal Beach (sites' max. range = 0.857–0.889). Finally, west-facing Rock Crusher beaches south of Vizcaino Point have the lowest HSV (max. = 0.74).

Recent and not-so-recent data (Spear 1979; U.S Navy 2006c) indicate breeding plovers can be found anywhere on the San Nicolas Island coast. Tender Beach has the most consistent and highest numbers by far (1993–2006). The northern beaches near Tranquility Beach, the Coast Guard beaches, and the Sand Spit have fluctuating but high numbers and high HSV. Red Eye beaches have lower HSV but are near the Tender Beach concentration and face north-west, which appears to be desirable on the islands. Numbers at south-facing Daytona Beach, Dutch Harbor, and Area 264/263 are erratic but declined over the survey period. Feral cats were removed from ev-ery beach listed (Harvey et al. 2008), and plovers should benefit quickly from their absence; San Nicolas Island "seabird restoration" was selected as mitigation for damages to seabirds from the effects of past releases of DDT.

Plover breeding on lower-HSV Rock Crusher beaches is explained by competition. This is not a new problem on southern beaches, (i.e., Elephant Seal Beach), but with protection in the Channel Islands, pinnipeds have overrun beaches where plovers historically nested, displacing birds to less suitable habitat. Efforts to accommodate all protected species are being made, but most nesting (2007) is confined to caliche terraces above Rock Crusher (max. = 0.725) and Coast Guard beaches (max. = 0.825) (H. Geller-man pers. comm.) rather than where historic nesting occurred. Rock Crusher compares to low-HSV but high-density nest sites at Vandenberg AFB. On winter surveys, San Nicolas has averaged 140 birds and exceeded 200 on recent surveys (USFWS 2007a). Winter counts are erratic. Tender Beach has consistently high numbers (2006b); over time, so did Red Eye and Coast Guard beaches and the Sand Spit but other northern beaches declined. Numbers were steady on the south coast although wintering flocks selected many different beaches on window-survey days.

3.1.3 Deductive predictions compared with known nest data

We used the recorded locations of nest sites to make quantitative assessments of the performance of deductive models that were based on environmental variables alone. We used the same nest-point data to evaluate our deductive-model predictions of habitat suitability that were used to generate our inductive models. We expected that the results would show that locations chosen by snowy plovers as nest sites have a higher mean HSV than non-nest locations. We evaluated the differences between mean HSV at nest and non-nest pixels with ANOVA and replicated randomization.

SUMMARY OF RESULTS: NEST/NO-NEST PIXEL MEANS RANDOMIZATION/ANOVA TESTS BY SITE								
Difference Significant						α =0.05	**Not Significant**	
Sites where *mean HSV higher* in pixels where nests recorded than in no-nest pixels								
801	833	841.2	851	882	981		781	962
	834	843	852	881.4	991		801.2	971
811	835	844	851.2		993			
812	834.56	845.6	854	9.567	991.5		831.23	995
811.23	837	841.6		961	98.915		838	
	837.89			961.22			855	
Sites where *mean HSV lower* in pixels where nests recorded than in no-nest pixels								
		853					853.5	
		851.5						

TABLE 8. Summary of deductive model performance in predicting recorded nest sites within recovery sites. Significance tests of model applied to Western Snowy Plover nest data.

Within beach survey sites, the differences in predicted habitat suitability between pixels with and without recorded nests were revealed by examination of maps, tabular data, and histograms and box plots. Differences were apparent at sites with comparatively high and low HSV. Large-scale maps of predicted HSV overlaid with recorded nest locations *(Figure 43)*, and histograms and box plots *(Figure 44)* are shown for two sets of beaches in Santa Barbara County that illustrate the pattern. Figures *43a, 44a* are south-facing beaches surrounding Coal Oil Point Reserve (COPR, CA-88, site 882, with adjacent beaches 881–884); figures *43b, 44b* are west-facing northern beaches at Vandenberg Air Force Base (VAFB N, CA-84, 841-846). Environmental conditions are very different. One region is very small and the other is huge. However, both are successful breeding (and wintering) sites with comparable amounts of data: roughly 3% of the 10-m pixels at each site have nests *(Table 8)*.

For models based on environmental variables alone, sites were under consideration as potential habitat regardless of nest data availability. To evaluate our deductive predictions using known nest data, the statistical significance of differences between nest and no-nest pixel groups was calculated separately for individual beaches and for combinations. Sites with data were considered individually. Sites without data when contiguous to beaches with data were aggregated. Effects upon significance by increasing the number of no-nest pixels were expected.

HSV differences were significance tested by ANOVA and Monte Carlo randomizations. ANOVA tested differences between observed (predicted) nest and no-nest pixel HSV means. Randomizations tested differences between observed (predicted) means and simulated HSV means. Mean HSV was higher in pixels where nests were recorded than in no-nest pixels for 37 of 40 sites and site combinations. The difference was significant at α=0.05 in 29 cases *(Table 8)*. Results were directly comparable *(Table 9)*. These patterns reinforce the validity of the model: the sites identified has having high habitat values were indeed more likely to be chosen as nest sites than other sites with lower values.

Mean predicted HSV at survey sites across the study region varied from ~0.692 to ~0.947 (mean = ~0.821 for all 73 sites). Pixels where nests were recorded had greater mean HSV than no-nest pixels and this relationship was valid across all levels of suitability. This was true for aggregated sites that had relatively high HSV across a small range of values, including every south or south-west facing site in Santa Barbara and Ventura Counties with nest data and their

FIGURE 43a. (RIGHT)
Site close-ups, known nest locations mapped with predicted HSV for Coal Oil Point Reserve.
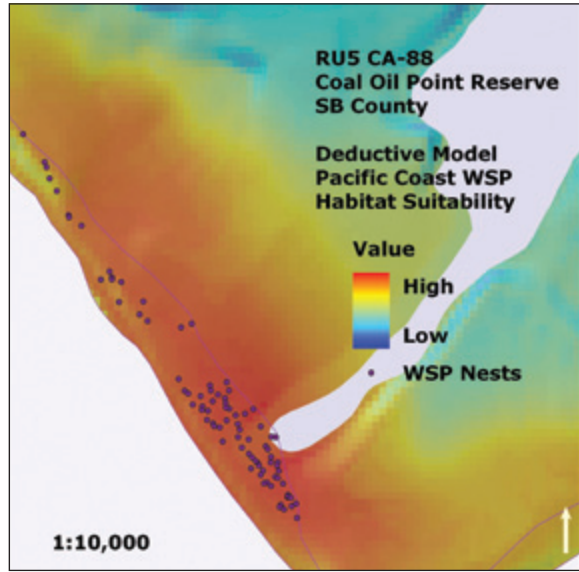
FIGURE 44a. (BELOW)
Plots of mean HSV at pixels with (red) and without known nests (blue) show similar patterns at sites with comparatively high and low HSV: Coal Oil Point Reserve and contiguous beaches.

RU5 CA-88
Coal Oil Point Reserve
SB County

Deductive Model
Pacific Coast WSP
Habitat Suitability

Value
High
Low
· WSP Nests

1:10,000

Model Habitat Suitability Values where WSP nests recorded

CA−88: Coal Oil Point UC Natural Reserve, 2001−2004 nest data, site number 881.4

Model HSV where no WSP nests recorded
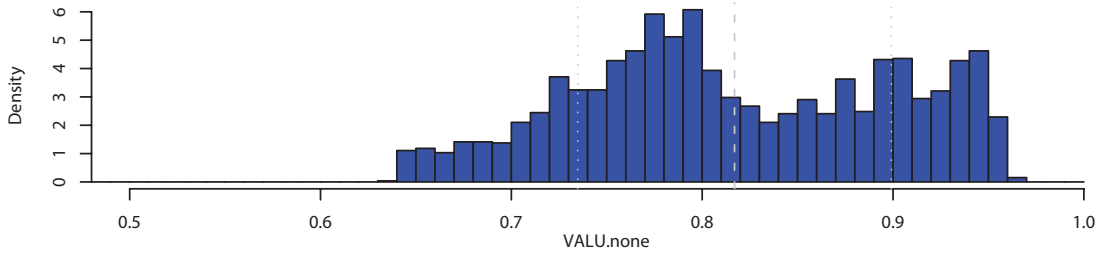
Ellwood Beach to Coal Oil Point to UCSB Campus Beach, HS Model 1K_13BSB, site number 881.4

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0
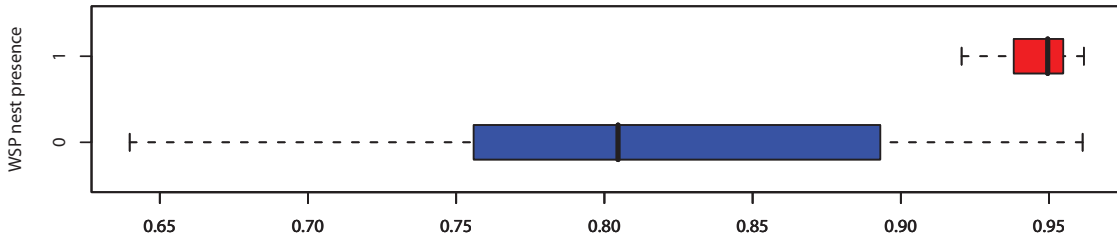
WSP Habitat Suitability Values, nest (n = 73) and non−nest (n = 2618) pixels, Model 1K_13BSB, site number 881.4

FIGURE 43b. (RIGHT)
Site close-ups, known nest locations mapped with predicted HSV for Vandenberg AFB, northern beaches, at San Antonio Creek.

RU5 CA–84 VAFB, N
(at San Antonio Creek)
SB County

**Deductive Model
Pacific Coast WSP
Habitat Suitability**

Value

High

Low

· WSP Nests

San Antonio Creek

1:10,000
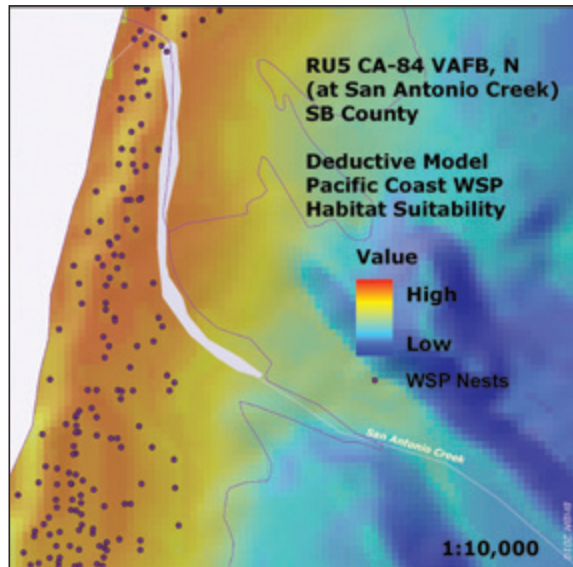
FIGURE 44b. (BELOW)
Plots of mean HSV at pixels with (red) and without known nests (blue) show similar patterns at sites with comparatively high and low HSV: Vandenberg AFB, northern beaches.

Model Habitat Suitability Values where WSP nests recorded

CA–84: Vandenberg AFB, All North Beaches, 1994–97, 1999–2000, 2002–06 nest data, site number 841.6

Model HSV where no WSP nests recorded

Vandenberg Air Force Base, All North Beaches, HS Model 1K_13BSB, site number 841.6

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 1224) and non–nest (n = 35979) pixels, Model 1K_13BSB, site number 841.6

COUNTY CA-SITE	BEACH SITE	N PIXELS/SITE		MODEL MEAN HSV PREDICTED		RANDOMIZATION α = 0.05 P H0 = TRUE	ANOVA α = 0.05 P > α	BEACH NAME INDIVIDUAL/ CONTIGUOUS
		nests	none	nests	none			
		Mean HSV higher for pixels where nests recorded than no-nest pixels						
SLO CA-78	781	49	541	0.886	0.877	0.1395-0.1469	0.1448	Estero Bluffs State Beach/ Villa Creek
CA-80	801	74	4779	0.848	0.822	0.0001-0.0008	0.0006	Morro Strand State Beach
	801.2	74	7696	0.848	0.839	0.2126-0.2181	0.2158	Morro Strand/ Morro Rock City Beach
CA-81	811	131	6929	0.885	0.879	0.0268-0.0324	0.0303	Morro Bay Sandspit - City of Morro Bay
	812	586	20119	0.856	0.805	0	1.16E-61	Morro Bay Sandspit - Montaña de Oro SP
	811.23	717	27963	0.861	0.826	0	3.02E-39	Morro Bay Sandspit - City + State + private
SLO CA-83	833	14	3667	0.886	0.838	0.0182-0.0226	0.0227	Oceano Dunes SVRA (ODSVRA) - day use
	831.23	14	9219	0.886	0.863	0.1498-0.1541	0.1569	Pismo State Beach to ODSVRA day use
	834	484	19319	0.763	0.738	0	8.97E-16	Oceano Dunes SVRA
	835	107	12527	0.819	0.767	0	5.37E-11	ODSVRA Oso Flaco Natural Area
	834.6	591	42814	0.773	0.746	0	6.62E-19	ODSVRA to Guadalupe-Nipomo Dunes NWR
	837	207	15828	0.870	0.789	0	4.15E-44	Guadalupe Restoration Site
SB CA-83	838	98	10301	0.813	0.805	0.4083-0.4241	0.4111	Rancho Guadalupe Dunes Preserve
	837.9	305	31401	0.852	0.795	0	5.44E-31	Guadalupe Rest. Site to Mussel Rock
CA-84	841.2	139	6062	0.826	0.750	0	3.94E-28	VAFB North - Minuteman Beach
	843	610	18399	0.778	0.741	0	1.04E-32	VAFB North - Shuman Beach
	844	438	7747	0.822	0.789	0	9.58E-35	VAFB North - San Antonio Beach
	845.6	37	3771	0.767	0.732	0	1.35E-06	VAFB North - Purisima North/Purisima Point
	841.6	1224	35979	0.799	0.752	0	1.82E-109	VAFB North - all beaches
CA-85	851	220	2937	0.901	0.880	0	1.38E-12	VAFB South - Wall Beach
	852	358	2833	0.910	0.870	0	2.52E-35	VAFB S - Surf Beach North (N)
	851.2	578	5770	0.907	0.875	0	3.77E-46	VAFB South - northern beaches
	854	223	1127	0.749	0.745	0.0047-0.0072	0.0059	VAFB S - Surf Beach North (S)
	855	432	1609	0.7055	0.702	0.0866-0.0979	0.0927	VAFB South - Surf Beach South
CA-88	882	73	1569	0.939	0.820	0	1.79E-35	Coal Oil Point UC Natural Reserve
						continued on next page		

TABLE 9. Performance of deductive model in predicting recorded nest sites within recovery areas. All sites. Significance tests of model applied to Western Snowy Plover nest data.

COUNTY CA-SITE	BEACH SITE	N PIXELS/SITE		MODEL MEAN HSV PREDICTED		RANDOMIZATION α = 0.05 P H0 = TRUE	ANOVA α = 0.05 P > α	BEACH NAME INDIVIDUAL/ CONTIGUOUS
		nests	none	nests	none			
Mean HSV higher for pixels where nests recorded than no-nest pixels								
	881.4	73	2618	0.939	0.817	0	5.33E-36	Ellwood Beach to (UCSB) Campus Beach
VEN CA-95	9.567	87	18419	0.924	0.895	0	3.84E-06	San Buenaventura SB to Hollywood Beach
CA-96	961	55	9869	0.937	0.901	0-0.0002	0.0001	McGrath State Beach
	962	16	3136	0.888	0.879	0.3545-0.3642	0.3586	Mandalay State Beach
	961.22	72	13200	0.926	0.897	0-0.0003	6.81E-05	Santa Clara River Mouth/ McGrath Mandalay SB
CA-97	971	15	2714	0.911	0.902	0.2226-0.2354	0.2275	Hollywood County Beach
CA-98	981	96	9633	0.904	0.879	0-0.0001	1.99E-05	Ormond Beach
CA-99	991	320	6293	0.894	0.849	0	3.82E-31	Naval Base Ventura County Mugu Lagoon - Ormond East
	993	124	6966	0.890	0.872	0.0104-0.0144	0.0124	NBVC Mugu Lagoon - Holiday Beach
	995	53	4175	0.928	0.925	0.6346-0.6388	0.6349	NBVC Mugu Lagoon - Eastern Arm Beach
	991.5	497	20189	0.897	0.883	0-0.0001	2.00E-05	NBVC Mugu Lagoon - entire
	98.915	593	29822	0.898	0.882	0	4.65E-09	Ormond Beach to Mugu Lagoon
Mean HSV lower for pixels where nests recorded than no-nest pixels								
SB CA-85	853	144	676	0.822	0.834	0.0071-0.0084	0.0077	Vandenberg AFB South - Surf Station Beach
	853.5	799	3412	0.739	0.742	0.1478-0.1573	0.1563	VAFB South - southern beaches
	851.5	1379	9182	0.804	0.824	0	2.76E-14	VAFB South - all beaches

TABLE 9 (continued). Performance of deductive model in predicting recorded nest sites within recovery areas. All sites. Significance tests of model applied to Western Snowy Plover nest data.

contiguous beaches, as well as for sites in southern San Luis Obispo and northern Santa Barbara counties with comparatively lower mean HSV across a greater range of values.

At eight single and aggregate beaches, mean HSV was higher for nest pixels than no-nest pixels, but results were not significant at α=0.05 (Table 8). Specific site details (Table 9) discussed above often explained divergence from the desired outcome. As expected, some site combinations had results that differed from sites considered independently. Disparities were most apparent when sites with comparatively few nest records were combined with adjacent no-data sites with higher mean HSV.

Insufficient data alone may have affected significance at some single sites (Table 8), particularly at larger sites with lower nest to no-nest pixel ratios (Table 9). Sites with relatively sparse data, either for limited years (e.g., Estero Bluffs State Beach/Villa Creek, site 781, and Rancho Guadalupe Dunes Preserve, site 838, which had 2005–2006 data only) or with few nests recorded (e.g., Mandalay State Beach, site 962, had 16 nests during 2003–2007; and Hollywood County Beach, site 971, recorded 15 nests for 2004, 2006–2007) had non-significant results. Each of these sites has provided additional data for further analysis.

Naval Base Ventura County Mugu Lagoon beaches had very high predicted HSV (see Table 7). Mul-

FIGURE 45. Mugu Lagoon nest sites: a) 1998–2000, b) 2001–2003, c) 2004–2006.

tiple years of data were available; for most beaches, differences between predicted HSV for nest and no-nest pixels were significant. Eastern Arm, site 995, had the highest mean (0.936) and maximum (0.980) HSV for the RU5 study area, however, differences between nest and no-nest pixels were not significant at α=0.05. We observed a pattern consistent with the intensive management and successful habitat restoration efforts at Mugu Lagoon (U.S. Navy 2002, 2005, 2006a). In *Figure 45*, Western Snowy Plover nests in *(45a)* 1998–2000, *(45b)* 2001–2003, and *(45c)* 2004–2006 indicate earlier nests more densely concentrated at Ormond East Beach, site 991. After restoration was completed in early 2002, more nesting occurred at Holiday Beach, site 993. Finally, distribution along the three beaches managed for plovers became more even and higher-HSV sites were selected as more nests were initiated at Eastern Arm, site 995. Differences between nest/no-nest HSV means will likely become further differentiated as more Western Snowy Plover nests are recorded at all Mugu Lagoon beaches. Nest/no-nest HSV comparisons at Holiday Beach support this: it was one of three sites (along with northern Morro Bay Sandspit (811) and Pismo State Beach (833)) where higher mean nest-pixel HSV was not significant at a more-stringent α=0.01 *(Table 9)*.

FIGURE 46a. Vandenberg AFB, southern beaches, CA-85: 1609 Western Snowy Plover nests recorded.

As at Mugu Lagoon, Pacific Coast Western Snowy Plovers are intensively monitored and managed and thrive at the other RU5 military reservation, Vandenberg Air Force Base (VAFB). At the northern and southern VAFB beaches, sites CA-84 and CA-85, extensive data for multiple years were available *(Table 8)*. Our deductive models predicted a wide range of habitat quality along the southern VAFB beaches, sub-sites 851–855, because of extreme variability across the entire suite of environmental predictors. HSV range from very high at the northern beaches to quite low in the south (means, 0.702–0.881; maxima, 0.793–0.939, Table 7), as our map *(Figure 28)* illustrates. *Figure 46* indicates the location and concentration of nests recorded for this site *(46a)*; histograms confirm the variability in predicted HSV from north to south by showing *(46b)* all beaches, *(46c)* northern beaches, and *(46d)* southern beaches.

These data and associated comprehensive VAFB annual reports are an opportunity for a more detailed analysis. When we compared predicted HSV at nest and no-nest pixels within the five southern beach sub-sites (CA-85; 851–855) and combinations (northern, southern, all sites), the results represented all possibilities *(Table 9)*. Three beaches, Wall Beach (851), and Surf Beach North to the north (852) and south (854) of Surf

Model Habitat Suitability Values where WSP nests recorded

CA–85: Santa Ynez River Mouth, Vandenberg AFB, All South Beaches, 1994–97, 1999–2000, 2002–06 nest data, site number 851.5

Model HSV where no WSP nests recorded

Santa Ynez River Mouth/Ocean Beach, Vandenberg Air Force Base, All South Beaches, HS Model 1K_13BSB, site number 851.5

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 1379) and non–nest (n = 9182) pixels, Model 1K_13BSB, site number 851.5

Station, plus the combination of the two beaches north of Surf Station (851.2) had significantly higher HSV at nest sites than at non-nest pixels. Southernmost Surf South Beach (855) had very slightly but not significantly higher HSV at nest pixels. Finally, the only locations within all of RU5 where the predicted HSV at recorded locations of Western Snowy Plover nests was lower than at no-nest pixels were here (at site 853, Surf Station; and in the site combinations 853.5 and 851.5).

The southern Vandenberg AFB beaches are environmentally diverse, but factors other than physical features probably explain why plovers selected lower rather than higher-HSV nesting

Model Habitat Suitability Values where WSP nests recorded

CA–85: Santa Ynez River Mouth, Vandenberg AFB, N South Beaches, 1994–97, 1999–2000, 2002–06 nest data, site number 851.2

Model HSV where no WSP nests recorded

Santa Ynez River Mouth, Vandenberg Air Force Base, northern South Beaches, HS Model 1K_13BSB, site number 851.2

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 578) and non–nest (n = 5770) pixels, Model 1K_13BSB, site number 851.2
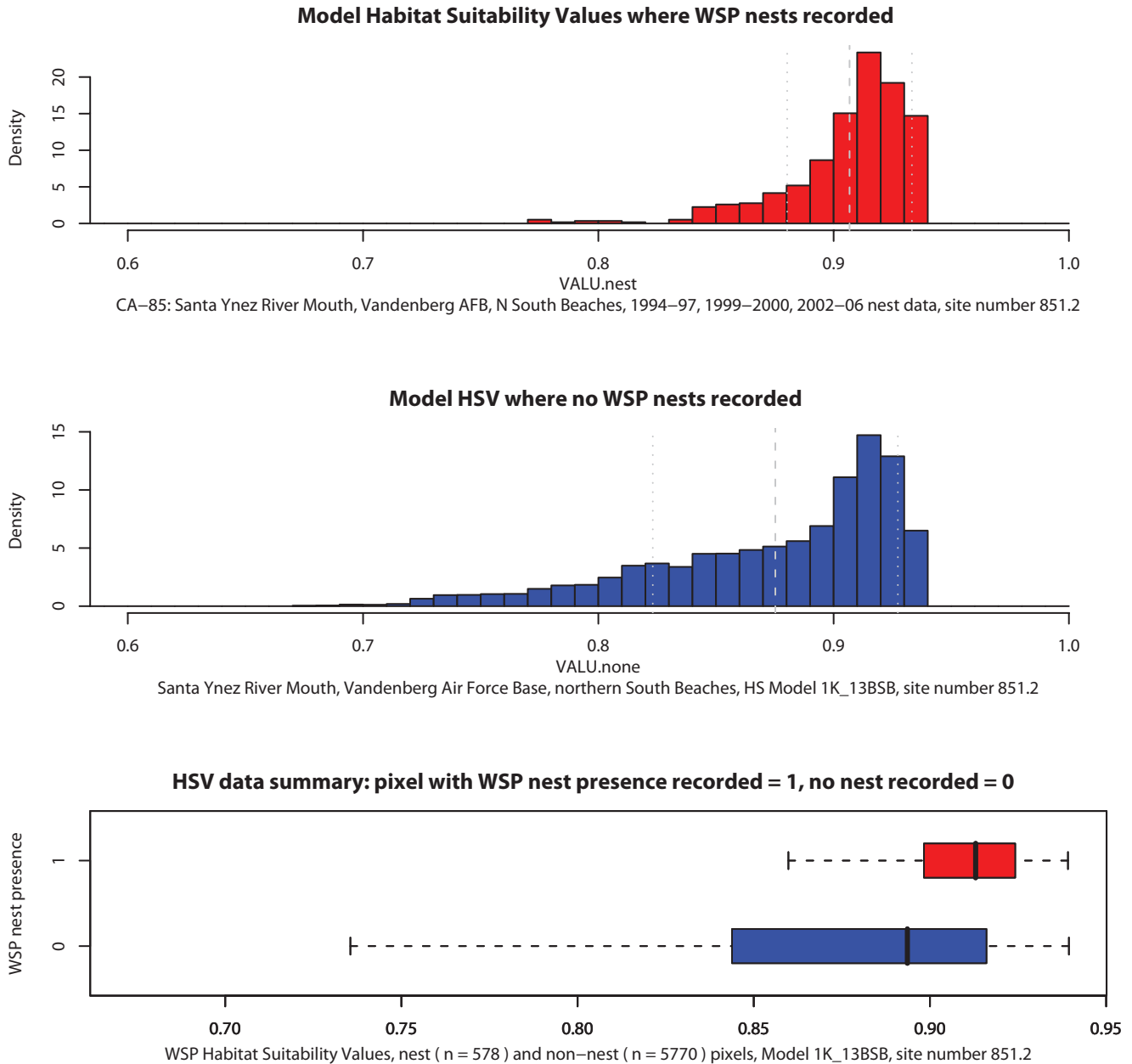
locations within site 853 and why ostensibly less-desirable habitat (e.g., site 855) was intensively utilized by nesting Western Snowy Plovers. Our five contiguous subsites correspond to Wall, Surf North, and Surf South beaches; values listed below are mean HSV. Wall Beach, site 851, farthest north, had the highest HSV at VAFB (0.881) and second-highest HSV in the region. Very narrow

Surf Beach South, site 855, was habitat at the edge of suitability, with lowest HSV (0.702) for any nest site. Surf Beach North was partitioned into three by land use and management strategies including restricted public and military access, controls on dogs, etc.: 1) The high-HSV (0.875) north end, site 852; 2) the narrower, slightly lower HSV (0.832), Surf Station Beach,

Model Habitat Suitability Values where WSP nests recorded

CA−85: Santa Ynez River Mouth, Vandenberg AFB, S South Beaches, 1994−97, 1999−2000, 2002−06 nest data, site number 853.5

Model HSV where no WSP nests recorded

Santa Ynez River Mouth, Vandenberg AFB, southern South Beaches, HS Model 1K_13B2SB, site number 853.5

HSV data summary: pixel with WSP nest presence recorded = 1, no nest recorded = 0

WSP Habitat Suitability Values, nest (n = 799) and non−nest (n = 3412) pixels, Model 1K_13B2SB, site number 853.5
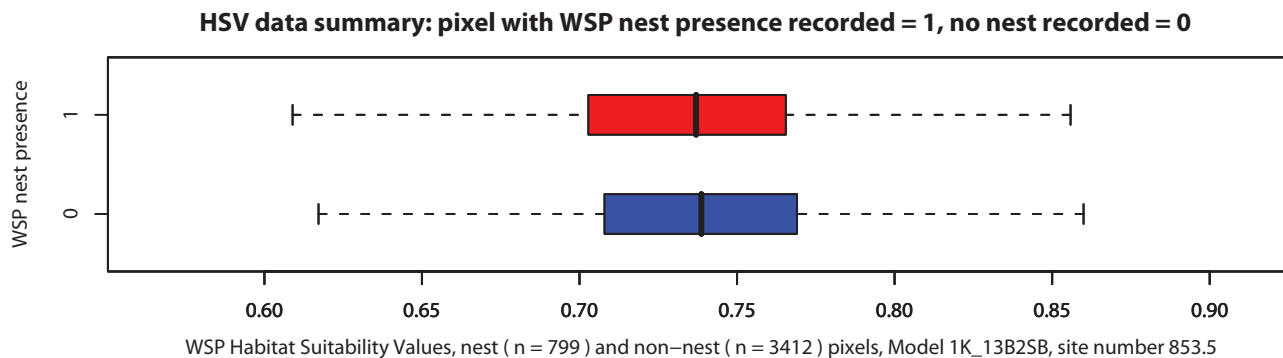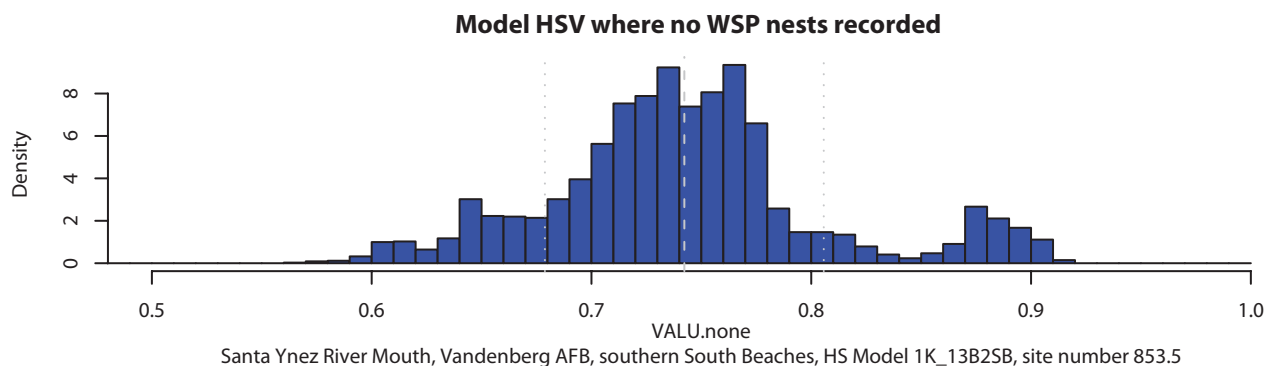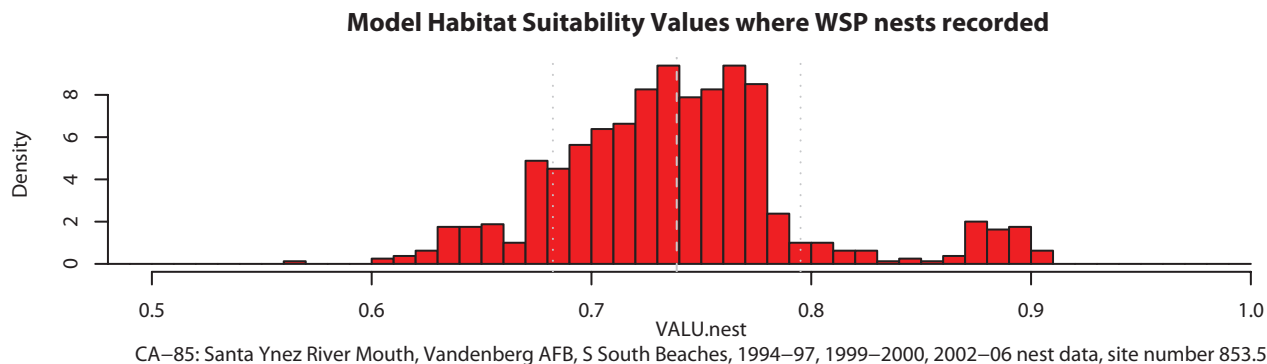
site 853, with railway station, public access, and a failed petition to delist Pacific Coast Western Snowy Plovers (USFWS 2006); and 3) the south end, site 854, even narrower but with access limited and higher HSV (0.746) than 855.

The sets of comparisons of predicted HSV at nest site pixels versus HSV at non-nest site pixels pro-

vides broad support for the deductive modeling approach. Even within the areas that are managed for Western Snowy Plovers, the sites chosen by plovers for nests have significantly higher HSV than those not chosen. The variations from this pattern are largely explainable by management differences on the ground.
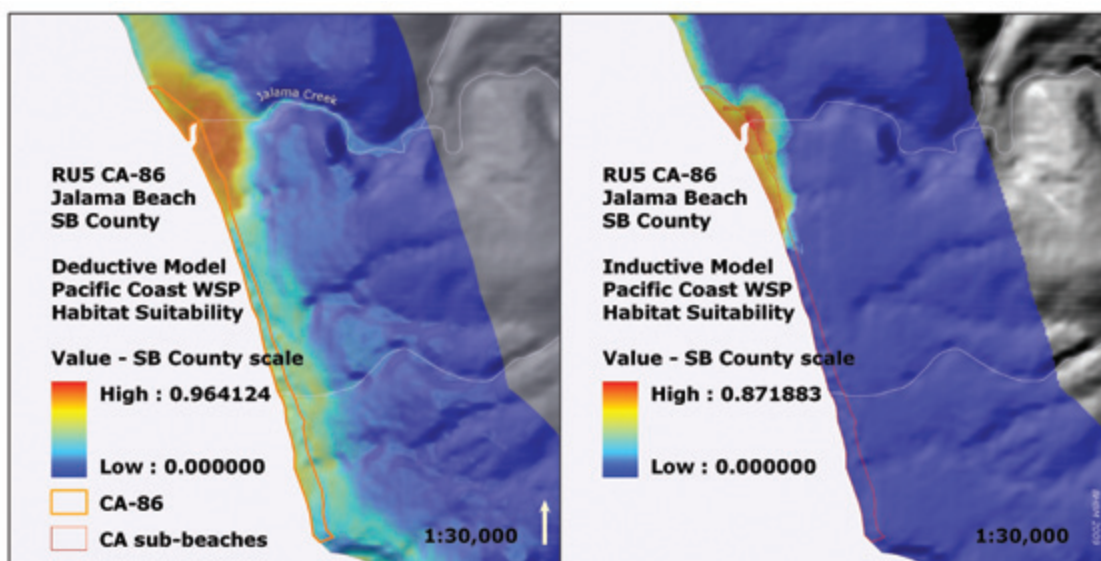
FIGURE 47. Comparison of deductive and inductive habitat models at Jalama Beach.

3.2 RESULTS OF INDUCTIVE MODELS

The inductive models of Western Snowy Plover habitat produced maps that missed large areas of known occupied winter or breeding habitat. Overall, where nest sites were provided as training data the models predicted high quality habitat while no habitat was predicted in areas without nest data. The rules that were generalized from existing sites and the physical parameters were not adequate to generalize to areas of the coast without nest site data.

Maxent produced habitat suitability maps that indicated suitable habitat existed only in areas where nest data were available. The program was unable to identify nearby, physically similar beaches as suitable habitat even with manipulation of a whole range of input assumptions (see Methods). Historic and even currently occupied sites without nest data were not identified as habitat.

The only exception where Maxent correctly identified potential habitat outside areas with training data was at Jalama Beach. This site, with extraordinarily high intrinsic habitat value, is a sheltered location between Point Arguello and Point Conception, along an otherwise rocky coastline with high winds and high surf where conditions unequivocally are unsuitable habitat. The results of both models *(Figure 47)* are similar in that they identify highest HSV around the mouth of Jalama Creek.

Jalama Beach is immediately adjacent to Vandenberg Air Force Base (VAFB) and ~23 km south of the southern VAFB beaches, which had a very large number of nest points used as model training data (Figure 46a and Table 9). Maxent was able to identify habitat to Jalama Beach presumably as a result of its closeness to this concentration of training data. Potentially, the effect was compounded by the disparity between desirable environmental conditions at Jalama Beach, and the poor or sub-optimal conditions at Surf and Surf South Beaches at VAFB, where extensive training data were obtained. Recall that our deductive model results indicated these southernmost VAFB beaches were an RU5 anomaly: the one location where habitat suitability values were not higher at nest sites than at non-nest sites *(Table 8)*, indicating the beaches were extensively used for nesting despite sub-optimal conditions. Given these data were (necessarily) used to train the SB inductive models, the results are not too surprising.

3.3 COMPARISON OF INDUCTIVE AND DEDUCTIVE MODEL RESULTS

Figures 48-50 illustrate major differences in predicted HSV generated by each approach. Inductive and deductive model outputs are compared for three regions within the three RU5 mainland analysis areas. Predicted HSV differences (figures on the left) were calculated by subtracting the pixel value for the inductive model from that of the deductive model, typically the one with higher HSV. Potentially, differences could range between (–1.0)–1.0; actual differences ranged between ~(–0.248)–0.955.

Difference maps are colored white (strongly positive) to black (negative). Strongly positive values indicated the HSV predicted by the deductive model was high (near 1.0), while at the same location the inductive model predicted low HSV (near 0.0). Positive values indicated the deductive prediction was the higher value. A negative value indicated the inductive model predicted higher suitability. A difference of 0.0 indicated models were in complete agreement. HSV predictions for inductive models (figures in the center) and deductive models (figures on the right) are scaled 0.0–1.0 and colored blue (0.0) to yellow to red (1.0). In this set of maps, to consistently interpret differences on a regional scale, values indicated next to the scale are those for the entire county area, not just the area pictured.

The region shown on northern San Luis Obispo County (SLO) maps *(Figure 48)* extends from the northern boundary of RU5 near San Carpoforo Creek, CA-69, south to Pico Creek, CA-76. Western Snowy Plover survey sites along this rocky coastline are almost all small pocket beaches that have historically (and sometimes recently) had nesting snowy plovers. The difference map *(48a)* indicates the disparity between predictions; the all-blue inductive model map *(48b)* indicates there are no locations of suitable habitat; and the deductive model map *(48c)* accurately identifies the location of multiple window survey sites.

However, no survey sites in this immediate area collect nest point data, and without that input, the inductive model could not identify suitable habitat. The closest location to Pico Creek with nest data is at Estero Bluffs State Park/Villa Creek, about 24 km southeast. It would seem that environmental conditions at Villa Creek might be similar enough to identify habitat further north (including two other beaches south of this set, at San Simeon State Beach) but the model could not capture these sites.

The south-facing Santa Barbara County coast from west of Santa Barbara Harbor (CA-90) to Carpinteria Beach (CA-91) is shown on the SB County maps *(Figure 49)*. The difference map *(49a)* indicates the disparity between predictions, with strongly positive values (white) indicating high HSV (deductive) and low HSV (inductive) along most of the beach. Indeed, the all-blue inductive model map *(49b)* indicates there are no locations of suitable habitat, and the deductive model map *(49c)* identifies multiple sites. No nest-point data exist for this location. Coal Oil Point (CA-88) is ~20 km west of Santa Barbara (CA-90), and has nearly identical conditions but is apparently not close enough to extrapolate the data.

East Beach (site 903) at Santa Barbara Harbor is predicted by the deductive model to have the highest habitat suitability for Western Snowy Plover in the county (HSV max. = 0.964; mean = 0.916). The inductive model's prediction of habitat suitability is, however, quite different (HSV max. = 0. 017; mean = 0.010). From a perspective of habitat conservation in general, and, more specifically, to encourage active management of Santa Barbara beaches for species' recovery, it is unfortunate that the models completely disagree.

The Ventura County maps show the southwest facing coast from San Buenaventura Beach (CA-95) to Mugu Lagoon (CA-99) *(Figure 50)*. This difference map *(50a)* reflects the presence of nest data to enable the inductive model to make predictions of suitable habitat; the predictions
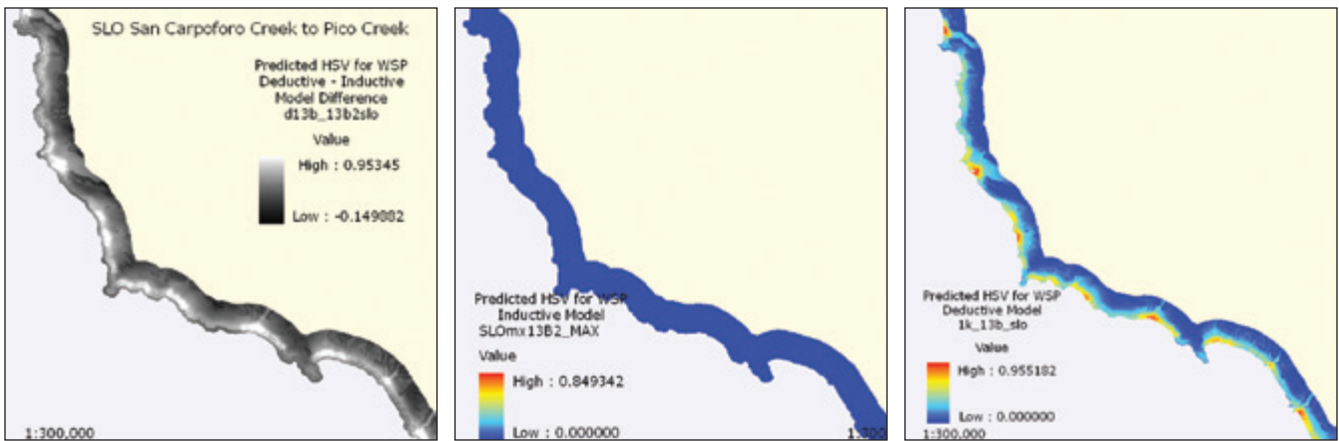
FIGURE 48. Northern San Luis Obispo County, San Carpoforo Creek to Pico Creek, CA-69 to CA-76: maps show a) differences between inductive and deductive models, b) inductive model results, and c) deductive model results.
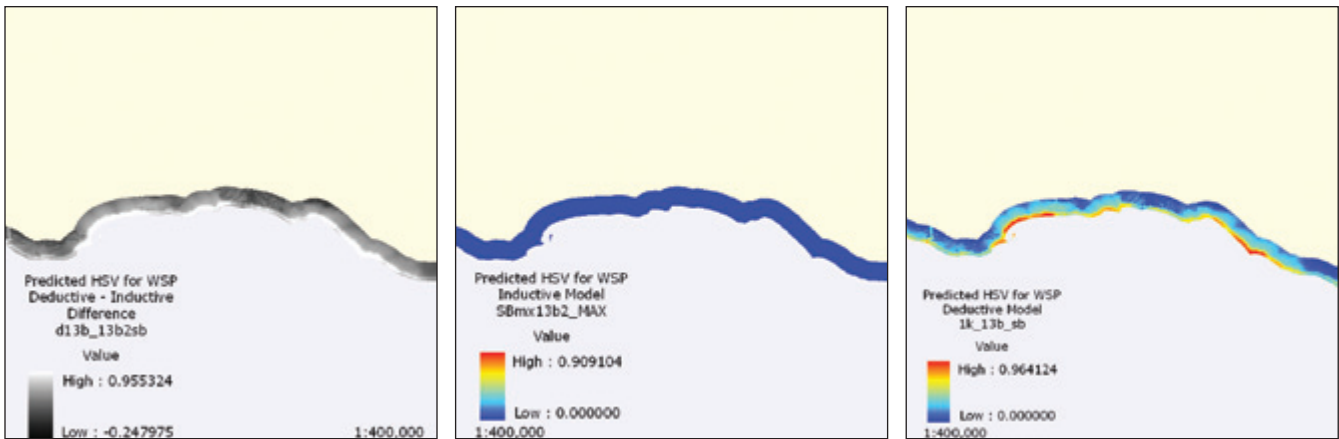
FIGURE 49. Southern Santa Barbara County, Santa Barbara Harbor to Carpinteria Beach, CA-90 to CA-91: maps show a) differences between inductive and deductive models, b) inductive model results, and c) deductive model results.
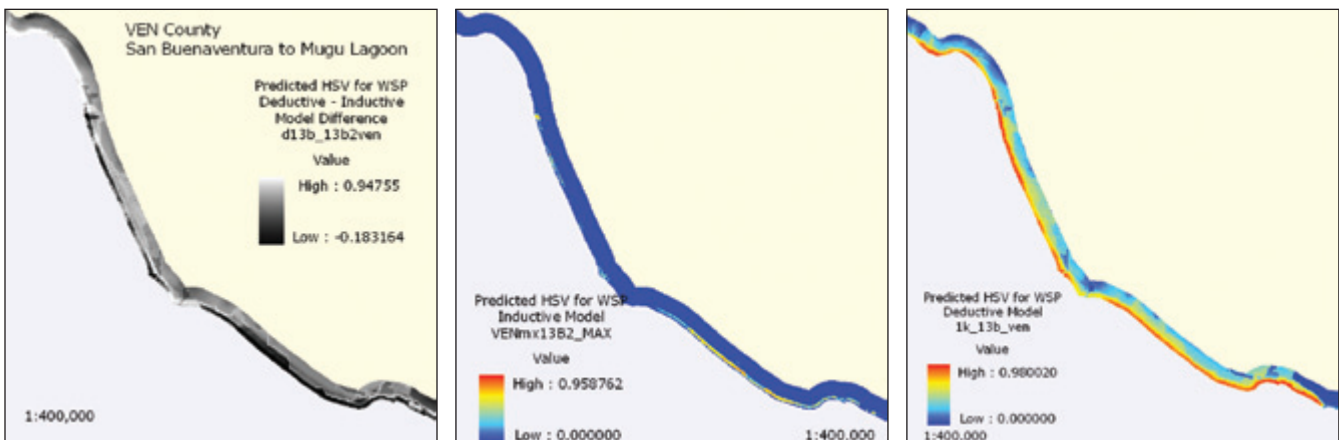
FIGURE 50. Ventura County, San Buenaventura to Mugu Lagoon, CA-95 to CA-99: maps show a) differences between inductive and deductive models, b) inductive model results, and c) deductive model results.

	INDUCTIVE [MAXENT] MODELS:		DEDUCTIVE [IDRISI] MODELS:	
	Primary models for comparison	**Alternative composite model models**	**Primary models for comparison**	**Minimization alternative model**
	SLOmx13B2_MAX	SLOmx13B2_AVG	1k_13BSLO	1k_13BSLO_4x25
mean	0.137	0.118	0.712	0.466
stdev	0.237	0.219	0.112	0.198
max	0.849	0.824	0.955	0.905
	SBmx13B2_MAX	SBmx13B2_AVG	1k_13B2SB	1k_13BSB_4x25
mean	0.167	0.146	0.722	0.470
stdev	0.258	0.246	0.104	0.181
max	0.909	0.872	0.964	0.916
	VENmx13B2_MAX	VENmx13B2_AVG	1k_13BVEN	1k_13BVEN_4x25
mean	0.204	0.158	0.839	0.668
stdev	0.267	0.233	0.101	0.197
max	0.948	0.849	0.980	0.950
	NCH	NCH	1k_13BNCH	1k_13BNCH_4x25
mean	no nest point data available for NCH		0.653	0.332
stdev	no directly comparable models		0.090	0.163
max			0.935	0.868

TABLE 10. Habitat suitability values from deductive and inductive models by county.

(50b) align almost exactly with nest points, and are indicated in yellow to orange. There are no nest data for San Buenaventura, the northernmost beach (CA-95), and comparatively very few nest points within a very large area for the next three sites, Santa Clara River Mouth/McGrath and Mandalay Beaches (CA-96), Hollywood Beach (CA-97), and Ormond Beach (CA-98). At the southernmost site, Mugu Lagoon (CA-99), there is an abundance of nest-point data. However, the model does not seem to extend predictions of suitable habitat much beyond the actual points. Finally, the deductive model map *(49c)* identifies most of this coastal strip as of high suitability, which is probably closer to reality.

Tabular results allow comparison of the inductive and deductive model results by county analysis area *(Table 10)*. Column headings are colored to make numbers easier to differentiate inductive (blue) and deductive (green) models. The primary models for comparison are indicated as such. We compare HSV predictions for the 150-m coastal "beach-width" strips and present the mean, standard deviation, and maximum values for each

area and each model. The northern California Channel Islands are not included with the inductive model results because no nest data are available and the two methods to project the models from the mainland to environmental data layers for the islands were spectacularly unsuccessful. All inductive models have lower maximum and mean habitat suitability values and much greater variability than the deductive models.

Alternative model results for both the inductive and deductive approach are also shown in *Table 10*. These allow a secondary comparison at the county level. For the inductive approach, both models were created at the same time from the 15-replicate composites. Our primary models were grids with the pixel value indicating maximum HSV achieved at that location (from among all 15 models). Within this table only, we designate each model version more specifically to better differentiate one from another. For San Luis Obispo (SLO), for example, the primary inductive model is indicated as "SLOmx13B2_MAX". The alternative models were grids with the pixel value representing the mean HSV (for the 15 models) at

any given location; for SLO, this model is indicated as "SLOmx13B2_AVG".

For the deductive models, the process used to create the primary models was described. The alternative models were the least-restrictive minimization option we tried. The minimization process was described, and is illustrated in *Figure 10*. It added another set of weights to environmental factors, which decreased the amount of area predicted as suitable, reduced overall HSV, and identified pixels with very high values for multiple variables. For San Luis Obispo, the primary deductive model is indicated "1k_13BSLO" and the alternative is called "1k_13BSLO_4x25". While site-by-site comparisons between all models further accentuates the disparity between the predictions for the inductive and deductive approach, complete comparisons are not included here. However, individual sites that retain a high predicted HSV after minimization may merit additional analysis.

We compared inductive and deductive model performance by beach. Mean and maximum values predicted at each site are compared. Results are shown for individual beach sites in San Luis Obispo *(Table 11)*, Santa Barbara *(Table 12)*, and Ventura *(Table 13)* Counties. Column headings are colored: inductive (blue) and deductive (green).

Differences between the inductive and deductive model predictions are even more evident in graphical comparisons for San Luis Obispo *(Figure 51)*, Santa Barbara *(Figure 52)*, and Ventura *(Figure 53)* Counties. The top two graphs compare mean HSV at individual window survey beaches predicted by the deductive model (green) and the inductive model (blue). Deductive model HSV are clustered to the right (higher HSV); inductive model HSV predictions are more variable but lower and are spread out on the left side of the graph (sites with nest data are always higher). The bottom two graphs compare values predicted at pixels where nests were recorded for the deductive model (green) and the inductive

model (blue). HSV means and standard deviation are indicated on all graphs.

Additional comparisons of inductive and deductive model results were not pursued because of the inability of inductive models to identify habitat outside of areas with training data. Further inspection of inductive model results, however, revealed sub-threshold (our 0.7 threshold for model evaluation) information that could be compared with deductive models. Even though Maxent models did not identify suitable habitat (e.g., values > 0.7) for non-training sites, the model values below this threshold did indeed indicate apparent gradations in habitat values.

After reclassifying the output of Maxent models to emphasize variation at low habitat values (generally <0.1; see Methods), other currently occupied and historically occupied beaches were seen to have greater HSV than sites never inhabited. These sites also corresponded visually to the sites identified by the deductive models. For example, in the northernmost part of RU5 (Figure 54), there are no locations with nest data to train the inductive model. Here, multiple pocket beaches identified by the deductive model as being of high to very high HSV (54a) are not apparent in the inductive model map (54b). When the inductive model map is reclassified using the threshold-based scale (54c), areas become visible which were not apparent before, particularly when the lower threshold-values are used (54d). Similar results are produced at Avila Beach (Figure 55), where no nesting currently occurs. The deductive model map correctly indicates habitat, which is confirmed by historic records (55a). The inductive model shows low habitat value when compared on the same scale (55b). Subsequent reclassification (55c) and visualization at lower scales (55d) brings out variation in HSV that show that the model interprets the site as having greater habitat value than its surroundings. This provides independent support for the deductive model.

TABLE 11. San Luis Obispo County: inductive and deductive model comparisons by beach site (**San Luis Obispo County site with nest point data).

	PREDICTED HABITAT SUITABILITY FOR PACIFIC COAST WSP	CA-SITE	INDUCTIVE MODEL HSV [MAXENT]		DEDUCTIVE MODEL HSV [IDRISI]	
			mean	max	mean	max
SLO	coastal zone, 150 m buffer		0.137	0.849	0.712	0.955
691	San Carpoforo Creek	CA-69	0.002	0.013	0.817	0.936
701	Arroyo Hondo	CA-70	0.003	0.006	0.699	0.776
711	Point Sierra Nevada	CA-71	0.016	0.055	0.748	0.793
721	Arroyo de la Cruz	CA-72	0.020	0.042	0.903	0.936
731	Sydney's Lagoon	CA-73	0.024	0.040	0.898	0.909
740	Point Piedras Blancas	CA-74	0.011	0.024	0.729	0.819
751	Arroyo Laguna	CA-75	0.026	0.082	0.893	0.907
761	Pico Creek	CA-76	0.057	0.125	0.867	0.941
771	San Simeon State Beach	CA-77	0.120	0.324	0.845	0.936
772	Santa Rosa Creek / SS SB	CA-77	0.202	0.334	0.878	0.913
781	** Estero Bluffs State Beach / Villa Creek	CA-78	0.481	0.769	0.877	0.918
791	Toro Creek	CA-79	0.528	0.676	0.819	0.910
801	** Morro Strand State Beach	CA-80	0.538	0.796	0.823	0.947
802	Morro Rock City Beach	CA-80	0.387	0.747	0.867	0.921
811	** Morro Bay Sandspit - City of Morro Bay	CA-81	0.560	0.849	0.879	0.926
812	** Morro Bay Sandspit - Montaña de Oro State Park	CA-81	0.441	0.830	0.807	0.918
813	Morro Bay Sandspit - private	CA-81	0.262	0.578	0.872	0.909
821	Avila Beach	CA-82	0.039	0.122	0.783	0.931
831	Pismo State Beach - N of Grand		0.417	0.670	0.872	0.931
832	Pismo State Beach - S of Grand		0.551	0.666	0.889	0.935
833	** Oceano Dunes SVRA day use	CA-83	0.534	0.830	0.839	0.940
834	** Oceano Dunes SVRA	CA-83	0.440	0.789	0.739	0.849
835	** ODSVRA Oso Flaco Natural Area	CA-83	0.534	0.784	0.768	0.930
836	Guadalupe-Nipomo Dunes National Wildlife Refuge	CA-83	0.270	0.664	0.737	0.853
837	** Guadalupe Restoration Site	CA-83	0.479	0.839	0.791	0.942

	PREDICTED HABITAT SUITABILITY FOR PACIFIC COAST WSP	CA-SITE	INDUCTIVE MODEL HSV [MAXENT]		DEDUCTIVE MODEL HSV [IDRISI]	
			mean	max	mean	max
SB	coastal zone, 150 m buffer		0.167	0.909	0.722	0.964
838	** Rancho Guadalupe Dunes Preserve	CA-83	0.506	0.795	0.805	0.946
839	Mussel Rock beach	CA-83	0.485	0.759	0.792	0.908
8310	Paradise beach		0.514	0.605	0.755	0.848
8311	Point Sal State Beach		0.485	0.520	0.692	0.758
8312	Brown's beach [local name]		0.465	0.525	0.794	0.851
841	** Vandenberg AFB North - Minuteman open access		0.444	0.785	0.737	0.844
842	** VAFB North - Minuteman Beach	CA-84	0.480	0.843	0.753	0.904
843	** VAFB North - Shuman Beach	CA-84	0.561	0.870	0.739	0.932
844	** VAFB North - San Antonio Beach	CA-84	0.686	0.853	0.791	0.929
845	** VAFB North - Purisima North	CA-84	0.588	0.816	0.733	0.825
846	** VAFB North - Purisima Colony	CA-84	0.691	0.820	0.729	0.825
851	** Vandenberg AFB South - Wall Beach	CA-85	0.716	0.861	0.881	0.933
852	** VAFB South - Surf Beach North (N end)	CA-85	0.685	0.856	0.875	0.939
853	** VAFB South - Surf Station Beach	CA-85	0.772	0.868	0.832	0.913
854	** VAFB South - Surf Beach North (S end)	CA-85	0.737	0.821	0.746	0.803
855	** VAFB South - Surf Beach South	CA-85	0.773	0.837	0.702	0.792
861	Jalama County Beach	CA-86	0.339	0.909	0.751	0.920
871	Hollister Ranch	CA-87	0.033	0.218	0.746	0.879
872	Gaviota State Beach		0.128	0.220	0.758	0.908
873	Refugio Beach State Park		0.100	0.187	0.786	0.903
874	El Capitan Beach State Park		0.023	0.078	0.702	0.818
875	Haskell's Beach		0.175	0.283	0.815	0.911
881	Ellwood Beach		0.336	0.400	0.762	0.814
882	** Coal Oil Point UC Natural Reserve	CA-88	0.446	0.800	0.825	0.962
883	Isla Vista Beach		0.152	0.273	0.721	0.877
884	Campus Beach		0.001	0.003	0.881	0.935
891	Goleta Beach	CA-89	0.055	0.127	0.846	0.960
901	Santa Barbara West Beach	CA-90	0.010	0.017	0.837	0.905
902	Santa Barbara Harbor	CA-90	0.009	0.016	0.882	0.952
903	Santa Barbara East Beach	CA-90	0.010	0.017	0.916	0.964
911	Carpinteria Spit Beach - Santa Claus Lane		0.070	0.129	0.935	0.958
912	Carpinteria City Beach	CA-91	0.063	0.090	0.831	0.922
913	Carpinteria State Beach	CA-91	0.058	0.079	0.816	0.875

TABLE 13. Ventura County: inductive and deductive model comparisons by beach site (**Ventura County site with nest point data).

	PREDICTED HABITAT SUITABILITY FOR PACIFIC COAST WSP	CA-SITE	INDUCTIVE MODEL HSV [MAXENT]		DEDUCTIVE MODEL HSV [IDRISI]	
			mean	max	mean	max
VEN	coastal zone, 150 m buffer		0.204	0.948	0.839	0.980
951	San Buenaventura Beach	CA-95	0.052	0.319	0.881	0.949
961	** McGrath State Beach	CA-96	0.373	0.948	0.901	0.978
9661	** Mandalay Beach - Reliant Energy sector	CA-96	0.407	0.627	0.947	0.965
962	** Mandalay State Beach	CA-96	0.277	0.769	0.880	0.958
971	** Hollywood County Beach	CA-97	0.419	0.805	0.902	0.949
981	** Ormond Beach	CA-98	0.538	0.853	0.879	0.950
991	** Naval Base Ventura County Mugu Lagoon - Ormond East Beach	CA-99	0.578	0.867	0.852	0.943
992	NBVC Mugu Lagoon Beach	CA-99	0.631	0.815	0.914	0.936
993	** NBVC Mugu Lagoon - Holiday Beach	CA-99	0.574	0.854	0.872	0.957
994	NBVC Mugu Lagoon - Family Beach	CA-99	0.485	0.781	0.928	0.971
995	** NBVC Mugu Lagoon - Eastern Arm Beach	CA-99	0.460	0.806	0.936	0.980
NCH	coastal zone, 150 m buffer				0.653	0.935
920	San Miguel Island	CA-92			0.753	0.902
930	Santa Rosa Island	CA-93			0.770	0.916
940	Santa Cruz Island	CA-94			0.755	0.835
1000	Naval Base Ventura County San Nicolas Island	CA-100			0.788	0.935

FIGURE 51. **San Luis Obispo County: comparison of deductive (green) and inductive model (blue) HSV predictions by survey site (n=25) and by nest sites (n=1699; beaches=8).**

Deductive model mean HSV at WSP window survey beaches (n=25): San Luis Obispo (SLO) County

SLO 150m coastal zone mean HSV >

Idrisi.1k13BSLO.sites

Inductive model mean HSV at WSP window survey beaches (n=25): SLO composite model

< SLO coast

Maxent.SLOmx13B2.MAX.sites

SLO Deductive model mean HSV where nests recorded (n=1699; beaches=8): HSV extracted to points

Idrisi.1k13BSLO.nests

SLO Inductive model HSV: Composite means of sample predictions for pixels where nests recorded

Maxent.SLOmx13B2.nests

FIGURE 52. Santa Barbara County: comparison of deductive (green) and inductive model (blue) HSV predictions by survey sites (n=33) and by nest sites (n=3027; beaches=13).

FIGURE 53. Ventura County: comparison of deductive (green)
and inductive model (blue) HSV predictions by survey sites
(n=13) and by nest sites (n=710; beaches=8).

Deductive model mean HSV at WSP window survey beaches (n=13): Ventura (VEN) County
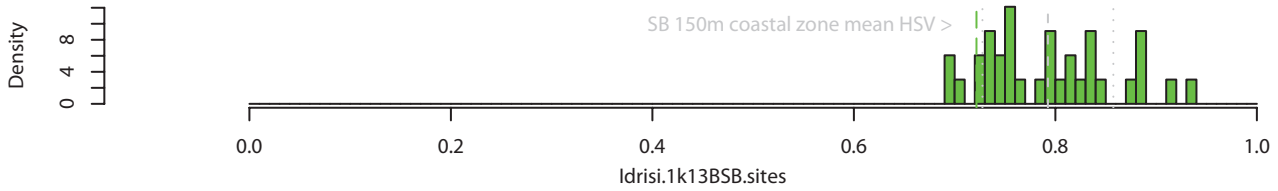
Inductive model mean HSV at WSP window survey beaches (n=13): VEN composite model
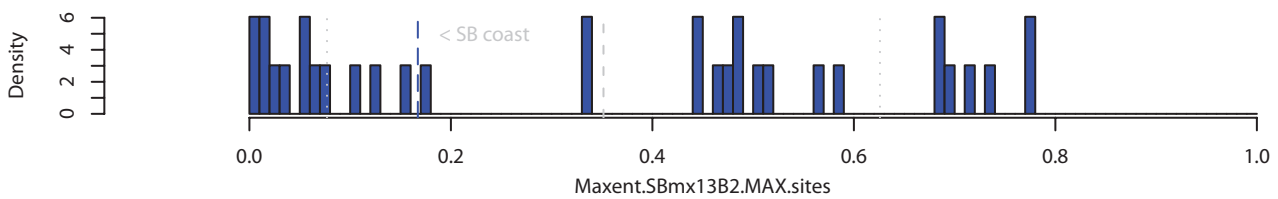
VEN Deductive model mean HSV where nests recorded (n=710; beaches=8): HSV extracted to points
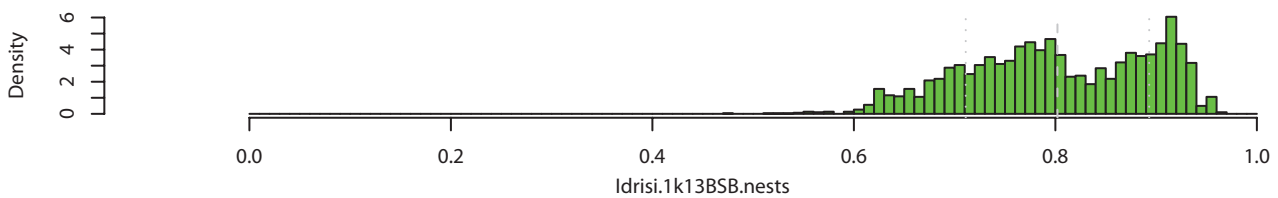
VEN Inductive model HSV: Composite means of sample predictions for pixels where nests recorded
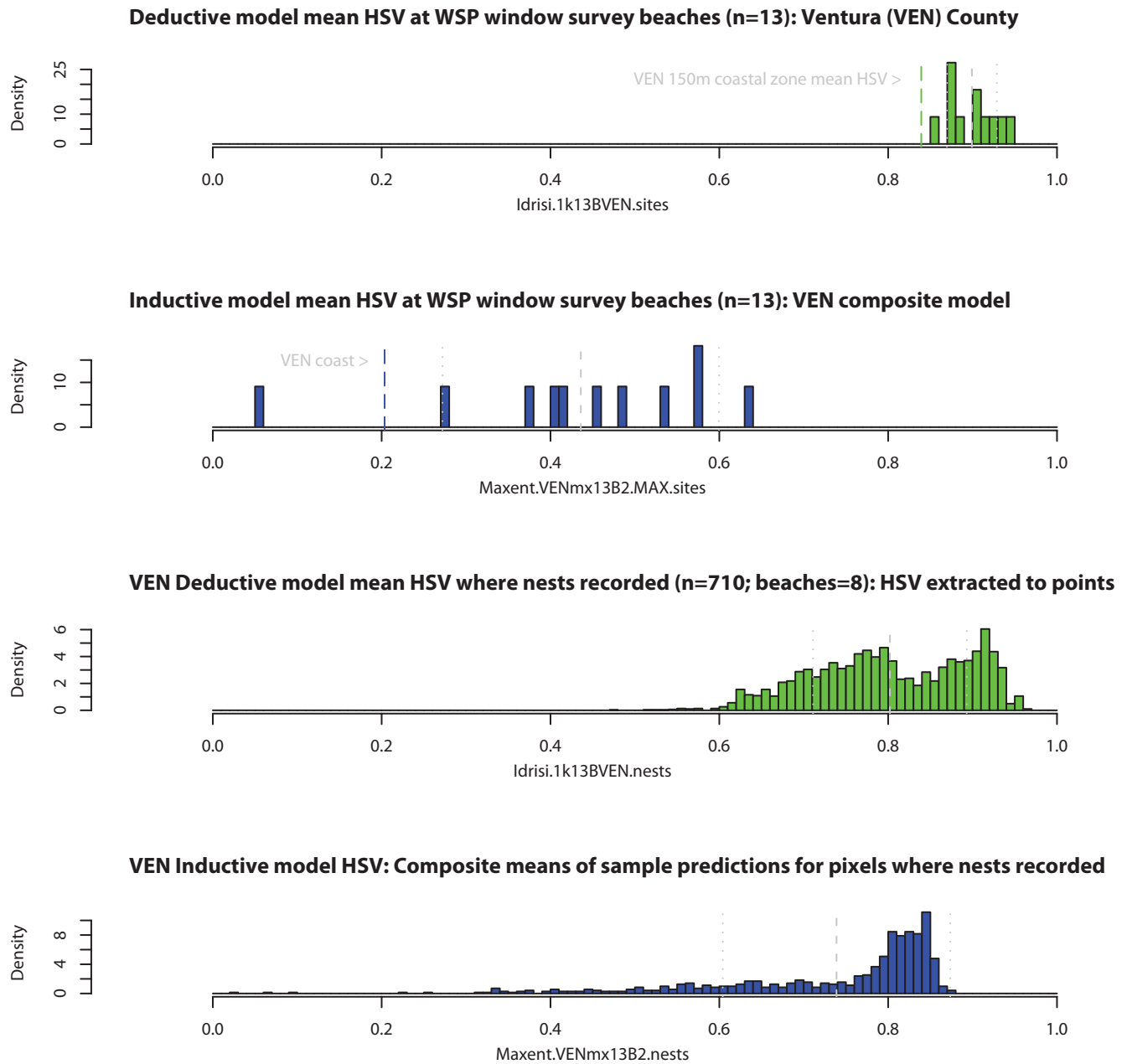
FIGURE 54. Comparison of a) deductive habitat suitability model results at high-HSV pocket beaches in northern San Luis Obispo County, with b) similarly-scaled inductive model, c) inductive model reclassified with threshold-values, and d) inductive model results with lower threshold-value classes.
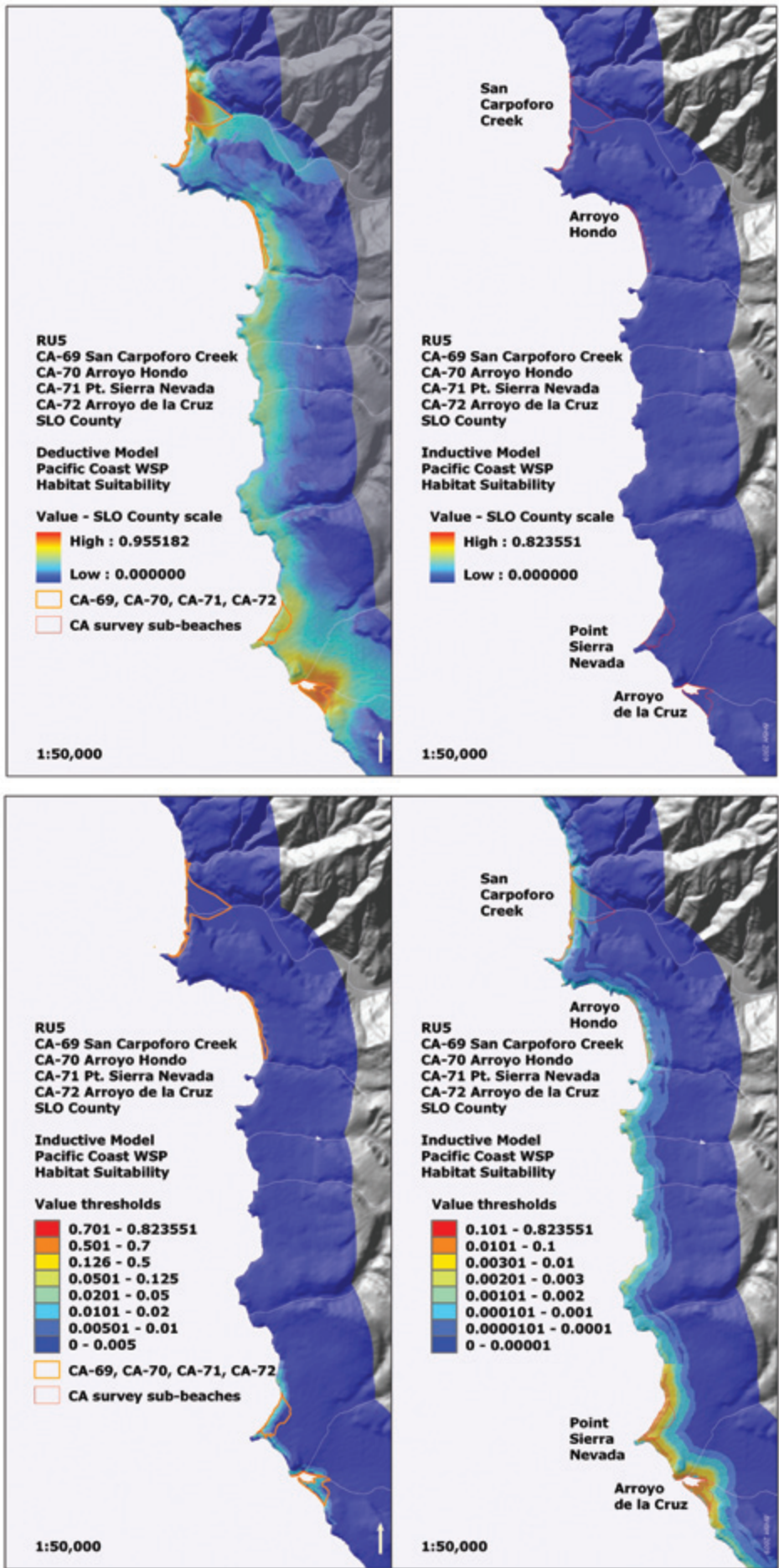
FIGURE 55. Comparison of a) deductive habitat suitability model results at Avila Beach, with b) similarly-scaled inductive model, c) inductive model reclassified with threshold-values classes, and d) inductive model results with lower threshold-value classes.
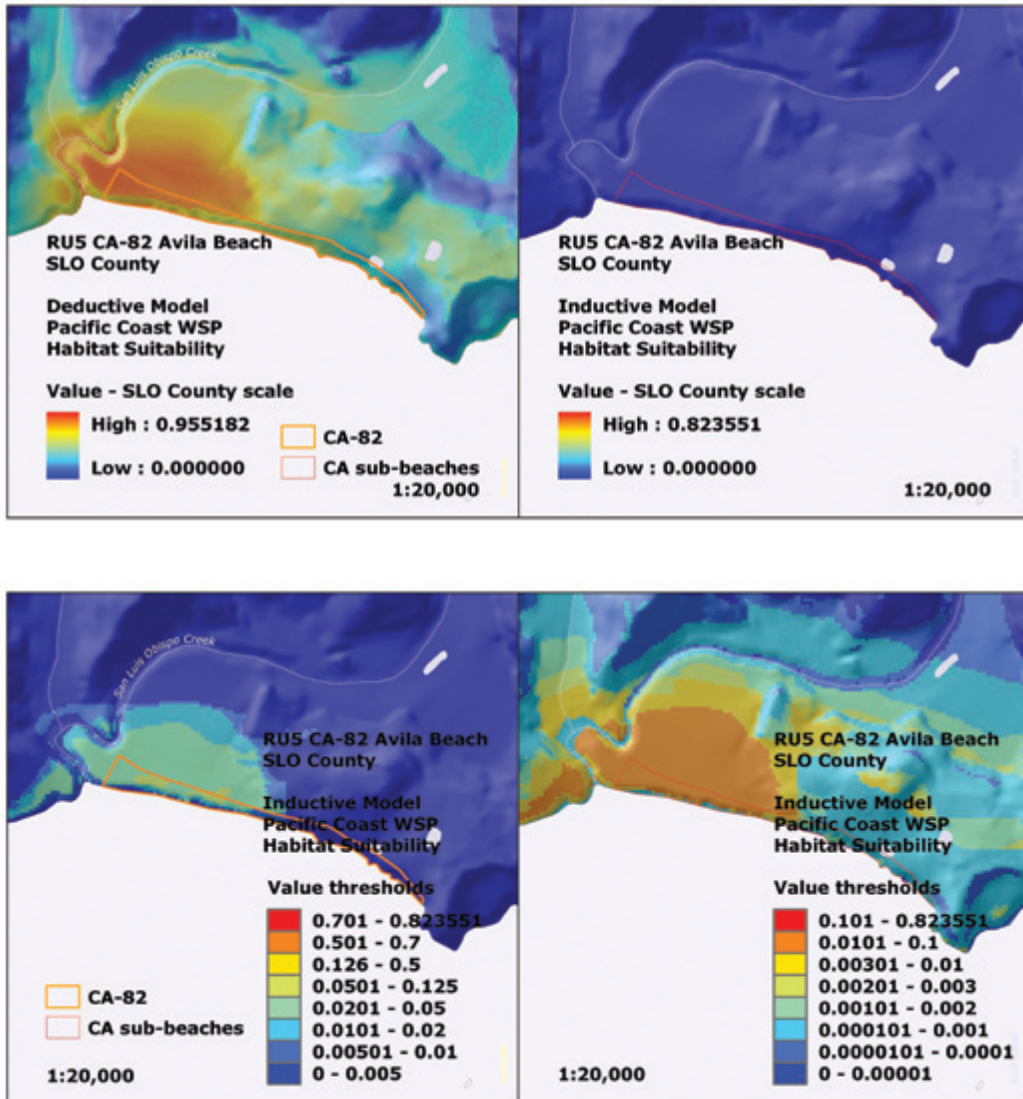
PHOTO BY CALLIE BOWDISH

The current trend in species distribution modeling is to extrapolate from location data to predict overall distribution, that is, an inductive approach (Guisan and Thuiller 2005; Araújo and Guisan 2006; Elith and Graham et al. 2006; Peterson et al. 2007). This approach is intuitively appealing because it allows the data to "speak for themselves" because the user does not make assumptions about what factors are or are not important to defining habitat for the species in question.

For rare and endangered species, however, this approach is problematic because the habitats that are left for species are not necessar-

ily those with the optimal conditions for the species (Lomolino and Channell 1995). Taking a strictly inductive approach runs the risk of overlooking sites that have appropriate conditions when the training data are insufficiently dispersed for the range of the species. In our example, inductive approaches were only successful at identifying non-occupied but suitable habitats in one location: immediately adjacent to a concentration of training data.

Given a niche is an abstract concept, like a model, when estimating the niche or distribution of a species, we are modeling the intersection of geographical space with

is a subset of the fundamental niche that represents the "space" that meets their requirements (Anderson et al. 2003; Soberón and Peterson 2005). On the other hand, model accuracy and predictive power suffer (Phillips et al. 2006) when predictions are made based on the constraints of a realized niche a threatened species occupies, rather than the fundamental niche that better estimates its potential or historical distribution.

We acquired Pacific Coast Western Snowy Plover nest point data from all RU5 sites that intensively monitor breeding birds, which included data from an environmentally diverse, geographically representative area. We knew, however, that the nest data available were not collected in the consistent and random manner a traditional and quantitatively rigorous inductive modeling approach required. Naturally, results from inductive models reflect patterns in the sample data. Survey effort and other sample selection biases affect model quality. We used a machine-learning approach designed to make inferences from incomplete data, but presence-only data do not provide negative examples (Phillips et al. 2004). Most datasets used for recent species' distribution modeling efforts have limitations (Stockwell and Peterson 2002b; Graham et al. 2004), and there has been an increased focus on methods to identify and "fix" problems (e.g., Guisan et al. 2006; Austin 2007; Elith and Graham 2009).

environmental space, and we need information about both. When a species is threatened by habitat loss or fragmentation, encroachment or disturbance, the species' occurrence data will violate other essential assumptions (Pearson et al. 2006): the species may not actually be present in all suitable areas, and absent where conditions are not suitable. Inaccurate correlations drawn between species' presences under sub-optimal environmental conditions, and their absences in highly suitable habitats make it difficult to infer their true requirements.

On one hand, a threatened species occupies a realized niche (Brown and Lomolino 1998) that

We used 50% of the point data for training final models and 50% for testing them. In later evaluations, 90% and 95% of the nest data were set aside for testing — or — to look at it another way, only 10% or 5% of the samples were used to train models. No improvement in prediction of known sites was discernable in the areas without training data; overall, performance decreased, particularly in areas like northern and central Ventura County where fewer data samples represented large beaches. Another solution would have been to discard or down-weight samples (Engler et al. 2004; Lutolf et al. 2006) from over-sampled locations, a common (if perhaps subjective) approach we did not try.

In an observation that directly applies to the Pacific Coast Western Snowy Plover in RU5, Phillips et al. (2009) observe that in areas transformed by human activity, biased samples may be an inherent part of the realized, current distribution of the species. Recent species' distribution modeling trials have specifically targeted sample selection bias and its implications for models. Their results indicated that model performance may be enhanced and uncertainty decreased by introducing a similar selection bias into the background data as in survey data (Phillips et al. 2009), sampling both sets from the same areas in lieu of acquiring background points from the entire region (Ferrier et al. 2002). Our background-point selection was constrained by narrowing the width of the coastal strip by 95% over the course of our modeling trials. Another approach uses presence data for similar taxa (i.e., Pacific shorebirds) to estimate true survey effort and produce "target-group" data for the background (Anderson 2003; Phillips et al. 2009). Additional parameterization of our inductive models might improve their predictive performance.

In contrast, a deductive approach provides a number of advantages for conservation planning in a heavily human-dominated landscape, even though it does depend on the existence of a well-developed natural history for the species in question. With this information, however, it can extrapolate the ideal conditions to locations where the species is no longer present and indeed is useful for identifying locations that would be excellent habitat if appropriate management were undertaken. Such sites are simply not ranked highly by inductive models when the training data are geographically clustered and the actual potential range is large.

It is reassuring that our deductive model of Western Snowy Plover distribution is supported by the inductive Maxent model when the scale is adjusted to visualize low habitat values. Via its independent pathway, it ranks sites that the deductive model identified as habitat (and are used by the species in current surveys) as higher than adjacent areas. Practical use of these Max-

ent results would require a sliding scale across the study area.

Our decision to develop models that were independent of site conditions that could be changed through management makes the results particularly useful for conservation planning, especially within the context of species recovery under the Endangered Species Act. The model results show the sites that would be occupied by adult Western Snowy Plovers (or even have nests) if they were managed for the species. The models quantify physical features (distance to coast, proximity of streams, substrate, landward boundary, wave height, etc.) and do not rely on, for example, presence of vegetation or wrack. These critical habitat features, and protection of disturbance, are then all it would take to support nesting plovers at these sites.

The deductive model also provides a tool to investigate the influence of changes in the physical environment on habitat suitability for Western Snowy Plover. The response of the model to changes in beach width, wave height, winds, beach slope and other factors in the model that will vary with climate change could provide estimates of the effect on the species from these phenomena.

The model results should also be useful for identifying, accurately delimiting, and assessing critical habitat for the species. Our deductive model gives gradations of habitat suitability within (and outside) existing recovery sites that might be used both to concentrate efforts within those sites and to reconfigure them during future recovery planning efforts.

The population viability analysis for the species, which was used in developing many facets of the draft and final Recovery Plan (USFWS 2001; 2007a), could be greatly improved by incorporating the detailed spatial information about habitat quality developed here. The PVA model (Nur et al. 1999) is spatially explicit, but does not incorporate variability in habitat quality within those

regions designated as habitat, and probably over-estimates habitat size and value in some areas and underestimates it in others. Our approach provides the tools to revisit this analysis, at least for RU5.

Finally, the model results reported here should provide the baseline information necessary to compare the efficacy of different management actions. We provide some examples of preliminary comparisons in the site-by-site discussions of our results. The density and productivity of plover sites can now be standardized to the quantified habitat values so that the results of various different management actions can be more easily compared. Production of a few chicks on a beach with low HSV can then be interpreted as a management success when compared with production of a similar number on a site with optimal physical conditions. The modeled HSV will be critical inputs to future assessments of the response of plovers to management actions.

If the modeling approach were in the future extended to the range of the species, it would provide numbers to put into context the differential productivity of different parts of the range, and importantly, provide a tool to explore the potential need for reallocation of effort in light of changes to the physical environment with global climate change. Notwithstanding the threat posed by long-term climate change, however, the model gives convincing information now to promote, encourage, or even mandate management for Western Snowy Plovers in locations that have optimal conditions but for which Section 9 prohibitions on take are not invoked because nesting does not occur.

The models developed and presented here are convincing evidence that many sites are indeed nesting habitat for Western Snowy Plover, but it is only ongoing beach disturbance (through unfettered recreational use, beach grooming, or other means) that consistently and chronically interferes with nesting. Recent observations of breeding adult Western Snowy Plovers in Los Angeles County, recorded during 2008 and 2009 window surveys, and the discovery of an attempted nest on a beach along the Santa Monica Bay in Los Angeles, located only with intense surveillance (Ryan et al. 2009; USFWS 2009b), are evidence that such nesting activities do occur on these high-quality beaches but are immediately destroyed. The model results, validated by the nest site and historic data, provide the basis for strong argument that take, as defined under the Endangered Species Act, is regularly occurring at high-HSV sites that have wintering populations of Western Snowy Plovers but are not managed for the species.

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