SHIFTING SANDS: SOCIAL CUES INFLUENCE THE LONG-TERM DYNAMICS OF SNOWY PLOVER DISTRIBUTION

By

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ABSTRACT

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Understanding the social and physical factors that influence the temporal and spatial distribution of a species is imperative for successful management. The Western Snowy Plover (*Charadrius nivosus nivosus*) selects for wide-open stretches of beach; yet within large expanses of ideal habitat, plover populations tend to be aggregated. Recent evidence suggests plovers may prioritize social information over ideal physical factors alone when selecting breeding locations. I analyzed data collected on an individually marked population of Snowy Plovers in Humboldt County, California from 2001 to 2018 to evaluate the influence of physical (beach width) and social (presence of conspecifics) landscape factors on the population's breeding distribution. Using an information-theoretic framework, I conducted incidence function models and model selection analyses to examine how physical and social factors influenced inexperienced breeder occupancy of approximately 100 km of plover habitat. Beach width influenced where plovers bred, however, inexperienced plovers were more likely to colonize sites occupied by experienced conspecifics. Reproductive success had minimal influence on settlement of inexperienced breeders the following season. This information suggests the species' successful recovery requires an added emphasis on social information for future habitat restoration efforts.

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INTRODUCTION

Ecologists strive to understand the landscape factors, both physical and social, that determine the distribution and abundance of species (Andrewartha and Birch 1954, Kotler 1984, Cody 1985). Under evolutionary theory, an individual's preference is to select habitat to maximize potential fitness gains (Rosenzweig 1981, Morris 2003). Fitness is influenced by the physical features of habitat, including: habitat structure and composition (Cody 1985), prey abundance (Orians and Wittenberger 1991), predator abundance (Kotler 1984, Morris 2003), and competitor presence (Bourski and Forstmeier 2000). Habitat selection is partially based on these physical features, and influenced by an individual's genetic and phenotypic variation (Duijns et al. 2015). These heterogenous choices often manifest themselves in a species' patchy distribution within suitable habitat; however, this patchy distribution cannot always be explained by physical information and intrinsic variation alone (Ahlering and Faaborg 2006). Most ecologists acknowledge the importance of social information to help explain this patchy distribution (Doligez et al. 2003, Ahlering and Faaborg 2006, Jones and Kress 2012).

Social information is acquired through direct signals from other individuals (i.e., conspecific attraction) and cues inadvertently provided by the behavior of individuals with similar requirements (i.e., public information; Danchin et al. 2004, Ahlering and Faaborg 2006). Conspecific attraction is defined as the tendency for individuals to select breeding sites near individuals of their own species (Ward and Schlossberg 2004), whereas public information (often referred to as performance-based conspecific attraction) emphasizes the ability of individuals to assess site quality based on the reproductive performance of conspecifics (Danchin et al. 2004, Campomizzi et al. 2008). In birds, these inadvertent social cues are thought to convey breeding location suitability and potential for breeding success for prospecting individuals (Stamps 2001, Ahlering and Faaborg 2006, Nocera et al. 2006). Social information benefits birds by limiting energy costs and reducing predation risk while prospecting for a breeding site (Bijleveld et al. 2010); adult and nest survival has been shown to increase for individuals that are influenced by social information (Powell 2001, Doligez et al. 2003, Pearson et al. 2014). Many avian taxa utilize social information for nest site selection, including: colonial seabirds (Kress 1983, 1997, Ward et al. 2011), raptors (Serrano and Tella 2003, Alonso et al. 2004, Serrano et al. 2004), territorial songbirds (Herremans 1993, Ward and Schlossberg 2004, Nocera et al. 2006, Ward et al. 2011), and shorebirds (Hötker 2000, Rioux et al. 2011, Cunningham et al. 2016).

Individual movement and habitat selection decisions are also influenced by experience. Experienced breeders (i.e., individuals that have bred at a location) are known to rely on their previous breeding success and site knowledge (i.e., personal information) when deciding whether to disperse or remain at a site (Danchin et al. 2004, Schmidt et al. 2010, Rioux et al. 2011). Inadvertent social cues may also influence dispersal in experienced birds, especially for failed breeders (Danchin et al. 1998, Rioux et al. 2011). For example, territorial Piping Plovers (*Charadrius melodus*) that failed to breed successfully dispersed the following season and settled closer to successful conspecifics from the previous season (Rioux et al. 2011). Inexperienced breeders (migrants and first-year breeders) do not have the advantage of personal information and thus may benefit more from social information by assessing social cues to guide breeding decisions (Reed and Oring 1993, Ward and Schlossberg 2004, Nelson 2007, Rioux et al. 2011, Rushing et al. 2015). For example, in Black-capped Vireos (*Vireo atricapilla*), an experiment using song playback resulted in a higher proportion of inexperienced birds settling in unoccupied habitat compared to experienced breeders (Ward and Schlossberg 2004).

The Western Snowy Plover (*Charadrius nivosus nivosus*) is a member of a 40-species clade including some of the world's most vulnerable taxa (Colwell and Haig 2019). The North American Pacific coast population is listed as Threatened under the Federal Endangered Species Act; in 1993 the U.S. Fish and Wildlife Service (USFWS) designated six recovery units (RU) (U.S. Fish and Wildlife Service 1993, 2007, Page et al. 2009) extending from Midway Beach, Washington to Bahia Magdalena, in Baja, Mexico (Page et al. 2009, Eberhart-Phillips et al. 2015). Throughout the coastal range, plovers breed from March (first eggs laid) to September (last chicks fledged; Page et al. 2009). Previous work has shown that plovers select breeding sites using physical cues, such as wide, open stretches of ocean-fronting beach, salt pans, and riverine gravel bars with an abundance of invertebrates (Muir and Colwell 2010, Brindock and Colwell 2011, Webber et al. 2013, Patrick and Colwell 2014, Pearson et al. 2014, Leja 2015, Colwell et al. 2019) – and that within these habitats, plovers select nest sites within sparse, patchy vegetation, which aides their ability to detect predators (Muir and Colwell 2010). Throughout this physically ideal habitat, plover breeding tends to be aggregated and large swaths of suitable beach habitat remain unoccupied each year (Patrick and Colwell 2018, Colwell et al. 2019). The role of conspecific attraction to explain this aggregated distribution remains unclear.

The species is social year-round (Page et al. 2009), forming non-breeding flocks at predictable locations (Papian 2018). During the breeding season (Page et al. 2009), plovers form loose aggregations (Patrick 2013, Patrick and Colwell 2018), and do not defend a classical, resource-based territory (Patrick and Colwell 2018). They are partial migrants, and may disperse within and between seasons (Page et al. 2009, Pearson and Colwell 2014). Within RU2 (i.e., Del Norte, Humboldt, and Mendocino counties of northern California), the population is maintained largely by immigrants (Mullin et al. 2010, Colwell et al. 2017*a*) that become site faithful (Edwards and Paton 1996, Colwell et al. 2007, 2010).

Based on the plover's social nature, social information should play an important role in selection of a breeding site. In support of this, Nelson (2007) found individuals established nests nearer conspecifics than expected by chance (i.e., confirmed conspecific attraction). Furthermore, a 10-year study in Humboldt County, California, found that plovers moved shorter distances in successive breeding seasons when they successfully bred (Pearson and Colwell 2014). And lastly, Patrick and Colwell (2018) confirmed the "semi-colonial" nature of Snowy Plovers by documenting a positive association between population size and spatial aggregation of nests. In other plover studies along the Pacific coast, breeding near conspecifics resulted in higher reproductive success, beyond the benefits of both physical and social variables (Powell 2001, Pearson et al. 2014). While there is evidence of the influence of conspecific attraction on nest distribution and hatching success in Snowy Plovers, it has not been examined in relation to the patchy and aggregated spatio-temporal distribution, which arises through the process of breeding site selection (Powell 2001, Pearson et al. 2014); this information could have a profound influence on habitat management and restoration efforts (U.S. Fish and Wildlife Service 2007).

Here, I investigated the importance of social information for breeding site selection by inexperienced (i.e., first-time breeding) Snowy Plovers in a low-density population in Humboldt County, California. I used an 18-year dataset (2001-2018) to assess the extent to which ecologically relevant physical and social factors influenced the distribution of nests from year to year. Specifically, I examined the temporal dynamics of breeding distribution and determined whether there was a correlation in breeding site selection from one season (i.e., year) to the next. I then examined the interactive influence of physical habitat traits and social information (i.e., both conspecific attraction and public information) on breeding site occupancy within suitable breeding habitat. Finally, I discuss the importance of my results for the species’ management through conservation measures such as habitat restoration, and artificial social attraction.

METHODS

Study Area

The study area encompassed approximately 85 km of ocean-fronting beaches and 15 km of gravel bars along the lower Eel River within Humboldt County (Figure 1; see Colwell et al. 2019). I excluded two breeding sites newly discovered in 2018 from the 2001-2018 dataset due to a lack of continuous survey efforts over the study period. Natural forces (e.g., tidal erosion, drifting sand, channel alterations) and anthropogenic effects (e.g., restoration) altered beach and gravel bar habitats each year. Habitat restoration and revegetation efforts (e.g., Little River State Beach and South Spit) also changed the amount of suitable breeding habitat between years. I used ArcMap Version 10.5.1 (Esri 2017) to draw 209 500-m diameter circles (cells) on beach and gravel bar habitats throughout the study area (174 cells along the north-south axis of ocean-fronting beaches, and 35 cells along the east-west axis of the Eel River); methods follow those detailed in Colwell et al. (2019).

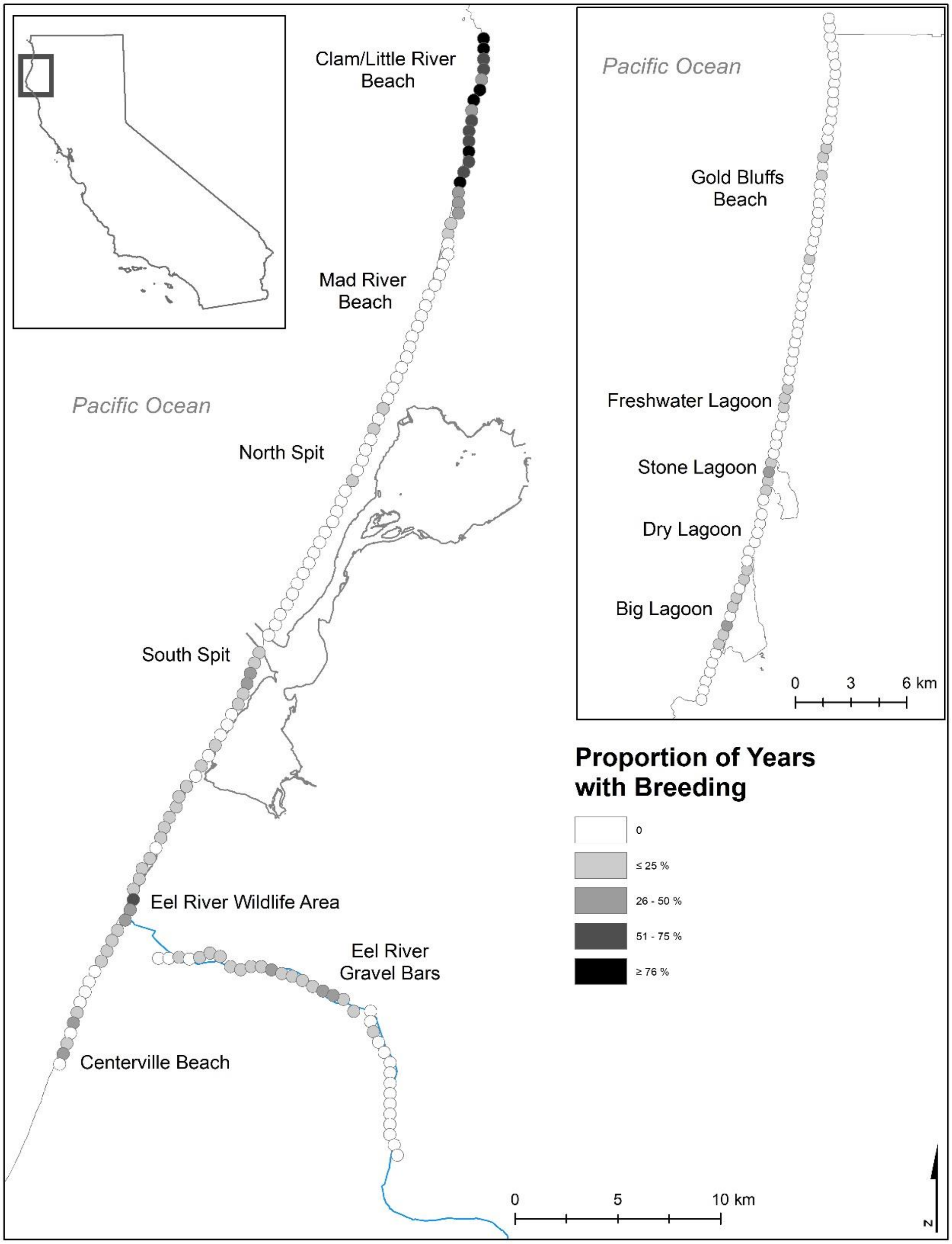

Figure 1. Ocean-fronting beaches and gravel bars of the lower Eel River in Humboldt County, California, USA, where observers monitored breeding Snowy Plovers for 18 years. Shaded circles are 500-m diameter plots showing the proportion of years in which at least one nest occurred.

Field Methods

I analyzed an 18-year (2001-2018) dataset consisting of nest locations [i.e., Universal Transverse Mercator (UTM) coordinates] derived from the fieldwork of observers working for Humboldt State University, private consultants, and State and Federal agencies. Each year, observers monitored breeding plovers from early March until the last chicks fledged in late August or early September. Researchers marked the majority (>95% annually) of breeding plovers in the study area with unique color bands and a USFWS unique metal band (see Colwell et al. 2017*a*), hence allowing for individual-based analysis of breeding activity and movements. I characterized an individual's origin (i.e., local recruit, immigrant) based on banding location. Moreover, I categorized individuals as experienced breeders if they had bred in the study area in a prior year, as opposed to inexperienced breeders (i.e., first year breeding in study area) (see Colwell et al. 2017*a*).

Observers systematically surveyed most sites at least weekly during the breeding season to locate and identify nests and identify (based on color bands) the owners. We increased surveys of sites to 2-3 times per week when we detected breeding adults. Surveyors walked slowly through habitats, while stopping occasionally to scan for plovers using binoculars and a spotting-scope. This frequent and systematic survey effort ensured we missed few nests. For each nest, observers determined the owner based on behaviors during courtship (e.g., male and female scraping) and parental behaviors (e.g., incubating eggs or brooding chicks). Furthermore, observers recorded the location of each nest [in World Geodetic System (WGS) 1984 UTM coordinates] using a Global Positioning System (GPS) attached to a personal digital assistant (e.g., Dell Axim x50) or with a Garmin GPS unit (Garmin eTrex 20). Observers monitored nests at least once per week to record nest activity, confirm the identity of tending parents, and determine nest fate (i.e., hatched or failed). We recorded nest activity by egg presence, observation of an incubating adult, plover tracks, or egg fragment presence and abundance. For this study, I classified a nest as successful if at least one egg hatched. In summary, the 18-year dataset had complete information on 1) their geographic coordinates, 2) the identity, origin, and experience of their tending adults, and 3) their fate.

Surveyors did not systematically monitor plovers during the entire nonbreeding season, however, they conducted yearly winter window surveys to gather winter flock information for a portion of the study period. Additionally, more focused nonbreeding surveys occurred during certain years (Brindock and Colwell 2011, Papian 2018). I used this data to determine winter flock locations and size estimates for eight consecutive years (2010 to 2017).

Observers conducted research in accordance with Federal, State, and university permits: USFWS # TE-73361A-1, California Department of Fish and Wildlife # SC0496; Department of Parks and Recreation # 18-635-009, and Humboldt State University IACUC #18/19.W.14-A.

Annual Dynamics of Breeding Distribution

Within Humboldt County, Snowy Plovers exhibited an aggregated breeding distribution with sections of beach or gravel bar often hosting multiple pairs, with long stretches of habitat unoccupied each season (Patrick 2013, Patrick and Colwell 2018, Colwell et al. 2019). I examined this variability by quantifying the proportion of the 18 years that plovers bred at a location (i.e., within a 500 m cell). For this analysis, I defined the breeding distribution for each of the 209 cells based on the presence of at least one nest within the cell for each year (Figure 1). In total, I included 1,052 nests over the 18-year study period.

To evaluate whether breeder presence in the previous year (*t0)* predicted presence the following year (*t*+1), I used contingency tables, chi-square analyses, and Fisher's exact test (n = 17). Additionally, I quantified the longest consecutive run of years that breeding occurred within each of the 209 cells.

Modeling Inexperienced Breeder Occupancy

I modeled inexperienced breeder occupancy following methods established by MacKenzie and co-workers (MacKenzie et al. 2002, 2003, 2018). I defined a cell as "occupied" for a given year if it had at least one nest with at least one inexperienced parent, as inexperienced breeders are assumed to not have the benefit of personal information in site selection (Ahlering and Faaborg 2006). Inexperienced breeders included immigrants from elsewhere along the Pacific Coast that had not bred previously in Humboldt County and yearlings hatched locally, which follows Nelson (2007). In total, 523 of the 1,052 nests had at least one inexperienced parent. I then calculated predictor and response values (i.e., occupancy) over the 18-year study period for each of the 209 cells.

I treated cell occupancy as categorical, as individuals often re-nested multiple times each season (Colwell et al. 2017*b*, 2018). This definition allowed me to calculate three response variables for each cell over the 18-year study: initial occupancy (i.e., occupancy in 2001), colonization rate (i.e., probability a cell became occupied by an inexperienced plover after not being occupied the previous year), and extinction rate (i.e., probability a previously occupied cell became unoccupied by inexperienced plovers the next season) (Table 1).

Table 1. Response and predictor variables used to model occupancy by inexperienced Snowy Plovers.

Type	Variable	Definition	Reasoning
Response	Initial occupancy (Ψ)	The presence of at least one nest with an inexperienced breeder within a 500-m cell during 2001 breeding season.	Examines the physical habitat feature hypothesized to influence selection of breeding habitat (Colwell et al. 2019).
	Colonization (γ)	The presence of at least one nest with an inexperienced breeder within a cell not occupied the previous season.	Examines the factors that lead to a cell becoming colonized by inexperienced breeders.
	Extinction (ε)	The absence of at least one nest with an inexperienced breeder within a cell occupied the previous season.	Response variable that examines the factors (or lack of) that leads to cell becoming extinct.
Predictor	Beach Width (*BW*)	The average of 20 beach width measurements for each of the three years of NAIP imagery within each 500-m cell.	Plovers select nest and breeding locations based on distance (m) between vegetation and edge of habitat as defined by ocean or river (Muir and Colwell 2010, Patrick and Colwell 2014, Colwell et al. 2019) in Humboldt County. See appendix A.
	Number of experienced breeders Current Year (*Expt1*)	The number of experienced breeders that had at least one nest within the 500-m cell during the current season.	Inexperienced breeders nest closer to experienced conspecifics (Nelson 2007).
	Number of experienced breeders Previous Year (*Expt0*)	The number of experienced breeders that had at least one nest within the 500-m cell the previous season.	Inexperienced birds nest closer to experienced birds (Nelson 2007); may use conspecifics for future settlement (Rioux et al. 2011).
	Winter flock size Current Year (*Flockt*)	The number of wintering birds within the 500-m cell during the winter flock survey preceding the current breeding season.	If inexperienced birds look for conspecifics at beginning of season, they should settle with residents from winter flocks (Papian 2018).
	Successful hatch of a nest PY (*Hatch*)	The presence of at least one nest that successfully hatched during the previous breeding season.	Individuals assess reproductive performance of conspecifics for future decisions in Piping Plovers (Rioux et al. 2011).

I derived five predictor variables based on literature and prior knowledge of the species (Table 1). I used average beach width (*BW*) along ocean fronting beaches and exposed gravel bars along the Eel River (i.e., areas with suitable plover habitat) as a surrogate for the overall physical habitat quality (see Appendix A; Muir and Colwell 2010, Brindock and Colwell 2011, Webber et al. 2013, Patrick and Colwell 2014, Pearson et al. 2014, Colwell et al. 2019). I also included four predictor variables based on conspecific attraction and public information (Table 1). The number of experienced breeders in the current (*Expt1*) and previous (*Expt0*) year, and the size of the winter flock (*Flockt*) evaluated the effect of conspecific attraction, while the presence of a hatched nest the previous year (*hatch*) examined the influence of public information. I scaled the three continuous conspecific attraction covariates within my analysis to aid in numerical convergence of models (Kery and Chandler 2016). I had sufficient data for the locations of winter flocks for 8 years (2010 to 2017) and hypothesized this covariate would influence where inexperienced plovers might nest the following breeding season. In addition to my analysis of the overall dataset (i.e., 17-year Analysis), I conducted a separate incidence function model analysis (i.e., 8-year Analysis) to assess the importance of the winter flock.

I analyzed occupancy in a two-step approach. First, I confirmed that cumulative detection probability of breeding individuals (i.e., pairs that initiated a nest) was high (>0.90) by performing a single season occupancy analysis for the 2016 breeding season (See Appendix B). A cumulative detection probability of greater than 0.95 was reached quickly (i.e., in as few as four weeks of survey effort) and thus providing ample statistical support to simplify my analysis and avoid incorporating the species detectability.

Next, I evaluated the importance of predictor variables in relation to cell occupancy, colonization, and extinction (Table 1) using the *colext* function within the "unmarked" package in Program R (R Development Core Team 2011, Kery and Chandler 2016). I included the winter flock size covariate (only years 2010 to 2017) and ranked 14 *a priori* models (8-year Analysis). Then, I analyzed the entire 18-year dataset, minus the winter flock covariate; in this case, I ranked 12 *a priori* models (17-year Analysis). For both analyses, I included average beach width as an initial occupancy covariate as this has been previously shown to be an important predictor for plover nesting activity in this population (Muir and Colwell 2010, Brindock and Colwell 2011, Patrick and Colwell 2014, Colwell et al. 2019). To appropriately incorporate my predictor variables into analyses, I did not calculate response probabilities for 2018 (MacKenzie et al. 2003, 2018).

The *colext* function is typically used to fit dynamic occupancy models; it estimates parameters for initial occupancy (Ψ), colonization (γ), extinction (ε), while modeling detection probability (p) to account for imperfect detection (Kery and Chandler 2016). These models are typically used for species that breed within a closed system (i.e., no immigration within a breeding season); however, by holding detection at a constant probability value of one (replicating the occupancy status for each cell), the model is equivalent to an incidence function model, which eases the assumption of a closed system (Hanski 1994, Braak et al. 1998, Kery and Chandler 2016).

Prior to analysis, I evaluated variables for collinearity and found Pearson's *r* values below 0.70 (*r* = 0.25 – 0.68) except for the two covariates that evaluated the number of experienced breeders in the previous and current year (Dormann et al. 2013). When examining *Expt0* and *Expt1*, 2 out of 17 years (2009, 2013) had correlation values greater than 0.70. I chose to include combinations of these covariates as all other values ranged below 0.70 (*r* = 0.37 – 0.69) and they represented different hypotheses for use of social information by inexperienced breeders. Additionally, I ran specific models that evaluated each covariate separately, and I did not want a loss in explanatory power for my model set (Carnes and Slade 1988, Graham 2003, Dormann et al. 2013). I did not include interaction terms between predictor variables as the effect of one covariate did not necessarily influence the effect of another (e.g., beach width does not influence effect of *Expt1*) and I wanted to minimize spurious findings that might result from interaction terms (Johnson and Omland 2004).

I used an information theoretic approach (Burnham and Anderson 2002, Anderson 2008) and model selection [using quasi-Akaike's Information Criterion (QAIC) (Akaike 1973, Burnham and Anderson 2002)] to evaluate the support for each model. I inferred the best fitting models based on Akaike weight (*w*), a probability calculated using the normalized likelihood from each ranked model. I used QAIC over Akaike's Information Criterion (AIC) as the global models for the 8-Year Analysis ($\hat{c}$ = 1.87) and 17-year Analysis ($\hat{c}$ = 2.27) were overdispersed. I then calculated the model-averaged parameter estimates on the logit scale for each model within seven ΔAIC values of the top model (Anderson 2008). Finally, I calculated odds ratios for each covariate in my top model, which provided a description of a parameter’s effect, rather than back-transforming estimates on the probability scale, as this avoided the potential for false interactions (Jones and Peery 2019).

RESULTS

Annual Dynamics of Breeding Distribution

Snowy Plovers bred in a patchy distribution, with long stretches of unused habitat punctuated by areas of aggregated nests (Figure 1). Over the 18-year period, plovers nested in 88 of the 209 cells (42%). No cell had nesting during every year of the study period and only eight cells had nesting in more than 75% of all years. By contrast, plovers bred in most cells (n = 56) for less than 25% of all years. From one year to the next, nesting activity of the population had a strong tendency to occur at the same locations ($P<0.005$, 17 comparisons; see Appendix C). This tendency was dynamic over longer periods of time; only 12 cells had nests in seven or more consecutive years. Conversely, 54 cells had nests in two or fewer consecutive years (Figure 2).

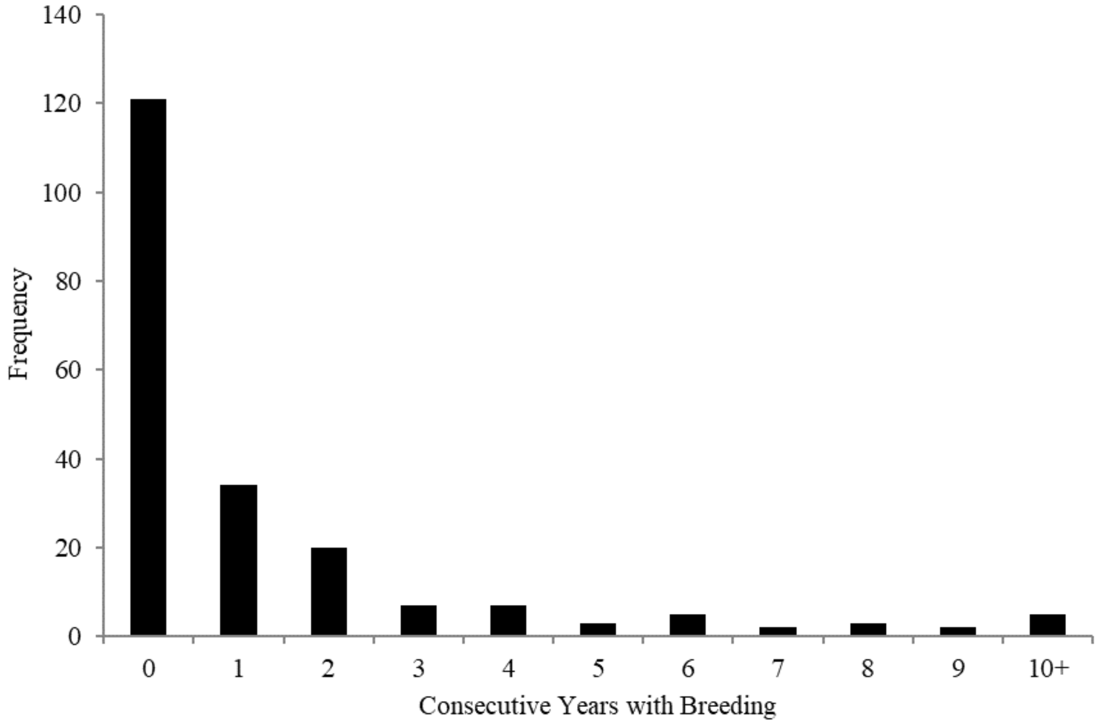

Figure 2. The temporal distribution (i.e., “runs”) of Snowy Plover occupancy of breeding locations (i.e., 500-m cells) showed that plovers bred at most locations for one or two years; few sites were occupied in multiple consecutive years.

Effect of Winter Flock

The top model within the 8-year Analysis included winter flock size as a colonization parameter (Table 2). This model held 52% of the Akaike weight. The second-ranked (18% Akaike weight) and third-ranked (12% Akaike weight) models included the winter flock size as an additional extinction parameter (Appendix D); however, this added variable was not a significant predictor for extinction, as evident by a positive coefficient value (contrary to what was expected) and confidence intervals that overlap zero (β= 0.057, 95% CI = -0.195, 0.309). This result indicates these models contained noninformative variables and did not need to be included within my model set (Anderson 2008). When I removed these two models, the top model remained the same and held 77% of the Akaike weight (Table 2). The new second-ranked model (13% Akaike weight) was identical to the top-ranked model without the winter flock size as a colonization predictor.

Table 2. A summary of top models predicting initial occupancy (Ψ), colonization (γ), and extinction (ε) of Snowy Plover breeding sites, including the presence (8-year Analysis) and absence (17-year Analysis) of a wintering flock. The null models representing physical habitat only for each analysis is shown.

Analysis	**Model**	**QAIC**	**ΔQAIC**	**ω**	***K***
8-year	Ψ(*BW*)γ(*BW*+*Expt1*+*Flockt*)ε(*Expt1*)	304.16	0.00	0.77	10
	Ψ(*BW*)γ(*BW*+*Expt1*)ε(*Expt1*)	307.79	3.63	0.13	9
	Ψ(*BW*)γ(*BW*+*Expt1*+*Flockt*)ε(*BW*+*Expt1*+*Flockt*+*Hatch*)	309.74	5.58	0.04	13
	Ψ(*BW*)γ(*BW*+*Expt1*)ε(*Expt1*+*Hatch*)	309.95	5.79	0.03	10
	Ψ(*BW*)γ(*BW*+*Expt0*+*Expt1*+*Flockt*)ε(*Expt0*+*Expt1*+ *Flockt*)	310.21	6.05	0.03	13
	Ψ(*BW*)γ(*BW*)ε(*BW*)p(.)	389.35	85.19	0.00	8
17-year	Ψ(*BW*)γ(*BW*+*Expt1*)ε(*Expt1*)	517.38	0.00	0.80	9
	Ψ(*BW*)γ(*Expt1*)ε(*Expt1*)	521.33	3.96	0.11	8
	Ψ(*BW*)γ(*Expt0*+*Expt1*)ε(*Expt0*+*Expt1*)	521.65	4.27	0.09	11
	Ψ(*BW*)γ(*BW*)ε(*BW*)p(.)	664.83	147.45	0.00	8

QAIC: Quasi Akaike's Information Criterion
ΔQAIC: change in QAIC between the top model and each additional model.
ω: the proportion of the total Akaike weight held by each model.
K: number of model parameters.

Within the 8-year Analysis, winter flock size positively influenced (β= 0.44, 95% CI = 0.10, 0.78) inexperienced breeder colonization (Appendix E). Odds ratios provide additional insight into the role of this covariate; colonization by inexperienced plovers was approximately 60% more likely at sites with a large winter flock (Table 3).

Table 3. Odds ratios expressing the strength of covariate relationships [average beach width (*BW*), the number of experienced breeders in the current year (*Expt1*), and winter flock size (*Flockt*)] on initial occupancy, colonization, and extinction of Snowy Plover breeding sites including the presence (8-year Analysis) and absence (17-year Analysis) of a winter flock.

Analysis	**Parameter**		**Odds Ratios**	**Lower CI**	**Upper CI**
8-year Analysis	Occupancy (Ψ)	Intercept	0.04	0.02	0.89
		BW	2.35	1.41	3.89
	Colonization (γ)	Intercept	0.03	0.02	0.04
		BW	1.49	1.09	1.93
		Flockt	1.56	1.22	2.00
		Expt1	3.86	2.62	5.69
	Extinction (ε)	Intercept	1.66	0.99	2.79
		Expt1	0.66	0.53	0.82
17-year Analysis	Occupancy (Ψ)	Intercept	0.06	0.04	0.12
		BW	2.77	1.72	4.47
	Colonization (γ)	Intercept	0.03	0.03	0.04
		BW	1.46	1.21	1.76
		Expt1	5.00	4.00	6.24
	Extinction (ε)	Intercept	2.37	1.66	0.03
		Expt1	0.64	0.55	0.74

*CI: Confidence Interval

Effect of Beach Width and Experienced Conspecifics

The top model for the 17-year Analysis (i.e., excluding the effect of winter flock) included average beach width as a parameter for initial occupancy and colonization. More importantly, the model included the number of experienced breeders as colonization and extinction parameters (Table 2). This model held 51% of the Akaike weight (Appendix F). The second-ranked model (18% Akaike weight) and third-ranked model (17% Akaike weight) included the presence of a successful nest as an additional extinction parameter; this added variable was not a significant predictor in either model (also indicating they were noninformative variables), as evidenced by a positive coefficient value and confidence intervals overlapping zero (β= 0.010, 95% CI = -0.58, 0.57). I removed these two models and ran the analysis with 10 *a priori* models. The top model remained the same and held 80% of the Akaike weight (Table 2). The new second ranked model (11% Akaike weight) was identical to the top-ranked model with beach width removed from the colonization parameter.

In the first year (2001), beach width predicted cell occupancy by inexperienced breeders. In subsequent years, the presence of experienced breeders correlated positively with colonization (β = 1.61, 95% CI = 1.27, 1.96) and negatively with extinction (β = -0.45, 95% CI = -0.66, -0.25) (Appendix G). Additionally, average beach width positively influenced colonization (β= 0.38, 95% CI = 0.12, 0.63); although average beach width was marginal within the 8 year-Analysis (β= 0.37, 95% CI = -0.02, 0.76).

Within the top model for the 17-year Analysis, colonization by inexperienced plovers was five times as likely at sites with experienced breeders present. Extinction probability decreased by approximately 56% with the presence of experienced breeders. Additionally, initial occupancy was more than twice as likely at sites with wide beaches (Table 3).

DISCUSSION

Three major findings arise from my study. First, as shown in previous studies of this population (Colwell et al. 2019), plover breeding distribution was dynamic, characterized by aggregations that often persisted from one year to the next; however, few sites persisted for long intervals. Second, although physical features of habitat (i.e., beach width) influenced where plovers bred, inexperienced plovers first bred at locations occupied by experienced conspecifics. Third, measures of reproductive performance (i.e., public information) did not influence future settlement decisions of inexperienced breeders. Each of these findings has consequences for plover conservation.

Plover Breeding is Dynamic

From one year to the next, nesting activity of the population tended to occur at the same locations; however, this long-term study shows that few breeding sites are occupied by plovers over a long period of time. This corroborates what we know about the nonterritorial nature of the species' social system and the ephemeral nature of the beach and gravel bar habitat along the Pacific coast. Breeding sites are continually changing, precipitated by a combination of natural forces and anthropogenic efforts that shape the physical state of available habitat (Muir and Colwell 2010, Brindock and Colwell 2011, Patrick and Colwell 2014, Leja 2015, Colwell et al. 2019), but modified by personal experience (Colwell et al. 2007, Pearson and Colwell 2014) and social information (Nelson 2007, Leja 2015, Patrick and Colwell 2018).

Using the same nest and beach width dataset as Colwell et al. (2019), I confirmed that beach width is the main physical factor driving breeder settlement decisions within Humboldt County: inexperienced birds bred at wider beaches, which is consistent with other research within the species' range (Patrick and Colwell 2014, Leja 2015, Colwell et al. 2019). However, despite having over 100 km of suitably wide beach and gravel bar habitat within Humboldt County, the majority of these site remain unoccupied. Physical factors alone are therefore unable to explain this breeding distribution. Investigating the additional role of social information provides insight into the aggregated distribution of breeding plovers (Patrick and Colwell 2018).

Inexperienced Breeders Utilize Conspecific Attraction

This is the first study to examine the influence of conspecific attraction in Snowy Plover breeding distribution at a large temporal and spatial scale, and the first since Nelson (2007) to investigate how prior breeding experience influences breeding locations. As with other colonial and territorial bird species (Kress 1983, Serrano et al. 2004, Ward and Schlossberg 2004, Hunt et al. 2017), these findings highlight the importance of conspecific attraction in a semi-colonial species (Ahlering and Faaborg 2006).

Social factors (e.g., experienced conspecifics, winter flock size) predicted inexperienced breeder colonization and extinction better than physical factors alone. I expanded on the findings of Nelson (2007), who used a different metric (distance to nearest nest), and confirmed inexperienced plovers settled at sites with experienced conspecifics. I also showed that winter flock size influenced the settlement decisions of inexperienced birds.

There are several reasons that conspecific attraction may be more prevalent in Snowy Plovers compared with other members of the *Charadrius* genus, particularly with this study population. In territorial species, such as the Piping Plover, prospecting males first find and defend a territory, then focus on obtaining a mate, often returning to a territory occupied in a prior year (Cairns 1982). With this resource defense strategy, winter flocks inevitably dissipate quickly at the beginning of the breeding season as resident individuals establish territories (Haig and Oring 1985); conspecific presence likely deters prospecting breeding individuals, as conspecific territories are already established (Cairns 1982). The Snowy Plover population within northern California does not defend a traditional territory (Page et al. 2009, Patrick and Colwell 2018) comprised of distinct boundaries guarded for an appreciable amount of time (Stamps 1994, Adams 2001); this allows prospecting individuals to focus on finding a mate. The presence of conspecifics (including individuals from the winter flock) likely attracts prospecting birds to a general location, enabling more mating opportunities. Additionally, Snowy Plovers are prone to dispersing within and between years (Stenzel et al. 1994, Pearson and Colwell 2014) to find and enhance breeding opportunities. The shifting distribution attests to this observation.

Snowy Plovers also have a relatively long breeding season (Warriner et al. 1986) compared to other avian species and are known to be social during the non-breeding season (Brindock and Colwell 2011). I confirmed the findings by Colwell et al. (2019), that inexperienced breeders were more likely to settle at sites with a large winter flock, which occur at predictable locations within Humboldt County year after year (Papian 2018). My results suggest some inexperienced breeders may arrive at the beginning of the breeding season, when winter flocks are still present, or are influenced by resident individuals that court within the winter flock and eventually nest nearby. This highlights the importance and challenges of understanding the social nature of interactions in winter flocks. If birds court, they may be influenced in their choice of a breeding site by their mate's experience.

The small population size within RU2 requires prospecting individuals, especially females, to move long distances within and between seasons to seek potential mates. The RU2 population size has ranged from 19 to 74 breeding individuals (Colwell et al. 2017*a*) and a large portion of suitable habitat (i.e., 120 cells) remained unoccupied over the 18 years. Additionally, most sites experienced relatively low reproductive success (Colwell et al. 2019), with unsuccessful breeders less likely to be site faithful the following season (Pearson and Colwell 2014). As such, sites within Humboldt County are more prone to extinction and colonization events because individuals seek out mates and may be forced to move substantial distances in the process. This likely places added importance for prospecting plovers to utilize social information within RU2 to limit the costs associated with finding a mate. Higher density populations, such as Coos Bay North Spit in RU1, have sites with larger breeding flocks (Lauten et al. 2019), limiting the need for breeders to disperse from a breeding site in search of another mate. Instead, individuals within these flocks can likely focus on the physical characteristics of a breeding location, as potential mates can be found nearby.

Hatching Success did not Influence Inexperienced Breeders

Contrary to expectations, hatching success, which was generally low in all but the last two years of the dataset, did not have a strong influence on inexperienced breeder occupancy. Hatching success was found to influence the settlement decisions of breeding Piping Plovers, a species that defends territories over a shorter breeding season (Cairns 1982, Rioux et al. 2011). By contrast, Snowy Plovers initiate nests asynchronously during their long (i.e., four month) breeding season (Powell 2001, Nelson 2007, Page et al. 2009, Saalfeld et al. 2012, Patrick and Colwell 2018), and are semi-colonial within the study area (Patrick and Colwell 2018). These aspects of the breeding biology afford individuals more opportunities to use social cues, such as reproductive performance to influence settlement decisions (Warriner et al. 1986, Colwell et al. 2010, 2017*b*, Wilson and Colwell 2010).

There are three potential reasons that public information (i.e., hatching success) did not influence inexperienced breeders. First, adult Snowy Plovers can move large distances with chicks in a short period of time (Page et al. 2009, Wilson and Colwell 2010, Patrick and Colwell 2018). For instance, Wilson and Colwell (2010) noted a male moved 2,723 m away from the nest site within the first three days of hatching. Snowy Plover broods may not remain within a cell for a sufficient duration for inexperienced breeders to gather public information and instead, may solely use conspecific attraction.

Second, the study population was considered a sink until 2016 (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014, Hudgens et al. 2014, Colwell et al. 2017*a*) owing to low reproductive success (Colwell et al. 2019). Only 354 out of 1,052 nests (34%) hatched over the 18-year study period and a smaller proportion survived to fledge; migrant breeders may not have had opportunities to assess nest success using the presence of chicks. Additionally, failed breeders are known to disperse, especially if they did not retain the previous season's mate (Pearson and Colwell 2014); thus, failed experienced breeders may not occupy the same cell the following season, limiting the potential for conspecific attraction. Third, while plovers produce multiple clutches within a season (Page et al. 2009), inexperienced birds would need to arrive early or remain late in the breeding season to evaluate reproductive performance. There is evidence that inexperienced breeders first initiate a nest later in the breeding season compared with experienced pairs (Warriner et al. 1986, Pearson and Colwell 2014); however, a better understanding of settlement timing within a season would help to ascertain whether inexperienced plovers arrived at a time when they could adequately assess hatch success. This provides support to further evaluate the within-season dynamics of inexperienced breeder arrival, to confirm the typical arrival times compared to nest initiation and evaluate the influence of nest clutches within a season.

Limitations

Several methodological facets of this study limit inference regarding the nature and mechanisms of social information in Snowy Plovers. I was only able to include approximately half of the nests (523 of 1,052) for my response variables when modeling occupancy due to the inability to differentiate conspecific attraction from personal information in experienced-only pairs. Additionally, it was difficult to determine how the presence of conspecifics influenced inexperienced breeder decisions within a breeding season. More than half of the nests in my analysis (352 of 523) belonged to pairs consisting of an inexperienced plover and experienced mate. Consequently, I was unable to determine which individual ultimately chose the breeding location. I also had limited information on the arrival times of inexperienced versus experienced breeding plovers.

I was unable to examine how sex might influence the settlement decisions of inexperienced breeders. Snowy Plovers have a unique mating system (serial polygamy) with typically male-only brood care (Warriner et al. 1986), while females are known to seek mates and may determine the ultimate location of the nest (Warriner et al. 1986, Page et al. 2009); based on these different behaviors, it is likely the importance of social information varies considerably by sex. While my results provide support for the hypothesis that inexperienced plovers use social information from experienced conspecifics at some point during the settlement process, future studies should focus on understanding inexperienced individuals' within-season settlement and mate decisions, and further evaluate differences in settlement decisions between sexes (Pearson and Colwell 2014).

Winter flock data did not differentiate between inexperienced and experienced breeders. Winter flocks are dominated numerically by individuals that breed elsewhere along the Pacific coast, especially Oregon (Papian 2018). Additionally, only a small percentage of fledged plovers within RU2 are philopatric and return the subsequent season (Colwell et al. 2007). Therefore, including inexperienced breeders in the winter flock likely had a minimal effect on inexperienced breeder occupancy influence the following season.

I only included one physical habitat covariate (i.e., beach width) which could limit the interpretation of my results. However, many studies have evaluated the physical factors of preferred plover habitat with the same conclusion—that the species prefers wide beaches, with gentle slopes, and little vegetation (Powell 2001, Muir and Colwell 2010, Patrick and Colwell 2014, Pearson et al. 2014, Leja 2015, Colwell et al. 2019); with these three covariates inevitably correlated (i.e., wider beaches typically have gentler slopes and less vegetation). Given this extensive evidence, it is unlikely that other physical factors needed to be included in my analysis.

CONSERVATION IMPLICATIONS

Within RU2, beach restoration to remove invasive European Beach Grass (*Ammophila arenaria*) and create open, sparsely vegetated habitats is a common management strategy (Muir and Colwell 2010, Dinsmore et al. 2014, Leja 2015, Raby 2019), with varying degrees of success in meeting recovery objectives (Colwell et al. 2007, 2019, Leja 2015). Clam Beach and South Spit Beach are two breeding locations within Humboldt County with similar site conditions and restoration strategies. Both sites have a consistent winter flock and wide beach habitat attributed to habitat restoration, which together increases occupancy. However, there is a stark contrast in reproductive performance between the sites. South Spit is currently the most important single breeding site within RU2 (Feucht et al. 2018), while Clam Beach has long been considered a population sink (Burrell and Colwell 2012).

In the last two decades, Clam Beach has had continuously low reproductive success due to predation by Common Ravens (*Corvus corax*) (Burrell and Colwell 2012). Inexperienced plovers are likely to keep selecting poor quality sites, such as Clam Beach, because of conspecific presence from the winter flock. Conversely, experienced breeders may eventually disperse to breeding locations with higher reproductive success (Rioux et al. 2011, Pearson and Colwell 2014), as has been documented in certain individuals (Colwell et al. 2017*b*). It is unlikely reproductive success will significantly increase unless innovative management strategies, such as those incorporated at South Spit, are considered to meet recovery objectives (U.S. Fish and Wildlife Service 2007).

South Spit has similar site conditions (i.e., winter flock and wide beaches); however, the placement of oyster shells (a key difference in restoration from Clam Beach) has increased reproductive success by enhancing nest and chick crypsis (Colwell et al. 2011). Additionally, nest predation is infrequent as corvid activity is low (Colwell et al. 2019). My results indicate that the winter flock and comparatively high density (i.e., conspecific attraction) of successful experienced breeders (i.e., public information) will likely continue to attract inexperienced plovers to the site. Focusing restoration efforts at sites such as South Spit could prove an effective management tool (Huxel and Hastings 1999). Additionally, at sites where conspecifics are lacking, managers need to anticipate long-term restoration and maintenance. Artificial decoys and vocalizations could be useful as an attractant, as they are known to be beneficial for species such as colonial seabirds (Kress 1983, 1997, Jones and Kress 2012). Although, plovers do not have the same social system and breeding site limitations that make for successful use of decoys in restoring seabird colonies (Kress 1997, Kim et al. 2009, Jones and Kress 2012). It is likely artificial methods would only have a temporary effect, with individuals continuing to prospect for real conspecifics that offer the advantages of mate choice and predator avoidance (Powell 2001, Page et al. 2009, Pearson et al. 2014).

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APPENDIX A

Appendix A. Delineation of suitable plover habitat and determination of cell beach width using remotely sensed aerial imagery.

I digitized beach habitat and determined average beach width (*BW*) using ArcMap version 10.5.1 (Esri 2017). I obtained National Agriculture Imagery Program (NAIP) imagery from the United States Department of Agriculture (USDA) Natural Resources Conservation Science (NRCS) Geospatial Data Gateway for 2005 (National Agriculture Imagery Program, 2005), 2010 (National Agriculture Imagery Program, 2010), and 2016 (National Agriculture Imagery Program 2016). I created each 500 m long and 1000 m wide cell in ArcMap (Esri 2017) using the Polygon Construction tool. I chose the length based on the typical movement distance for adults rearing chicks and to standardize my sample size (i.e., cells) for future analyses (Wilson and Colwell 2010). I chose the width to adequately measure the furthest extent of beach width habitat.

I created a new polygon shapefile and digitized available beach habitat within each site for each NAIP year at a maximum scale of 1:1500 using the Polygon Construction tool to create three digitized beach habitat shapefiles. I then used the Create Fishnet tool to overlay a 25 by 25-m grid over the digitized beach habitat. I removed all vertical lines, clipped the horizontal lines to the suitable habitat polygons, and then calculated the average beach width value for each cell using the Calculate Geometry tool (Figure 3). I confirmed this method produced similar indices of habitat width for each year, as determined by strong positive correlations (r = 0.665 - 0.741, all $p < 0.05$)

between each NAIP year (i.e., 2005-2010, 2010-2016, 2005-2016); I then obtained an overall average beach width for each cell.

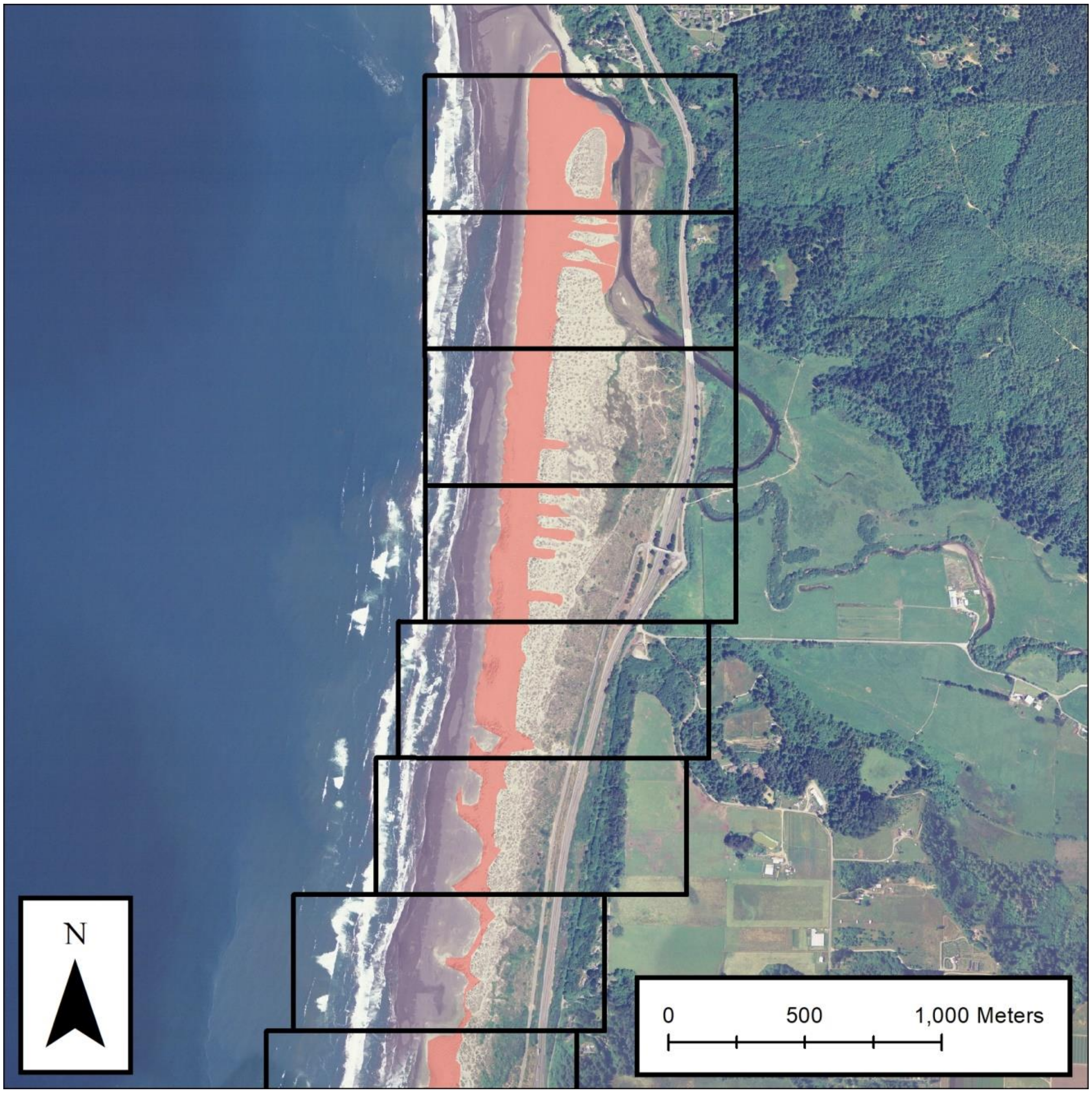


Figure 3. An example of the digitization method to determine average beach width (*BW*) within suitable beach (highlighted in red). Figure is a 2005 National Agriculture Imagery Program (NAIP) image of Little River State Beach in Humboldt County. Edge of the wave slope to the edge of the European Beach Grass dominated and/or vegetated dunes comprised suitable habitat. The black rectangles represent the 500-m long by 1000-m wide cells.

APPENDIX B

Appendix B. Confirmation of high detection probability utilizing single season occupancy models

Occupancy modeling can be an effective tool to incorporate species detectability and reduce the error in population-level modeling (MacKenzie et al. 2002, 2018); however, models that incorporate a species detectability create a more complex analysis (MacKenzie et al. 2005, 2018). This added complexity may be unnecessary if detection is high (>0.90). I predicted intensive monitoring efforts over the 18-year study period resulted in few missed nests (see Colwell et al. 2019); therefore, cumulative detection probability would be extremely high for a given year.

To test this prediction, I performed a single season occupancy model on a candidate model set of 10 *a priori* models with the *Occupancy Estimation with Detection <1* (Occupancy) function in program MARK Version 9.0 (White and Burnham 1999) for a subset of 2016 breeding locations within Humboldt County. The Occupancy function in Program R is typically used to fit single season occupancy models; estimating parameters for occupancy (Ψ) while also modeling detection probability (p) based on replicate survey occasions to account for imperfect detection (MacKenzie et al. 2002, 2018). I chose 2016 for this analysis because there was detailed survey date and plover location data for each survey.

For this single season analysis, “occupancy” is defined as the probability a plover used a cell at some point during the 2016 breeding season (MacKenzie et al. 2018). This definition is different than my overall analysis, which defined response variables based solely on the individuals associated with a nest. Defining occupancy based solely on individual presence allows for a more conservative detection probability estimate and is more representative of traditional single season occupancy models (MacKenzie et al. 2002, 2018). With this definition, there is a possibility a cell could be occupied even though a nest was missed or predated; however, this was unlikely to occur due to intensive monitoring efforts and observers' ability to efficiently determine nest predation and abandonment. Ultimately, if detection probability of individuals is high, it can be inferred that the detection probability of the individuals associated with nests would be substantially higher.

To calculate detection probability, I considered one week during the 2016 survey season to constitute one replicate survey (i.e., occasion) as the entire study area was covered at least once each week. In total, I included 20 replicated detections for each cell during the 2016 breeding season. Response and predictor variables thought to influence detection are provided in Table 4.

Table 4. Response and Predictor variables used to model single season occupancy and detection probability by Snowy Plovers.

Variable	Definition	Reasoning
Use (Ψ)	The presence of at least one Snowy Plover within a 500-m cell during 2016 breeding season.	Response variable to examine if a physical indicator for suitable habitat (i.e., *BW*) influences occupancy during 2016 breeding season.
Detection probability (p)	The probability of detecting a Snowy Plover at an occupied site during one survey.	Response variable to determine cumulative detection probability for the 2016 breeding season.
Beach Width (*BWt*)	The average of 20 beach width measurements for the 2016 NAIP image within each 500-m cell.	Plovers select nest and breeding locations based on distance (m) between vegetation and edge of habitat as defined by ocean or river (Muir and Colwell 2010, Patrick and Colwell 2014, Colwell et al. 2019) within Humboldt County.
The presence of a nest during breeding season (*Nest)*	The presence of at least one nest within a 500-m cell during 2016 breeding season.	Adult plovers will remain near an active nest to incubate and tend chicks (Page et al. 2009, Wilson and Colwell 2010). Detectability should increase.
Detection probability is linear over time (*T*)	The ability to detect a plover either increases or decreases linearly over time, or is constant (i.e., for the 20 survey occasions).	Detectability should not change throughout the season (i.e., plover detectability the same at beginning, middle, and end of breeding season).
Detection probability is quadratic over time (*T*^2)	The ability to detect a plover is highest during the middle of the survey period (i.e., 20 survey occasions).	Detectability should increase during the middle of the season, when more nests are active and adults are actively courting (Page et al. 2009, Colwell et al. 2010).

I used model selection and AIC corrected for small sample sizes (AICc) (Hurvich and Tsai 1989, Burnham and Anderson 2002) to evaluate support for each model based on Akaike weight (w) as the data were not substantially overdispersed ($\hat{c} = 1.0388$). I then calculated the cumulative detection probability for the top model using the equation: $1 - (1 - a)^{b}$. In this equation, a represents the estimated parameter for detection probability and b is the number of replicated units (Rodtka et al. 2015).

The top model included time as a quadratic function and the presence of at least one nest as parameters for detection probability, and beach width in 2016 as a parameter for occupancy. This model held 73% Akaike weight. The second-ranked model (27% Akaike weight) also included time as a quadratic function, but also included beach width in 2016 as parameter for detection probability (Table 5). Assuming detection probability was quadratic (with a peak in detection probability during the middle of the season) over time, cumulative detection probability reached 0.95 in as little as four occasions (i.e., surveys) for the 2016 breeding season at locations with known nests (Figure 4). Even for cells without nests, the cumulative detection probability exceeded 0.90 in 16 occasions.

Table 5. A list of *a priori* models predicting occupancy (Ψ) and detection probability (p) of Snowy Plover breeding sites for the 2016 breeding season. The top models are shown, ranked by Akaike weight (**ω**).

Model	**AICc**	**ΔAICc**	**ω**	***K***
p(*T*+*t*^2+*nest*) Ψ(.+*BWt*)	1144.05	0.00	0.73	6
p(*T*+*t*^2+*nest*+*BW*) Ψ(.+*BWt*)	1146.04	2.00	0.27	7
p(*T*+*t*^2+*nest*) Ψ(.)	1187.56	43.52	0.00	5
p(*T*+*nest*) Ψ(.)	1211.80	67.75	0.00	4
p(*T*+*t*^2) Ψ(.+*BWt*)	1269.11	125.07	0.00	5
p(*T*+*t*^2+*BWt*) Ψ(.)	1312.34	168.30	0.00	5
p(*T*+*t*^2) Ψ(.)	1318.15	174.10	0.00	4
p(.) Ψ(.)	1339.72	195.67	0.00	2
p(*T*) Ψ(.)	1340.10	196.06	0.00	3
p(*t*)Ψ(.)	1342.31	198.26	0.00	21

AIC: Akaike's Information Criterion
ΔAIC: change in AIC between the top model and each additional model.
ω: the proportion of the total Akaike weight held by each model.
K: number of model parameters.

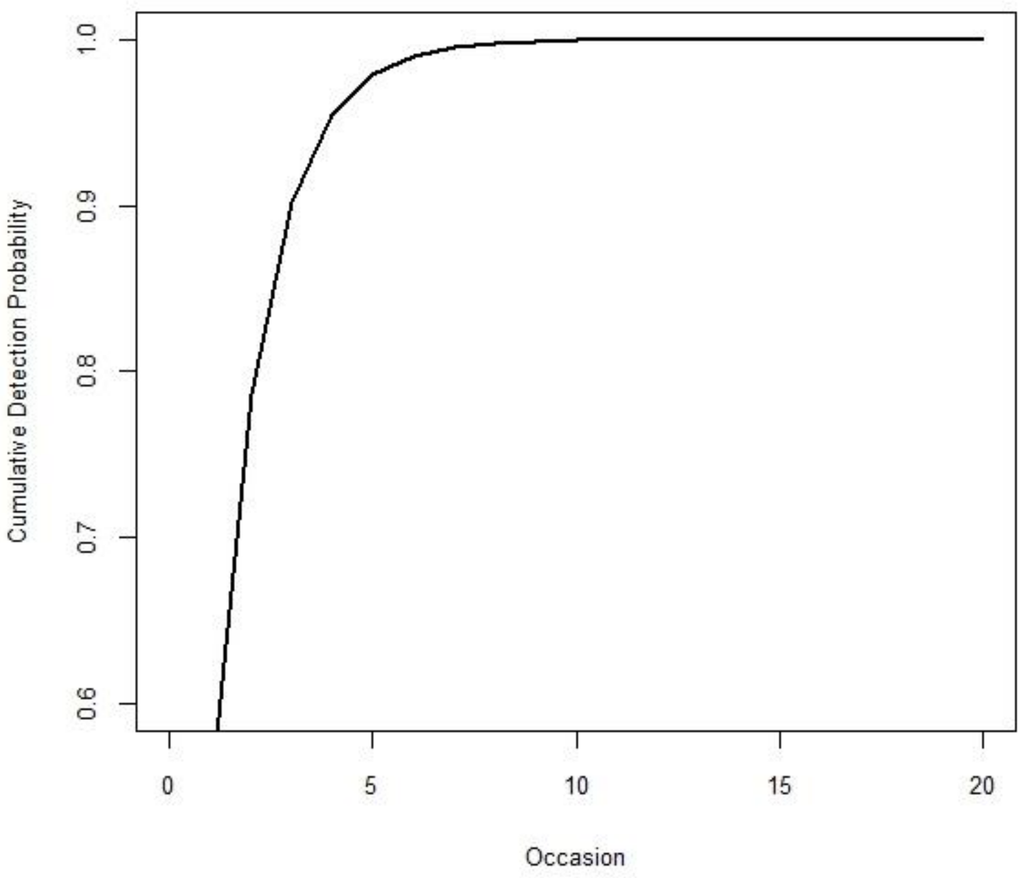
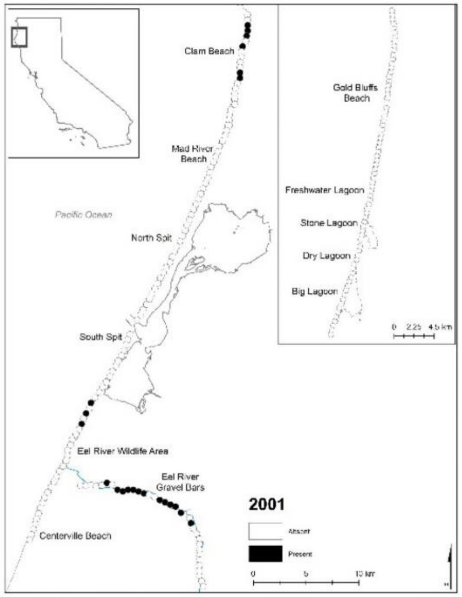


Figure 4. Cumulative detection probability was reached in four occasions for the top model [i.e., p(*T+t^2+nest*) Ψ(*BWt*)], analyzing 2016 breeding data.

APPENDIX C

Appendix C. Ocean-fronting beaches and gravel bars of the lower Eel River in Humboldt County, California, USA, where observers monitored breeding Snowy Plovers for each year over the 18-year study period. Black circles are 500-m diameter plots which had at least one nest present within a given year.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Centerville Beach
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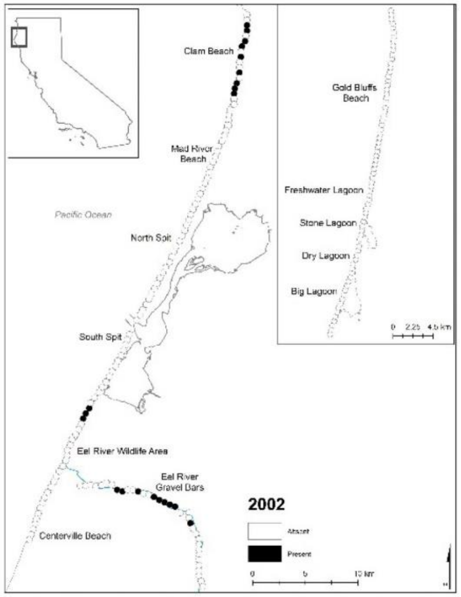
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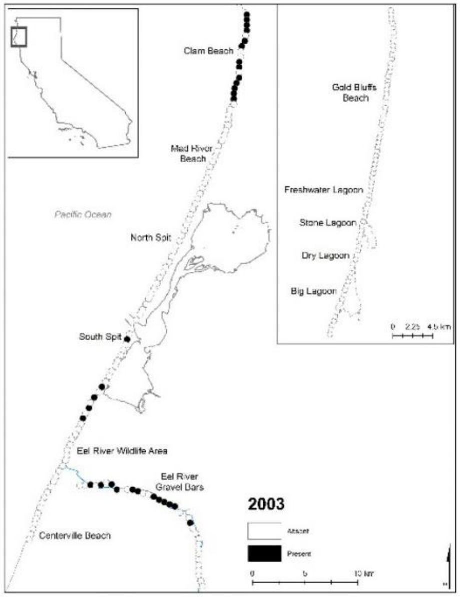
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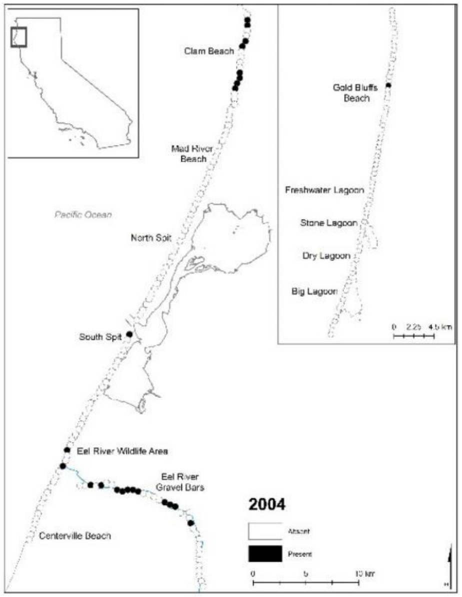
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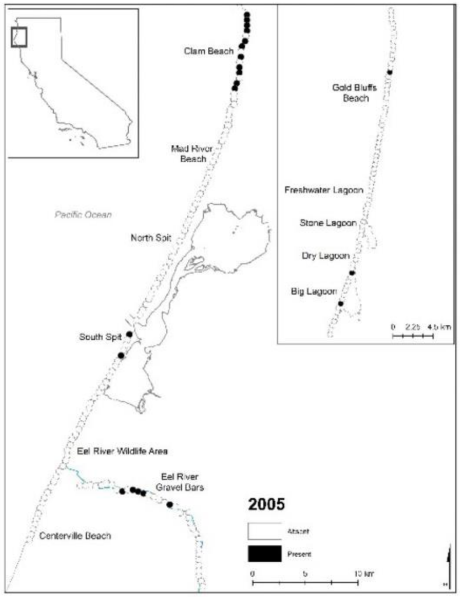
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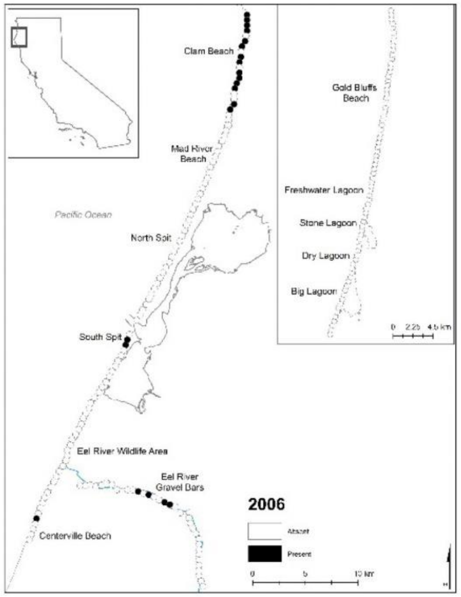
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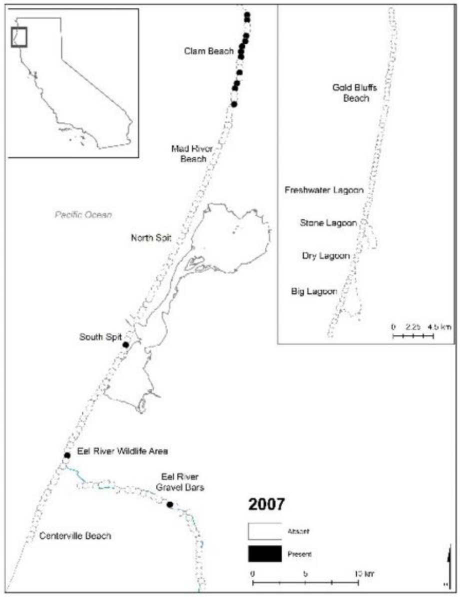
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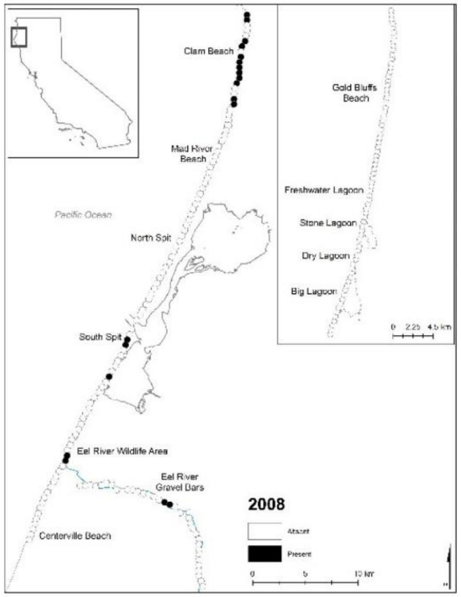
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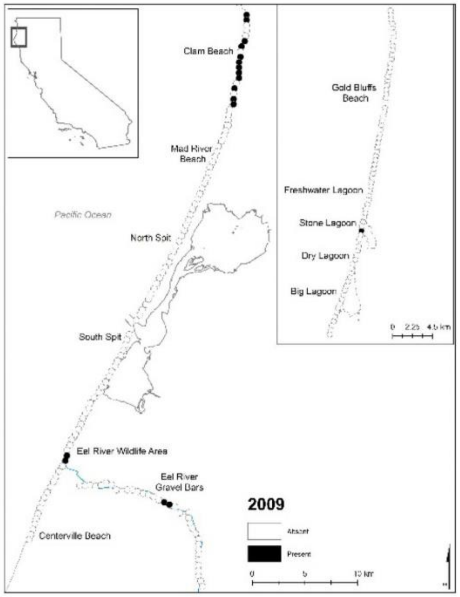
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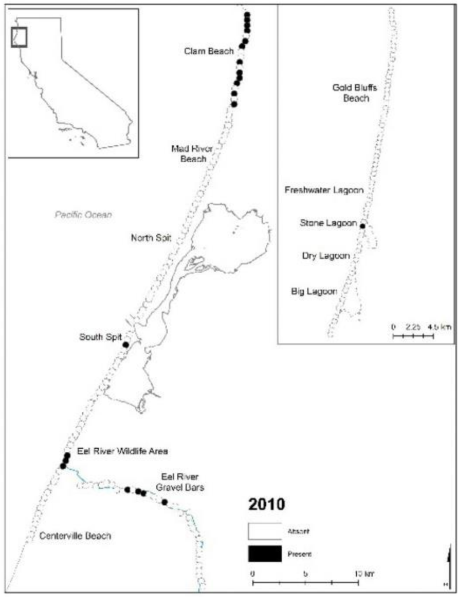
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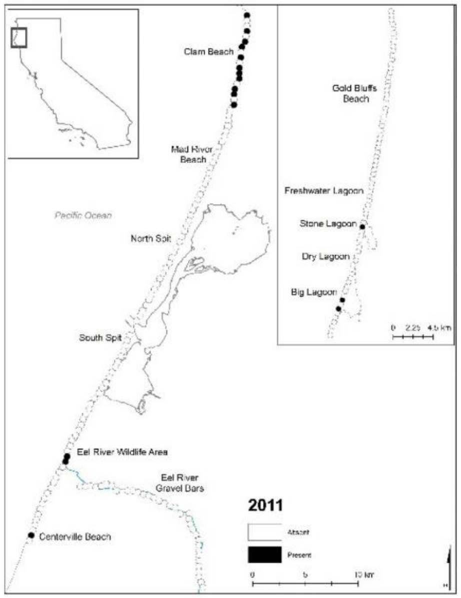
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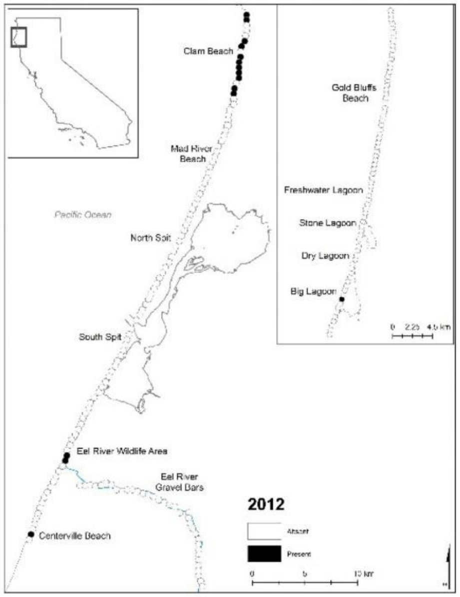
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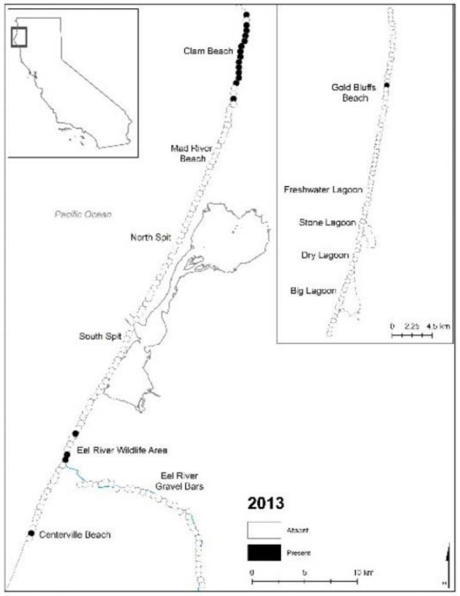
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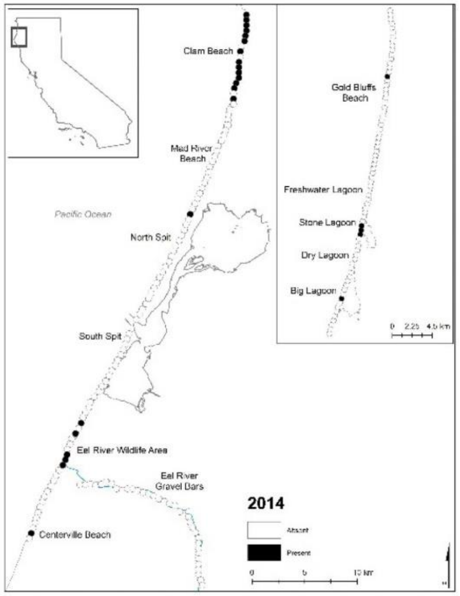
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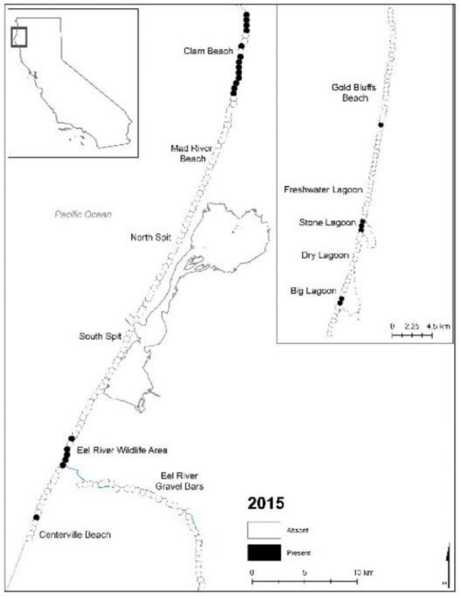
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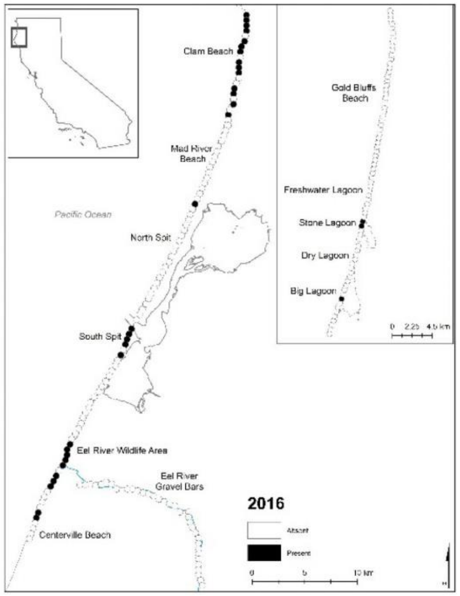
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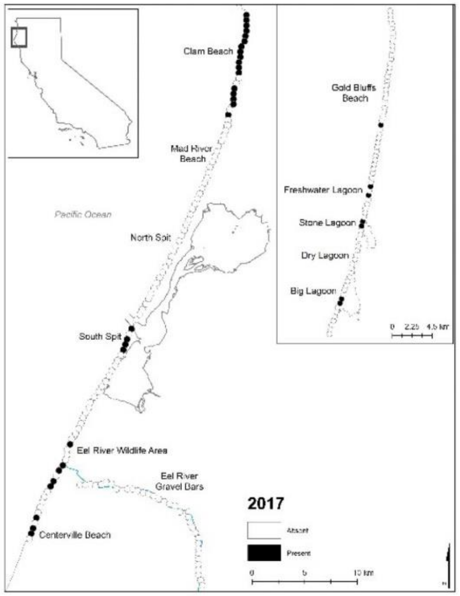
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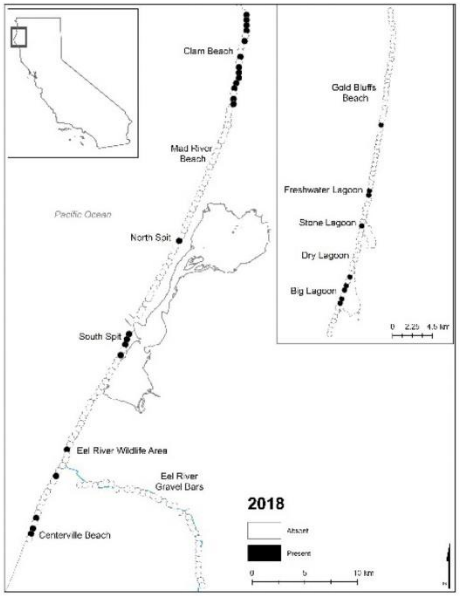
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APPENDIX D

Appendix D. Ranking of 14 *a priori* models predicting occupancy (Ψ), colonization (γ), extinction (ε) of Snowy Plover breeding sites. Models evaluate eight years (2010 – 2017) of breeding data. The top models for each analysis are shown, ranked by QAIC weight **(ω)**.

Model	**QAIC**	**ΔQAIC**	**ω**	***K***
Ψ(*BW*)γ(*BW+Expt1+Flockt*)ε(*Expt1*)p(.)	304.16	0.00	0.52	10
Ψ(*BW*)γ(*BW+Expt1+Flockt*)ε(*Expt1+Flockt*)p(.)	306.28	2.12	0.18	11
Ψ(*BW*)γ(*Expt1+Flockt*)ε(*Expt1+Flockt*)p(.)	307.03	2.86	0.12	10
Ψ(*BW*)γ(*BW+Expt1*)ε(*Expt1*)p(.)	307.79	3.63	0.08	9
Ψ(*BW*)γ(*BW+Expt1+Flockt*)ε(*BW+Expt1+Flockt+Hatch*)p(.)	309.74	5.58	0.03	13
Ψ(*BW*)γ(*BW+Expt1*)ε(*Expt1+Hatch*)p(.)	309.95	5.79	0.03	10
Ψ(*BW*)γ(*BW+Expt0+Expt1+Flockt*)ε(*Expt0+Expt1+Flockt*)p(.)	310.21	6.05	0.03	13
Ψ(*BW*)γ(*BW+Expt1+Flockt*)ε(*Hatch*)p(.)	313.57	9.41	0.00	10
Ψ(*BW*)γ(*BW+Expt1*)ε(*Flockt*)p(.)	316.82	12.65	0.00	9
Ψ(*BW*)γ(*BW+Flockt*)ε(*Flockt)*p(.)	347.08	42.92	0.00	9
Ψ(*BW*)γ(*BW+Expt0*)ε(*Expt0*)p(.)	372.69	68.53	0.00	10
Ψ(*BW*)γ(*BW*)ε(*BW*)p(.)	389.35	85.19	0.00	8
Ψ(*BW*)γ(*BW*)ε(*Hatch*)p(.)	390.62	86.46	0.00	8
Ψ(.)γ(.)ε(.)p(.)	398.48	94.32	0.00	5

QAIC: Quasi Akaike’s Information Criterion
ΔQAIC: change in QAIC between the top model and each additional model.
ω: the proportion of the total Akaike weight held by each model.
K: number of model parameters.

APPENDIX E

Appendix E. Model averaged occupancy (Ψ), extinction (ε), and colonization (γ) coefficient estimates for the 8-year Analysis top model [Ψ(*BW*)γ(*BW*+*Expt1*+*Flockt*)ε(*Expt1*)p(.)] in logit scale.

Parameter	**Estimate**	**Standard Error**	**Lower 95% CI**	**Upper 95% CI**
BW Ψ	0.85	0.35	0.16	1.55
Expt1 γ	1.40	0.30	0.82	1.99
Flockt γ	0.44	0.17	0.10	0.78
BW γ	0.37	0.20	-0.02	0.76
Expt1 ε	-0.42	0.16	-0.73	-0.11

CI: Confidence Interval

APPENDIX F

Appendix F. Ranking of 12 *a priori* models predicting occupancy (Ψ), colonization (γ), extinction (ε) of Snowy Plover breeding sites. Models evaluate 17 years (2001 – 2017) of breeding data. The top models for each analysis are shown, ranked by QAIC weight (ω).

Model	**QAIC**	**ΔQAIC**	**ω**	***K***
Ψ(*BW*)γ(*BW+Expt1*)ε(*Expt1*)p(.)	517.38	0.00	0.51	9
Ψ(*BW*)γ(*BW+Expt1*)ε(*BW+Hatch+Expt1*)p(.)	519.44	2.06	0.18	11
Ψ(*BW*)γ(*BW+Expt1*)ε(*Expt1+Hatch*)p(.)	519.59	2.21	0.17	10
Ψ(*BW*)γ(*Expt1*)ε(*Expt1*)p(.)	521.33	3.96	0.07	8
Ψ(*BW*)γ(*Expt0+Expt1*)ε(*Expt0+Expt1*)p(.)	521.65	4.27	0.06	11
Ψ(*BW*)γ(*BW+Expt1*)ε(.)p(.)	537.47	20.09	0.00	8
Ψ(*BW*)γ(*BW+Expt1*)ε(*Hatch*)p(.)	539.19	21.82	0.00	9
Ψ(*BW*)γ(*BW+Expt0*)ε(*Expt0*)p(.)	634.26	116.89	0.00	9
Ψ(*BW*)γ(*BW*)ε(*BW*)p(.)	664.83	147.45	0.00	8
Ψ(*BW*)γ(*BW*)ε(.)p(.)	665.38	148.01	0.00	7
Ψ(*BW*)γ(*BW*)ε(*Hatch*)p(.)	667.08	149.71	0.00	8
Ψ(.)γ(.)ε(.)p(.)	691.22	173.84	0.00	5

QAIC: Quasi Akaike's Information Criterion
ΔQAIC: change in QAIC between the top model and each additional model.
ω: the proportion of the total Akaike weight held by each model.
K: number of model parameters.

APPENDIX G

Appendix G. Model averaged occupancy (Ψ), extinction (ε), and colonization (γ) coefficient estimates for the 17-year Analysis top model [Ψ(*BW*)γ(*BW*+*Expt1*)ε(*Expt1*)p(.)] in logit scale.

Parameter	**Estimate**	**Standard Error**	**Lower 95% CI**	**Upper 95% CI**
BW Ψ	1.02	0.33	0.37	1.67
Expt1 γ	1.61	0.17	1.27	1.96
BW γ	0.38	0.13	0.12	0.63
Expt1 ε	-0.45	0.10	-0.66	-0.25

CI: Confidence Interval